

**FINE SCALE CLIMATIC AND SOIL VARIABILITY EFFECTS ON PLANT SPECIES COVER ALONG THE  
FRONT RANGE OF COLORADO, USA**

by

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**Fine Scale Climatic and Soil Variability Effects on Plant Species Cover along the Front Range of  
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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

## ABSTRACT

Cumming, W.F. Preston (Ph.D., Geography)

FINE SCALE CLIMATIC AND SOIL VARIABILITY EFFECTS ON PLANT SPECIES COVER ALONG THE FRONT RANGE OF COLORADO, USA

Thesis directed by Professor Susan W. Beatty

Fine scale studies are rarely performed to address landscape level responses to microclimatic variability. Is it the timing, distribution, and magnitude of soil temperature and moisture that affects what species emerge each season and, in turn, their resilience to fluctuations in microclimate. For this dissertation research, I evaluated the response of vegetation change to microclimatic variability within two communities over a three year period (2009-2012) utilizing 25 meter transects at two locations along the Front Range of Colorado near Boulder, CO and Golden, CO respectively. To assess microclimatic variability, spatial and temporal autocorrelation analyses were performed with soil temperature and moisture. Species cover was assessed along several line transects and correlated with microclimatic variability. Spatial and temporal autocorrelograms are useful tools in identifying the degree of dependency of soil temperature and moisture on the distance and time between pairs of measurements. With this analysis I found that a meter spatial resolution and two-hour measurements are sufficient to capture the fine scale variability in soil properties throughout the year. By comparing this to *in situ* measurements of soil properties and species percent cover I found that there are several plant functional types and/or species origin in particular

that are more sensitive to variations in temperature and moisture than others. When all seasons, locations, correlations, and regional climate are looked at, it is the month of March that stands out in terms of significance. Additionally, of all of the vegetation types represented at these two sites C<sub>4</sub>, C<sub>3</sub>, native, non-native, and forb species seem to be the most sensitive to fluctuations in soil temperature, moisture, and regional climate in the spring season. The steady decline in percent species cover the study period and subsequent decrease in percent species cover and size at both locations may indicate that certain are unable to respond to continually higher temperatures and lower moisture availability that is inevitable with future climatic variability.

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## **Chapter 1. Introduction and Rationale**

### **1.1. Introduction**

Species distributions may be restricted by their intolerance to the physical environment or by biotic factors that exclude species from otherwise favorable sites. Studies point to the likelihood of future changes in the composition of plant communities under climate change (Ford 1982, Leadley & Reynolds 1992, Pastor & Post 1986, Emanuel et al. 1985, Overpeck & Bartlein 1991, Woodward 1992, Field et al. 1992, Sternberg et al. 1999, Chapin 2003, Ellsworth et al. 2008). In many forest-steppe transitional communities such changes could be dramatic because of the sensitivity of these landscapes to regional climate, length of growing season, air and soil temperatures, as well as precipitation and resulting soil moisture (Kuramoto & Bliss 1970, Billings 1987, Sturges 1989, Evans & Fonda 1990, Chapin et al. 1992, Noble 1993, Risser 1995, Shadangi & Nath 2008, CWCB 2008).

### **1.2. Spatiotemporal soil variability**

Over the past several decades, studies on the spatial and temporal soil heterogeneity faced by plants have progressed from purely descriptive accounts to detailed spatial-statistical and time-series analyses (Hutchings et al. 2000). For soil resources that show a high level of spatial and temporal variation, data from a single time period or location may not provide an adequate view of the resource environment experienced by plants during a growing season. Subsequently, samples need to be taken and the measurements repeated as conditions change to determine if they are changing (Douaik et al. 2011).

In terrestrial plant communities soil resource heterogeneity influences plant growth and competitive interactions (Einsmann et al. 1999, Fransen et al. 2001, Garcia-Palacios et al. 2011, 2012), the coexistence of species and species diversity (Levine 1974, Grime 1979, Bell et al. 2000), and spatial patterns of species distribution (Snaydon 1962, Palmer 1990, Nicotra et al. 1999, Gallardo et al. 2005). Plants also alter spatial patterns of soil properties (Hendrickson & Robinson 1984, Breshears et al. 1997, Finzi et al. 1998, Villegas et al 2010, Li et al. 2013), leading to dynamic interactions between fine-scale patterns within vegetation and soil and, theoretically, to close correlation between the two.

### **1.3. Plant functional types**

The study of plant functional types (PFTs) has been widely emphasized as an alternative to determining species composition for the evaluation of the influence of climatic changes, differences in the atmospheric composition and land-use changes over present day plant communities around the world (Box 1996, Woodward & Cramer 1996, Diaz & Cabido 1997, Pausas 1999, de Miguel et al. 2010, Pekin et al. 2011). In spite of some conceptual differences, it is agreed in most definitions that PFTs are groups of plants similar in terms of traits and similar in their responses to certain environmental conditions (soil conditions, temperature, moisture, disturbance regimes) and/or in their effects on ecosystem processes (biomass production, litter decomposition) (Pillar & Orloci 1993a, b, Box 1996, Noble & Gitay 1996, Woodward & Cramer 1996, Lavorel & Garnier 2002, Pillar & Sosinski 2003). Based on the assumption of a relationship between form and function (Barkman 1988), the structural-functional approach permits the use of visible structural attributes as substitutes for functional

patterns. Thus, these have been widely used as basic features for PFT classifications and, when possible, further complemented by physiological traits (Box 1996, Weiher et al. 1999, Perez-Harguindeguy et al. 2013).

The methods to elaborate PFT classifications follow different approaches. Groups of plants may be derived by numerical analysis, with a selection of traits related to environmental variables, or may be deduced based on features that are assumed to have certain functionality in the system (Bugmann 1996, Noble & Gitay 1996, Woodward & Cramer 1996, Kleyer et al. 2012). Classifications become useful when plant types are determined for a particular purpose.

#### **1.4. Ecotones**

In ecology, an upper and lower treeline is generally highlighted by an additional transition zone (ecotone) found between this boundary and the open (grassland) vegetation (Odum 1979, Sumegi et al. 2012). In an ecotone area there would be an intermingling of individuals from the adjacent units with no one group dominating the others. Moreover, the extent of this area varies in accordance with the nature of the peripheral habitat factors. For example, eighty kilometers south of Boulder, CO the ecotone may be several kilometers wide whereas near Boulder the ecotone is only 450 m. wide. The greater breadth of the ecotone comes as a result of local physiography. Valleys erode out between sedimentary outcrops running parallel to the foothills produce a broad zone in which peripheral habitat factors favor one association in one location while within a meter the habitat favors another association (Roach 1948). Closer to the study areas, there is an abrupt change from habitats favoring grassland associations to habitats favoring montane associations.

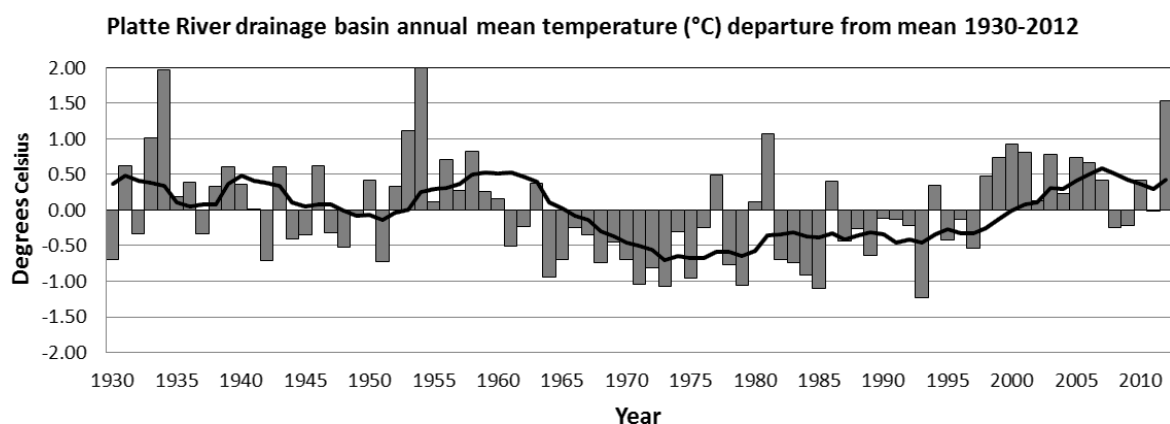
Typical vegetation responses at forest edges include: increased tree basal area, tree density, and shrub cover because of enhanced light availability (Wales 1972, Ranney et al. 1981, Williams-Linera 1990, Matlack 1994). Recent work has also recognized that vegetation structure and composition changes within the field edge (Goldblum & Beatty 1999, Meiners & Pickett 1999, de Lafontaine & Houle 2007, Porensky & Young 2013). An increase in the presence of non-native species, and high species richness, diversity and total cover are characteristic of both forest and field edges (Chen et al. 1992, Matlack 1993, Fraver 1994, Meiners & Pickett 1999).

Semi-natural grasslands are generally very species rich, and contain several species that are confined to these types of plant communities (Zobel 1992, Bachmann et al. 2005, Price & Morgan 2010). The plant distribution within these ecotones is influenced by many factors. The physiography of these areas is important because it produces differences in microclimate and soil moisture. Ecotones that separate forests and steppe are highly sensitive to variation in environmental factors (Neilson 1993, Kupfer and Cairns 1996, Loehle 2000, Hochstrasser et al. 2002, Danz et al. 2011). Ecotones provide a useful area for comparative studies, but they also indicate to land managers a potential front of invasion for non-native and/or harmful species.

### **1.5. Climate change in Colorado**

The accumulation of greenhouse gases in the atmosphere is very likely the cause of most of the increase in global average temperatures (IPCC 2007). In North America, temperatures have increased by 1°C in the past 30 years (CCSP 2008). In Colorado, temperatures have increased similarly over the same time period likely due to anthropogenic

activities. Climate models predict that Colorado will warm between 1-2°C by 2025 and 1.5° and 3°C by 2050 (IPCC 2007). These projections also suggest that typical summer monthly temperatures will be as warm as or warmer than the hottest 10% of summers that occurred between 1950 and 1999 (Figure 1.1.). In all parts of Colorado, no consistent long-term trends in annual precipitation have been detected. Variability is high, which makes detection of trends difficult. Climate model projections do not agree whether annual mean precipitation will increase or decrease in Colorado by 2050 (CWCB 2008). Colorado's climate since 1930 shows a warm period during the 1930s and the 1950s, a cool period through the 1960s and 1970s, and a consistent upward trend in the 10-year average since about 1970 (Figure 1.1.). The temperature has increased by 1°C from 1957 to 2006 (50 years) and by 1.1°C from 1977 to 2006 (30 years).



**Figure 1.1.** Annual mean temperature (°C) departure from mean 1930-2012 for the Platte River drainage basin climate division. The 10-year moving average (black curve) highlights low frequency variations in the record (Data source: NCDC Climate Divisions, see <http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp>).

This variability in temperature and precipitation will inevitably have an effect on the resistance and resilience of grassland communities. Different plant communities, when exposed to changes in temperature and precipitation, will respond in different ways and, crucially, at



different rates. Some experimental evidence suggests that diverse plant communities are more resistant and resilient (Frank & McNaughton 1991) and that plant traits, such as life history and growth rate, strongly influence community response to climate change and other stresses (Leps et al. 1982, MacGillivray et al. 1995, Diaz & Cabido 1997, Wardle et al. 1997).

In order to retain both historical ecosystem function and aesthetic value that native plants provide, maintaining plant species diversity is an important goal of habitat managers in semi-arid environments (West 1993, Fulbright 1996). Disturbance is considered to be one of the main factors influencing species richness in plant communities (Collins et al. 1995, Mackey & Currey 2001). Historically disturbance is thought of as being a temporary change in average environmental conditions that causes a pronounced change in an ecosystem. Climate change will inevitably introduce this type of change. This low level change that is compounded as anomalous conditions continue from one year to the next greatly affects both annual and perennial species. The semi-arid conditions that exist along the eastern slope of the Front Range of Colorado are particularly susceptible to these slowly changing conditions. An increase in temperature by a single degree Celsius or a decline in precipitation by a single centimeter can have profound effects on the productivity and composition of species adapted to these conditions.

Climate manipulations in natural grasslands are increasing in abundance (Harte & Shaw 1995, Grime et al. 2000, Fay et al. 2000, Buckland et al. 2001) and most of these studies have reported rapid community and ecosystem responses to warming and precipitation changes. Most systems have proven unresponsive to new climate regimes after 1–5 years (Dukes et al.

2005, Grime et al. 2000), yet there remains the overwhelming idea that ultimately, plant communities will see major shifts in composition and structure with long-term changes in temperature and precipitation (IPCC 2007), which may have dire consequences for species conservation (Thomas et al. 2004).

Impacts of recent climate change on plant communities are already evident, as geographic distributions shift poleward and toward higher elevations and some species disappear altogether (Graberr et al. 1994, Beebee 1995, Crick et al. 1997, Parmesan et al. 1999, Thomas & Lennon 1999, Pounds et al. 1999, Fitter & Fitter 2002, Sanz-Elorza et al. 2003, Bertin 2008, Sakio & Masuzawa 2012). To forecast ecological change under continued climate warming and variable moisture regimes, a better understanding of the relative importance of direct responses by individual species and functional groups to climate is needed (Ives 1995, Davis et al. 1998, Post et al. 1999, Walther et al. 2002, Schmitz et al. 2003, Parmesan 2006).

Climate change models differ with regard to projected changes in annual precipitation amounts in the central U.S., but they are in agreement with predictions that the dynamics of event distribution will become more variable (Groisman et al. 1999, Houghton et al. 2001, Petrie et al. 2012). General circulation models predict precipitation events of a greater magnitude, but with longer intervening dry periods and reduced frequency. The longer dry periods between storms will generally lead to reduced soil moisture levels (Knapp et al. 2002). Substantial changes in moisture availability and temporal variability will undoubtedly impact ecosystems in which productivity is limited by water availability (Sala et al. 1988, Weltzin et al. 2003, Miranda et al. 2009, Hao et al. 2010, Holub et al. 2013).

Diaz and Eischeid (2007) used PRISM (Parameter-elevation Regressions on Independent Slopes Model) data to analyze the effects of elevation on temperature during a 1979 to 2006 study period and found a 1°C average increase along the Front Range of Colorado (1610-2195 m). Colorado's temperature trends are consistent with multiple independent analyses showing widespread warming in the West (Udall & Bates 2007, Mote et al. 2005, Stewart et al. 2005, Diaz & Eischeid 2007). Regonda et al. (2005) observed that the onset of spring warm spells (defined as seven days greater than 12°C) shifted to an earlier date over the period 1950-1999. Knowles et al. (2006) found the greatest warming was generally observed at the higher elevations in the Interior West, with the most warming observed in March.

The Colorado Water Conservation Board's (CWCB) Climate Change in Colorado synthesis report 2008 provides detailed assessments of past and future climatic variability in Colorado. In this study, all regions examined within the state warmed during the 30 year study period (1977-2006), except for the far southeast corner, in which there was a slight cooling trend (CWCB 2008). Colorado's highly variable climate is a consequence of high elevations and the complex topography of the mountains, plains, and plateaus. Climate varies spatially and temporally, and different climatic variables fluctuate in distinct ways.

Climate models project Colorado will warm 1-2° C by 2025, relative to the 1950-1999 baseline, and 1.5-3° C by 2050. The 2050 projections show summers warming by 2.75° C and winters by 1.5° C (Wolter & Allured 2007). These projections also suggest that typical summer monthly temperatures will be as warm as or warmer than the hottest 10% of summers that occurred between 1950 and 1999. As an illustration, mid-21<sup>st</sup> century summer temperatures on

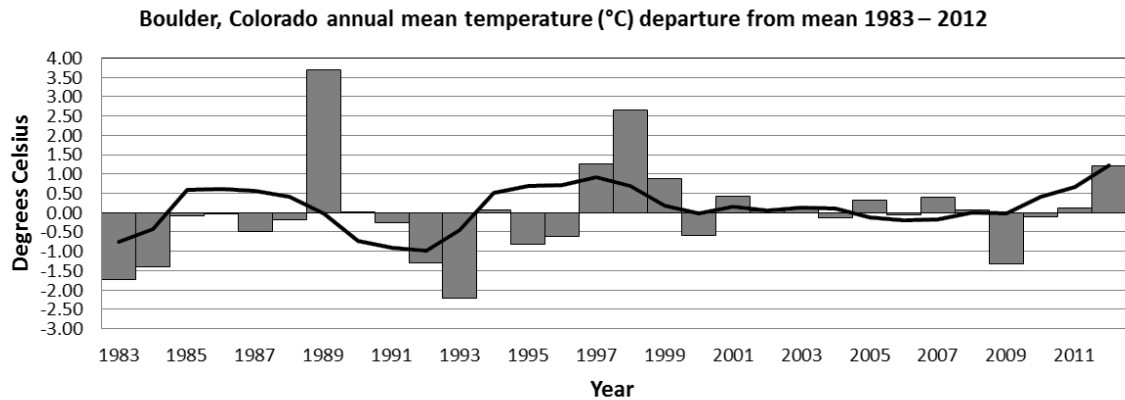
the Eastern Plains of Colorado are projected to shift westward and upslope, bringing into the Front Range temperature regimes that today occur near the Kansas border.

In contrast to temperature, in all parts of Colorado, no consistent long-term trends in annual precipitation have been detected. Variability is high, which makes detection of trends difficult. Climate model projections do not agree whether annual mean precipitation will increase or decrease in Colorado by 2050. The multi-model average projection shows little change in annual mean precipitation, although a seasonal shift in precipitation does emerge. Projections show little change in annual mean precipitation with a decrease in late spring and summer and an increase in winter precipitation. Water year precipitation ranges from roughly half the long-term average in a dry year to double the average in a wet year and varies across the state. Throughout the West, less frequent and less severe drought conditions have occurred during the 20<sup>th</sup> century than revealed in the paleoclimate records over the last 1000 years (Meko et al. 2007).

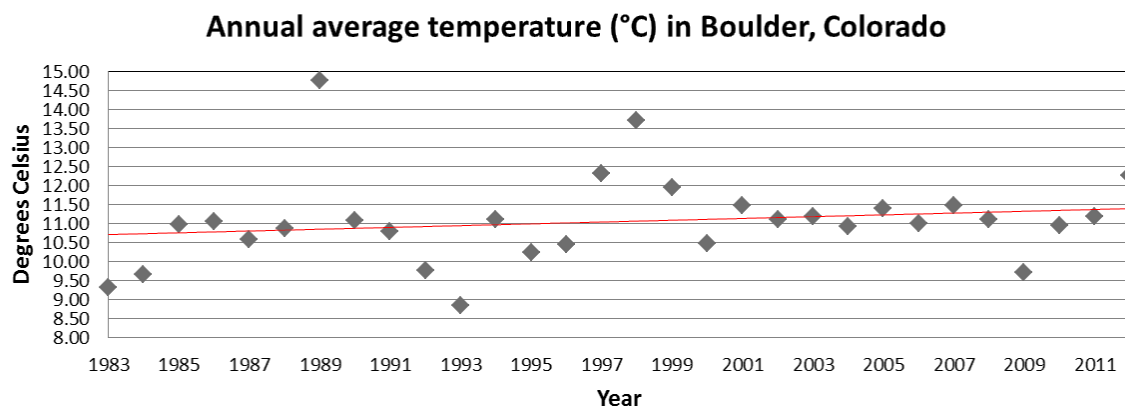
For a quick analysis of the variable climate close to the research sites climate data for Evergreen, Colorado and Boulder, Colorado was gathered from The Western Regional Climate Center (WRCC) for the years 1983-2012. A t-test was performed on the slope of average temperature, precipitation, and snowfall at each climate station and p-values are reported here. The Evergreen station is located at 2133 m approximately 20 km from the White Ranch site and the Boulder station is located at 1655 m and approximately 3.5 km from the Shanahan Ridge Site. For both sites there were periods of missing data (December 1, 1983 – June 30, 1984 and September 1 – 30, 1984 at the Evergreen site and August 1, 1989 – March 31, 1990, August

1 – 31, 1993, November 1 – December 31, 1997, and November 1, 1998 – April 30, 1999 at the Boulder site). For both sites mean substitution of missing data with the average was performed in order to correct for lost data. Replacement of this data did not significantly change the outcome of the 30-year averages for temperature or precipitation. The Boulder, CO site, it must be noted, was moved several times during this study period, beginning in on the grounds of the Central Fire Station of Boulder (40° 02'N, 105° 16'W, 1640 m) from 1983-1989 and then moving to the National Institute of Standards and Technology (40 40'N, 105 16'W, 1670 m) from 1990 to the present. The Evergreen Colorado site has been located at its present location since 1962 (39° 38'N, 105° 19'W, 2133 m).

The temperature records for the Boulder, Colorado station show the departure from the 30-year mean with the 10-year moving average (Figure 1.2.A) and the linear regression for the 30-year trend in the mean (Figure 1.2.B). Boulder's climate since 1983 shows a consistently cool period through 1998 (with a few exceptional years), and a consistent average to slightly above average trend in the 10-year average from about 1999 to 2007 with a few cool years before greatly increasing once again in 2012 (Figure 1.2.A). Overall, Boulder has significantly warmed 0.75°C in the past 30 years ( $t=2.40$ ,  $p=0.02$ ) (Figure 1.2.B).



A.

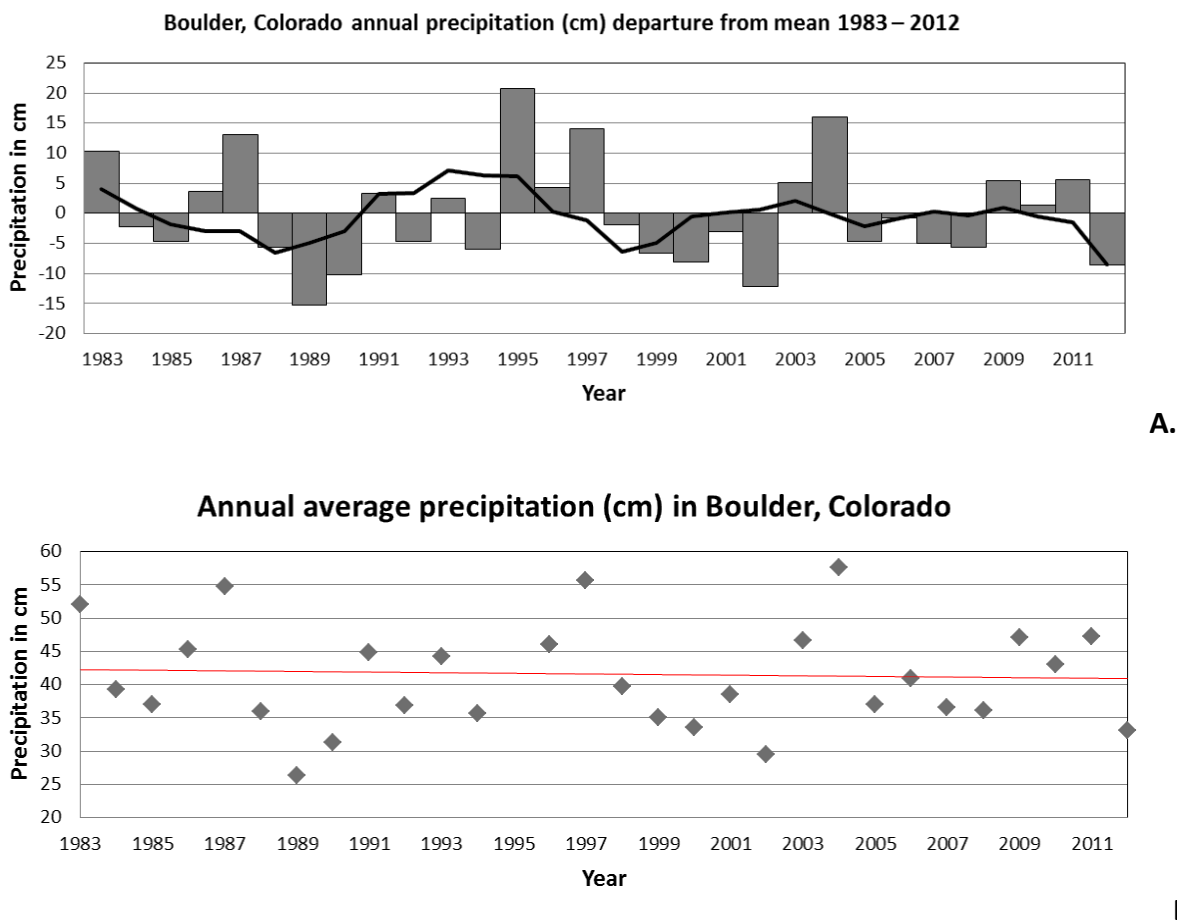


B.

**Figure 1.2.** Annual mean temperature (°C) at Boulder, Colorado. A. Boulder, Colorado annual mean temperature (°C) departure from mean 1983 – 2012. The 10-year moving average (black curve) highlights low frequency variations in the record. B. Annual average temperature (°C) in Boulder, Colorado. Over this thirty year period there has been a 0.75° C increase in temperature (red line) ( $t=2.40$ ,  $p=0.02$ ).

The precipitation records show the departure from the 30-year mean with the 10-year moving average (Figure 1.3.A) and the linear regression for the 30-year trends in the mean (Figure 1.3.B) for the Boulder, Colorado station. According to the precipitation records, very little long-term trend in annual precipitation can be detected (Figure 1.3.A), although ten of the fifteen years since 1998 have been below average in terms of precipitation. Overall, there has

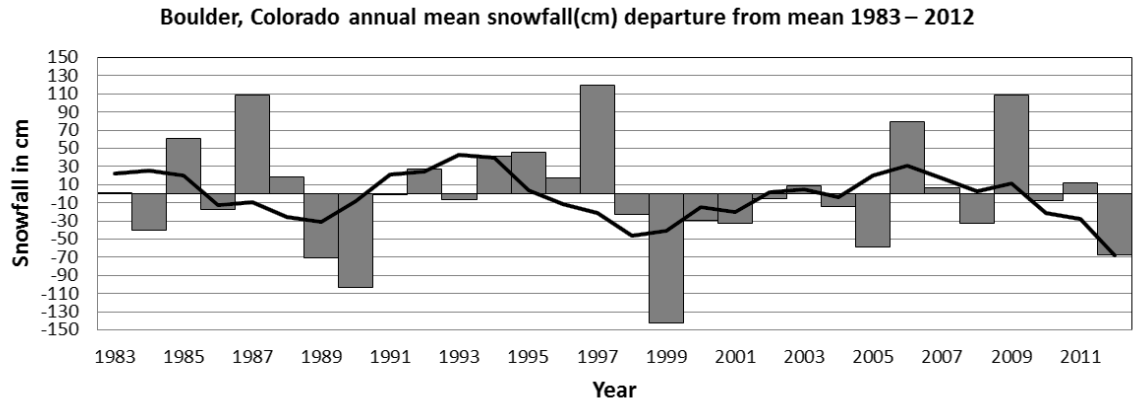
been an insignificant, but interesting 1.2 cm decrease in the past 30 years ( $t = -1.30$ ,  $p = 0.20$ ) (Figure 1.3.B).



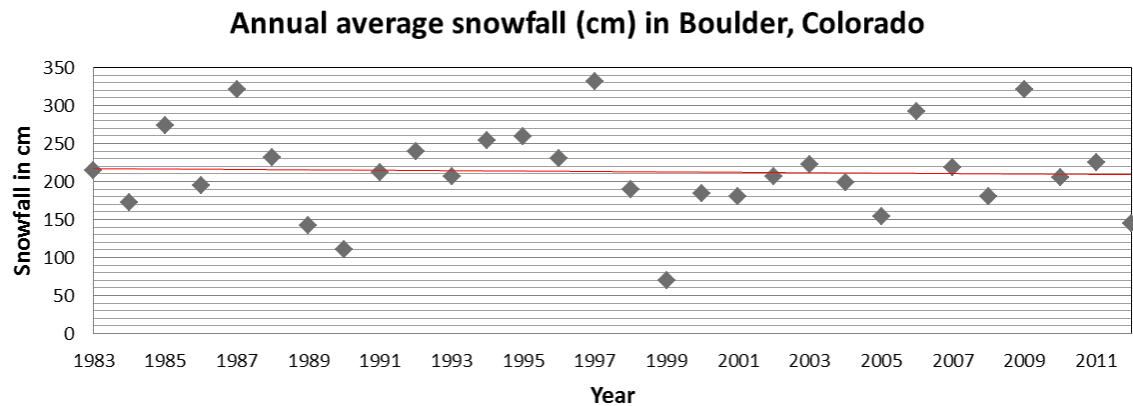
**Figure 1.3.** Annual mean precipitation (cm) at Boulder, Colorado. A. Boulder, Colorado annual mean precipitation (cm) departure from mean 1983 – 2012. The 10-year moving average (black curve) highlights low frequency variations in the record. B. Annual average precipitation (cm) in Boulder, Colorado. Over this thirty year period there has been a 1.2 cm decrease in precipitation (red line) ( $t = -1.30$ ,  $p = 0.20$ ).

The snowfall records show the departure from the 30-year mean with the 10-year moving average (Figure 1.4.A) and the linear regression for the 30-year trends in the mean (Figure 1.4.B) for the Boulder, Colorado station. According to the snowfall records, very little long-term trend in annual snowfall can be detected (Figure 1.4.A), although ten of the fifteen

years since 1998 have been below average in terms of precipitation. Overall, there has been an insignificant 10 cm decrease in the past 30 years ( $t=0.34$ ,  $p=0.73$ ) (1.4.B).



A.



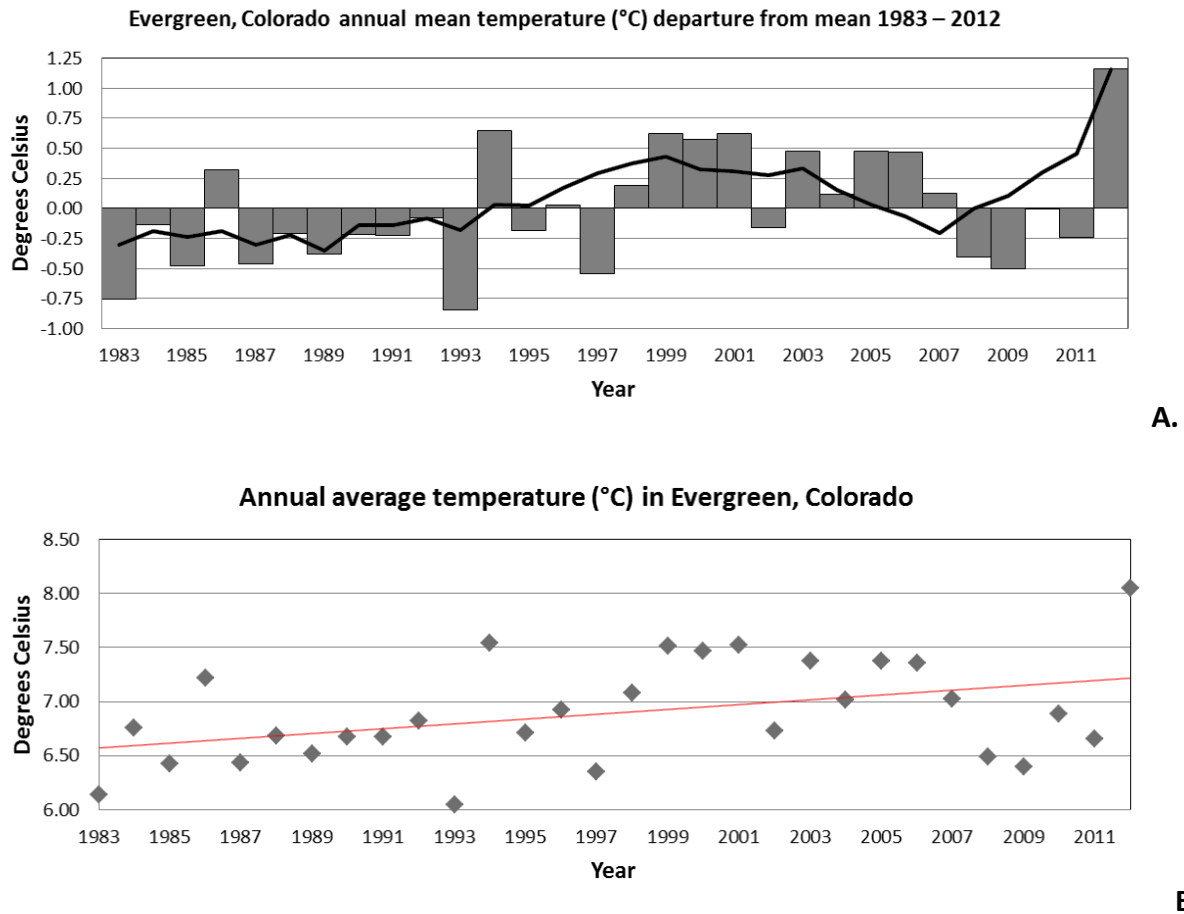
B.

**Figure 1.4.** Annual mean snowfall (cm) at Boulder, Colorado. A. Boulder, Colorado annual mean snowfall (cm) departure from mean 1983 – 2012. The 10-year moving average (black curve) highlights low frequency variations in the record. B. Annual average snowfall (cm) in Boulder, Colorado. Over this thirty year period there has been a 10 cm decrease in snowfall (red line) ( $t=0.34$ ,  $p=0.73$ ).

The temperature records for the Evergreen, Colorado station show the departure from the 30-year mean with the 10-year moving average (Figure 1.5.A) and the linear regression for the 30 and 50-year trends in the mean (Figure 1.5.B). Evergreen's climate since 1983 had a



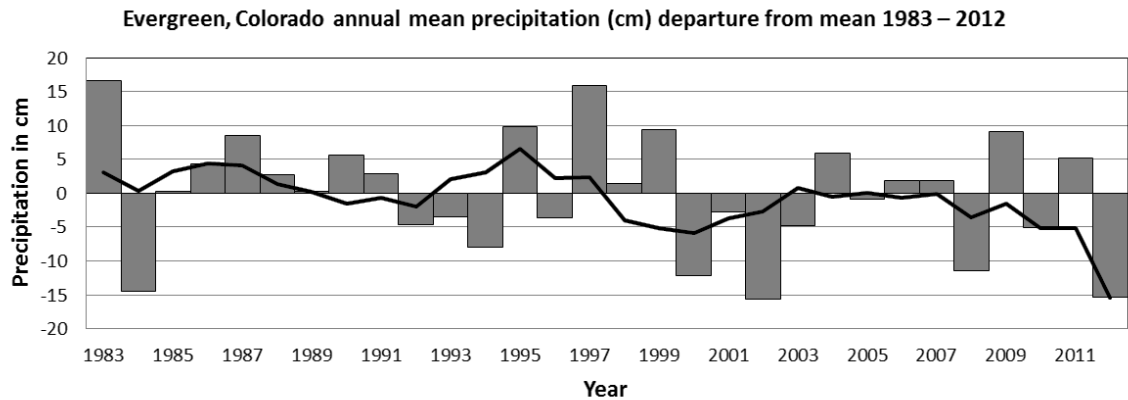
consistently cool period from 1983-1997 (with the exception of 1994) and a generally warm period from 1998-2007. Evergreen had another cool period from 2008-2011 and then an exceptionally warm 2012. Overall, Evergreen has significantly warmed  $0.65^{\circ}\text{C}$  in the past 30 years ( $t=2.98$   $p=0.005$ ) (Figure 1.5.B).



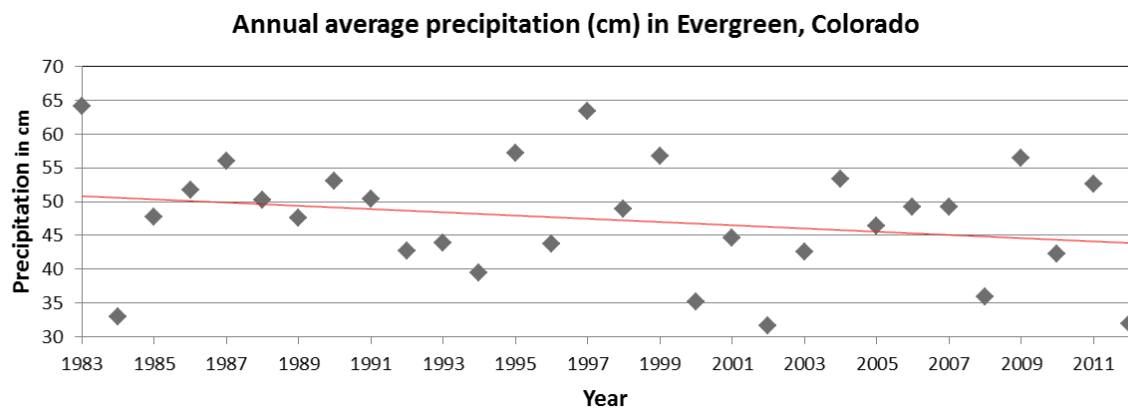
**Figure 1.5.** Annual mean temperature ( $^{\circ}\text{C}$ ) at Evergreen, Colorado. A. Evergreen, Colorado annual mean temperature ( $^{\circ}\text{C}$ ) departure from mean 1983 – 2012. The 10-year moving average (black curve) highlights low frequency variations in the record. B. Annual average temperature in Evergreen, Colorado. Over this thirty year period there has been a  $0.4^{\circ}\text{C}$  increase in temperature (red line) ( $t=2.98$ ,  $p=0.005$ ).

The precipitation records show the departure from the 30-year mean with the 10-year moving average (Figure 1.6.A) and the linear regression for the 30-year trends in the mean

(Figure 1.6.B) for the Evergreen, Colorado station. According to the precipitation records, very little long-term trend in annual precipitation can be detected. Overall, there has been an insignificant, but interesting 7 cm decrease in precipitation over the past 30 years with high variability within that ( $t=-0.26$ ,  $p=0.79$ ) (Figure 1.6.B).



A.

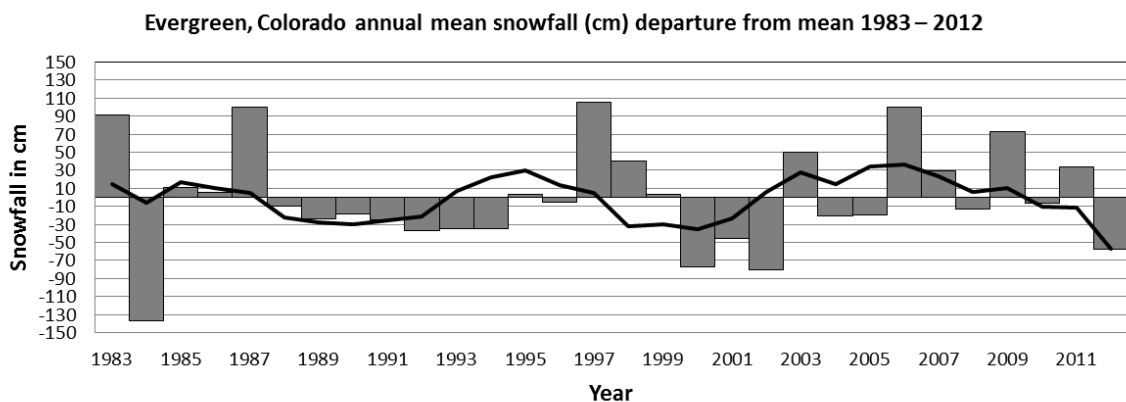


B.

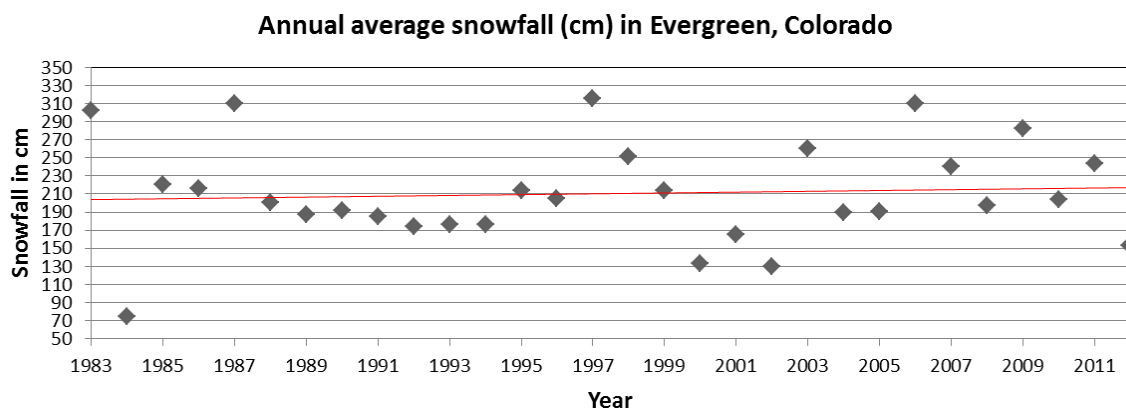
**Figure 1.6.** Annual mean precipitation (cm) at Evergreen, Colorado. A. Evergreen, Colorado annual mean precipitation (cm) departure from mean 1983 – 2012. The 10-year moving average (black curve) highlights low frequency variations in the record. B. Annual average precipitation (cm) in Evergreen, Colorado. Over this thirty year period there has been a 7 cm decrease in precipitation (red line) ( $t=-0.26$ ,  $p=0.79$ ).

The snowfall records show the departure from the 30-year mean with the 10-year moving average (Figure 1.7.A) and the linear regression for the 30-year trends in the mean

(Figure 1.7.B) for the Evergreen, Colorado station. According to the snowfall records, very little long-term trend in annual snowfall can be detected (Figure 1.7.A), although eight of the fifteen years since 1998 have been below average in terms of precipitation. Overall, there has been an insignificant 12 cm increase in the past 30 years ( $t=-0.22$ ,  $p=0.82$ ) (1.7.B).



A.



B.

**Figure 1.7.** Annual mean snowfall (cm) at Evergreen, Colorado. A. Evergreen, Colorado annual mean snowfall (cm) departure from mean 1983 – 2012. The 10-year moving average (black curve) highlights low frequency variations in the record. B. Annual average snowfall (cm) in Evergreen, Colorado. Over this thirty year period there has been a 12 cm increase in snowfall (red line) ( $t=-0.22$ ,  $p=0.82$ ).

## 1.6. Monthly variance in air temperature, precipitation, and snowfall

When monthly temperature (°C), precipitation (cm), and snowfall (cm) were analyzed for trends over the 30 year period, several months seemed to be important in terms of changes over time. In Boulder, there were few months in particular that stood out with most others showing little change per month in terms of temperature (Table 1.1.). The months that display the greatest increase in temperature are November (3°C), March (1.9°C), December (1.6°C), and January (1.6°C).

At Evergreen more variable conditions were observed, but with a few significant similarities. There are a few months with increases of note once more, with July (2°C), March (1.2°C), and August (1°C). The increase in March of 1.2°C once again brings this month out as a potential month to continue to monitor in terms of its relationship to vegetation.

For the precipitation, although highly variable, several months show an interesting amount of change over the period of record in Boulder, having a 3.9 cm decrease in November, 2 cm decrease in June, and 1.8 cm decrease in March. In Evergreen there are a few months of note with November having a 2.9 cm decrease, August with a 2.7 cm decrease, June with a 2.3 cm decrease, and March with a 1.9 cm decrease. In an area that is moisture limited, a decrease of even 1 cm may affect species growth depending on when the loss occurs. With March having an increase in temperature, resulting in a warmer environment for germination or possibly emergence of plant species, and a decrease in precipitation on average the result would be a stronger negative plant community response.

In terms of snowfall, several months stand out once again. November had a great decrease in average snowfall, with Boulder dropping an average of 40.5 cm and Evergreen

decreasing an average of 28.5 cm. As has been discussed earlier in this paper, the variability over recent times at these two sites, with 2012 being extremely dry and warm, may display a threshold in precipitation and temperature that each species reacts differently to.

**Table 1.1.** Changes in temperature, precipitation, and snowfall between 1983 and 2012. Highlighted cells indicate statistical significance ( $p < 0.05$ ).

	Boulder			Evergreen		
January	1.6°C ↑	0.3cm ↑	9.0cm ↑	0.6°C ↑	0.5cm ↑	12.0 ↑
February	0.6 ↓	0.3 ↑	15.0 ↑	1.0 ↓	1.2 ↑	8.0 ↑
March	1.9 ↑	1.8 ↓	5.0 ↓	1.2 ↑	1.9 ↓	9.0 ↑
April	1 ↑	0.7 ↑	14.5 ↓	0.3 ↑	2.4 ↑	11.5 ↑
May	0.1 ↓	0.25 ↑	4.0 ↑	0.2 ↑	0.3 ↓	5.0 ↑
June	0.6 ↑	2.0 ↓	0	0.7 ↑	2.3 ↓	0
July	1.4 ↑	0.7 ↑	0	2.0 ↑	1.9 ↓	0
August	0.6 ↑	0.8 ↑	0	1.0 ↑	2.7 ↓	0
September	1.3 ↑	0.4 ↑	7.0 ↓	0.7 ↑	0.05 ↓	4.0 ↓
October	0.2 ↑	1.4 ↑	8.0 ↑	0.2 ↑	0.6 ↓	11.0 ↑
November	3.0 ↑	3.9 ↓	40.5 ↓	0.8 ↑	2.9 ↓	28.5 ↓
December	1.6 ↑	1.1 ↑	23.0 ↑	0	1.7 ↑	39.5 ↑
	Temp	Precip	Snow	Temp	Precip	Snow

### 1.7. Study system

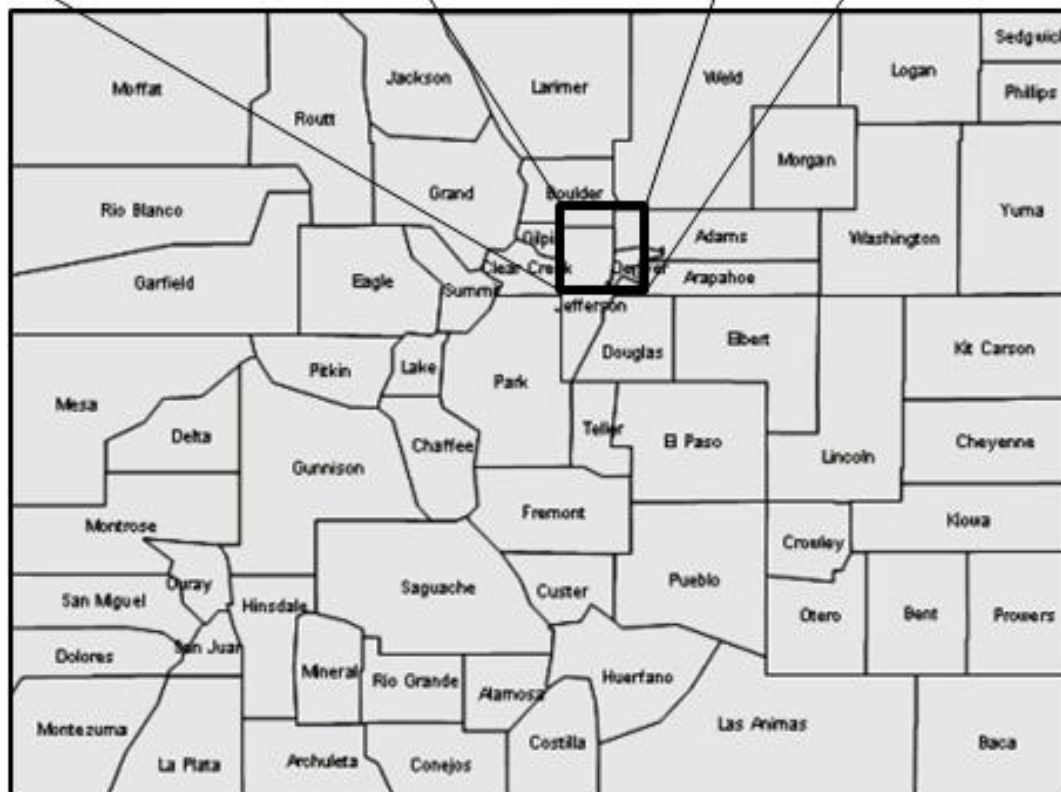
Two study sites are located in the montane zone (~1750-2300 m) of the eastern slope of the northern Colorado Front Range on the City of Boulder's Open Space and Mountain Parks Shanahan Ridge (elevation 1756 m; 39°57'30.8"N, 105°15'44.6"W) and the Jefferson County's White Ranch Open Space (elevation 2282 m; 39°48'32.3"N, 105°17'4.2"W) (Figure 1.9.). The Colorado Front Range is the easternmost range of the Rocky Mountains, extending north to south ~150 km from the Wyoming border paralleling the Great Plains. The majority of this land

mass is composed of a core of acidic Precambrian intrusive rocks, which frequently contain intrusions of acidic Tertiary plutons (Madole 1973). Toward the east at elevations below ~2400 m, outside the mineralized belt, are a series of narrow sedimentary formations of cuestas and hogbacks. Soils along the Front Range are highly variable but are usually Mollic Cryoll soils dominant with rocky, thin, coarsely textured and shallow slightly acidic characteristics (Johnson & Cline 1965, NRCS 2013). With a cryic soil temperature regime, the Cryolls are the soils of the northern latitudes. They have a xeric, ustic, or udic soil moisture regime and are moderately extensive in the western U.S. Conditions at each site are summarized in Table 1.2.

**Table 1.2.** Average soil conditions at study sites.

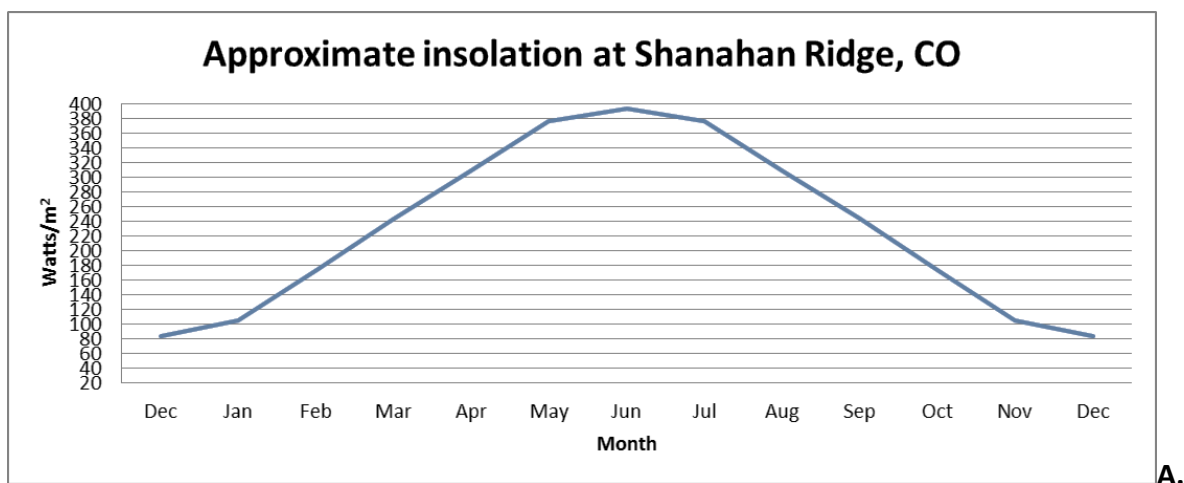
	% Sand	% Silt	% Clay	pH	% Organic Matter
<b>Shanahan Ridge</b>	76.46	9.79	13.75	4.79	5.10
<b>White Ranch</b>	76.54	14.54	8.92	5.61	5.11

Climate stations located near both sites show mean annual temperature ranges from 10.8° C at an elevation of 1655 m for 1983-2012 (Boulder, Colorado station, Western Regional Climate Center, Reno, NV) to 7.0° C at 2133 m (Evergreen, Colorado station, Western Regional Climate Center, Reno, NV) for 1983-2012. Precipitation ranges from 49.9 cm at 1655 m to 47.0 cm at 2133 m over the same periods as temperature.

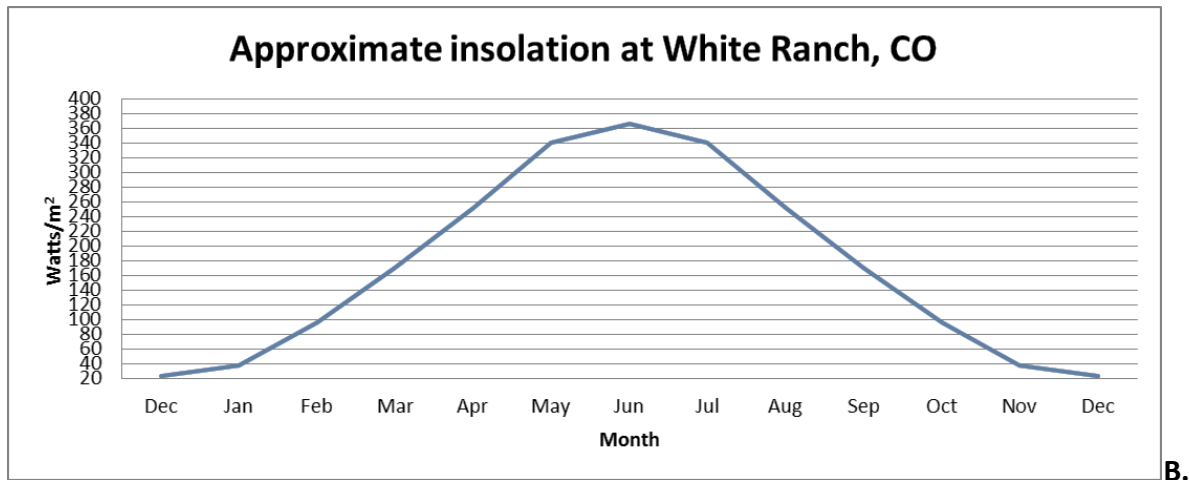


**Figure 1.9.** Map of counties of Colorado and Google Earth inset map of the study region, including approximate locations of sites at White Ranch Open Space and The City of Boulder Open Space and Mountain Park’s Shanahan Ridge area property.

The amount of solar radiation reaching each site plays an important role in species development (Sims et al. 1978, Middleton 1991, Breshears et al. 1997, Martens et al. 2000, Bennie et al. 2006). In the northern hemisphere, east/southeast slopes will have lower soil moisture due to higher amounts of evaporation due to increased insolation. Additionally, steeper slopes will have lower amounts of soil moisture due to increased draining rates. Shanahan Ridge has a 67° east/northeast southwest aspect with a significant amount of insolation during the morning through afternoon due to little to no tree coverage to its south and east. White Ranch has a 21° north/northeast facing aspect, with most of its tree cover occurring in the eastern portion of the transect which shades the site during morning hours. Insolation amounts were approximated throughout the year. The average over an entire year for an ENE 15° slope (Shanahan Ridge), which will vary with aspect, is 242.9 W/m<sup>2</sup> per day, and a NNE 22.5° slope (average of a 15° and 30° slope and approximate to the 23° at White Ranch) is 185 W/m<sup>2</sup> (Buffo et al. 1972) (Figure 1.10.).

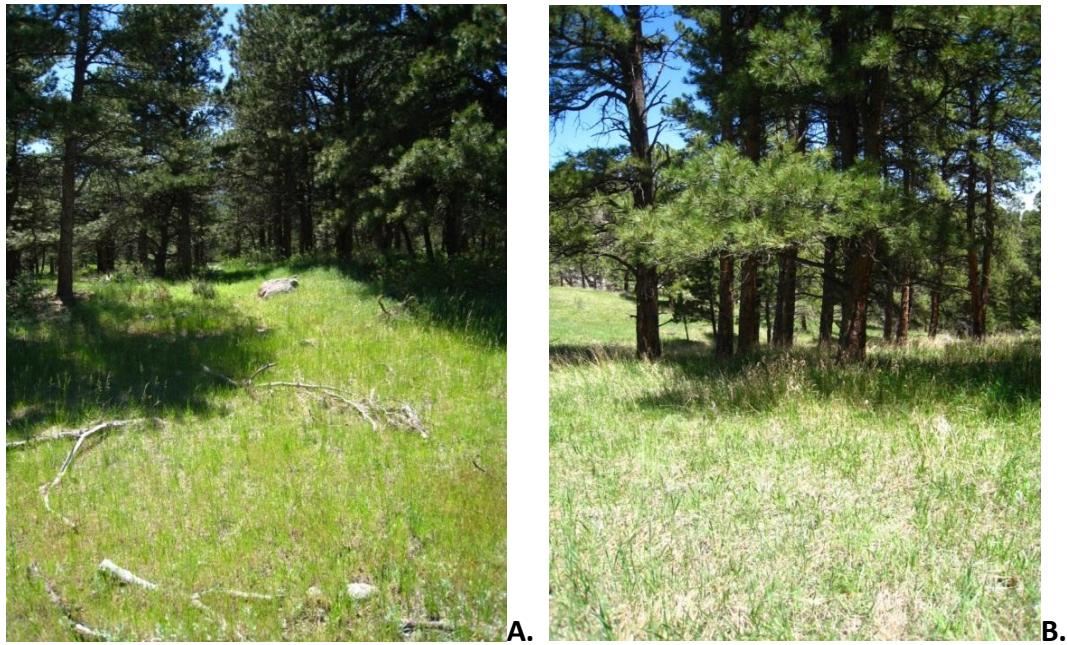






**Figure 1.10.** Approximate clear-sky insolation throughout the year at 40° north latitude, NNE aspect and 15° slope (Shanahan Ridge, A.) and 40° north latitude, ENE aspect and 23° slope (White Ranch, B.) (Adapted from Buffo et al. 1972).

This region includes a wide array of vegetation, including shortgrass steppe, shrub-steppe, and open woodland stands of ponderosa pine (*Pinus ponderosa*) (Figure 1.11.). In terms of disturbance, the Shanahan Ridge area in Boulder experienced widespread (minimum 42 hectare extent) fire in 1870 (Sheriff & Veblen 2006), while White Ranch Open Space has little known history of wildfire (Gartner 2008). Cattle grazing became an integral part of life in the 19th century in the region and livestock numbers are believed to have peaked in the late 1890's to early 1900's (Marr 1961), and most of the area has not been grazed since the 1960's, but by the 1970s due to the purchase and preservation of open spaces along the rapidly developing Front Range, grazing had nearly ceased. However, grazing by ungulate species such as elk and deer is still an apparent factor on these landscapes today.



**Figure 1.11.** Photos of the Shanahan Ridge (A.) and White Ranch Sites (B.) taken in summer of 2011.

Latitudinal and elevational plant species distributions along the Front Range of Colorado have been attributed to temperature and moisture, as typically influenced by elevation and topographic position (Peet 1981, 1988, Allen et al. 1991). Vegetation along the lower-montane region varies along elevational gradients and can be found in several structural states, from open, park-like stands of ponderosa pine near the forest-steppe ecotone and on south-facing xeric sites to more dense stands on north-facing mesic slopes.

### **1.8. Research objectives**

Finer scale models of climate and vegetation comparisons generally receive less attention than coarser scale predictive models (Paruelo & Lauenroth 1996), however research has shown that they need to be addressed (Franklin et al. 2013). By examining biotic and abiotic

variability across boundaries and at a fine scale, a better understanding regarding what site factors define what type of species establish yearly under varying conditions.

The first objective of this research is to illustrate the use of autocorrelograms as tools to identify the degree of dependency of soil temperature and moisture on the distance and time between pairs of measurements and how to take advantage of this dependency along several line-transects that cross the forest-steppe ecotone. The magnitude of spatial and temporal variation of soil temperature, moisture, and several additional soil properties across a transition zone would invariably show some autocorrelation depending on the season. This type of study will add to the understanding of fine-scale soil properties and their relationship to the greater landscape in terms of land management influence and future climatic variability.

The second objective was to use *in situ* measurements to determine the effects of changes in soil temperature and moisture on plant functional types and species origin. Different species and species groups (PFTs, native, non-native, annual, and perennial, etc.) will respond to environmental gradients differently. If species with different traits show similar response to environmental gradients and potential environmental change, then how does the variability in these gradients at the fine scale help determine community composition?

The present study adds to current literature by directly examining the modifying effects of plant coverage type (PFTs and species origin), fine scale soil property variation, micro and macro climate. This research will also assess these combinations and their relationship to environmental gradients and conditions.

## **1.9. Research organization**

This dissertation is organized into four chapters. Chapter one is a general introduction to this study. Chapter two is focused on the results generated from the spatiotemporal soil moisture and soil temperature data as well as the soil sample nutrient, organic matter, texture, and pH analysis. By determining spatial and temporal autocorrelation breaks in significance within each of these two variables at the meter scale for spatial and hourly/weekly/seasonal scale for temporal I established a model for future research at the fine-scale. Chapter three is focused on the results generated from correlation analysis of soil conditions, PFTs, and species origin. Comparing which plant functional type and species origin relate to the yearly microclimatic variability can give insight into how future climate change will influence this community as well as possibly explain the sub-decadal climate variability and its role in resilience and resistance. Chapter 5 summarizes the lessons learned from this study and pinpoints the importance of my results in ecosystem studies and management of grassland communities in the face of climate change. I also provide thoughts for further research needs based on my results.<sup>8</sup>

## **Chapter 2. Detection of spatial and temporal soil variability at a forest-steppe ecotone**

### **2.1. Introduction**

Over the past several decades, studies on the spatial and temporal soil heterogeneity faced by plants have progressed from purely descriptive accounts to detailed spatial-statistical and time-series analyses (Parton 1984, Nash et al. 1991, Getis and Ord 1992, Anselin 1995, Brundson et al. 1996, Moran et al. 2009, Shumway & Stoffer 2010). For soil resources that show a high level of spatial and temporal variation, data from a single time period or location may not provide an adequate view of the resource environment experienced by plants during a growing season. Due to the spatial and/or temporal variability of soil properties, numerous samples need to be taken and the measurements need to be repeated as conditions change or to determine if they are changing (Douaik et al. 2011).

Within traditional soil science, soil survey values for soil properties are predicted for the majority of locations in the region where the values are not actually measured (Burgess & Webster 1980, Webster 1985). Analysis of the relationships among soil properties traditionally uses classical statistics, which do not consider spatial autocorrelation and would not be appropriate due to the limitation of their assumptions of the independence and normality of sampling data and are not suitable for repeated sampling from a single spatial location (Biggar & Nielsen 1976, Subler et al. 1995, Iqbal et al. 2005, Sharma et al. 2011). Instead, spatial statistics are thought to be more powerful analytical tools for the analysis of spatially dependent variation of various soil physical properties (Vieira et al. 1981, Warrick et al. 1986, Loscano & Hatfield 1992, Kutilek & Nielsen 1994, Iqbal et al. 2005, Sharma et al. 2011), soil moisture (Yeh et al. 1986, Tomer & Anderson 1995, Schwanki et al. 2000), soil temperature

(Davidoff & Selim 1988, Yates et al. 1988, Lascano & Hatfield 1992, Some'e et al. 2011) soil biochemical properties (Bonmati et al. 1991, Sutherland et al. 1991), soil microbiological processes (Aiken et al. 1991, Rochette et al. 1991), and ecological parameters (Trangmar et al. 1985, Webster 1985, Robertson 1987, Isaaks & Srivastava 1989, Rossi et al. 1992, Garcia-Palacios et al. 2012, Chiao et al. 2012). Since the measurements are often spatially dependent, the description gained by this method may not be complete. Treating the measurements as spatially correlated and using the knowledge of the spatial distribution provides additional information. Spatial autocorrelation analysis is suitable to reveal relationships among sample sites in a geographic space, where arrangement of sample sites could be irregular (random) or regular (line-transect) (Sokal & Thomson 1987). The variability is the outcome of many processes acting and interacting across a continuum of spatial and temporal scales and is inherently scale-dependent (Parkin 1993, Nunan et al. 2002, Becker et al. 2006). Generally, samples collected close to one another are more similar than samples collected at greater distances (Tobler 1970, Miller 2004). Although the soil is assumed to be relatively uniform, quantitative measures of the spatial variance structure within any one soil unit are not common.

In many ecosystems, it would be expected to find strong spatial autocorrelation of soil properties due to the combined effects of physical and chemical processes as well as the strong ecological relationships between variables (Beckett & Webster 1971, Trangmar et al. 1985, Robertson 1987, van den Pol-van Dassel et al. 1998, Walter et al. 2002, Bekele and Hudnall 2006). Because soil resources can have large effects on plants, it is important to have a detailed

understanding of how the resources available to plants change over both space and time. The overriding thought in ecology is that environmental variability at the scale of meters is usually less important and less correlated with community structure than at coarser scales, such as meso-scale (tens of meters or greater) or macro-scale (kilometers or greater). However, the effects of purely spatial factors or random variation in environmental factors are typically more important on this micro-scale, whereas the meso- and macro-scales may rather reflect habitat structure and average values that don't directly correspond to an individual plant response. Abiotic factors may play a significant role on a micro-scale level, for example, in habitats with high substrate heterogeneity or in habitats that are primarily structured by a single physical factor (Neustupa et al. 2012).

Soil properties may exhibit spatial dependencies at scales smaller than the scale at which sampling was performed (Cambardella et al. 1994, Fu et al., 2011, Liu et al. 2013). Observations of these soil properties along line-transects are commonly made at equal intervals and consequently may be considered as a continuous series in a statistical sense. As stated by Kendall and Stuart (1968), this continuity implies a relationship or interdependence between adjacent observations along the line-transect. When observing some environmental phenomenon along a line-transect where one observation is less than the mean of all of the observations, the most likely recording of the immediately adjacent observations will also be less than the mean. This is in contrast to the common assumption of completely random values where knowledge of one value would provide no information in regard to the adjacent observations. If the observations along a line-transect are evenly spaced and have no missing

values, the data may be evaluated by autocorrelation analysis. Autocorrelation provides a means of determining the average extent of the mutual dependence of adjacent observations in time and in space. Quantitatively, it may serve to emphasize the continuous, orderly nature of soils and soil properties in contrast to the premise of independent, randomly distributed characteristics (Lanyon & Hall 1981).

Webster and Cuanalo (1975) investigated larger scale observations in soil morphological, physical, and chemical properties. The results of their autocorrelation analysis showed that patterns of soil properties coincided with the average dimension of the parent geological strata. Campbell (1978) calculated the semi-variance of observations, a similar technique to compare the spatial variation of soil properties within soil map delineations. From observations made at 10 m intervals, he found that the semi-variance was different for two properties within one delineation and for the same property between two delineations. Thus, he concluded that contrasting spatial variation existed in each case and that this variation needed to be considered when making observations of these soil properties (Lanyon & Hall 1981). Buchter et al. (1991) measured soil properties, including soil-water characteristic curves, particle size, saturated hydraulic conductivity, and bulk density along two parallel 100 m line-transects separated by 60 cm and found that the parameters had strong periodic behavior with a main cycle of 50 m. Nash et al. 1991 indicated that the range of dependence in time for soil moisture and rainfall was different for the entire transect when compared to individual transect segments. In general, water content showed a significant correlation in time between 3 to 5 lags, whereas rainfall showed a significant correlation in time between 2 to 25 lags. Soil



moisture lagged behind rainfall by a few lags. The response time to rainfall was short in the surface soil but increased with depth to as much as 10 lags at 135 cm. Cain et al. (1999) sampled soil nitrogen availability over space and time and found that both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  varied in both space and time depending on age of the site and vegetation occurrence. Downes and Beckwith (1951) found soil pH to vary by a full unit within a meter of apparently uniform soil. Vieira et al. (1981) used geostatistical methods (kriging) to determine the spatial variability of 1280 field-measured infiltration rates. They utilized a grid pattern to determine the spatial extent necessary to determine sample size necessary to successfully reproduce the infiltration rate across the field. Canton et al. (2004) showed that the simultaneous monitoring of rainfall, soil moisture and runoff at short intervals shows the different responses of soil surfaces to rainfall and the influence of rainfall partitioning on soil moisture patterns.

In addition to spatial variability, knowledge of temporal changes in soil conditions is highly desirable when making connections with vegetation responses. Many studies have looked at the temporal variability of soil moisture (Vinnikov et al. 1996, Western et al. 2002, Lauzon et al. 2004, Li et al. 2011, Mittelbach & Seneviratne 2012) and temperature (Kuzyakova & Stahr 2006, Katterer & Andren 2009, Vinnikov et al. 2011). With climatic variation being one of the most important forces structuring the world's ecological communities, the changes over time of soil conditions in sensitive natural plant communities will determine which species will continue to thrive and which species will be forced to become locally extinct.

The soils along the forest-steppe ecotone of the Colorado Front Range exhibit diverse spatial patterns because of discontinuities in soil processes or other localized effects such as

past tectonic uplift, parent material, weathering, transportation of materials, etc. (Birkeland et al. 2003, Dethier et al. 2003). These patterns are largely a function of historical factors, such as forestry practices, agricultural activities, fire, and climatic patterns. Resource availability has long been recognized as important in determining patterns in the diversity of organisms (Grime 1979, Tilman 1982). The main factors determining spatial heterogeneity at the local level are resource availability and response to environmental variables that have a direct impact on plant growth or on available resources. In times of climatic uncertainty, information on the current health of the natural resources is important both ecologically and economically. Soil physical properties such as soil temperature, moisture, and texture have a direct effect on the nutrient availability, water holding capacity, germination of seeds, plant growth, as well as other soil processes and conditions (Mzuku et al 2005). Therefore, an adequate understanding of the spatial and temporal variability in these properties is essential to the management of ecosystem sustainability in this area.

This study illustrates the use of autocorrelation analysis and autocorrelograms as tools to identify the degree of dependency of soil temperature, moisture and several laboratory derived soil variables on the distance and time between pairs of measurements and how to take advantage of this dependency along several line-transects that cross the forest-steppe ecotone along the Front Range of Colorado, USA. The study had three objectives:

- The first was to evaluate the magnitude of spatial and temporal variation of soil temperature and moisture across a transition zone from forest to steppe.

- The second was to investigate the usefulness of this type of statistical analysis as a tool to describe soil variability that could be incorporated in future studies.

This type of study will add to the understanding of fine-scale soil properties and their relationship to the greater landscape in terms of land management influence and future climatic variability.

## **2.2. Methods**

### **2.2.1. Study area**

Two study sites are located in the montane zone (~1750-2300 m) of the eastern slope of the northern Colorado Front Range. The first is in the City of Boulder's Open Space and Mountain Parks Shanahan Ridge area (elevation 1756 m; 39°57'30.8"N, 105°15'44.6"W) and the second is located in Jefferson County's White Ranch Open Space area (elevation 2282 m; 39°48'32.3"N, 105°17'4.2"W) (Figure 1.9.). Soils along the Front Range are highly variable but are usually Mollic Cryoll soils dominant with rocky, thin, coarsely textured and shallow slightly acidic characteristics (Johnson & Cline 1965, NRCS 2013). With a cryic soil temperature regime, the Cryolls are the soils of the northern latitudes. They have a xeric, ustic, or udic soil moisture regime and are moderately extensive in the western U.S. Climate stations located near both sites show mean annual temperature ranges from 10.7° C at an elevation of 1655 m for 1983-2012 (Boulder, Colorado station, NOAA/NWS Cooperative, Boulder, Colorado) to 7.0° C at 2133 m (Evergreen, Colorado station, Western Regional Climate Center, Reno, NV) for 1983-2012. Precipitation is less variable between the two sites as temperature, ranging from 49.9 cm at 1655 m to 47.0 cm at 2133 m over the same periods as temperature.

This region includes a wide array of vegetation, including shortgrass steppe, shrub-steppe, and open woodland stands of ponderosa pine (*Pinus ponderosa*) (Figure 1.8.). Since the origin of the present forest stands, these areas have remained relatively undisturbed. The Shanahan Ridge area in Boulder experienced widespread fire (minimum 42 hectare extent) in 1870 (Sheriff & Veblen 2006), while White Ranch Open Space has little known history of widespread wildfire (Gartner 2008). Cattle grazing at both locations continued through the late 1960s. With acquisition of both site locations by local governments came a cease to this practice. However grazing by native ungulates continues (elk, deer). Latitudinal and elevational plant species distributions along the Front Range of Colorado have been attributed to temperature and moisture, as typically influenced by elevation and topographic position (Peet 1981, 1988, Allen et al. 1991).

The average lapse rate of an air parcel is 6-10°C/1000m, with a dry air parcel being influenced by the dry adiabatic lapse rate of 10°C/1000m and a saturated air parcel being influenced by the moist adiabatic lapse rate of 6-9°C/1000m. The two sites differ in elevation by approximately 500 meters, which is the same as the two city stations described previously, giving a 3-5°C difference in annual temperatures between Boulder and Evergreen. The slope plays a role in the amount of run-off, water penetration and evapotranspiration. The White Ranch site is slightly steeper with a 23% slope over the 15% at Shanahan Ridge.

Aspect has a very large effect on its own. For example, a south facing slope would have higher actual evaporation (lower potential evapotranspiration) versus a northern aspect based on the reduced amount of leaf area on south facing slopes depending on the elevation (higher

elevation sites receive more rainfall because as the air is forced up the side of a mountain to a higher elevation the air cools, can hold more moisture, reaches the lifted condensation level, or the point at which the air is completely saturated, and if pushed up even higher, the moisture in the air will precipitate out). Shanahan Ridge has a 67° east/northeast southwest aspect with a significant amount of insolation during the morning through afternoon due to little to no tree coverage to its south and east. White Ranch has a 21° north/northeast facing aspect. The White Ranch site is unique in particular to most ecotone or transitional studies. Here, the location of the treed area is below the grassland portion, giving it more shade in the earlier parts of the day. The major insolation is later in the morning into late afternoon (Table 2.1). These variances in slope and aspect may give insight into the variations in soil conditions.

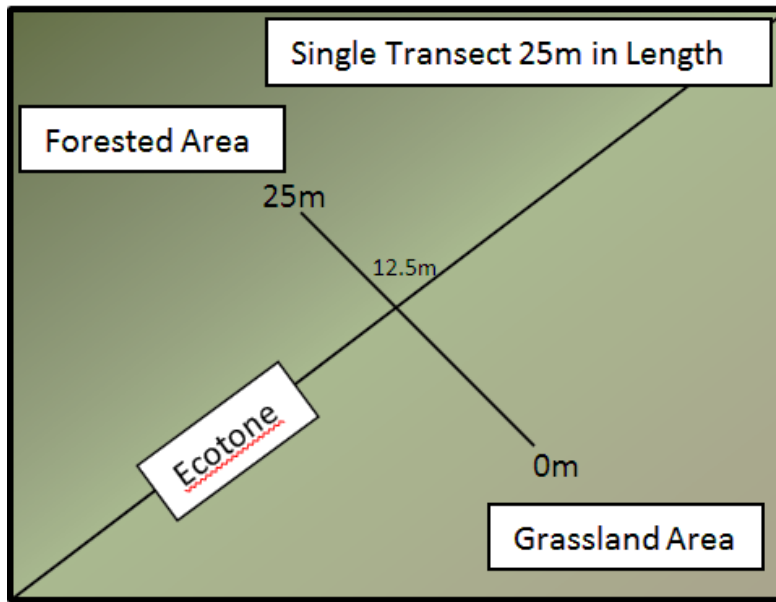
**Table 2.1.** Line-transects along the Front Range of Colorado, USA.

Site Name	From	To	UTM E	UTM N	Elevation	Slope	Aspect
	Veg Type	Veg Type			(m)	(%)	(°)
<b>Shanahan Ridge</b>	Shortgrass Prairie Steppe	<i>Pinus ponderosa</i> woodland	477595.8	4423197.3	1750	15	67
<b>White Ranch</b>	Shortgrass Prairie Steppe	<i>Pinus Ponderosa</i> woodland	475642.8	4406584.8	2280	23	21

### **2.2.2. Microclimate analyses**

In order to allow for analysis of spatial and temporal microclimate variation, field data were collected continuously from June 13<sup>th</sup>, 2009 through September 21<sup>st</sup>, 2012. Sites were identified in the fall of 2008 and spring of 2009 through collaboration with local land managers. Sites were at the lower elevational margin of Ponderosa pine distribution where ecotones with shortgrass steppe were available, and were along the Front Range of the Colorado Rockies near Boulder and Golden, CO.

Line-transects were located perpendicular to the ecotone at each site (Figure 2.1.), with Shanahan Ridge oriented along a 67° aspect and White Ranch oriented along a 21° aspect. In early June, 2009 one 25 m line-transect was laid out at Shanahan Ridge and one 25 m line-transect at White Ranch. All measurements of soil temperature had a regular sampling interval of 1 m in the grassland (meters 0-11) and forested (meters 14-25) portions of the line-transect with finer resolution of 0.5 m across the ecotone (11.5, 12.5 and 13.5 meters respectively). Measurements of soil moisture had a sampling interval of 6.25 meters along the entire line-transect equating to five total sampling points. This scale was continued through the May 22<sup>nd</sup> of 2011. At this time the resolution of the fine-scale sampling was reduced to two meter intervals up to meter 12, a point located at 12.5 m, and then continuing on from meter 13 through meter 25. This spacing preserved sensitivity to fine-scale variability while allowing deployment of sensors to increase line-transect replication. The 6.25 m spacing for soil moisture was maintained throughout the study and across both line-transects.



**Figure 2.1.** Diagram of line-transect layout and orientation

### 2.2.3. Soil temperature

From June 21<sup>st</sup>, 2009 through May 22<sup>nd</sup>, 2011 the upper 10 cm of soil temperature was measured using Thermochron iButtons (Model #DS1921G, Embedded Data Systems, Lawrenceburg, KY, USA). Due to a lack of reliability in battery life, low moisture contact resistance, the longevity of the study, and the acquisition of additional funding, the decision was made to change measurement devices in the summer of 2011 to HOBO Pendant data loggers (Onset Computer Corporation, Bourne, MA, USA). All sensors measure temperature at contact points between soil and sensors. The sensors were inserted into the soil and were as close to a 10 cm depth as possible. The accuracy of the iButtons is  $\pm 1^{\circ}\text{C}$  and resolution of  $0.5^{\circ}\text{C}$ . The HOBO data loggers have an accuracy of  $\pm 0.53^{\circ}\text{C}$  and a resolution of  $0.14^{\circ}\text{C}$ .

Sensors were calibrated before placement in the field. Sensors at the White Ranch site were removed on September 21<sup>st</sup>, 2012 and calibration was rechecked at this time. For this



calibration, ten sensors were chosen at random and immersed in a bowl of melted ice to determine the 0°C reading. Next, sensors were placed in a pot of slowly boiling water to determine the 100°C reading. All iButton sensors used in calibration read to within  $\pm 1^\circ\text{C}$  or better and HOBO data loggers read to within  $\pm 0.53^\circ\text{C}$  or better. Further discussion of the accuracy and sensing methodology of iButtons can be found in Hubbard et al. 2005.

#### **2.2.4. Soil moisture**

Soil moisture was measured with EC-5 soil moisture sensors and recorded using Em5b data loggers (Decagon Devices, Inc., Pullman, WA, USA). The sensors measure the dielectric constant of the media and approximately a liter of volumetric water content (VWC) surrounding the probe with an accuracy of  $\pm 3\%$  VWC and 0.1% VWC resolution in mineral soil. The sensors were inserted into the soil at a 45 angle extending from a depth of 5-10 cm. The VWC in the soil (also called the volume wetness or volume fraction of soil water) represents the fraction of the total volume of soil that is occupied by the water contained in the soil. For example, a measurement of 0.111 VWC would represent an 11.1% water content of a cubic meter volume of soil.

#### **2.2.5. Spatial and temporal autocorrelation**

Classical parametric statistics cannot be used to evaluate autocorrelated data without violating the central assumption of sample independence. Yet virtually all environmental samples are autocorrelated: samples taken from locations close to each other tend to be more similar than samples taken farther apart. As Tobler's first law of Geography states "Everything is related to everything else, but near things are more related to each other (Tobler 1970)."

Spatial statistics provides a means for defining spatial autocorrelation and for using the knowledge about its strength and scale to interpolate the value of the variants at unsampled locations. The same can be thought of when dealing with temporal autocorrelation, but through the use of time-series analysis rather than geostatistics, the temporal 'closeness' of the data can be determined.

Autocorrelation is defined as the relationship among values of a variable that is attributable to some underlying ordering of these values within a geographic space or across time (Griffith 1987). The analysis is based on the correlation of pairs of observations from a series and is analogous to Pearson's correlation coefficient (Sokal & Thomson 1987). The separation of the observations in each pair is an integral number of distance or time units within the series. If the number of distance units (commonly referred to as a lag) is selected as  $k$ , then each pair of observations in the series that is separated by a lag of  $k$  forms a new observation. This new observation becomes part of a set of values compiled in a similar fashion for all possible combinations of X and Y for a particular value of  $k$  in the original data. An autocorrelation coefficient ( $r_k$ ) of the X values with Y values may then be calculated. Calculation of an  $r_k$  is repeated for successive  $k$  values, with a set of  $r_k$ 's being formed. The value of  $r_k$  may vary from +1 to -1 (Kendall & Stuart 1968, Cliff & Ord 1973, Anderson 1976, Lanyon & Hall 1981, Griffith 1987, Box et al. 2008).

In the current study I investigated spatial patterns of soil temperature sampled at the scale of 1 and 2 meters and temporal patterns of soil temperature and moisture for monthly intervals (determined using daily averages that were then averaged monthly). To examine this

fine-scale structure's statistical significance, I calculated Global Moran's I spatially and the autocorrelation function temporally for each line-transect at different intervals (time and space) between points. The initial hypotheses were that there would be some autocorrelation between points closer to one another. The null hypothesis ( $H_0$ ) was that there is a non-zero autocorrelation present in the population ( $0 \leq r_k$ ), i.e. no autocorrelation present. On the other hand, the alternate hypothesis ( $H_1$ ) was that there is a zero autocorrelation present in the population ( $r_k=0$ ), i.e. there is spatial or temporal autocorrelation present. For time-series analysis, both correlograms and semi-variograms are often used to display autocorrelation. They show the same information, but the trends are reversed. For this research I prefer correlograms over variograms, because correlograms more easily demonstrate the negative and positive autocorrelations.

Several tiers of data were used for spatial autocorrelation. From June 21<sup>st</sup> of 2009 through May 22<sup>nd</sup> of 2011 the spatial resolution of sampling points for soil temperature was every meter along the 25 meter line-transect resulting in a sample size of  $n=25$ . Significance values for this sample size is 0.39 ( $p<0.05$ ) and 0.51 ( $p<0.01$ ). From May 23<sup>rd</sup> of 2011 through September 21<sup>st</sup> of 2012 the spatial resolution of sampling points was every other meter. This resulted in a sample size of  $n=13$  for this time period for soil temperature. Significance values for this sample size is 0.54 ( $p<0.05$ ) and 0.84 ( $p<0.01$ ). Due to the spatial resolution for soil moisture sampling ( $n=6.25$ ), soil moisture was eliminated from spatial autocorrelation analysis. Although sample sizes for analysis were lower than normally desired for statistical analysis ( $n=30$  or higher is desirable), the distributions were determined to be normal with an average

of 70% of daily values falling within two standard deviations of the mean across the transect and throughout the study period for both soil temperature and soil moisture.

With a sampling interval of one hour for temporal analysis, which has been consistent since the summer of 2009, occasional loss of data for a few hours up to a week at a time was an inevitable occurrence due to sensor error. Daily averages for both soil temperature and soil moisture were used in order to maintain consistency in analysis. For temporal analysis listwise (or casewise) deletion imputation was used in order to remove all null data points. Because the data were missing at completely random, due either to sensor malfunction or animal disturbance (eating through cords or pulling sensors out of the ground), this was determined to be the best method and is very common in large data set analysis. However, if there are large amounts of data missing then the power of the analysis will be reduced. For this research there were not significant amounts of missing data that would affect the spatial or temporal analysis.

In spatial analysis it is important to have consistent data across the space being studied because if autocorrelation lags are to be determined missing data points eliminate the needed adjacent points. When using daily average composites over a month the loss of data reduces this problem slightly, but when more than a few days are missing interpolation methods need to be implemented. For this interpolation I used the available data from the same month either earlier or later in the study to see the magnitude of change from one point to another and filled in the missing data as best as possible. For example, if meter 20 of October, 2010 was missing, I would look at meters 19 and 21 of June 2009 and 2011 and see where meter 20 fell in between these and would fill in the missing data based on meters 19 and 21 of October, 2010. With this

method I wanted to avoid increasing the amount of autocorrelation that would have occurred if imputation methods such as using the average of that month (say all other October values available in the study period) or averaging September and November, 2010 to fill in the gap were used. Magnitude of differences was important part of this study and I wanted to retain as much of that fine-scale variability as possible when possible.

ArcGIS does not have the ability to batch spatial analysis. Therefore, for spatial Moran's I analysis I used daily averages that were then averaged for each month between June 2009 and September 2012. For temporal time-series autocorrelation analysis I used daily averages in order to preserve the fine scale sensitivity to diurnal changes in soil temperature and moisture. Data collection was begun in June 21<sup>st</sup> of 2009 and ended in September 21<sup>st</sup> of 2012. Full years were recorded in 2010 and 2011 (with the exception of missing data). Total days recorded in 2009 were 195 and the number of days recorded in 2012 was 265. For  $n=195$  significance values were 0.14 ( $p<0.05$ ) and 0.18 ( $p<0.01$ ). For  $n=265$  significance values were 0.12 ( $p<0.05$ ) and 0.16 ( $p<0.01$ ). Significance values for the full year ( $n=365$ ) is 0.10 ( $p<0.05$ ) and 0.13 ( $p<0.01$ ).

Spatial autocorrelation among soil temperature was tested using the Moran's I method. This is a measure of spatial autocorrelation that accounts for the two-dimensional and bi-directional nature of spatial datasets (Kelejian & Prucha 2001). Moran's I (Moran 1950) tests for global spatial autocorrelation for continuous data. It is based on cross-products of the deviations of the mean. It is calculated as:

$$I = \frac{N}{\sum i \sum w_{ij}} \frac{\sum i \sum j (X_i - \bar{X})(X_j - \bar{X})}{\sum i (X_i - \bar{X})^2}$$

where  $N$  is the total number of observations indexed by  $i$  and  $j$ ,  $X$  is the variable of interest,  $\bar{X}$  is the mean of  $X$ , and  $w_{ij}$  is a matrix of spatial weights,  $w_{ij}=1$  if locations  $i$  and  $j$  are adjacent and zero otherwise (Kelejian & Prucha 2001). A positive Moran's  $I$  value indicates a positive autocorrelation with a value of +1 indicating total correlation. A negative Moran's  $I$  value specifies a negative autocorrelation with a value of  $-1$  indicating complete dispersion. A value of zero is a random spatial pattern.

ArcGIS 10.1 was used for calculating Global Moran's  $I$  for both soil temperature and soil moisture daily values averaged for each month during the study period, totaling 40 months. Daily values for soil temperature and moisture were averaged for each month from June 2009 through September of 2012. UTM coordinates were converted from Latitude and Longitude measurements collected at each site and added to each spreadsheet. Microsoft Excel .csv files were created for all months and imported into ArcGIS 10.1. Inputs for the Moran's  $I$  analysis were as follows: Inverse distance, where the impact of one variable on another decreases with distance, was used as the spatial relationship conceptualization and due to the linear nature of the transects Euclidian distance was used as the distance measurement.

Moran's  $I$  in ArcGIS also produces a z-score value that indicates whether or not the null hypothesis can be rejected. In this case, the null hypothesis states that there is no spatial clustering (things are not autocorrelated). In order to determine if this z-score is significant, it is

compared to the range of values for the 0.05 confidence level. If the score was below -1.96 or greater than 1.96 it was determined to be significant.

Temporal autocorrelation among soil temperature and soil moisture was tested using the *web:reg correlogram* add-in (Annen 2004) for Microsoft Excel. Daily averages for soil temperature and moisture for each year (January 1 – December 31) were used. Time-series data were then input into the add-in, the autocorrelations of the raw data were analyzed for hourly time lags in order to detect autocorrelation values. The formula for calculating the autocorrelation function is as follows:

$$r_k = \frac{\sum_{t=k+1}^n [(x_t - \bar{x})(x_{t-k} - \bar{x})] / (n - k)}{\sum_{t=1}^n (x_t - \bar{x})^2 / n}$$

where  $x$  is the data series,  $k$  is the lag (in hours), and  $\bar{x}$  is the sample mean. The autocorrelation function  $r_k$  measures the strength of the relationship between  $x_t$  and  $x_{t+k}$ .

### 2.3. Results and discussion

Investigators have shown increasing interest in analyzing measured soil parameters for their interdependency over space, i.e., to study the dependency of a measured parameter on location in the field. Typically semi-variograms and autocorrelograms have been used to study the spatial structure of soil properties. Some of the first research to study the effects of soil variability on soil conditions looked at leaching characteristics of field soils (Biggar and Nielsen 1976), infiltration rates (Vieira et al. 1981, Sisson and Wierenga 1981), soil moisture (Al-Kayssi et al. 1990) and surface temperatures (Vauclin et al. 1982, Davidoff et al. 1986, Al Kayssi et al. 2002).

Coarse-scale differences in average seasonal soil temperatures ( $^{\circ}\text{C}$ ) and soil moisture VWC ( $\text{m}^3/\text{m}^3$ ) existed for the two research sites (Table 2.2). At Shanahan Ridge air temperatures and soil temperatures vary in their relationship throughout the study period, with 2009 and 2010 having  $1^{\circ}\text{C}$  warmer average soil temperatures than air temperature, while 2011 and 2012 were the opposite, having warmer air temperatures than soil (Table 2.2.). White Ranch on the other hand has consistently warmer soil temperatures than air. Although the air temperatures may heat up faster during the day, the heat held in the soil later into the evening (and the air temperature cooling down quicker) and throughout the night would make the average soil temperatures (usually) warmer than the air temperature. The specific heat of soil moisture is higher than the air aboveground, the air in soil pore space, and the sand, silt, and clay minerals composing the soil itself, therefore the soils ability to retain that heat longer explains this relationship. The possible reasons for 2011 and 2012 at Shanahan Ridge being different from this reason may be related to the increased snowfall in 2011 possibly insulating the soil longer and reducing the air temperatures influence and the anomalously low precipitation levels early in the spring of 2012 reducing the moisture in the soil necessary in heat retention while increasing evaporation at the same time. White Ranch's topography and tree cover may help reduce the influences of reduced precipitation and increased temperatures by insulating and protecting the site from increased evaporation while maintaining snow cover for longer (Table 2.2.).

Although both sites vary fairly little in terms of soil volumetric water content on average, the amount of precipitation and snowfall vary a great deal (Figure 2.2.). Precipitation

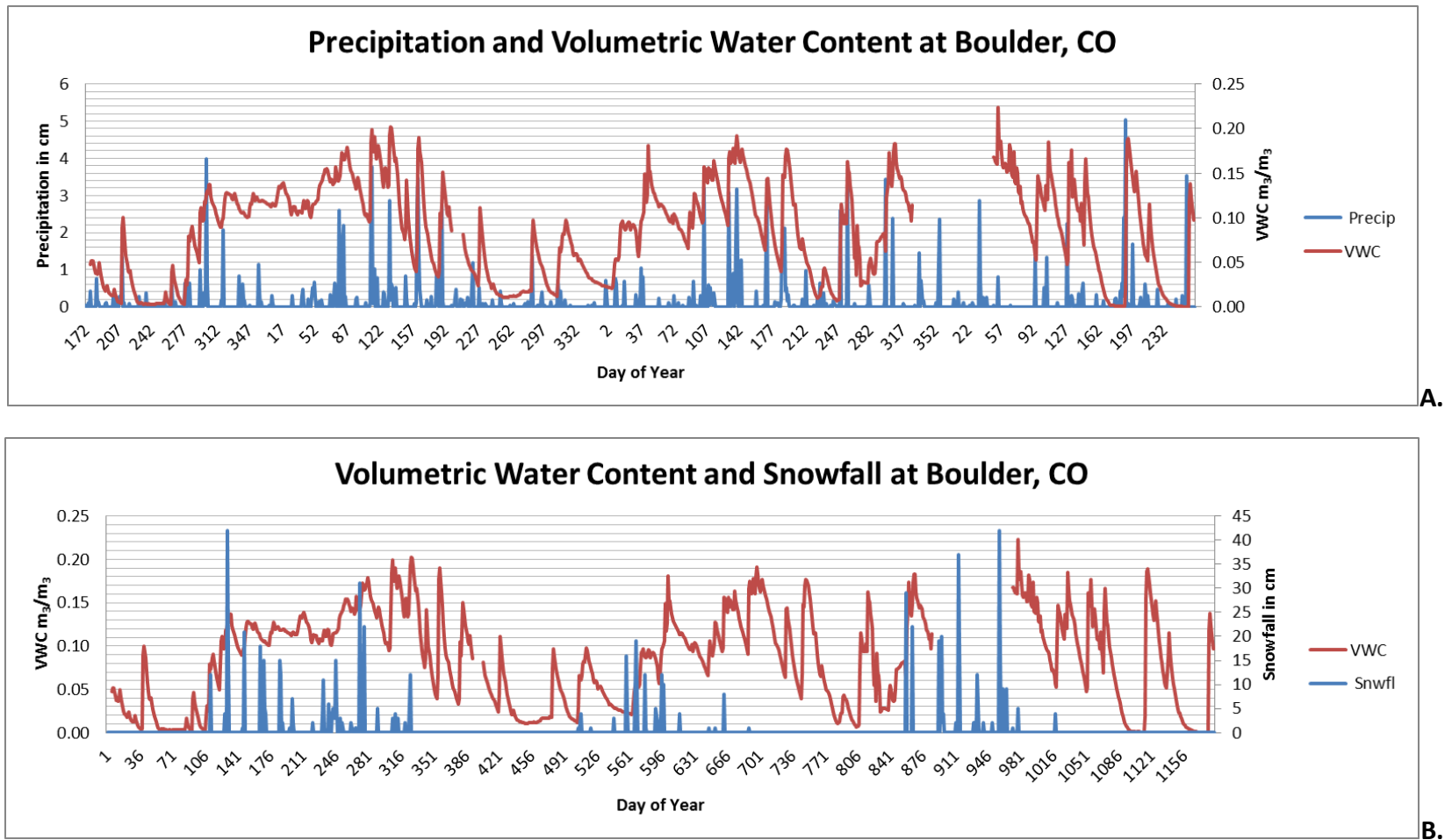


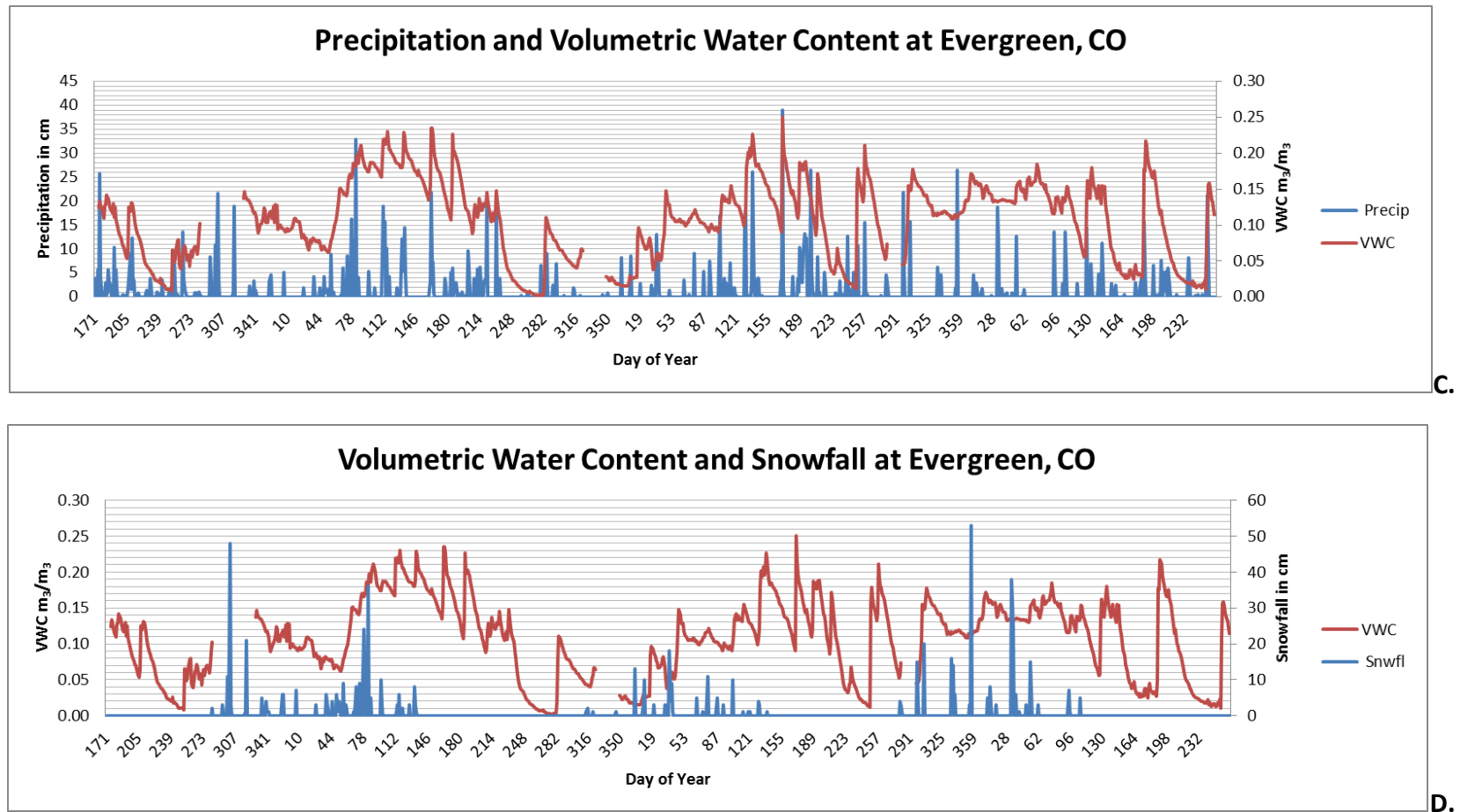
in the form of both rainfall and snow tends to create a lag in soil moisture in terms of the residence time in the top 10 cm (depth of sensor burial). As should be expected, the lag periods after a snowfall are longer than a rain event. Both soils here have high sand content compared to silt and clay (76.5% average at both sites), which equates to greater pores space and therefore higher percolation (drainage) rates following precipitation events.

**Table 2.2.** Average soil temperature and moisture at Shanahan Ridge, CO and White Ranch, CO over the study period.

\*June-December to coordinate with study period, \*\*January-September to coordinate with study period.

	<b>Shanahan/Boulder</b>	<b>Shanahan/Boulder</b>	<b>Evergreen/White</b>	<b>Evergreen/White</b>
	<b>Soil/Air Temp °C</b>	<b>Soil Moist/Precip/Snow cm</b>	<b>Soil/Air Temp °C</b>	<b>Soil Moist/Precip/Snow cm</b>
<b>2009</b>	13.7/12.4°C*	0.06 VWC/26.6 cm/171* cm	9.6/8.6°C*	0.08 VWC/32.2 cm/133 cm*
<b>2010</b>	11.9/10.9	0.09/51.6/205	7.6/6.9	0.11/42.3/204
<b>2011</b>	10.9/11.2	0.10/56.7/225	7.5/6.6	0.11/52.5/244
<b>2012</b>	13.3/14.2**	0.08/34.1/106**	10.1/9.78**	0.11/28.8/123**
<b>1983-2012 Average</b>	NA/10.8	NA/49.9/213	NA/7.0	NA/47/210





**Figure 2.2.** Precipitation, snowfall, and volumetric water content throughout the study period (June 20, 2009 – September 21, 2012) at Boulder, CO (A.,B.) and Evergreen, CO (C.,D.).

### 2.3.1. Spatial variability

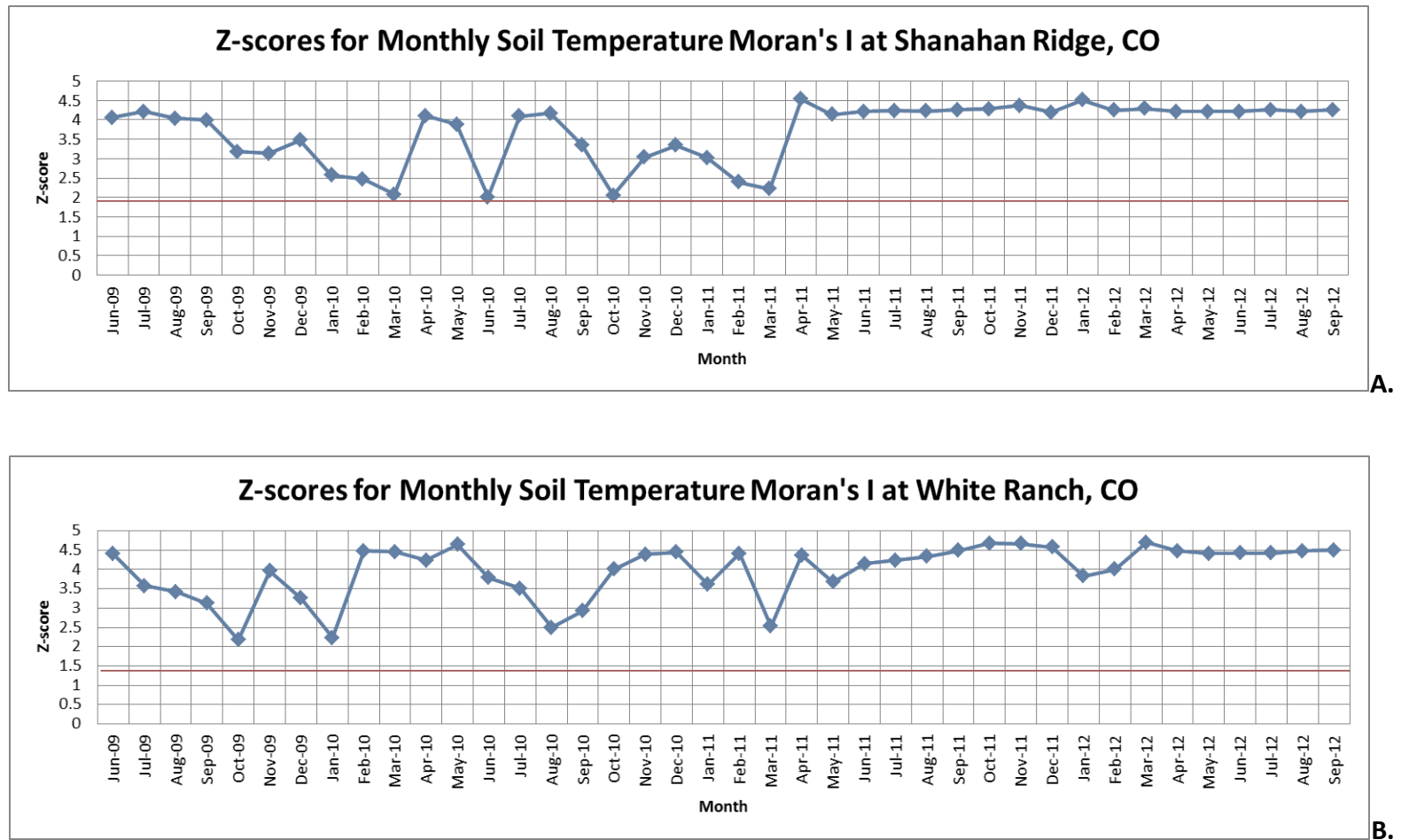
From June 21<sup>st</sup>, 2009 through May 22<sup>nd</sup>, 2011 the spatial resolution for soil temperature was recorded every meter. Each meter is represented as a single lag in the autocorrelation (i.e. meter 0 to 1 would be lag 1). As with many environmental variables the further away from the sample point one gets, the less correlation there is likely to be. Generally along each line-transect there is an initially strong autocorrelation with a sharp decline at some interval away from the beginning.

Moran's I analysis showed that soil temperatures display significant spatial autocorrelation during many months ( $p < 0.05$ ). Usually Moran's I values can be standardized so that, based on an assumption of a normal distribution, the positive or negative aspects of the correlation and correlation significance levels can be tested (Anselin 1995, Levine 2004). Z-scores from Moran's I analysis show that all months are suitably significant to perform analysis on these smaller sample sizes (Figure 2.3.). When daily soil temperature averages are composited over each month from June 2009-September 2012 there are no distinct pattern in months (Figure 2.4.), however there is a distinct increase in clustering (Moran's I closer to +1) when moving through the study period from single meter spatial lags to two meter lags. In May of 2011 the spatial resolution of sampling was increased from one meter to two meters. This change is evident in the plot of Moran's I (Figure 2.4.).

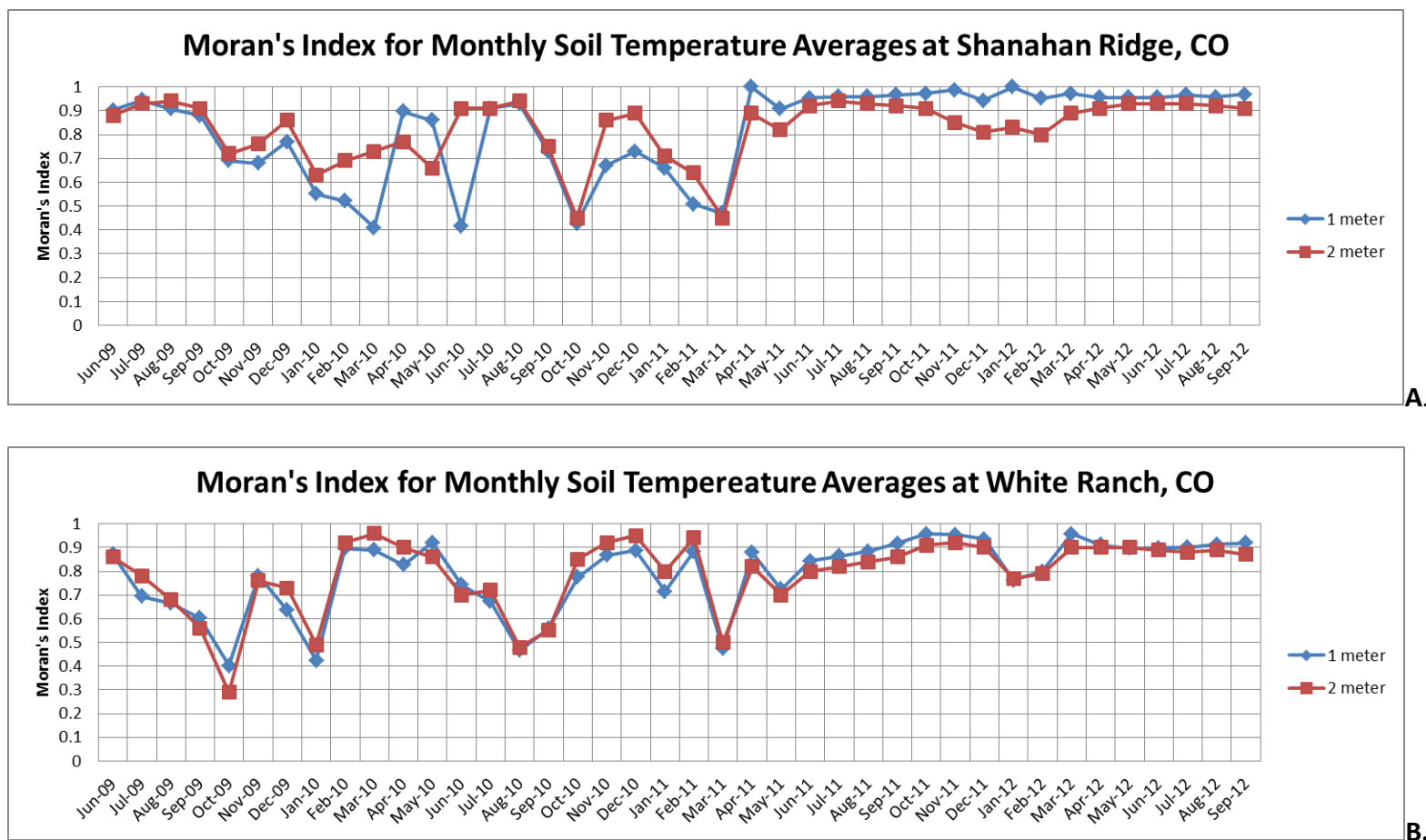
Studies have shown the importance of spatial variability of soil properties in species growth (Cambardella et al. 1994, Fu et al., 2011, Douaik et al. 2011, Liu et al. 2013). Analysis of the relationships between these variables need to incorporate spatial autocorrelation in order

to fully capture the variability of the site, and therefore, the variability of germination and persistence locations (Biggar & Nielsen 1976, Subler et al. 1995, Iqbal et al. 2005, Sharma et al. 2011). Spatial statistics are thought to be powerful analytical tools for the analysis of spatially dependent variation of soil temperature (Davidoff & Selim 1988, Yates et al. 1988, Lascano & Hatfield 1992, Some'e et al. 2011). Moran's I is a quantitative way to display this variability of soil conditions. A simple way of showing this variability across the site and through time is looking at the variance (standard deviation) across space and time, because soil resources can have large effects on plants, it is important to have a detailed understanding of how the resources available to plants change.

Standard deviations of soil temperature across the transect as well as throughout time at the two sites shows that there is a consistent trend across the transect (across the ecotone) that is repeated each year (Figure 2.5.). This information is important to species growth (Sharma et al. 2011). With the more variable the site the potential for changes in patterns of species cover that would in turn affect the microsite in a feedback. Both sites show a decrease in variance as a change across the transect takes place. Although the deviations change slightly from one year to the next, the pattern of deviation remains fairly constant.

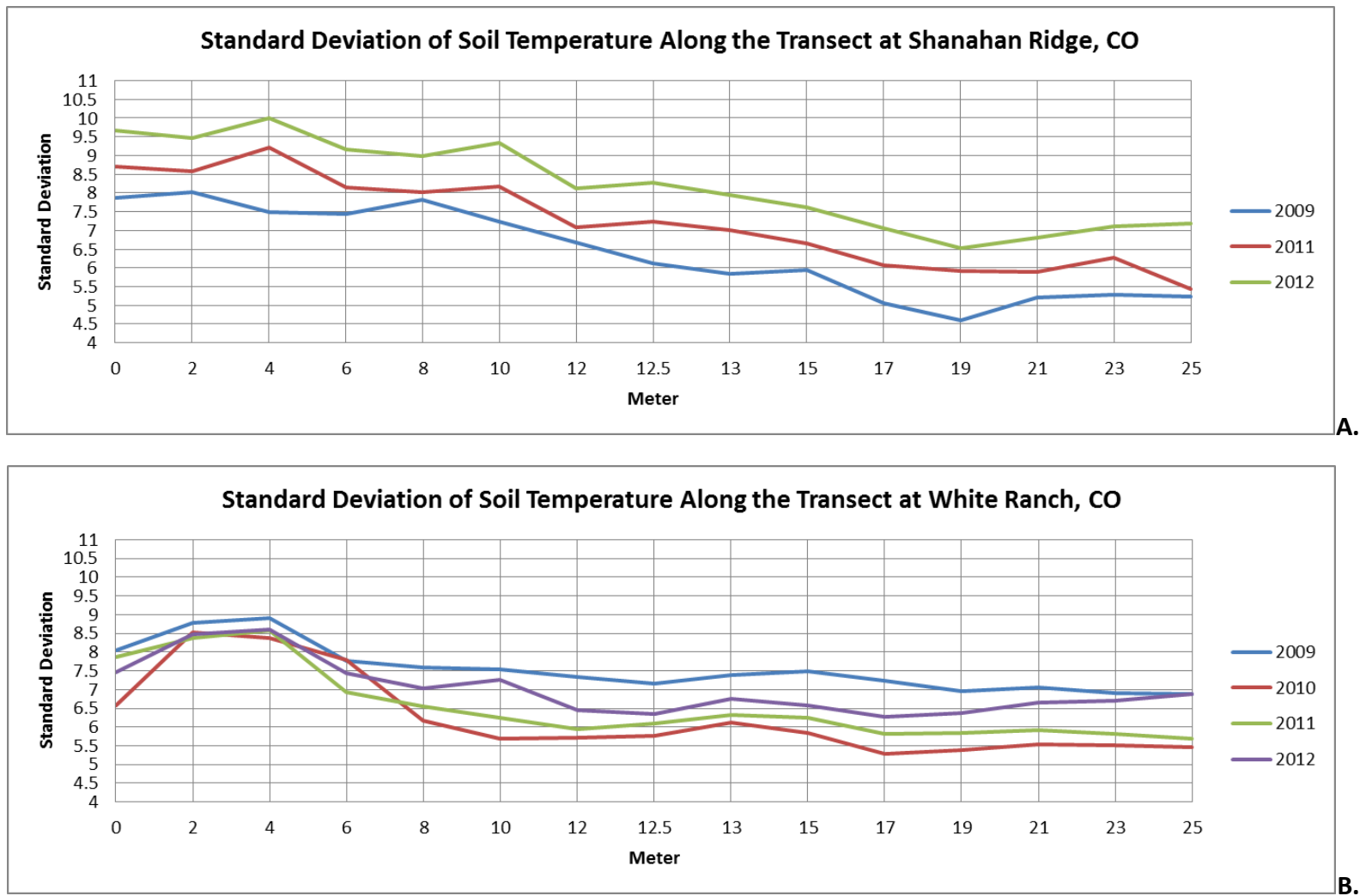


**Figure 2.3.** Z-scores for Moran's I spatial autocorrelation analysis of available average daily soil temperature ( $^{\circ}\text{C}$ ) for all months at Shanahan Ridge (A.) and White Ranch (B.). Values greater than 1.96 indicate significance at the  $p < 0.05$  level (red line).



**Figure 2.4.** Spatial autocorrelation of available average daily soil temperature ( $^{\circ}\text{C}$ ) for all months at Shanahan Ridge (A.) and White Ranch (B.). Values closer to +1 indicate clustering and closer to 0 indicate no relationship.





**Figure 2.5.** Standard deviation of soil temperature mean along the transect, across the ecotone for the years 2009-2012 at Shanahan Ridge (A.) and 2009, 2011, and 2012 at White Ranch (B.)

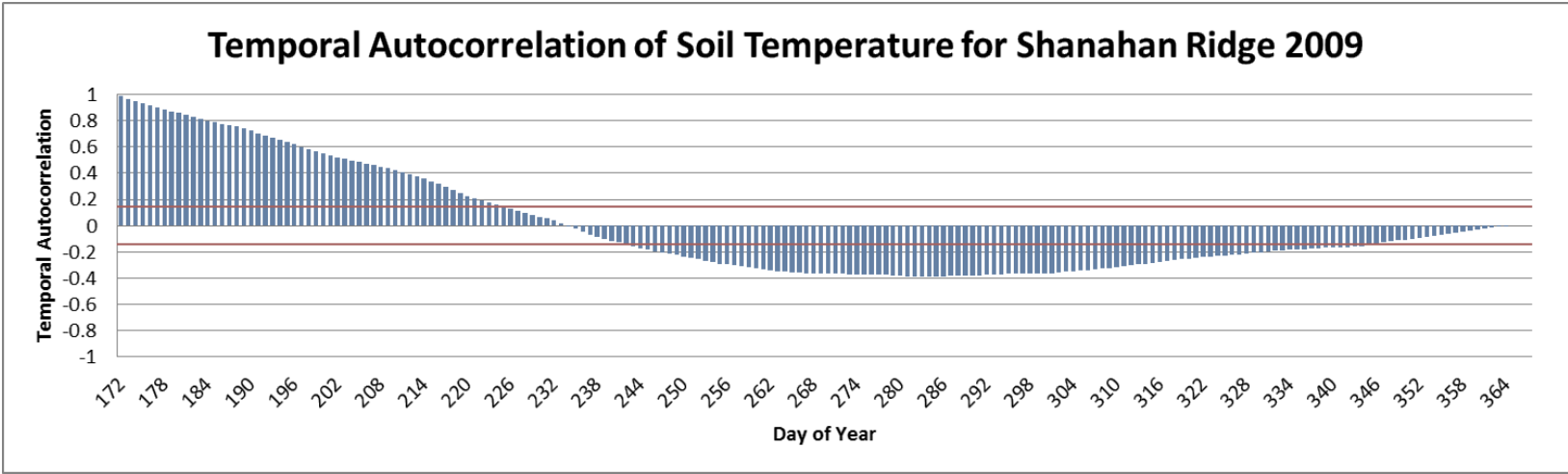
### 2.3.2. Temporal variability

Knowledge of temporal changes in soil conditions is highly desirable when making connections with vegetation responses. Many studies have looked at the temporal variability of soil moisture (Vinnikov et al. 1996, Western et al. 2002, Lauzon et al. 2004, Li et al. 2011, Mittelbach & Seneviratne 2012) and temperature (Kuzyakova & Stahr 2006, Katterer & Andren 2009, Vinnikov et al. 2011). With climatic variation being one of the most important forces structuring the world's ecological communities, the changes over time of soil conditions in sensitive natural plant communities will determine which species will continue to thrive and which species will be forced to become locally extinct.

At the Shanahan Ridge, CO site the initial autocorrelation between hours for soil temperature were very high, with 2009 beginning at 0.98, 2010 (0.99), 2011 (0.98), and 2012 (0.99) (Figure 2.6. A-D). At White Ranch, CO the initial autocorrelation values were also very high with 2009 beginning at 0.96, 2010 (0.98), 2011 (0.99), and 2012 (0.99) (Figure 2.6. E-H). Although the previous soil temperature values begin highly correlated with the next value, moving further into the year shows varying degrees of decline. In 2009 at Shanahan Ridge, there were 54 days between the initial data point (June 21<sup>st</sup>, 2009) and the day where insignificance at the 0.05 level was reached (August 14<sup>th</sup>). Between 2010 and 2012 similar time lags were found before insignificance at the 0.05 level was reached, 2010 (72 days, March 14<sup>th</sup>), 2011 (69 days, March 11<sup>th</sup>), and 2012 (78 days, March 19<sup>th</sup>) (Figure 2.6. A-D). It must be noted that 2009 data collection began in mid-June, whereas the remaining years all begin on January 1<sup>st</sup>. In 2009 at White Ranch, there were 35 days between the initial data point (June 21<sup>st</sup>, 2009)

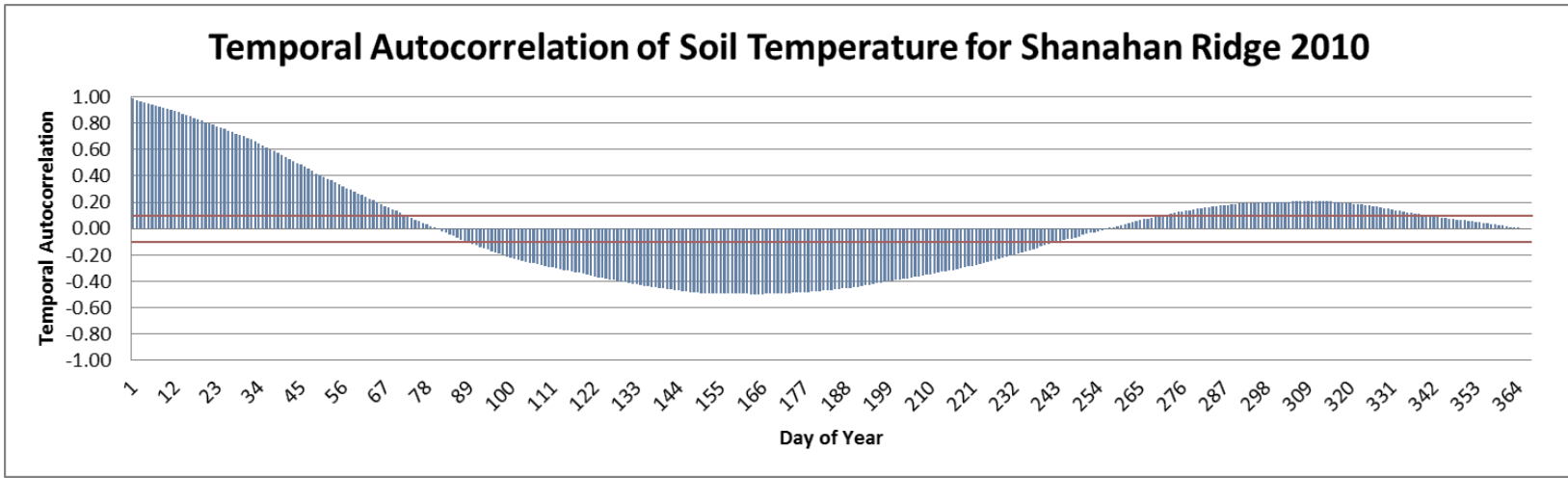
and the day where insignificance at the 0.05 was reached (July 26<sup>th</sup>). Between 2010 and 2012, as with Shanahan Ridge there were similar time lags once again before insignificance at the 0.05 level was reached, 2010 (74 days, March 16<sup>th</sup>), 2011 (73 days, March 15<sup>th</sup>), and 2012 (78 days, March 19<sup>th</sup>) (Figure 2.6. E-H).

It is evident from this analysis that the month of March plays a key role in species growth and subsequent coverage in these locations. Interestingly, the two sites differ very little in terms of timing of autocorrelation. If the ability to generalize across locations in terms of the variability (Figure 2.5.) across space and time (Figure 2.6.), the utility of studies such as this would become important in studying vegetation response to climate change and microsite variability.

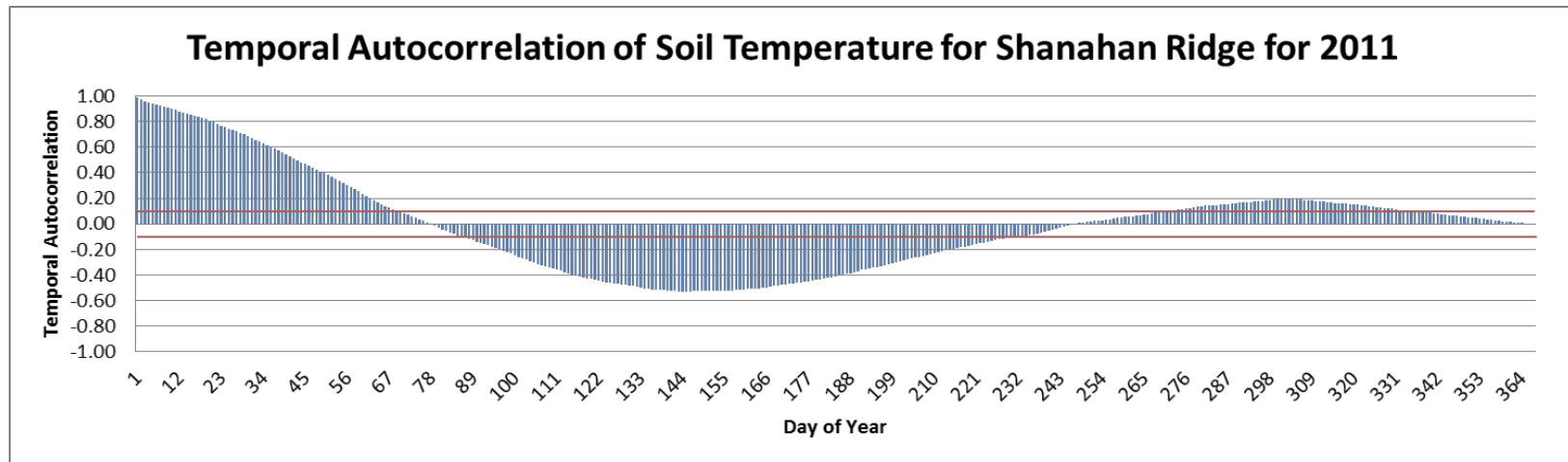


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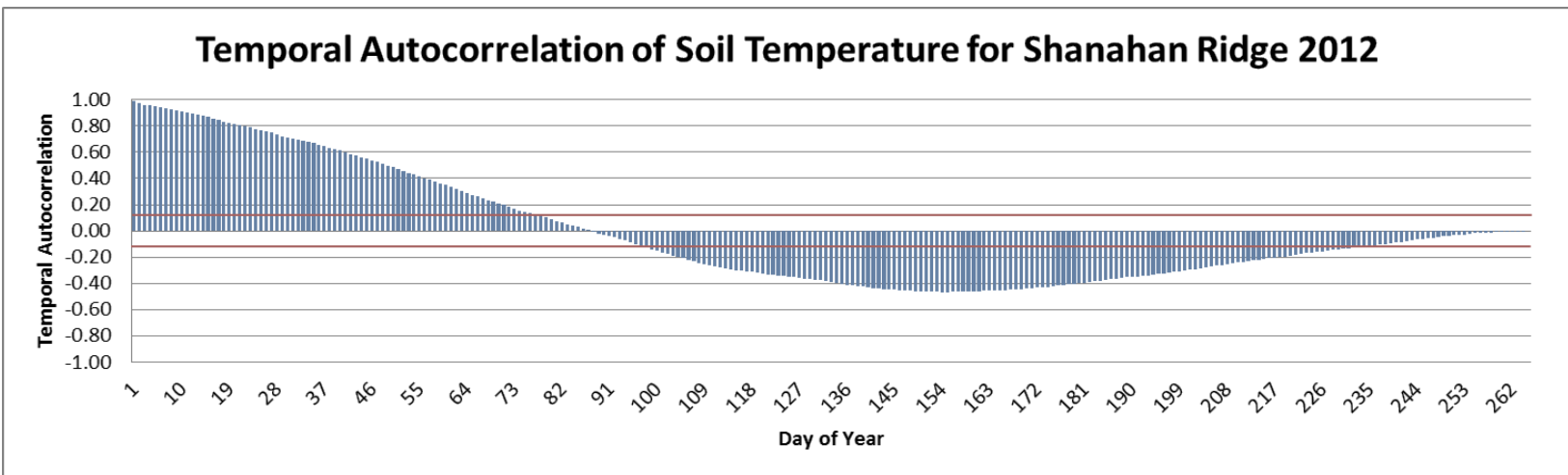
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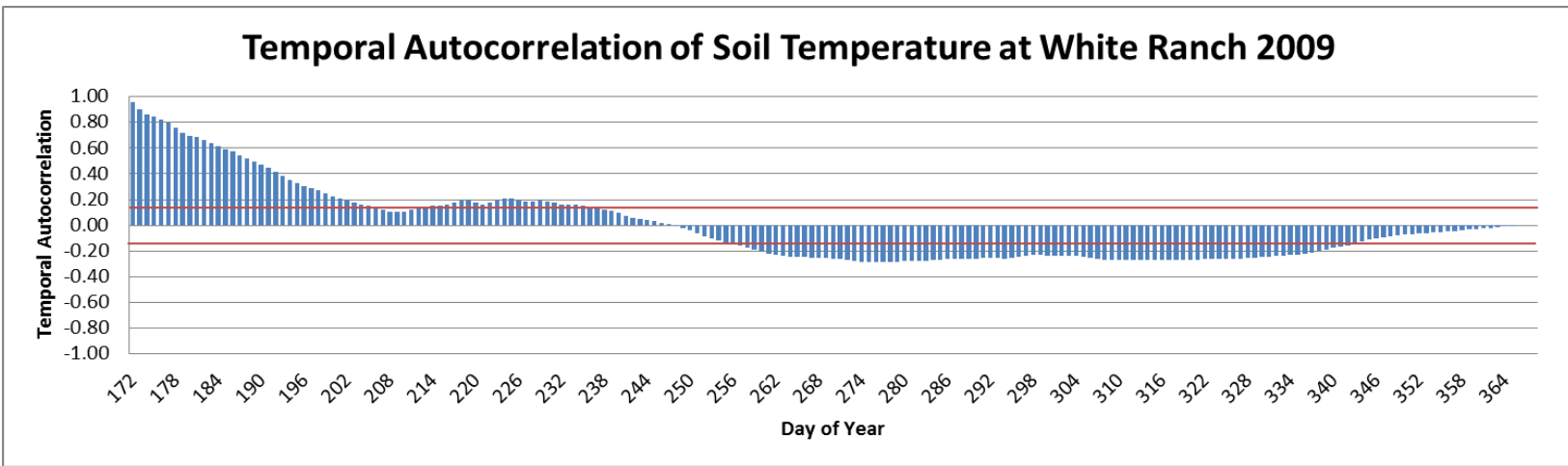
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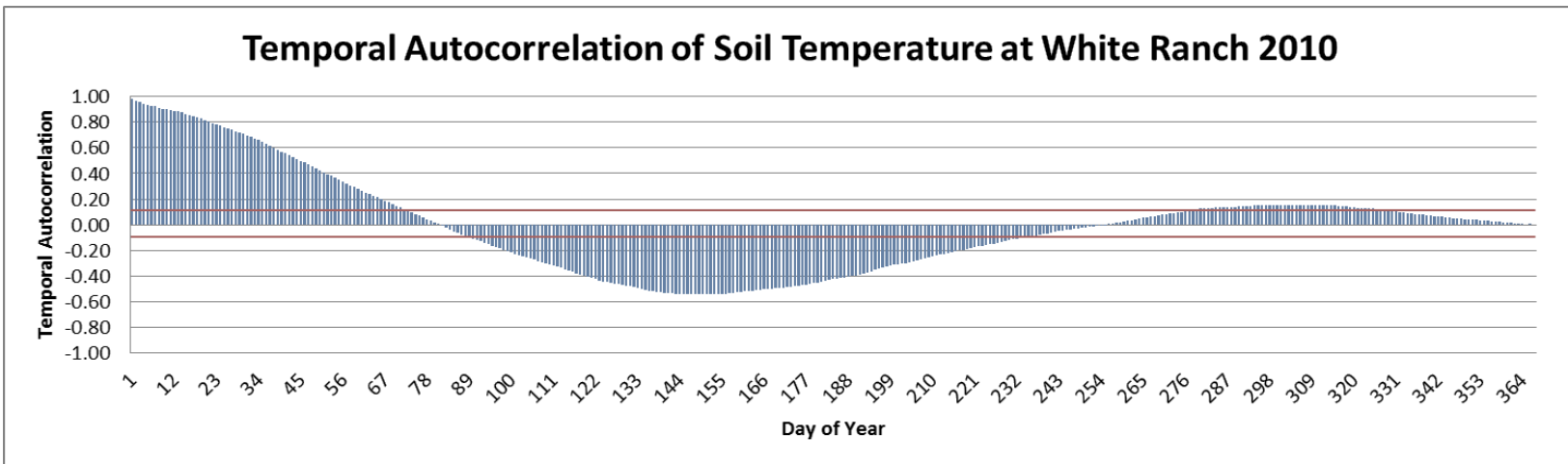
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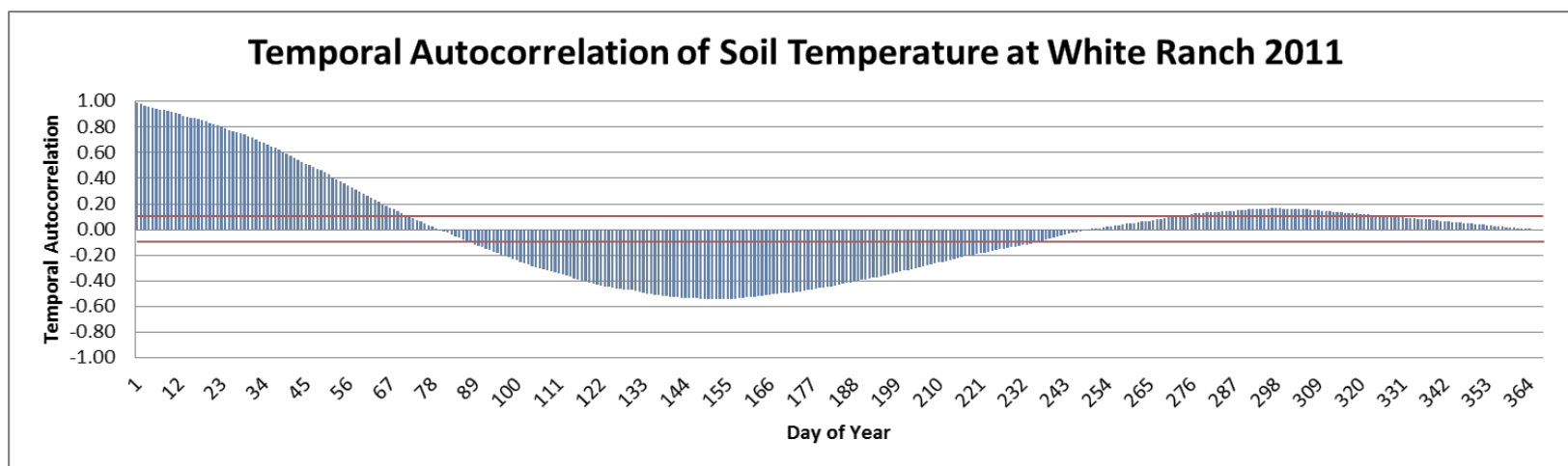
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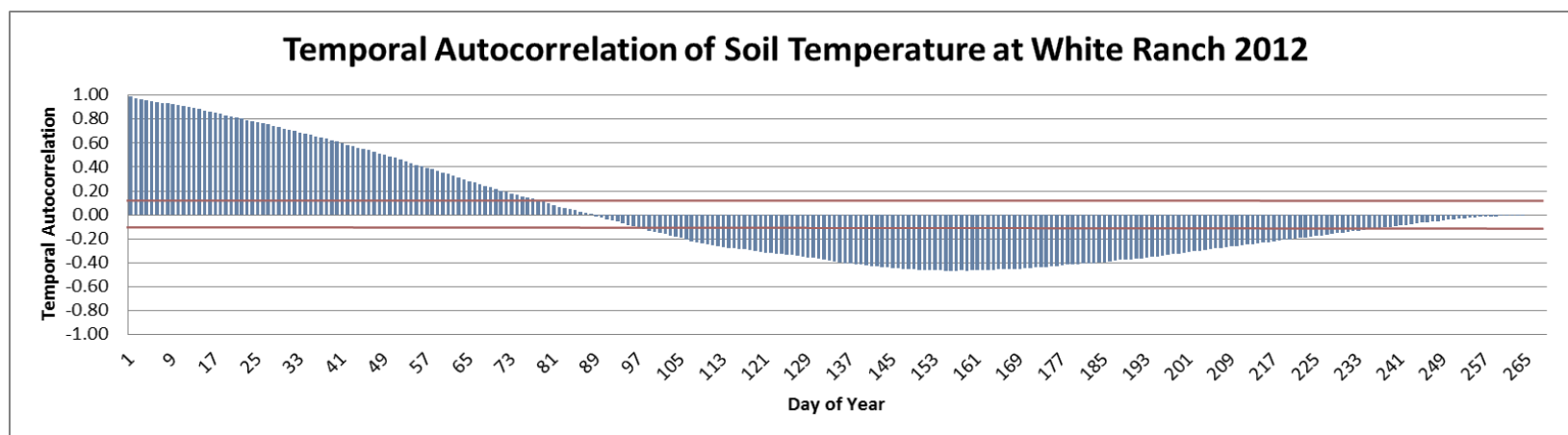


F.



G.

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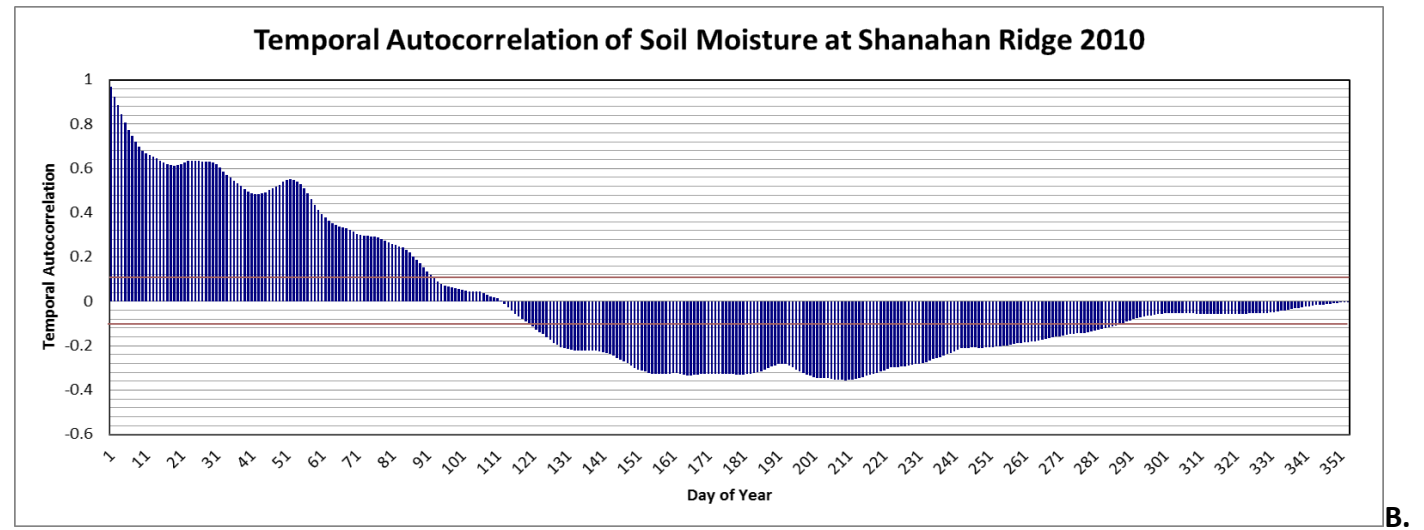
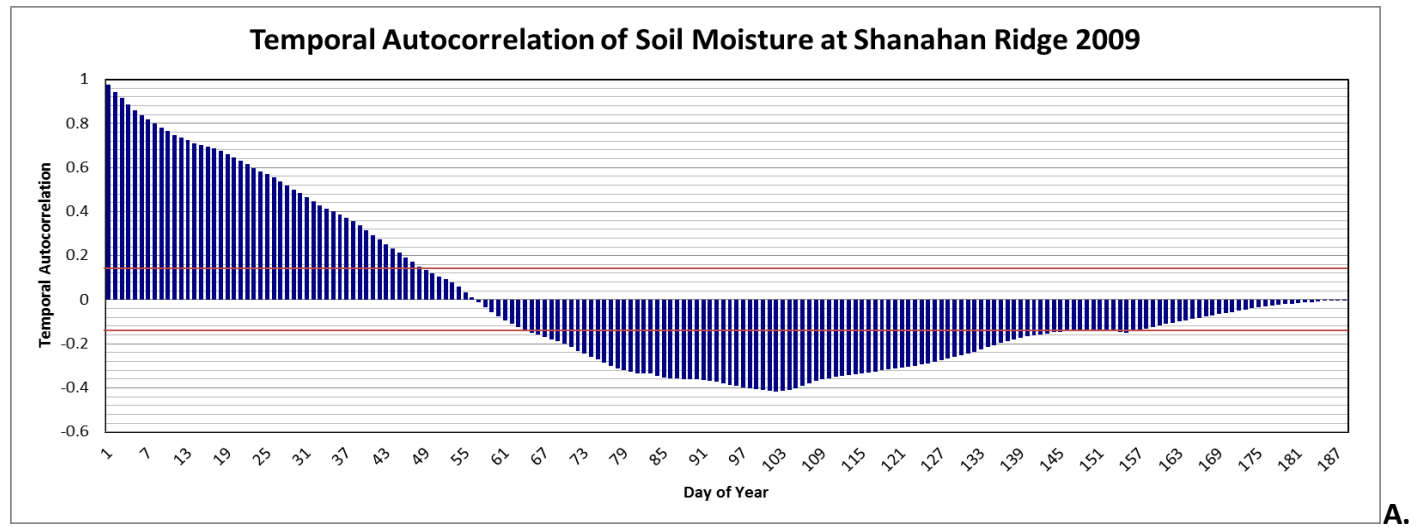


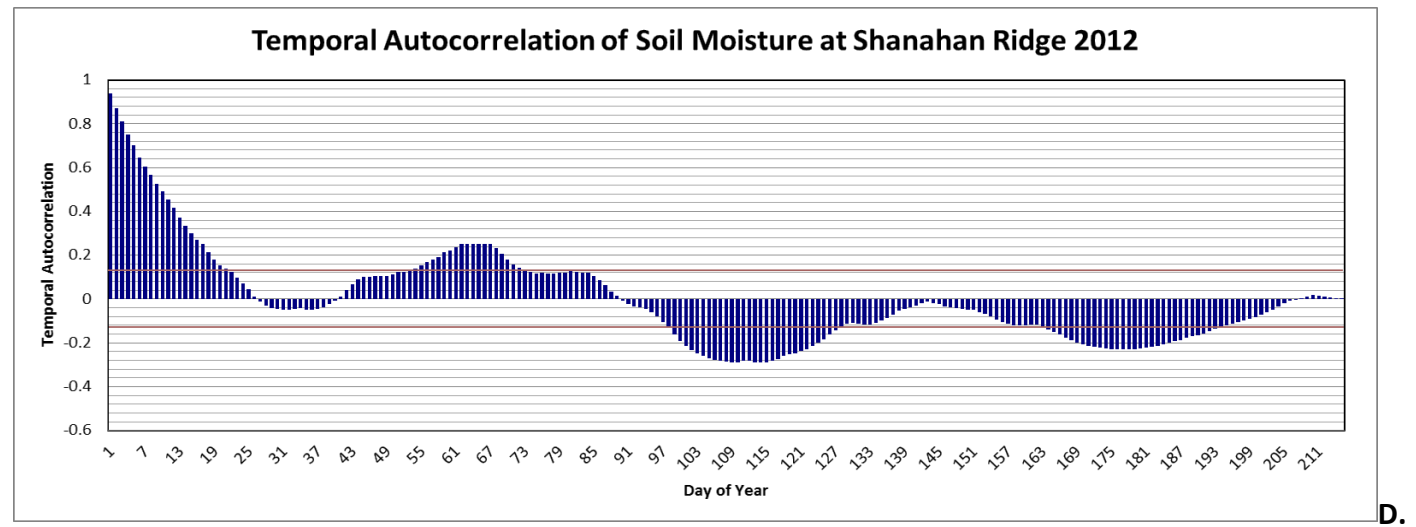
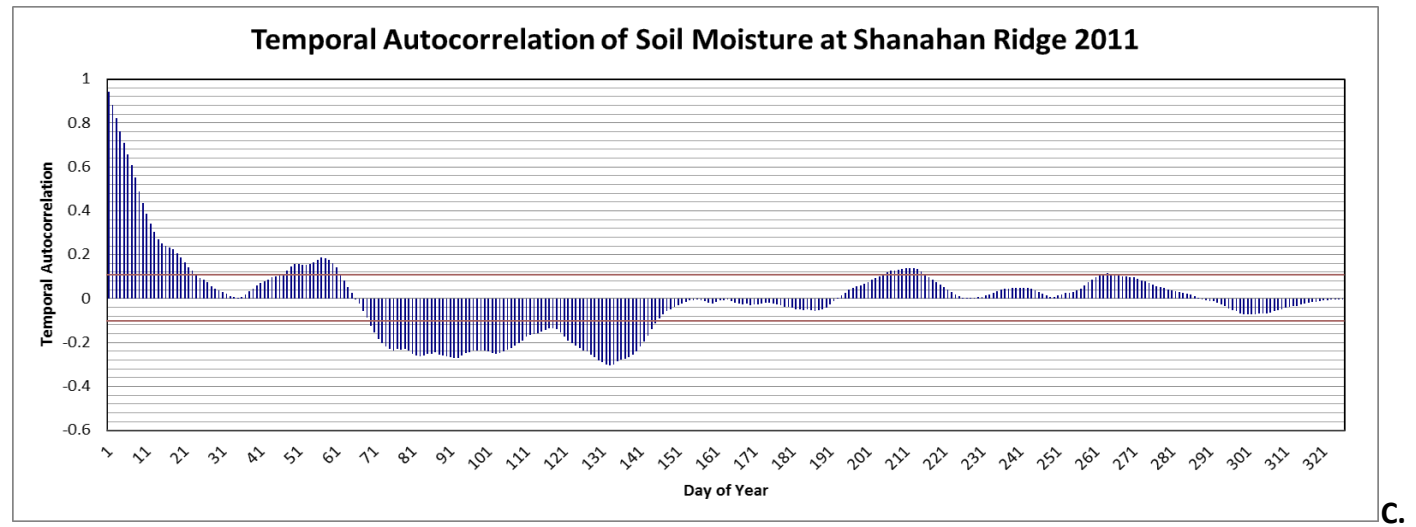
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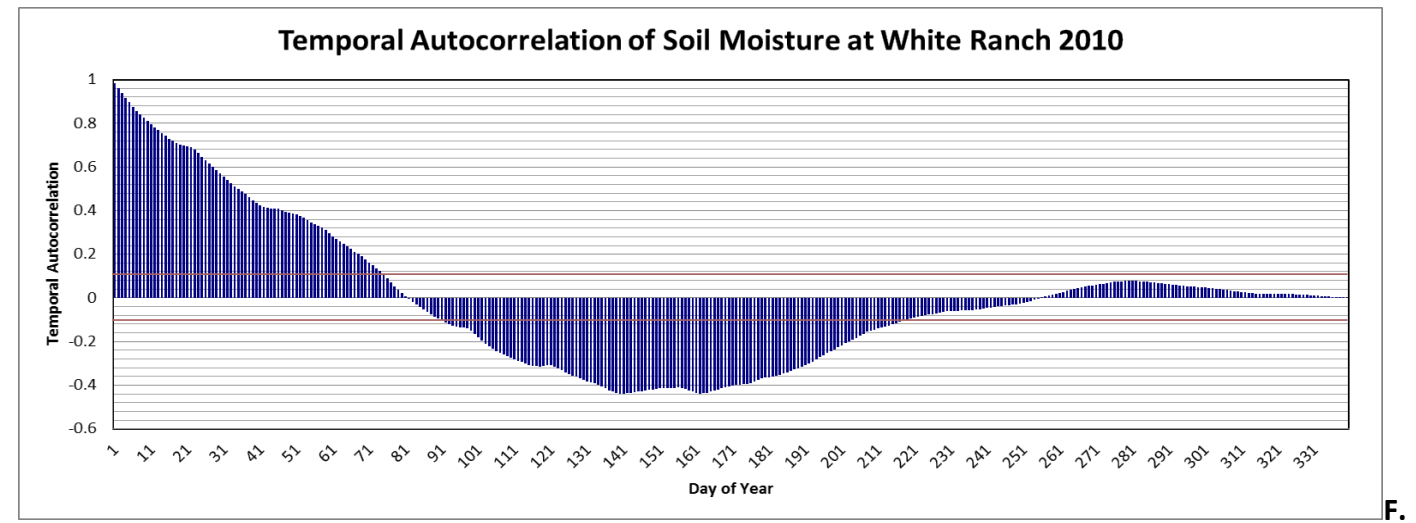
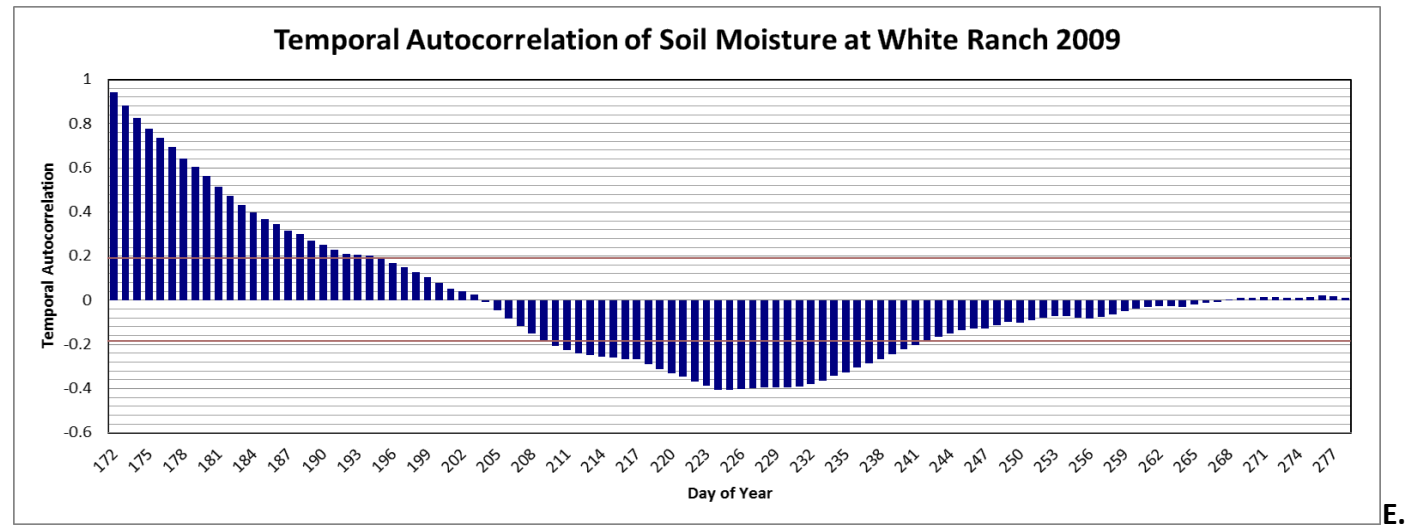
**Figure 2.6.** Temporal autocorrelation of average daily soil temperatures (°C) sampled for 2009 (A., E.), 2010 (B., F.), 2011 (C., G.), and 2012 (D., H.) at Shanahan Ridge, CO and White Ranch, CO sites. For a sample size of  $n=195$  (2009), the significance level ( $p<0.05$ ) is reached at 0.14 correlation coefficient (upper and lower red line), 0.10 for  $n=365$  (2010 and 2011), and 0.12 for  $n=265$  (2012).

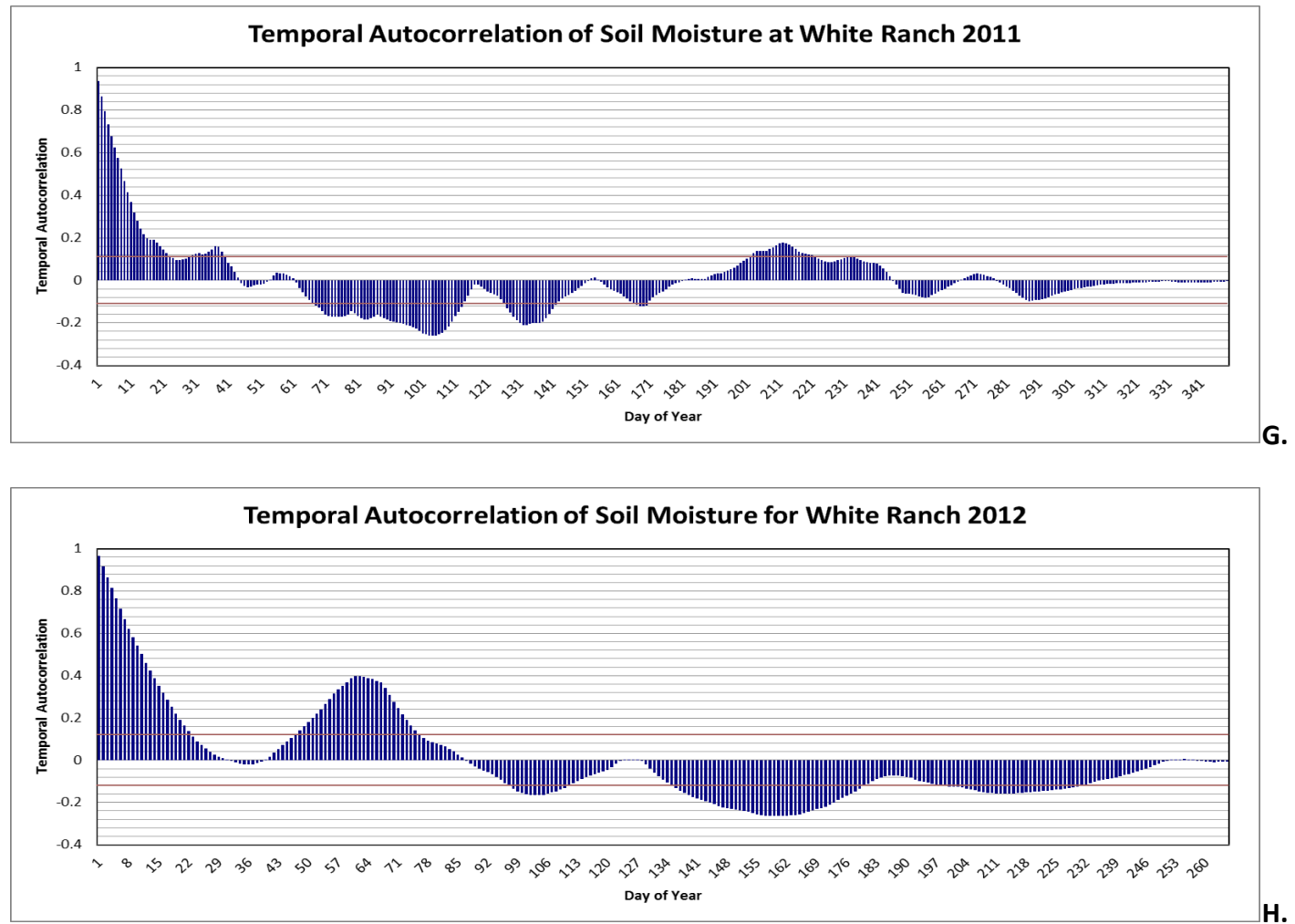
At the Shanahan Ridge, CO site the initial autocorrelation between hours for soil moisture were very high, with 2009 beginning at 0.97, 2010 (0.97), 2011 (0.94), and 2012 (0.94) (Figure 2.7. A-D). At White Ranch, CO the initial autocorrelation values were also very high with 2009 beginning at 0.94, 2010 (0.98), 2011 (0.94), and 2012 (0.96) (Figure 2.7. E-H). Although the previous soil moisture values begin highly correlated with the next value, moving further into the year shows varying degrees of decline with time. In 2009 at Shanahan Ridge, there were 49 days between the initial data point (June 21<sup>st</sup>, 2009) and the day where insignificance at the 0.05 level was reached (August 9<sup>th</sup>). Between 2010 and 2012 similar time lags were found before insignificance at the 0.05 level was reached, 2010 (93 days, April 4<sup>th</sup>), 2011 (24 days, January 24<sup>th</sup>), and 2012 (23 days, January 23<sup>rd</sup>) (Figure 2.7. A-D). As with soil temperature, it must be noted that 2009 data collection began in mid-June, whereas the remaining years all begin on January 1<sup>st</sup>. In 2009 at White Ranch, there were 25 days between the initial data point (June 21<sup>st</sup>, 2009) and the day where insignificance at the 0.05 was reached (July 16<sup>th</sup>). Similar to Shanahan Ridge there was a higher time lag in 2010 than 2011 and 2012, with 2010 reaching insignificance in 75 days (March 16<sup>th</sup>), 2011 (24 days, January 24<sup>th</sup>), and 2012 (24 days, January 24<sup>th</sup>) (Figure 2.7. E-H).







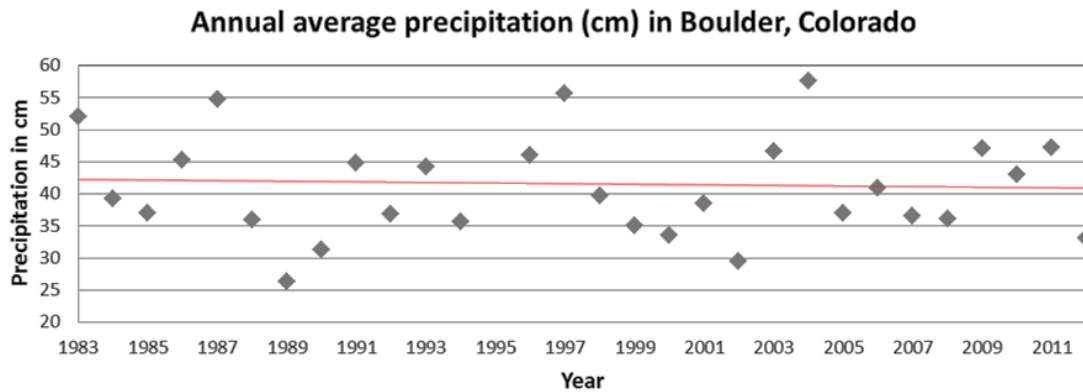




**Figure 2.7.** Temporal autocorrelation of average daily soil moisture ( $\text{m}^3/\text{m}^3$ ) sampled for 2009 (A., E.), 2010 (B., F.), 2011 (C., G.), and 2012 (D., H.) at Shanahan Ridge, CO and White Ranch, CO sites. For a sample size of  $n=195$  (2009), the significance level ( $p<0.05$ ) is reached at 0.14 correlation coefficient (upper and lower red line), 0.10 for  $n=365$  (2010 and 2011), and 0.12 for  $n=265$  (2012).

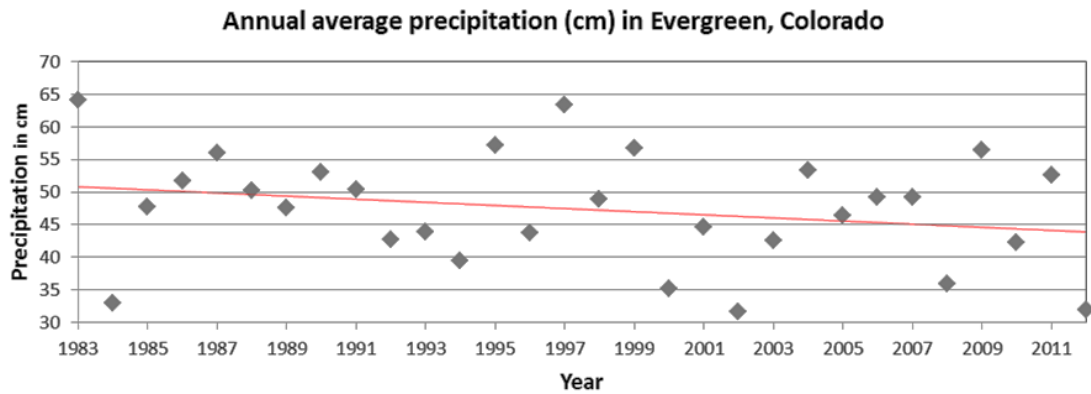
The results from this analysis suggest that researchers in this area could reduce the number of temporal measurements of soil moisture to a minimum of once daily during all seasons while still capturing the variability. The fine-scale nature of this sampling technique allows more accurate daily average soil temperature and moisture estimation for each site and, therefore can inform recommendations for temporal variability assessment. However, the timing of the measurements should also be discussed.

Deviations from the 30-year average (1983-2012) (Table 2.1.) precipitation for Boulder and Evergreen were compared to these seasons to look at the issue of timing of precipitation events. The spring season at Shanahan Ridge for the years 2009 and 2010 were above the thirty year average of 25.2 cm of precipitation (34.4 and 33 cm respectively) for Boulder while the years 2011 and 2012 were below and significantly below average (23.5 and 8.8 cm respectively). With drier conditions in 2011 and 2012 (meaning fewer precipitation events) higher autocorrelation values would extend into the season, up to days or weeks in between rain events. Interestingly the summer season shows the opposite relationship here with the years 2009 and 2010 being below normal (12.4 and 17.8 cm) and the years 2011 and 2012 being above average (20 and 20.3 cm respectively) (Figure 2.8.).



**Figure 2.8.** Precipitation for Boulder, CO for the years 1983-2012. An overall 1.2 cm reduction in precipitation has occurred over this period (red line). Average for time period was 49.9 cm.

The spring at White Ranch shows similar relationships in the spring thirty year average of 20.9 cm at Evergreen. The years 2009 and 2010 were above average precipitation years (32.5 and 23.5 cm) while 2011 and 2012 were below and again significantly below average (19.4 and 9.4 cm respectively). The thirty year average for the summer season is 20.4 cm, very near the spring average. The variability in deviation from the average for the years 2009 and 2011 were positive (22 and 23.4 cm) while 2010 and 2012 were negative (16 and 14.3 cm respectively) (Figure 2.9).



**Figure 2.9.** Precipitation for Evergreen, CO for the years 1983-2012. An overall 7 cm reduction in precipitation has occurred over this period (red line). Average for time period was 47.7 cm.

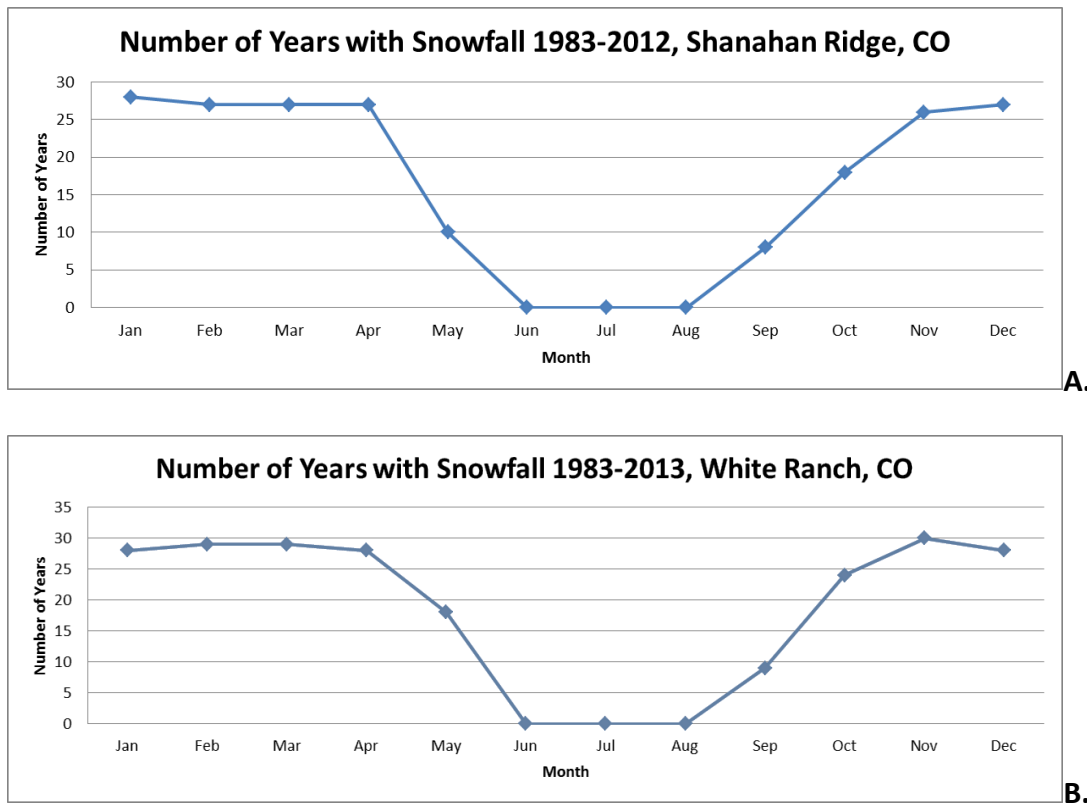
The reason that these relationships may be important is based on the timing of precipitation versus the totals. Soil moisture is the direct link between precipitation and ecological systems. Therefore, understanding the effects of precipitation on soil moisture has been a central goal for hydrologists and soil physicists for many years (Noy-Meir 1973) and remains an active field of research (Eagleson 2002). The basic phenomena associated with precipitation events—interception, infiltration, and runoff—are relatively well understood; the main difficulty lies in describing rates of soil moisture change between precipitation events (McAuliffe 2003). These rates are driven chiefly by evaporation from soils, transpiration by plants, horizontal and vertical soil water transport, and hydraulic redistribution of soil water, all of which depend in complex ways on vegetation and soil characteristics and on the timing and size of precipitation inputs.

In arid and semiarid ecosystems, there is a good correlation between event size and infiltration depth: Water from larger rainfall events infiltrates more deeply (Sala et al. 1981),

but infiltration, storage, and use depend on the season and on patterns of organismal activity. In summer, evaporation and transpiration remove nearly all water from shallow soil layers within days of rainfall, so that in the absence of rapid drainage through macropores, water does not infiltrate deeply into the soil profile. In winter, evaporation and transpiration are limited, so water can accumulate and infiltrate deeper into the soil profile. Changes in the seasonality or variability of precipitation are likely to affect the distribution of soil moisture in space and time, with ramifications for the performance of species and their interactions with other organisms (Weltzin et al. 2003).

It is not uncommon to see spring snows occur into early May (Figure 2.11.), with 10 years showing snowfall in May at Shanahan Ridge and 18 years at White Ranch during the 1983-2012 recording period. Similarly, the variability between the fall seasons for the years 2009-2011 was similar between years, perhaps also due in part to the low variability in late fall air temperatures, which reduces the flux. Both of these seasons demonstrate that changes in overall air temperature and its effects on soil temperature can cause the correlations between points along a line-transect to change. Spring of 2011 was on average 2.3° C warmer than both 2010 and 2012. Interestingly, fall of 2009 was 0.5° C and 1° C warmer than 2010 and 2011 and similarly shows a lower initial autocorrelation value with less negative values further into the season. With spring temperatures increasing (Chapter 1), most of this precipitation will come in the form of rainfall that has been seen to drain fairly quickly (Figure 2.7.) (Menzel & Fabian 1999, Easterling et al. 2000)



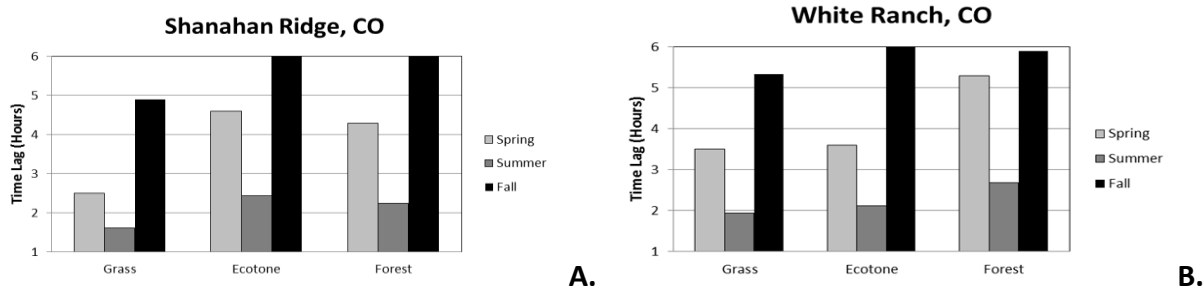


**Figure 2.11.** Number of years out of thirty year period (1983-2012) that recorded snowfall.

### 2.3.3. Temporal variability across the transect

Separating soil temperature into Grassland, Ecotone, and Forest across each season can determine the minimum interval for temporal resolution needed for effective data collection in similar landscapes. In the Shanahan Ridge grassland habitat, sampling intervals of two hours in the spring, one hour in the summer, and four hours in the fall will capture the variability in soil temperature (Figure 2.12.A). The ecotone habitat would require a sampling interval of four hours in the spring, two hours in the summer, and six hours in the fall will capture the variability (Figure 2.12.A). Finally, for the forest habitat, a sampling interval of four hours in the spring, two hours in the summer, and six hours in the fall will capture the variability in soil temperature (Figure 2.12.A). Similarly at White Ranch these intervals increase slightly in the grassland to

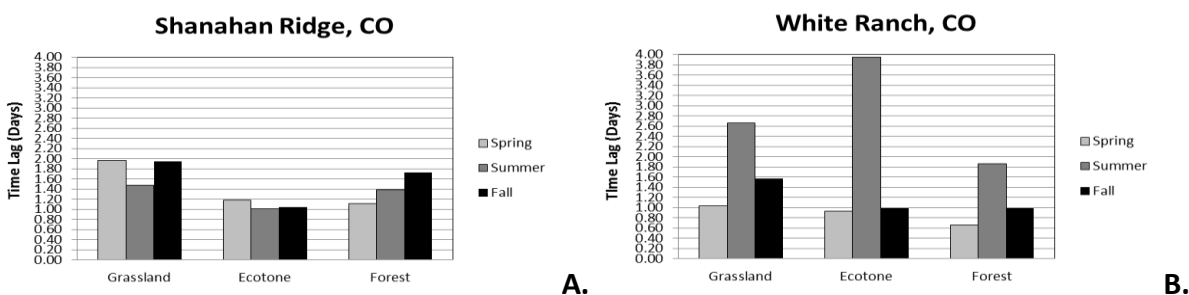
three hours in the spring, nearly two in the summer, and five hours in the fall (Figure 2.12.B). This increase is likely due to the variation in insolation between the two sites (both are south facing, however White Ranch has the forest cover below the grassland patch giving shade until later in the day extending onto the grassland). Surrounding the ecotone, the variability can be captured with three-hour intervals in the spring, two hour intervals in the summer, and six hour intervals in the fall (Figure 2.12.B). The forest habitat can be sampled at five hours in the spring, two hours in the summer, and five hours in the fall (Figure 2.12.B). All of these breakdowns could be reduced to the next lowest hour in order to standardize the intervals at similar locations with similar temperature and moisture variability. This could be used by researchers as an effective methodology for environmental sampling that preserves sensitivity to inherent variability.



**Figure 2.12.** Autocorrelation lags (in hours) out to six hour intervals for average seasonal temperatures ( $^{\circ}\text{C}$ ) across the entire line-transect and all sample points at Shanahan Ridge (A.) and White Ranch, CO (B.).

As was discussed with soil moisture earlier, the temporal variability needed in sampling intervals is greatly reduced in in both research locations. Depending on the resolution of soil moisture measuring equipment, the grassland at the Shanahan Ridge site could be measured every 1.8 days in both the spring and fall and 1.4 days in the summer (Figure 2.13.A). The

ecotone would need to be measured at daily intervals in order to capture the variability (Figure 2.13.A). The forested area of the Shanahan Ridge site would need to be measured daily in the spring, 1.4 days in the summer, and 1.6 days in the fall (Figure 2.13.A). White Ranch provides a much different scenario for sampling with daily intervals in spring, two and a half days in the summer, and 1.6 days in the grassland in fall (Figure 2.13.B). The ecotone would need a 0.8 of a day intervals in the spring, a very long 3.8 days in the summer, and daily in the fall (Figure 2.13.B). Finally, the forested area would require a 0.6 daily interval in the spring, 1.8 days in the summer, and daily in the fall (Figure 2.13.B).



**Figure 2.13.** Autocorrelation lags (in days) out to six hour intervals for average seasonal moisture (VWC as a % of a  $m^3/m^3$  of soil) across the entire line-transect and all sample points at Shanahan Ridge (A.) and White Ranch, CO (B.).

## 2.4. Conclusions

Spatial and temporal autocorrelation analysis techniques offer alternative methods to conventional statistics for the estimation of parameters and their associated variability. Moran's I analysis demonstrated that there was variability in the patterns of spatial variability for soil temperature at both of the field sites, while correlogram autocorrelation demonstrated that there were significant similarities between sites in terms of the temporal variability in soil

temperature and moisture throughout the study period. However, there are also significant differences in terms of specific intervals of soil temperature due to aspect of each site. This suggests that spatial relationships derived from one set of measurements for one field site may have applicability at other field sites within the same or similar landscapes for some soil conditions, but would need more analysis of local climate, site conditions (slope, aspect, soil type), and desired outcomes before beginning and committing to any spatial or temporal resolution. Because spatial relationships are strongly influenced by the scale of the sampling, further work may inform whether or not this approach will be useful for extrapolating spatial information obtained at the field scale to the watershed or regional scale.

Depending on the season the above resolutions could be adjusted per season if desired. Analysis of temporal variability showed that there were similarities in soil temperature in the spring and fall seasons at two sites along the Front Range of Colorado. The differences between the two sites in terms of elevation, slope, and aspect play a role in the variability in soil conditions making the generalization that similar conditions exist across the Front Range difficult. The higher variability and lack of temporal autocorrelation in summer suggests the need for further research into the relationship between percent vegetation cover and individual microsite fluctuations with variable seasons. Temporal analysis of soil moisture showed slightly varying seasonal responses, elucidating the need for a further analysis of soil temperature and moisture effects on each other at individual sites.

## **Chapter 3. Four years of plant functional type and species origin response to microclimatic variability along a forest-steppe ecotone**

### **3.1. Introduction**

Ecologists have recognized the importance of diverse plant communities in maintaining invasion resistant ecosystems (MacArthur & Wilson 1967, Goodman 1975, Pimm 1991, Von Holle et al. 2003, Barthram et al. 2005, Thiele et al. 2010, Yurkonis et al. 2012). Increased diversity has been positively correlated with increased community productivity and stabilization (Naeem et al. 1994, Tilman et al. 1997, Anderson & Inouye 2001, Tilman et al. 2001, Marquard et al. 2009, Wacker et al. 2009) because of more complete use of resources (Tilman 1997, Levine & D'Antonio 1999, MacDougall et al. 2009, Kuebbing et al. 2013,). In natural ecosystems the composition, vigor, and maturity of members of the plant community affect competition among species and have potentially profound implications for soil properties (Sauer et al. 2006). There have been many attempts to describe and explain the relationships between soils and vegetation (Morison et al. 1948, Webb 1969, Goodland & Pollard 1973, Grubb 1977, Golley et al. 1978, Alban 1982, Gartlan et al. 1986, Haase 1990, Johnston 1992, Ruggiero et al. 2002, Cachovanova et al. 2012). Variation of soil properties may also result from topographic heterogeneity (Huddleston & Riecken 1973, Daniels et al. 1987, Honeycutt et al. 1990, Feldman et al. 1991, Brubaker et al. 1993, Fu et al. 2004, Wu et al. 2008). The resultant soil-vegetation and soil-landscape interrelationships therefore should be expected to be more complex than either of the two considered separately (Chen et al. 1997, Kubota et al. 2004, Kim and Yu 2009).

Various factors have been investigated to determine their influence on competition between woody and herbaceous plants including aspect, micro-topography, disturbance, and

soil pathogens (Wilson & Tilman 1993, Matlack 1994, Mills & Bever 1998, Aerts 1999, Peltzer 2001, Weigelt & Jolliffe 2003, Haugo et al. 2013). When nutrient and water supplies are abundant, the primary competition is for light. In nutrient-poor environments, however, there is poor consensus on the dominant mechanism. Ultimately, a combination of site factors and soil properties produce either a positive or negative feedback on individual plant species, which determines the composition of the plant community.

A group of species that share morphological and physiological traits and play a similar role in an ecosystem can be referred to as a functional type (Lauenroth et al. 1978, Hawkins & MacMahon 1989, Paruelo & Lauenroth 1996, Blondel 2003, Voight et al. 2007). Plant functional types (PFTs) provide a logical link between physiological and life history strategies at the plant level and processes at the ecosystem level (Chapin 1993). The definition of PFT has received a lot of attention in ecology (Walker 1992, Leishman & Westoby 1992, Boutin & Keddy 1993, Golluscio & Sala 1993, Chapin 1993, Paruelo & Lauenroth 1996, Blondel 2003, Voight et al. 2007). Plant communities in semi-arid regions have exhibited widespread and rapid changes in response to changes in climate and land use in the past and are expected to be among the most sensitive to the accelerated climate changes and increasing intensity of land use that future decades are likely to bring (IPCC 1996a, b). An important approach for assessing the complex responses of these communities is to identify PFTs and characterize the functional response of each type to a suite of environmental conditions (Golluscio & Sala 1993, Epstein et al. 1997, Diaz & Cabido 1997, Marby et al. 2000, Cipriotti & Aguiar 2005).

Many studies of the regional distribution of PFTs have focused on C<sub>3</sub> and C<sub>4</sub> plants (Teeri & Stowe 1976, Stowe & Teeri 1978, Werger & Ellis 1981, Hattersley 1983, Li 1993, Wan & Sage 2001, Pyankov et al. 2010) and their distribution along elevation gradients (Chazdon 1978, Tieszen et al. 1979, Boutton et al. 1980, Cavagnaro 1988, Epstein et al. 1996, Wang et al. 2013). Cook and Irwin (1992) studied the distribution of shrubs, graminoids, and forbs in relation to climatic variables in the western Great Plains and the eastern portion of the Great Basin. Many past studies that relate to PFTs were based on the relative number of species within each and, therefore were underestimating the abundance of each, which would reduce the impact that climatic factors would have on each. However, Paruelo and Lauenroth (1996) showed that seasonal distribution of precipitation and temperature can control certain PFTs at a regional scale.

Increasing evidence suggests that PFT diversity is more important to ecological integrity than plant species diversity (Walker 1992, Power et al. 1996, Sala et al. 1996, Hooper & Vitousek 1997, Tilman et al. 1997, Mack & D'Antonio 1998, Xu et al. 2004, Fakude et al. 2008). Research implies that native species evolved to fill selected ecological roles because they differ in nutrient accumulation, storage, conservation strategies, and concentration (Parrish & Bazzaz 1976, McJannet et al. 1995, Carrera et al. 2000, Duke & Caldwell 2001, Reich et al. 2001). These species may be utilizing soil nutrients from separate spatial and temporal niches (Berendse 1979, McKane et al. 1990, Golluscio & Sala 1993, Reich et al. 2001, Perkins & Nowak 2013), allowing them to coexist.

Over the last decade the use of functional traits of organisms as a method to produce generic rules on community dynamics in response to environmental change has gained increasing momentum (McGill et al. 2006, Suding et al. 2008, Sandel et al. 2010, Cantarel et al. 2013). This is particularly evident in vegetation studies. The analysis of responses of traits associated with persistence, regeneration, and dispersal to environmental gradients should assist in a more mechanistic understanding of community ecology and species richness (McGill et al. 2006). As is prevalent in many disciplines (Fox & Brown 1993, Wilson 1999, Hood et al. 2006), functional types can be used to aggregate the large diversity of species within an area into groups with similar trait expressions to allow for easier analysis of trends.

Ecotones that separate forests and grasslands are highly sensitive to variation in environmental factors (Neilson 1993 Kupfer and Cairns 1996, Loehle 2000, Hochstrasser et al. 2002, Danz et al. 2011). Not only do these ecotones provide a useful area for comparative studies, but they also indicate to land managers a potential front of invasion for non-native and/or harmful species. Changes in abiotic factors at these boundaries may favor a plant community that differs from those found in interior forests. Recent work has recognized that vegetation structure and composition changes within the field edge (Williams-Linera 1990, Matlack 1994, Meiners & Pickett 1999 Goldblum & Beatty 1999, Meiners & Pickett 1999, de Lafontaine & Houle 2007, Porensky & Young 2013). An increase in the presence of non-native species, and high species richness, diversity, and total cover are characteristic of both forest and field edges (Chen et al. 1992, Matlack 1993, 1994, Fraver 1994, Meiners & Pickett 1999).



### 3.2. Microclimate and vegetation

Davis et al. (2005) suggested that contemporary ecology tends to consider vegetation change in a series of largely separate events that focus on different causes of vegetation change, e.g., species introduced from other regions of the world, disturbances that create gaps and initiate succession, and global change. In reality, all these influences are likely to be important to a greater or lesser extent and will interact within any particular plant community (Shaw et al. 2002, Zavaleta et al. 2003a, b, Norby & Luo 2004, Amatangelo et al. 2008, Naudts et al. 2011, Garcia-Palacios 2013), and an understanding of these influences and interactions is essential in understanding, managing, and restoring ecosystems more effectively in the future.

Microclimate is defined as the suite of climatic conditions measured in localized areas near the earth's surface (Geiger et al. 2003). The term may refer to areas as small as a few square feet or as large as many square miles. Another contributing factor to microclimate is the slope or aspect of an area. South-facing slopes in the Northern Hemisphere and north-facing slopes in the Southern Hemisphere are exposed to more direct sunlight than opposite slopes and are therefore warmer for longer. Regional, finer scale, models of climate and vegetation comparisons generally receive less attention than coarser scale predictive models (Paruelo & Lauenroth 1996), however research has shown that they need to be addressed (Franklin et al. 2013). By examining biotic and abiotic variability across boundaries and at a fine scale, a better understanding regarding what site factors define what type of species establish yearly under varying conditions. The objective of this research was to use *in situ* measurements to determine

the effects of changes in soil temperature and moisture on plant species. Several questions were asked:

- How do groups of species with similar trait expressions respond to environmental gradients?
- Does the environment determine which species coexist?

Much effort has been devoted to assess which combinations of traits determine species adaptations to different environmental conditions. The present study adds to current literature by directly examining the modifying effects of percent plant coverage type, fine scale soil property variation, micro and macro climate.

### **3.3. Methods**

#### **3.3.1. Study area**

Two study sites are located in the montane zone (~1750-2300 m) of the eastern slope of the northern Colorado Front Range on the City of Boulder's Open Space and Mountain Parks Shanahan Ridge (elevation 1756 m; 39°57'30.8"N, 105°15'44.6"W) and the Jefferson County's White Ranch Open Space (elevation 2282 m; 39°48'32.3"N, 105°17'4.2"W) (Figure 1.9.). Soils along the Front Range are highly variable but are usually Mollic Cryoll soils dominant with rocky, thin, coarsely textured and shallow slightly acidic characteristics (Johnson & Cline 1965, NRCS 2013). With a cryic soil temperature regime, the Cryolls are the soils of the northern latitudes. They have a xeric, ustic, or udic soil moisture regime and are moderately extensive in the western U.S. Climate stations located near both sites show mean annual temperature ranges from 10.8° C at an elevation of 1655 m for 1983-2012 (Boulder, Colorado station,

NOAA/NWS Cooperative, Boulder, CO) to 7.0° C at 2133 m (Evergreen, Colorado station, Western Regional Climate Center, Reno, NV) for 1983-2012. Precipitation is less variable between the two sites, ranging from 49.9 cm at 1655 m to 47.0 cm at 2133 m over the same periods as temperature.

This region includes a wide array of vegetation, including shortgrass steppe, shrub-steppe, and open woodland stands of ponderosa pine (*Pinus ponderosa*) (Figure 1.11.). Since the origin of the present forest stands, these areas have remained relatively undisturbed. The Shanahan Ridge area in Boulder experienced widespread fire (minimum 42 hectare extent) in 1870 (Sheriff & Veblen 2006), while White Ranch Open Space has little known history of widespread wildfire (Gartner 2008). Cattle grazing at both locations continued through the late 1960s. With acquisition of both site locations by local governments came a cease to this practice. However grazing by native ungulates continues (elk, deer). Latitudinal and elevational plant species distributions along the Front Range of Colorado have been attributed to temperature and moisture, as typically influenced by elevation and topographic position (Peet 1981, 1988, Allen et al. 1991).

For every approximately 305 meter rise in elevation the environmental lapse rate is approximately 2.2°C. The two sites differ in elevation by approximately 500 meters, which is the same as the two city stations described previously, giving the nearly 3°C difference in annual temperatures between Boulder and Evergreen (Table 2.1.). The slope plays a role in the amount of run-off, water penetration and evapotranspiration. The White Ranch site is slightly steeper with a 23% slope over the 15% at Shanahan Ridge. Aspect has a very large effect on its own. A

south facing slope would have more evaporation versus a northern aspect. At Shanahan Ridge there is a 67° southwest aspect with a significant amount of insolation during the morning through afternoon. White Ranch has a 21° northwest aspect. The White Ranch site is unique in particular to most ecotone or transitional studies. Here, the location of the treed area is below the grassland portion, giving it more shade in the earlier parts of the day. The major insolation is later in the morning into late afternoon. These variances in slope and aspect may give insight into the variations in soil conditions.

### **3.3.2. Soil analyses**

Line-transects were located across the ecotone at each site (Figure 2.1.). In the summer of 2009 one 25 m line-transect was laid out at Shanahan Ridge and one 25 m line-transect at White Ranch. All measurements of soil temperature had a regular sampling interval of 1 m in the grassland (meters 0-11) and forested (meters 14-25) portions of the line-transect with finer resolution of 0.5 m across the ecotone (11.5, 12.5 and 13.5 meters respectively).

Measurements of soil moisture had a sampling interval of 6.25 meters along the entire line-transect equating to five total sampling points. This scale was continued through the spring of 2011. At this time the resolution of the fine-scale soil temperature was reduced to two meter intervals up to meter 12, a point located at 12.5 m, and then continuing on from meter 13 through meter 25. This spacing preserved sensitivity to fine-scale variability while allowing deployment of sensors to increase transect replication. The 6.25 m spacing for soil moisture was maintained throughout the study and across all line-transects.

### **3.3.3. Soil temperature**

From June 21<sup>st</sup>, 2009 through May 22<sup>nd</sup>, 2011 the upper 10 cm of soil temperature was measured using Thermochron iButtons (Model #DS1921G, Embedded Data Systems, Lawrenceburg, KY, USA). iButtons were calibrated before placement in the field. First, ten sensors were chosen at random and immersed in a bowl of melted ice to determine the 0°C reading. Next, sensors were placed in a pot of slowly boiling water to determine the 100°C reading. All sensors read to within  $\pm 1^\circ\text{C}$ . Further discussion of the accuracy and sensing methodology of iButtons can be found in Hubbart et al. 2005. Due to a lack of reliability in battery life, low moisture contact resistance, the longevity of the study, and the acquisition of additional funding, the decision was made to change measurement devices in the summer of 2011 to HOBO Pendant data loggers (Onset Computer Corporation, Bourne, MA, USA). All sensors measure temperature at contact points between soil and sensors. The sensors were inserted into the soil and were as close to a 10 cm depth as possible. The accuracy of the iButtons is  $\pm 1^\circ\text{C}$  and resolution of  $0.5^\circ\text{C}$ . The HOBO data loggers have an accuracy of  $\pm 0.53^\circ\text{C}$  and a resolution of  $0.14^\circ\text{C}$ . Based on consistency and completeness of data White Ranch was used for soil temperature and vegetation correlations.

### **3.3.4. Soil moisture**

During the same study period, soil moisture was measured with EC-5 soil moisture sensors and recorded using Em5b data loggers (Decagon Devices, Inc., Pullman, WA, USA). The sensors measure the dielectric constant of the media and approximately a liter of volumetric water content (VWC) surrounding the probe with an accuracy of  $\pm 3\%$  VWC and  $0.1\%$  VWC

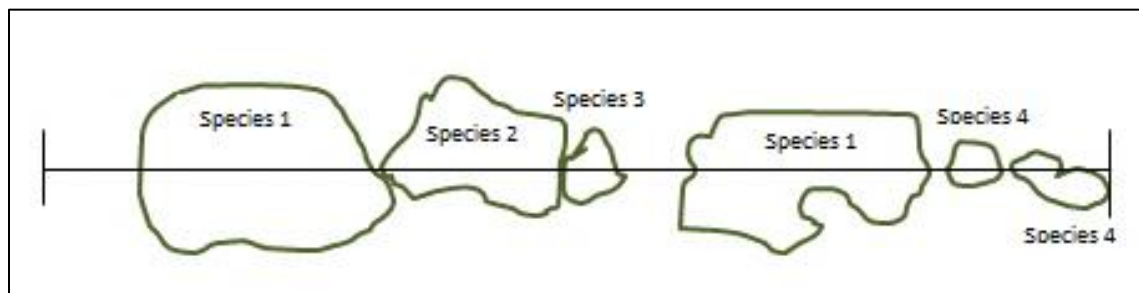
resolution in mineral soil. The sensors were inserted into the soil at a 45 angle extending from a depth of 5-10 cm. The VWC in the soil (also called the volume wetness or volume fraction of soil water) represents the fraction of the total volume of soil that is occupied by the water contained in the soil. For example, a measurement of 0.111 VWC would represent an 11.1% water content of a  $\text{m}^3$  volume of soil. Similar to soil temperature, soil moisture values were used from White Ranch to evaluate correlations with vegetation.

### **3.3.5. Species composition**

Transects are advantageous and efficient in studies of communities at transition zones or in contiguous stages of ecological succession. One method of transect sampling, the line-intercept method, is especially efficient at determining relative estimates of plant density. In this method, data are tabulated on the basis of plants lying on a straight line cutting across the community under study. Placement of transect lines is important. If the specific desire is to study a community transition or some ecological gradient, then the transect should transverse that transection or gradient.

The line intercept method has been shown to be effective in ecotone and grassland communities to show successional changes. Line-transects give data on the percent cover of individual species along the line, as well as the variation of the microsite conditions that are present, and therefore may describe the invasibility of these areas. The line-intercept method in particular is used as a tool to 1) quickly determine community structure and 2) investigate the relationship between plant species and any independent variable present along a transitional zone (Tansley & Chipp 1926, Canfield 1941).

On July 20, 2009 single line-transects were laid out at White Ranch (am) and Shanahan Ridge (pm) perpendicular to the ecotone. All vascular plant species were recorded and a plant species list was prepared for each site. Weber and Whittman (2001) was used for field identification. Each species was assigned a percent cover for each meter along the transect. This method gives a good quantification of the percent coverage and/or size of species and/or the potential loss of species with anomalous weather conditions from year to year. In the below example, species 1 would have approximately 50% coverage for the meter represented (Figure 3.1.).



**Figure 3.1.** Line intercept method

Species percent cover was measured each July from 2009-2012 at the two research sites within two days of each other in order to assure consistency. In addition to plant species, rock, sticks, and bare ground were measured between each meter interval. The changes in percent cover were compared to the abiotic condition changes in order to determine if there is a relationship.

The set of species co-existing in a given community constitute a PFT if they have similar functional characteristics related to one ecosystem service (Pla et al. 2012). The idea of creating PFTs is to obtain a set of species having the same role in the ecosystem. Several authors have

summarized the relationship between traits and ecosystem services (Carpenter et al. 2009, Lavorel et al. 2011). Because a PFT is a collection of organisms with similar suites of co-occurring functional attributes they have similar responses to external factors and/or effects on ecosystem processes (de Bello et al. 2010). For this study, species were placed in several different PFTs and/or species origin groups (native or non-native) in order to compare them to various soil characteristics for possible correlation of habitat and species (Table 3.1.).

**Table 3.1.** Species list with plant functional type and species origin designations (A. Shanahan Ridge, CO and B. White Ranch, CO). N=Native, I=Introduced, P=Perennial, A=Annual, F/H=Forb/Herb, G=Graminoid, and S=Shrub/Subshrub.

<i>Andropogon gerardii</i>	N	C4	P	G
<i>Ambrosia psilostachya</i>	N	C3	A	F/H
<i>Artemisia ludoviciana</i>	N	C3	P	S
<i>Bromus tectorum</i>	I	C3	A	G
<i>Carex heliophila</i>	N	C3	P	G
<i>Elymus elymus</i>	N	C3	P	G
<i>Erigeron sp.</i>	N	C3	P	F/H
<i>Heterostipa comata</i>	N	C3	P	G
<i>Opuntia macrorhiza</i>	N	C3	P	S
<i>Poa compressa</i>	I	C3	P	G
<i>Psoralidium tenuiflorum</i>	N	C3	P	F/H
<i>Rosa woodsii</i>	N	C3	P	S
<i>Silene antirrhina</i>	I	C3	A	F/H
<i>Thlaspi arvense</i>	I	C3	A	F/H
<i>Tragopogon dubius</i>	I	C3	A	F/H

A.

<i>Achillia lanulosa</i>	N	C3	P	F/H
<i>Agropyron intermedium</i>	I	C3	P	G
<i>Allium cernuum</i>	N	C3	P	F/H
<i>Artemisia ludoviciana</i>	N	C3	P	S
<i>Aster porteri</i>	N	C3	P	F/H
<i>Astragalus flexuosus</i>	N	C3	P	F/H
<i>Bouteloua gracilis</i>	N	C4	P	G
<i>Bromus inermis</i>	I	C3	P	G
<i>Carex heliophila</i>	N	C3	P	G
<i>Chenopodium album</i>	N	C3	A	F/H
<i>Heterotheca villosa</i>	N	C3	P	S
<i>Koeleria macrantha</i>	N	C3	P	G
<i>Penstemon strictus</i>	N	C3	P	F/H
<i>Poa compressa</i>	I	C3	P	G
<i>Tragopogon dubius</i>	I	C3	A	F/H

B.

### 3.3.6. Soil analysis

Soil varies continuously, and measurements of almost any property made at different places will differ (Webster & Oliver 1990). Variation from place to place is often substantial, and is a major source of uncertainty in soil survey. However, understanding this variation and how it



relates to species variation can give more insight into how one affects the other and vice versa. Soil conditions at both Shanahan Ridge and White Ranch were used for correlation analysis with vegetation.

Soil samples were collected in June of 2009 and again in June of 2011 in order to determine any potential changes in composition over the study period. Soil texture, organic matter, and pH were determined in the Geography Department Soil Lab (CU Boulder).

Several laboratory analyses were conducted in order to determine the various soil conditions present within each site. Soil sample texture was determined using particle size analysis through the hydrometer method. Soil samples were oven dried at 105°C for 24 hours and then ashed in a combustion furnace for 8 hours at 580°C. Samples were then run through a 2mm sieve to separate coarse materials and soil. Coarse texture soils like sand consists mostly of large pores which empty of water when a relatively small force is applied. Fine texture soils have a broader pore size distribution and larger particle surface area. The percentage of sand, silt and clay in the inorganic fraction of soil is measured in this procedure.

The hydrometer method is based on Stoke's law governing the rate of sedimentation of particles suspended in water. The sample is treated with a sodium hexametaphosphate (SHMP) solution that binds clay and silt particles into aggregates by adding 100g of soil and 50ml of reverse osmosis water to 200ml bottles and shaken for 24 hours to completely cover all particles with SHMP solution. The density of the soil suspension is determined with a hydrometer calibrated to read in grams of solids per liter after the sand settles out and again after the silt settles. The contents of each bottle are poured into a graduated cylinder and

reverse osmosis water is added up to the 1000ml mark. Cylinders were covered and shaken 10 times to fully mix the solution. Cylinders were then placed on the counter and a timer was set for 40 seconds. After this time a hydrometer reading was taken to determine the amount of sand that has settled out of the solution (hydrometer reading is the suspended silt/clay amount in suspension). Samples were covered once more and shaken 10 times. Cylinders were then placed on the counter and a timer was set for 2 hours. After this time a hydrometer reading was taken to determine the amount of sand and silt had settled out of the solution (hydrometer reading is the clay amount in suspension). At both time intervals temperature readings were also taken. Since hydrometers are reading the specific gravity (relative density) of the liquid that it is immersed in, the temperature of the water would affect the density of the solution. Therefore temperature readings need to be made in order to correct for this. For each degree above 20°C (which all temperatures were) I added 0.36 gm/l to the readings. Results of this analysis are reported as the percentages of mineral fraction: % sand, % silt, and % clay.

Organic matter influences many of the physical, chemical, and biological properties of soil. It can also affect the water holding capacity, nutrient contributions, biological activity, and water and air infiltration rates. Organic matter was determined by oven drying samples for 105°C for 24 hours and then ashed in a muffle furnace at 580°C for 8 hours. Soil samples were measured before and after being placed in the oven and again after ashing in order to determine organic matter percentage.

Soil pH was measured by using an Orion instruments pH meter (model 710A) on a 1:1 soil: water mixture. 30g of soil samples were added to 30ml of reverse osmosis water in a

100ml cylinder. The solution was stirred for 30 seconds using a glass stir stick. Samples were then read for 10 seconds to determine pH.

In the fall of 2011 soil samples were sent to Colorado State University's Soil Testing Lab (Fort Collins, CO) to test for nitrate nitrogen, phosphorous, and potassium. Additionally, this lab tested organic matter, pH, and texture which were used as validation for tests done already performed above at The University of Colorado in Boulder.

### **3.3.7. Statistical analysis**

Correlation and regression analysis are related in the sense that both deal with relationships among variables. The correlation coefficient is a measure of linear association between two variables. Values of the correlation coefficient are always between -1 and +1. A correlation coefficient of +1 indicates that two variables are perfectly related in a positive linear direction, a correlation coefficient of -1 indicates that two variables are perfectly related in a negative linear sense, and a correlation coefficient of 0 indicates that there is no linear relationship between the two variables.

The square of the correlation coefficient, coefficient of determination ( $r^2$ ), is a useful value in linear regression. This value represents the fraction of the variation in one variable that may be explained by the other variable. Thus, if a correlation of 0.80 is observed between soil temperature and vegetation percent cover 80% of the total variation in vegetation percent cover can be explained by the linear relationship between soil temperature and percent cover. The other 20% of the total variation in percent cover remains unexplained.

Neither regression nor correlation analyses can be interpreted as establishing cause-and-effect relationships. They can indicate only how or to what extent variables are linearly associated with each other. The correlation coefficient measures only the degree of linear association between two variables. Any conclusions about a cause-and-effect relationship must be based on the judgment of the analyst.

This study used correlations of microsite abiotic variables and percent vegetation cover to aid in the quantification of heterogeneity differences imposed by a variable microclimate. In order to evaluate the minimum level of significance ( $p < 0.05$ ,  $p < 0.01$ ) of the correlation coefficient a student t-test was performed. When performing this test, if  $t$  exceeds that for the chosen level of probability then the null hypothesis is rejected: the correlation is significant.

### **3.4. Results and discussion**

Vegetation and soils are dynamic systems, and relationships between particular vegetation parameters and soil properties at any one time may not always reflect the suitability of the plant species present to that set of soil conditions. There may, for example, be a delay in the response of plant populations to changes in soil properties. For purposes of reference the air temperature, soil temperature, precipitation, and soil moisture averages for each year have been included here (Table 3.2.).

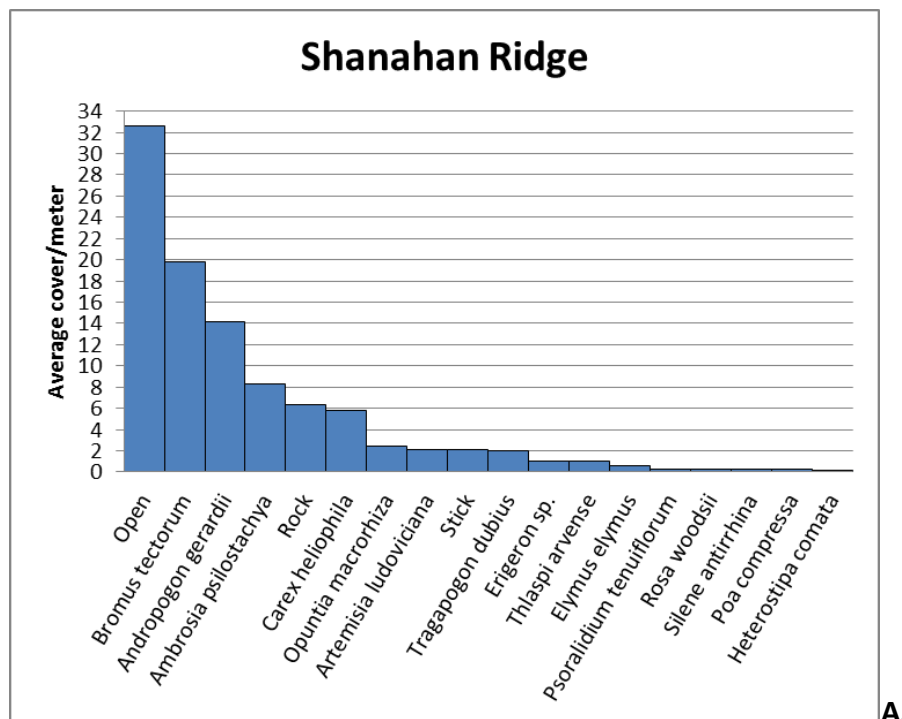
**Table 3.2.** Average soil temperature and moisture at Shanahan Ridge, CO and White Ranch, CO over the study period.

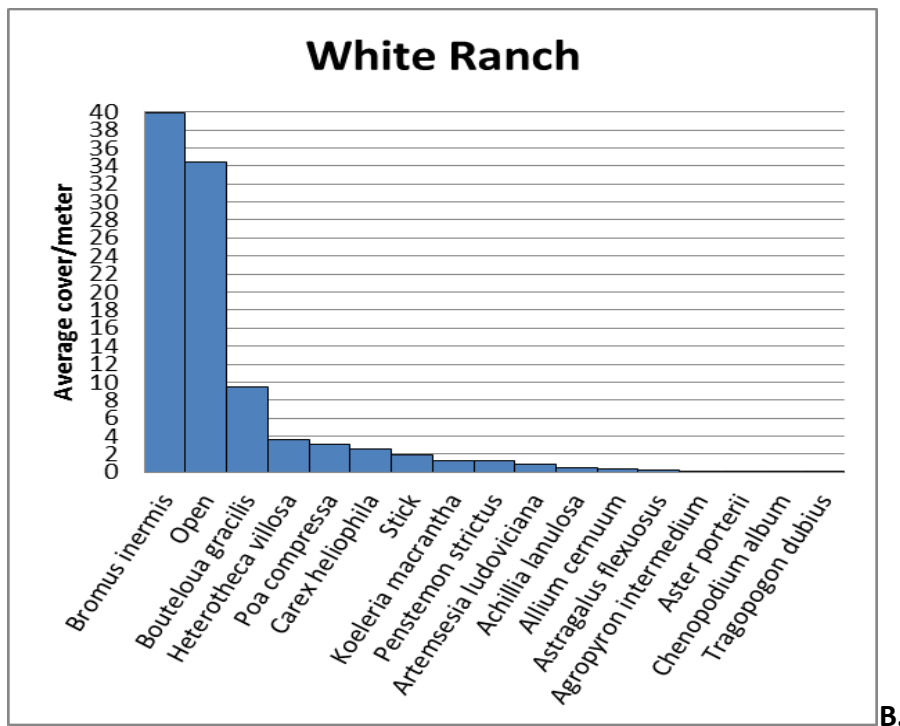
\*June-December to coordinate with study period, \*\*January-September to coordinate with study period.

	<b>Shanahan/Boulder</b> Soil/Air Temp °C	<b>Shanahan/Boulder</b> Soil Moist/Precip/Snow cm	<b>Evergreen/White</b> Soil/Air Temp °C	<b>Evergreen/White</b> Soil Moist/Precip/Snow cm
<b>2009</b>	13.7/12.4°C*	0.06 VWC/26.6 cm/171* cm	9.6/8.6°C*	0.08/32.2 cm/133 cm*
<b>2010</b>	11.9/10.9	0.09/51.6/205	7.6/6.9	0.11/42.3/204
<b>2011</b>	10.9/11.2	0.10/56.7/225	7.5/6.6	0.11/52.5/244
<b>2012</b>	13.3/14.2**	0.08/34.1/106**	10.1/9.8**	0.11/28.8/123**
<b>1983-2012 Average</b>	NA/10.8	NA/49.9/213	NA/7.0	NA/47/210

### 3.4.1. Dominant Species

In terms of species composition (Table 3.1. and Appendix A and B.) at the individual sites, several species stand out as dominant within each site (Figure 3.2.). Not only do particular non-native species such as *Bromus inermis* and *Bromus tectorum* dominate the sites in terms of coverage, but bare ground accounts for a large portion of the surface area. The bare ground may influence neighboring species because of a different regime in soil temperature and moisture.

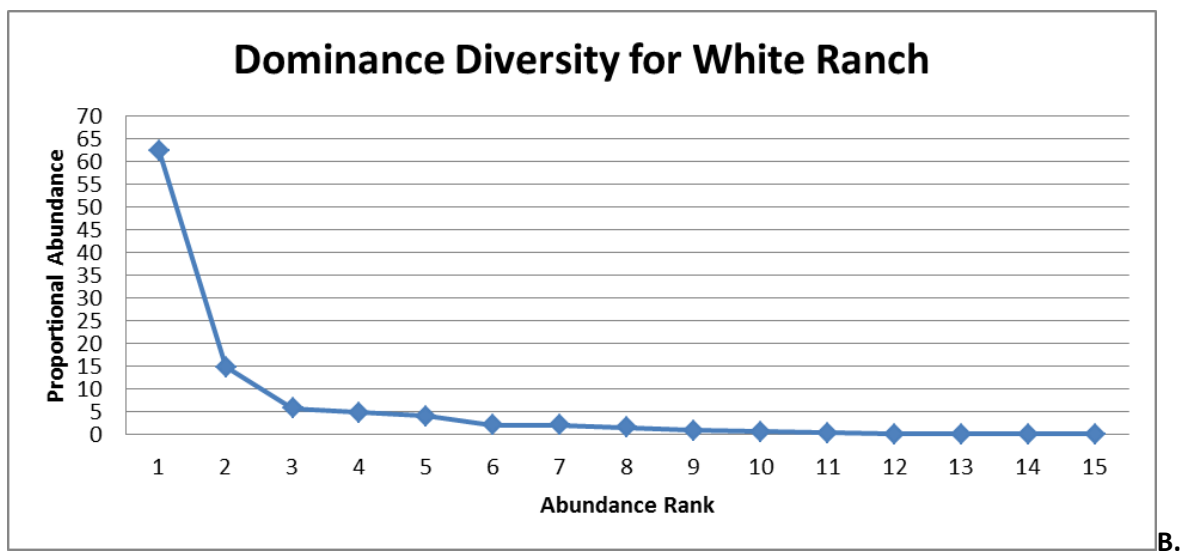
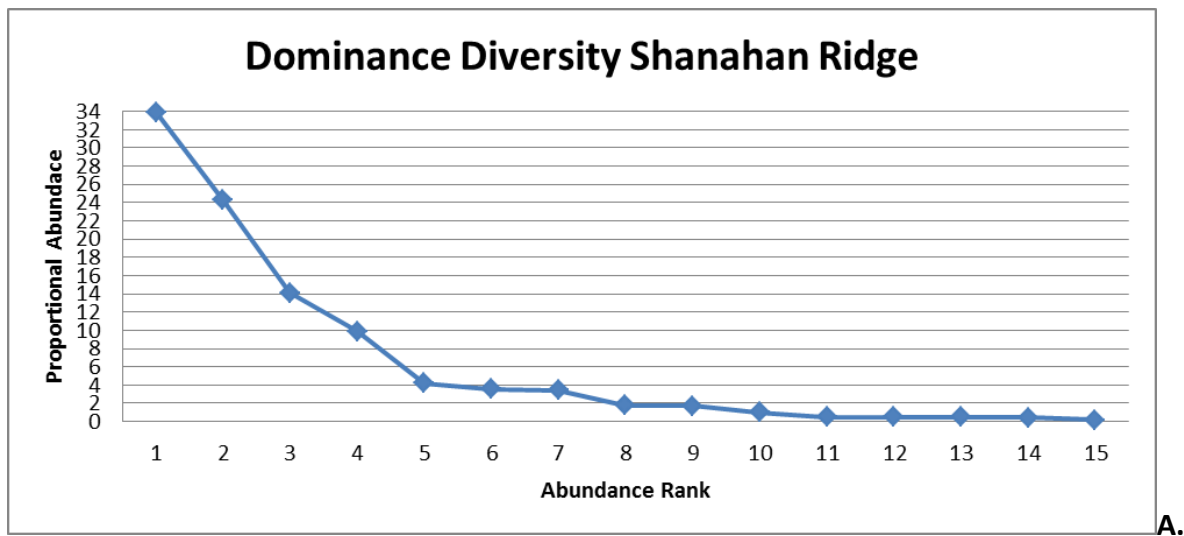




B.

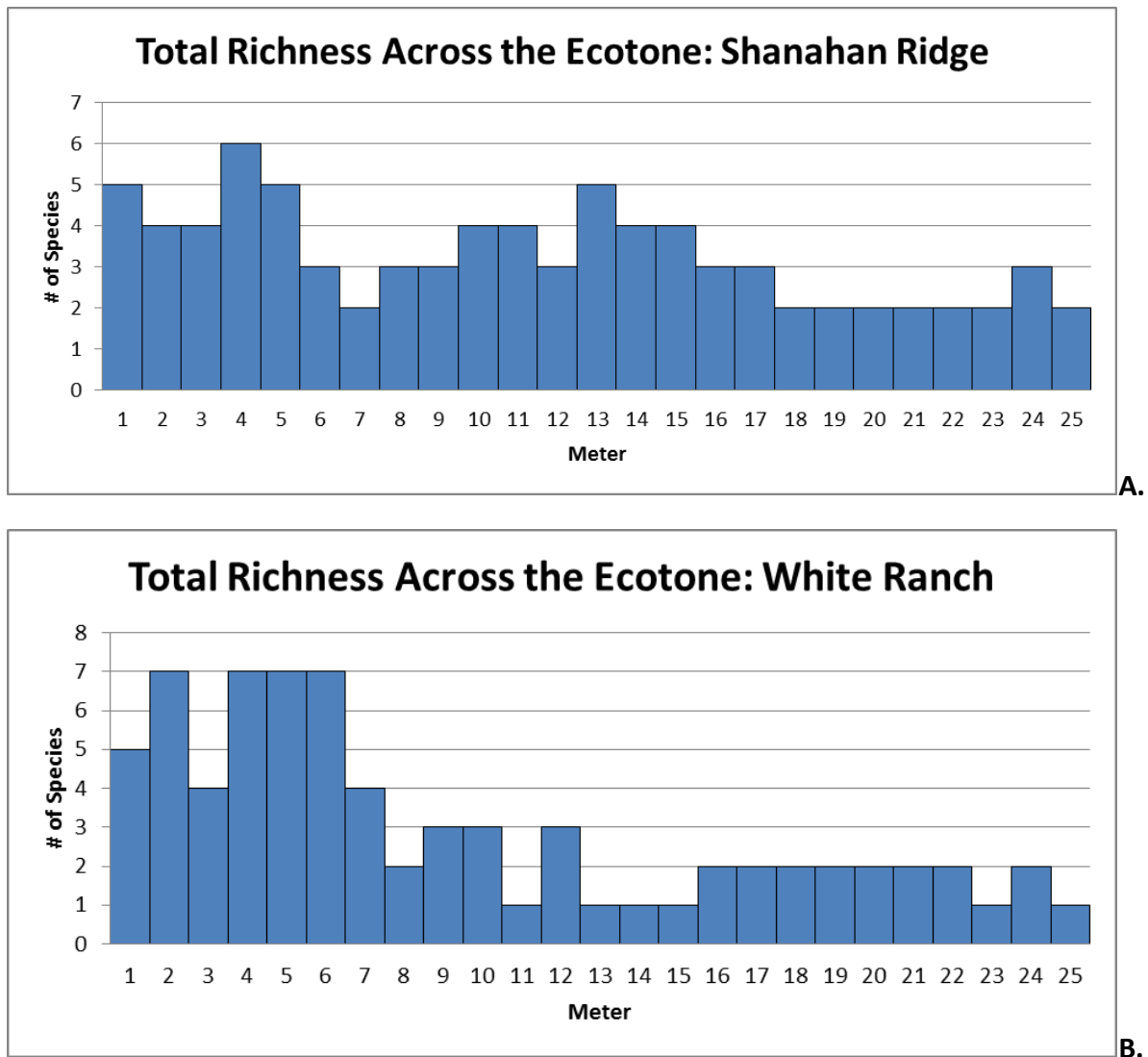
**Figure 3.2.** Average cover of species per meter at Shanahan Ridge (A.) and White Ranch (B.).

A graphical way of representing species diversity is to plot the proportion of each species' cover vs. its rank (from most abundant to least abundant). Though it doesn't yield a simple number for comparison, this way of representing diversity is perhaps the best of all, since it conveys the most information. Note that the greater the slope of the line, the less diverse (especially less "even") the sample. (Figure 3.3.). The species richness varies across the transect, and is impacted by the proportion of bare ground (Figure 3.4.). If the above average cover figures are used in conjunction with the below a better picture of the sites in terms of species dominance comes forward.



**Figure 3.3.** Dominance diversity curves for Shanahan Ridge (A.) and White Ranch (B.).





**Figure 3.4.** Species richness across each transect at Shanahan Ridge (A.) and White Ranch (B.).

Biological communities vary in the number of species they contain. A knowledge of this is important in understanding the structure of the community. Communities dominated by one or a few species have a low evenness while those that have a more even distribution of species have a high evenness. The Shannon-Weiner index (Shannon & Weaver 1949) was developed from information theory and is based on measuring uncertainty and has been used to discuss

the variability in grassland communities (Taft et al. 2006, Jastrzebska et al. 2009, Kopec et al. 2010). The degree of uncertainty of predicting the species of a random sample is related to the diversity of a community. If a community is dominated by one species (low diversity), the uncertainty of prediction is low; a randomly-sampled species is most likely going to be the dominant species. However, if diversity is high, uncertainty is high. The species diversity change throughout the study period was examined and effective number of species determined in order to reduce the number of species that are of highest dominance that will be used in later chapters for correlation analysis discussion (Table 3.3.).

**Table 3.3.** Shannon-Weiner index values and resultant effective species numbers for 2009-2012 at the Shanahan Ridge and White Ranch sites.

	2009	2010	2011	2012	
S-W Index	1.38	1.32	1.20	1.12	Shanahan Ridge
Effective Species Number	3.97	3.74	3.30	3.07	
S-W Index	1.32	1.47	1.41	1.14	White Ranch
Effective Species Number	3.74	4.33	4.08	3.12	

### 3.4.2. Soil temperature

In order to determine how soil temperature may affect the percent cover of plant species each season, correlations of percent cover along the transect and soil temperatures were performed with each PFT and species origin (native and non-native). Since species composition and soil temperatures vary with each meter along the length of the transect these relationships further define the ecotone and how potential changes in microclimate will affect species percent cover.

At White Ranch during the spring months of 2010-2012, there was generally a low correlation between non-native species and soil temperature until the year 2012, which was an extremely dry and warm spring along the Front Range, with precipitation being 10 cm below the thirty year average (40 cm in 2012 compared to 50 cm average Table 3.1.) (Figure 3.5.A). The compounded effects of three years of at or higher than average (2010 (7.0°C), 2011 (6.7°), and 2012 (8.1°)) (Table 3.2.) temperatures for this location may be an indication that it may not only be that particular year's temperature, but a residual of effects from seasons past in terms of soil temperature and resultant lower soil moisture availability. Percent cover for the dominant non-native species, *Bromus inermis* (Smooth brome), across the entire line-transect for the years 2010 (36.8), 2011 (40.6), and 2012 (37.6) (Figure 3.2.) follow this trend with a bit cooler temperatures in 2011 came an increase in percent cover. This may also be related to the location along the line-transect of the majority of the non-native species. Smooth brome extends from the ecotone into the understory, which would have the lower temperatures indicating a negative relationship with higher temperatures. Overall, non-native species percent cover was the lowest in the year 2012 (Appendix B) which correlates with the negative relationship with higher soil temperatures. In terms of native species, both 2011 and 2012 show a significantly positive correlation with soil temperature in spring, opposite of non-native species percent cover (in particular 2012). With higher temperatures in the grassland, and therefore affected by higher air temperatures a positive relationship along the line-transect would be noticeable.

A similar scenario is presented for C<sub>3</sub> and shrub vegetation at this site. During the spring season in general, there is a positive response in vegetation growth to soil temperature. In 2011, native species, C<sub>4</sub> and C<sub>3</sub> species, shrubs, graminoids, forb/herbs, and perennial species all show a positive response to soil temperature (i.e. when temperature increases so does vegetation percent cover). At the White Ranch site there is a single C<sub>4</sub> species (*Bouteloua gracilis*, Blue grama) that occurs only in the grass portion of the line-transect and had increases of 5-10 cm coverage in the year 2011 for the meters that it occurred. This may influence the increased correlation with soil temperature during this year. Because of the dominance of C<sub>3</sub> species there is a more statistically significant relationship with soil temperature here. Similar to native and non-native species percent cover, there is a positive correlation with average air temperatures seen in 2010 and 2011 and a very negative relationship with the anomalous year of 2012 (Table 3.1.). At this site, shrubs, graminoids, and perennial species are the dominant species group in terms of percent cover along the line-transect. *Heterotheca* sp. (Pursh), *Eriogonum umbellatum* (Sulphur flower), and *Geranium caespitosum* (Geranium) are the dominant species of subshrub along the line-transect and occur only in the grass portions. As with non-native species, an increase in temperature shows a decrease in percent cover of these species along the line-transect.

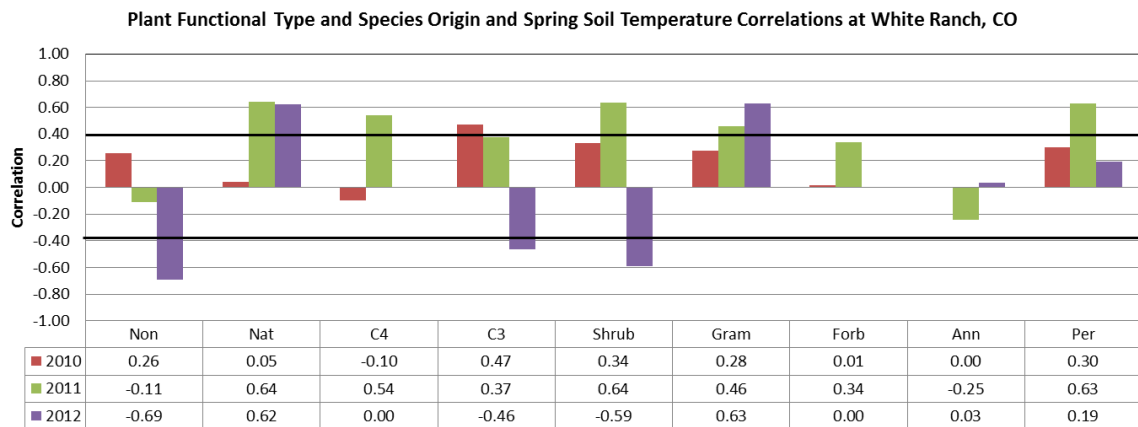
Interestingly, there is a gradual increase in percent cover of graminoid species although smooth brome shows a decrease with increased temperature in the understory, there is an increase in its percent cover further out into the grassland area (Appendix B). The response of graminoid species such as *Koeleria macrantha* (Junegrass), *Carex heliophila* (Sun sedge), and

*Poa compressa* (Canada bluegrass) is marginally increasing over the years, but generally stable or slightly decreasing. Many species are present and with an increase in temperature may merely show low to no growth in years that are too warm, only to increase in size and percent cover per meter the next year with more favorable conditions. However, with any lingering effects or a compounding effect of multiple years of above average temperature the likelihood of emergence decreases. With 2011 being the coolest in relation to average temperature, its positive relationship with perennial species percent cover is evident with a significant (0.63) correlation. At this site, the response of Smooth brome to yearly temperature and moisture variability shows the greatest significance.

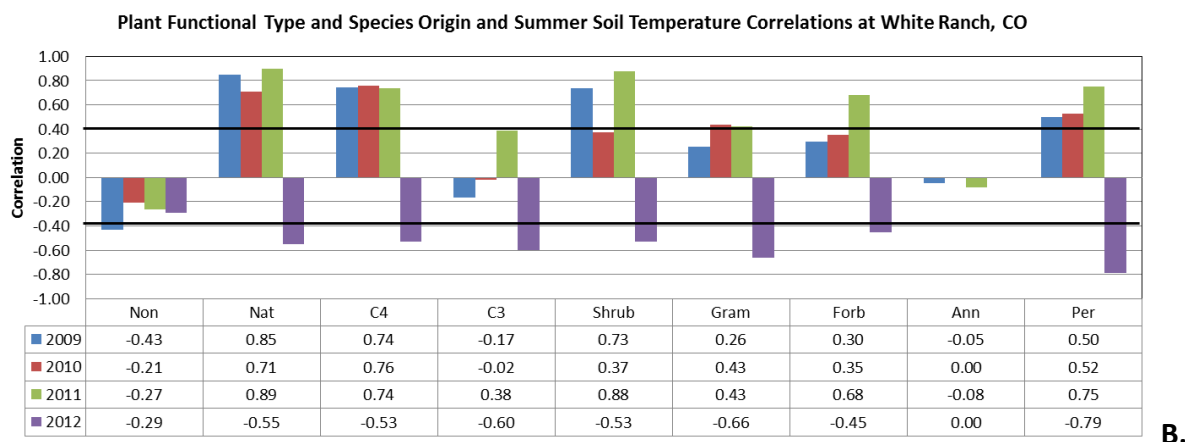
Moving further along in the year into the summer season shows a different vegetation response to soil temperature at White Ranch (Figure 3.5.B). A mostly negative response to soil temperature is evident in the non-native species relationship while a significantly positive response by native species is observed for the years 2009-2011. However, in 2012 the relationship with native species switches to a negative response. This trend continues with C<sub>4</sub>, C<sub>3</sub>, shrub, graminoid, forb, and perennial species as well. Generally, throughout the study period there is a positive response to soil temperature by native, C<sub>4</sub>, shrub, graminoid, forb/herb, and perennial species. Soil temperature data recording was initiated in 2009, a generally cool year overall (0.3° C below average) and is evident in the analysis.

The percent cover of perennial species at this site makes the timing of significant temperatures to emergence of these species the most significant relationship. Depending on the year, the germination of species later in the spring and earlier into summer is possible if

cooler temperatures prevail until later in the season. The anomalously high temperatures of 2012 that extended from spring into summer had an effect on the varying species groups and are evident with significant and nearly significant negative correlations with all species groups (except for the low percent cover annuals). As was discussed for the spring season, and is even more significant during the summer, non-native species in general show a decrease in percent cover through the study period and can be seen here. The highest percent cover of non-native species was during the 2009 season. The possible amplification between the forest understory and grassland during this season (highest difference in average) gives an explanation of this highly negative correlation. As grassland temperatures rise compared to the understory the percent cover of non-natives decline, although the highest percent cover of non-natives (predominantly Smooth brome) are the highest in the understory.

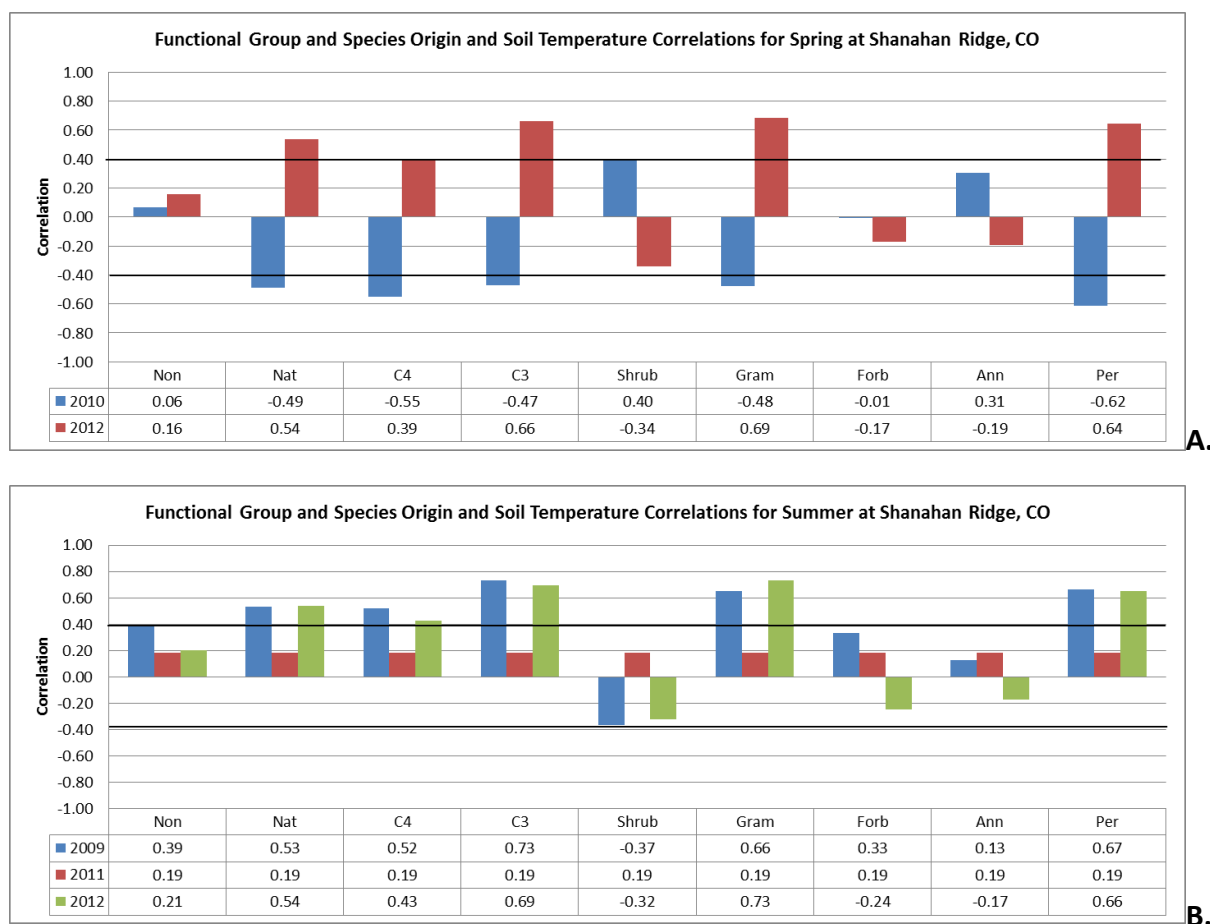


**A.**



**Figure 3.5.** Plant functional type and species origin correlations with soil temperature in spring (A) and summer (B) at White Ranch, Colorado. All graphs have a significance value of  $\pm 0.39$  for  $n=25$  at  $p<0.05$  and  $\pm 0.51$  at  $p<0.01$ , upper and lower black lines.

At Shanahan Ridge during the spring months of 2010 and 2012, percent cover for the dominant non-native species, *Bromus tectorum* (Cheatgrass), across the entire line-transect for the years 2010 (36) and 2012 (6) follow the trend of decreased soil moisture and increased soil temperatures (Figure 3.2.). Cheatgrass is located along the ecotone where the moderate temperatures provided by the increased shading and decreased loss of soil moisture due to lower evaporation rates provided by the increased tree cover as well. Unlike White Ranch, there are four species that make up the majority of species cover, however the two highest percentages are of *Bromus tectorum* (20%) and *Andropogon gerardii* (14%). During the spring of 2010 being cooler and wetter than 2012 (Figure 3.2.) the relationship between these two species is evident. *Bromus tectorum* is a non-native, C<sub>3</sub>, Annual and *Andropogon gerardii* is a native, C<sub>4</sub>, perennial. It is apparent from this that these two species, regardless of functionality or origin rely on spring temperatures (related to moisture) to be sufficient for growth.



**Figure 3.6.** Plant functional type and species origin correlations with soil temperature in spring (A) and summer (B) at White Ranch, Colorado. All graphs have a significance value of +/- 0.39 for  $n=25$  at  $p<0.05$  and +/- 0.51 at  $p<0.01$ , upper and lower black lines.

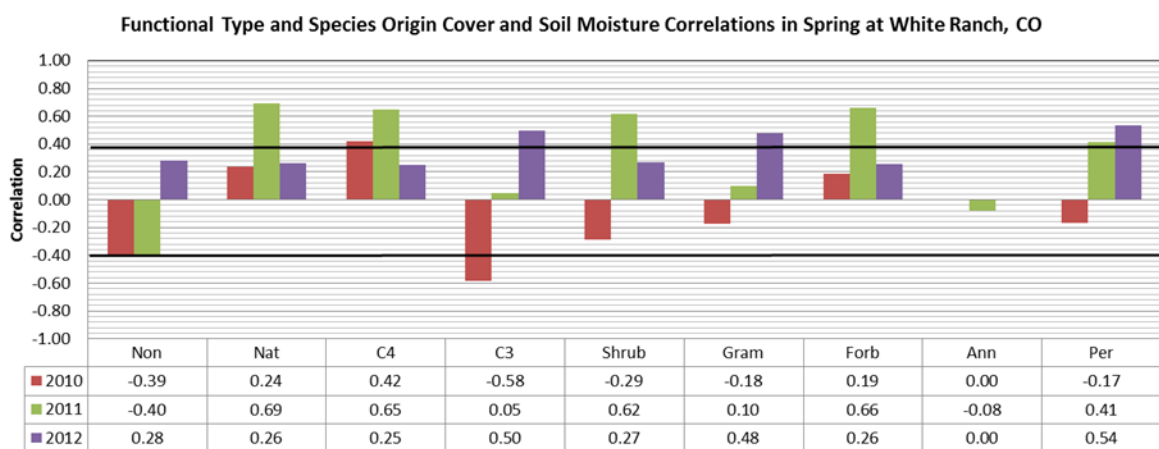
### 3.4.3. Soil moisture

In the North American shortgrass steppe, where most of the precipitation occurs during the warm season (late spring through summer), water availability is skewed towards the upper layers (Sala et al. 1992). The spring season at White Ranch shows a mostly positive correlation between soil moisture, PFTs, and species origin (Figure 3.7.A.). The highest moisture level in 2010 is negatively correlated with non-native,  $C_3$ , shrub, graminoid, and perennial species. Interestingly enough, the two highest spring moisture values in 2010 and 2011 are negatively

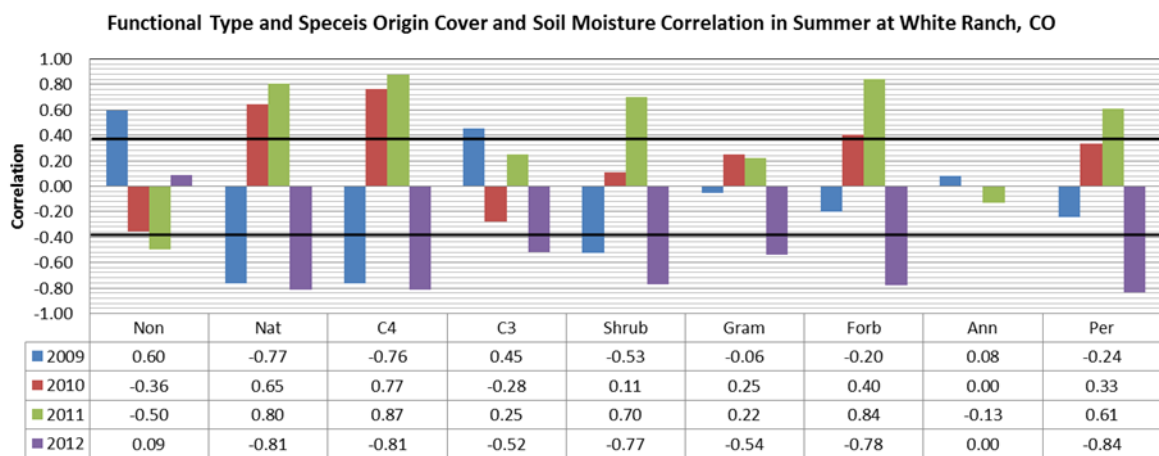


correlated with non-native species while the driest year, 2012, shows a positive correlation. The more moderately moist year of 2011 shows the strongest correlations between moisture and vegetation types.

The summer season again shows the most variability depending on the year (Figure 3.7.B.). With the summers of 2009 and 2012 being the driest in terms of soil moisture (Table 3.2.), there is a negative correlation with native, C<sub>4</sub>, shrubs, graminoids, forbs, and perennials. With native, C<sub>4</sub>, shrub, graminoid, forb, and perennial species there is a mostly positive correlations for the years 2010 and 2011, the wetter years.



**A.**

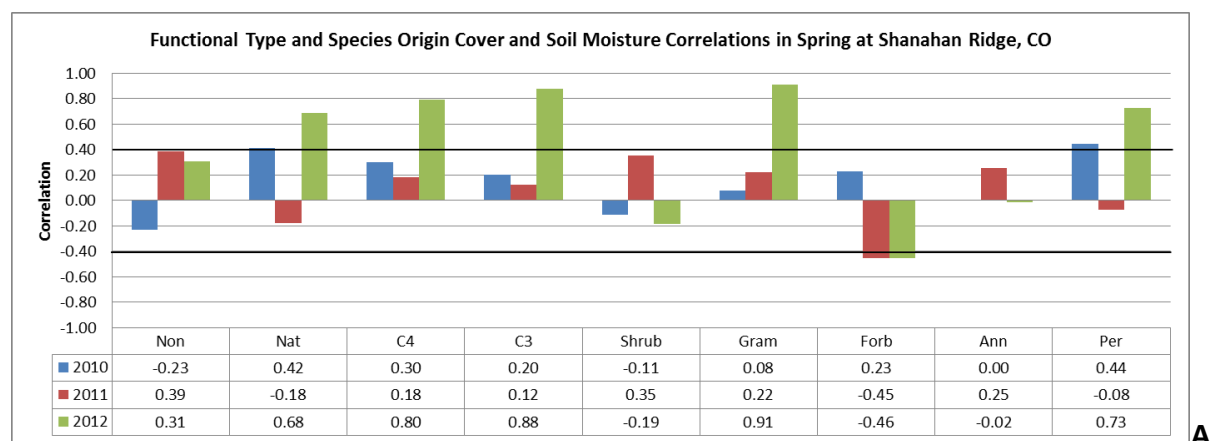


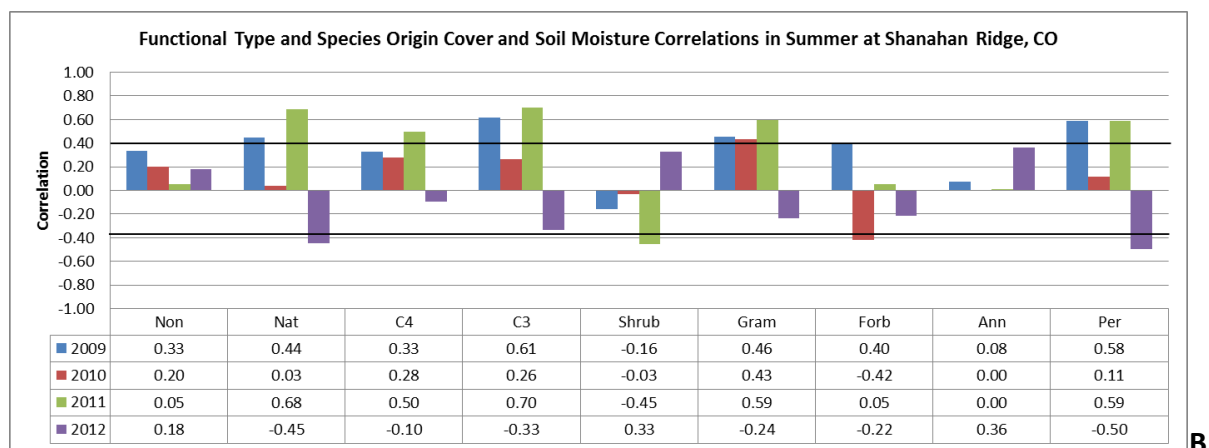
**B.**

**Figure 3.7.** Plant functional type and species origin correlations with soil moisture in spring (A) and summer (B) at White Ranch, Colorado. All graphs have a significance value of +/- 0.39 for n=25 at  $p<0.05$  and +/- 0.51 at  $p<0.01$ , upper and lower black lines.

The spring season at Shanahan Ridge shows a mostly positive correlation between soil moisture, PFTs, and species origin (Figure 3.8.A.). The strongest correlation that can be observed here is the positive relationship between native, C3, C4, Graminoid species (*Andropogon gerardii*, *Ambrosia psyllostachya*, and *Carex heliophila*) while the dominant non-native species (*Bromus tectorum*) does marginally positive as well.

The summer season again shows the most variability depending on the year (Figure 3.8.B.). With the summers of 2009 and 2012 being the driest in terms of soil moisture (Table 3.2.), there is a negative correlation with native, C<sub>4</sub>, shrubs, graminoids, forbs, and perennials. With native, C<sub>4</sub>, shrub, graminoid, forb, and perennial species there is a mostly positive correlations for the years 2010 and 2011, the wetter years.





**Figure 3.8.** Plant functional type and species origin correlations with soil moisture in spring (A) and summer (B) at Shanahan Ridge, Colorado. All graphs have a significance value of +/- 0.39 for  $n=25$  at  $p<0.05$  and +/- 0.51 at  $p<0.01$ , upper and lower black lines.

With this research, I wanted to determine if species with similar traits would respond similarly to a variable microsite over several years. With an increasingly variable climate and related soil conditions presented for species this relationship may be more of a concern in the future. Climate, in particular mean annual rainfall, affects species composition, functional trait diversity and net primary production in grasslands (Sala et al. 1988; Huxman et al. 2004; Sandel et al. 2010). These ecosystems are highly sensitive to changes in both rainfall amount and variability because their production is often water limited during at least part of the growing season (Sala et al. 1988, Esser 1992, Briggs & Koelliker 2001). In some grassland regions, however, climate change scenarios predict an increase in mean annual precipitation (Meehl et al. 2006, Schoof et al. 2010). Thus, understanding how changes in precipitation will affect community structure and dynamics is essential for the development of predictive models of ecosystem responses to future scenarios of climate change.

Based on these data one observation is that it is becoming increasingly apparent that specific species (PFT or species origin) matter in terms of a community response to fluctuations in microsite. If composition is more C<sub>3</sub> rather than C<sub>4</sub> or if there are natives or non-natives present is of importance, but even more important is the specific species of C<sub>3</sub>, C<sub>4</sub>, native, non-native, perennial, annual, etc. The dominant species at White Ranch (*Bromus inermis*, *Bouteloua gracilis*, *Heterotheca villosa*, and *Poa Compressa*) and Shanahan Ridge (*Bromus tectorum*, *Andropogon gerardii*, *Ambrosia psilostachya*, and *Carex heliophila*) all have variable functions and origins.

Recently, Gerten et al. (2008) simulated ecosystem responses (including grasslands) to increased or decreased annual precipitation, as well as the impacts of short-term droughts during the growing season. They concluded that total annual precipitation is a more important driver of net primary production (NPP) than changes in the size and frequency of precipitation events within a growing season. In contrast, experiments have demonstrated that within-season variability in rainfall alters NPP in both mesic and arid grasslands (Knapp et al. 2002, Heisler- White et al. 2009, Thomey et al. 2011).

Functional traits result from historical selection pressures and have been directly related to abundance patterns in response to environmental drivers (Grime 2001, Lavorel & Garnier 2002, Goldberg & Hartman 2003). In herbaceous communities, key response traits include water use efficiency (e.g. C<sub>3</sub> vs. C<sub>4</sub>; forbs vs. grasses) (Craine et al. 2001, Gough et al. 2012) traits that reflect selection pressures for capturing space, sunlight and the efficient use of limiting resources.

The physiological characteristics of C<sub>4</sub> plants such as a high optimum temperature range and minimal photorespiration give them an advantage in warm environments compared to C<sub>3</sub> plants, which dominate under cooler conditions (Long 1999). As a result, C<sub>4</sub> and C<sub>3</sub> plant distributional patterns are significantly correlated with temperature (Cabido et al. 1997, Wan and Sage 2001, Mo et al. 2004). At Shanahan Ridge and White Ranch the results from this research have shown that both C<sub>3</sub> and C<sub>4</sub> species have declined with increased soil temperatures. C<sub>3</sub> species would be expected to exhibit this decline, but the percent cover of C<sub>4</sub> species declining since 2009 is interesting and should be continually monitored to determine the response in 2013 and beyond. The dominant C<sub>4</sub> species' at the two sites (*Andropogon gerardii* and *Bouteloua gracilis*) both happen to be perennial species as well and are more likely influenced by soil moisture more than soil temperature.

The potential loss of perennial species with predicted climate change (Craine et al. 2011) will increase the ability of annual species to become more influential and opportunistic in these areas. Each species has a unique combination of functional traits (Eviner 2004) and a more complete understanding of the functional consequences of climate change for grasslands will require broad advances in our understanding of plant species and communities. With a more variable precipitation regime and warmer temperatures predicted the species that rely on consistent moisture (perennials) may suffer. At the Shanahan site, *Andropogon gerardii*, a perennial, did not fluctuate much over the four years studied (13.6, 13.4, 15.4, 14.4 averages for each year 2009-2012). The average soil moisture increased (Table 3.2.) throughout the

study, so, once again, the increased moisture was more important to these species than the increased temperature.

Non-native plant species pose a significant threat to native plant species and natural communities (D'Antonio et al., 1999, Vitousek, 1990). As some habitats have been invaded far more successfully than other habitats (Harrison, 1999, Stohlgren et al., 1999), plant ecologists are urgently trying to accurately quantify the environmental differences between heavily invaded and less invaded sites. At Shanahan Ridge and White Ranch the dominant species are *Bromus tectorum* and *Bromus inermis*, with percent cover average controlling the coverage of species (*tectorum* being an average of 20% cover and *inermis* being 40% cover). Although these species are limited by soil moisture along each transect, they differ in their function with *tectorum* being an annual and *inermis* being a perennial. Annuals are frequently found in abundance in areas with pronounced seasonal climates, frequent disturbances, and in areas of low soil fertility (Stohlgren et al. 2005). In response to these environments, annuals grow rapidly to maturity, and complete reproduction in a short season. In contrast, perennial species grow during multiple growing seasons, and, in more favorable climates and soils, occupy less-frequently disturbed sites, take longer to reach maturity and reproduction, and accumulate biomass over several years. Therefore, if conditions are more variable, with fluctuating precipitation, subsequent soil moisture, and then changing soil temperatures, then the species that have been adapted to these changes (natives) over tens of years to centuries will be more adapted to these changes (Sheley & James 2010, Byun et al. 2013).

Both native and non-native species, once more, declined in percent cover over the study period. One of the more apparent declines was in *Bromus tectorum*. This C3, Annual, Non-native species occurred mostly along the ecotone where soil temperatures were more moderate and soil moisture was slightly higher than the grassland, yet had more sunlight than the strictly forested areas. The increased in soil temperatures from 2009-2012 (Table 3.2) may have had the greatest influence on the germination of this annual species.

#### **3.4.4. Soil resources**

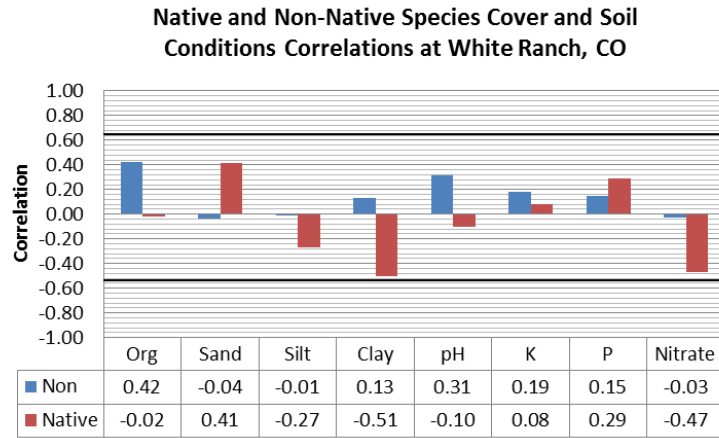
Although, there are no significant relationships between vegetation and soil variables (organic matter (OM), pH, potassium (K), phosphorous (P), and nitrate (N)) at the White Ranch site, there are a few distinctions to be made between clay content and nitrate in relation to native species (Figure 3.9.A.). At the Shanahan Ridge site OM, pH, K, P, and N all show stronger, if not significant, relationships with native species overall (Figure 3.10.A.). There are only two soil characteristics, organic matter and pH at White Ranch, that show a positive relationship with non-native species, further reinforcing a generalist perspective when dealing with these particular species. Additionally, at White Ranch the location of the dominant non-native species Smooth brome is in the understory, which is higher in organic matter content based on tree cover and a generally higher percent cover and density of this particular species. The higher pH may also be related to the percent cover of Ponderosa pine litter where these species occur. With a much higher percent cover of native species at Shanahan Ridge these relationships may display a better picture of relationships of PFTs, species origin, and soil conditions. With the

majority of species occurring in the grassland portion of the line-transect the lower organic matter content would explain the negative relationship with all species groups.

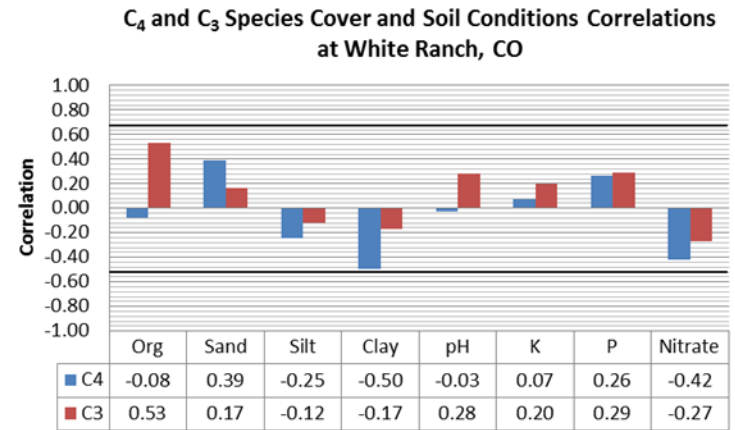
At White Ranch sand, silt, clay content; K, P, and N content are all similarly correlated among both C<sub>3</sub> and C<sub>4</sub> species (Figure 3.9.B.). At Shanahan Ridge every soil parameter is either positively or negatively correlated similarly between C<sub>3</sub> and C<sub>4</sub> plant species (Figure 3.9.B). For OM, sand, silt, and clay content, White Ranch vegetation shows a fairly strong correlation, both positive and negative with shrubs, graminoids, and forb/herbs (Figure 3.9.C.). For pH value, the relationship is variable and for K, P, and N the relationship gains strength both positive and negative once more. At Shanahan Ridge these correlations are highly variable, with none of the relationships being similar between the three types of vegetation (and graminoids being the most variable in levels of correlation) (Figure 3.10.C.).

At the White Ranch site, OM, K, and P are all positive correlated with annual species. Organic matter, sand content, pH, K, and P are all correlated with increased perennial growth while silt and clay content and N content are negatively correlated with perennial growth (Figure 3.9.D.). At the Shanahan Ridge site few similarities exist. Organic matter, sand content, K, and N content are negatively correlated with perennial growth while silt and clay content, pH, and P are all positively correlated with perennial species percent cover (Figure 3.10.D.). Interestingly, annual species at the Shanahan Ridge site show an opposing relationship to the same parameters and should be noted.

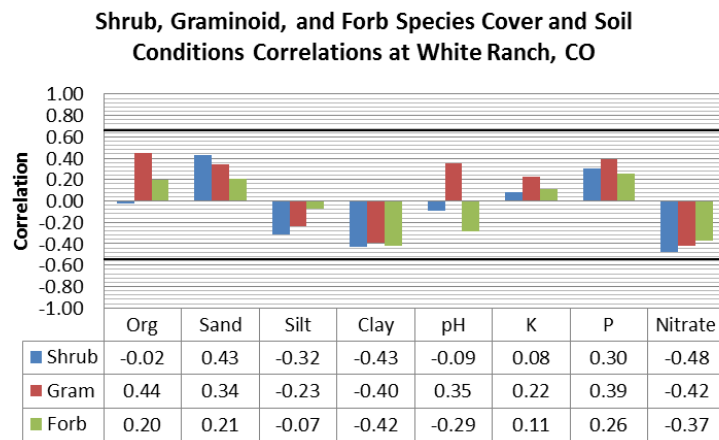




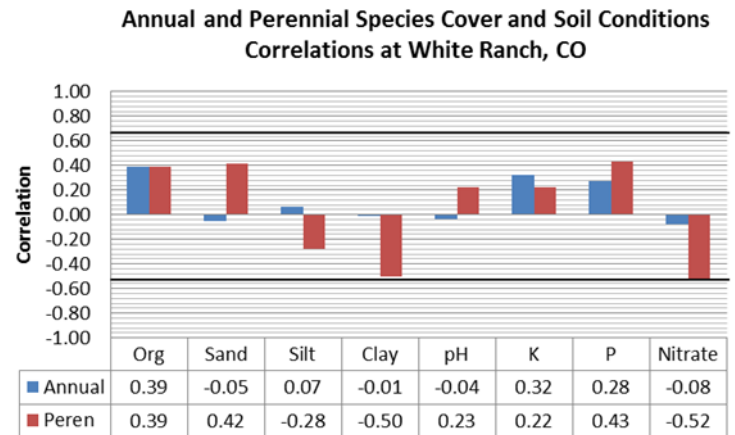
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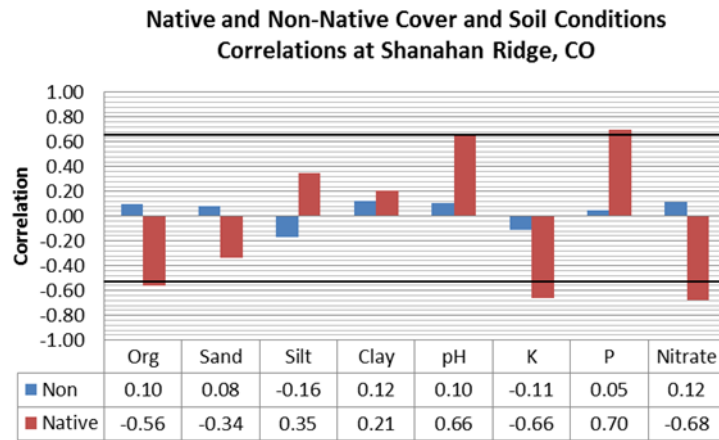


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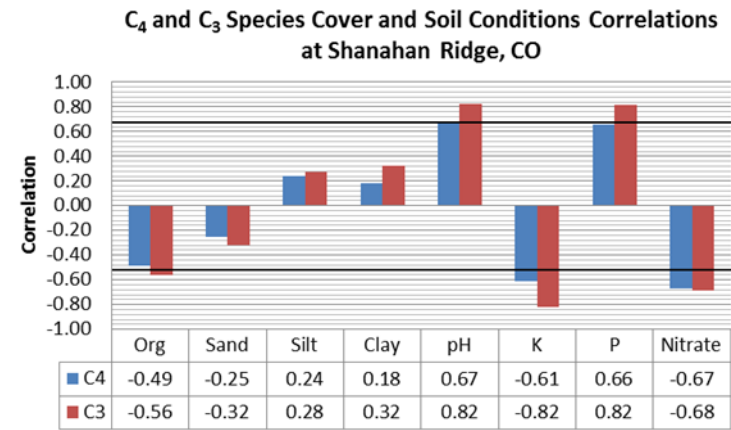


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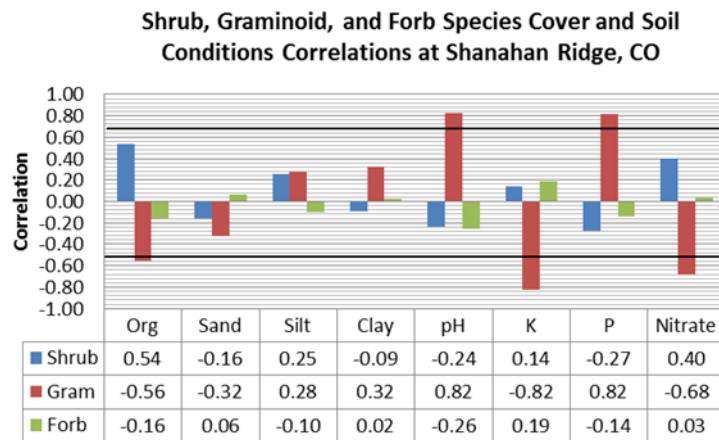
**Figure 3.9.** Individual soil traits correlated with functional groups and species origin at White Ranch, CO. A. represents native and non-native species compared to soil conditions. B. represents C<sub>4</sub> and C<sub>3</sub> species. C. represents Shrub/Subshrub, Graminoid, and Forb/Herb species. D. represents Annual and Perennial species (All graphs have a significance value of +/- 0.39 for n=25 at p<0.05 and +/- 0.51 at p<0.01, upper and lower black lines).



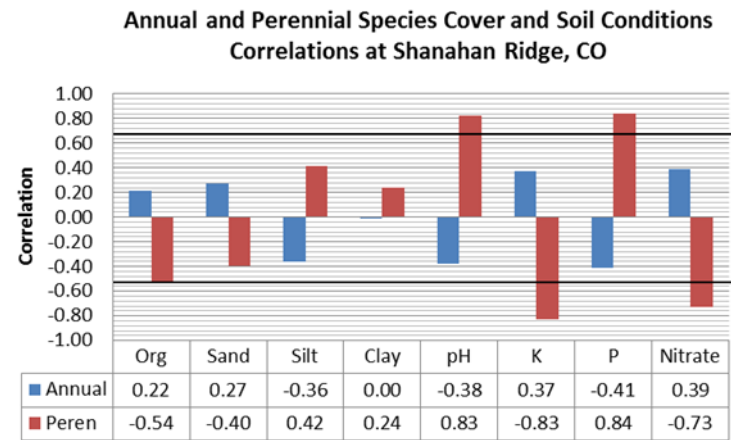
A.



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**Figure 3.10.** Individual soil traits correlated with functional groups and species origin at Shanahan Ridge, CO. A. represents native and non-native species compared to soil conditions. B. represents C<sub>4</sub> and C<sub>3</sub> species. C. represents Shrub/Subshrub, Graminoid, and Forb/Herb species. D. represents Annual and Perennial species (All graphs have a significance value of +/- 0.39 for n=25 at p<0.05 and +/- 0.51 at p<0.01, upper and lower black lines).

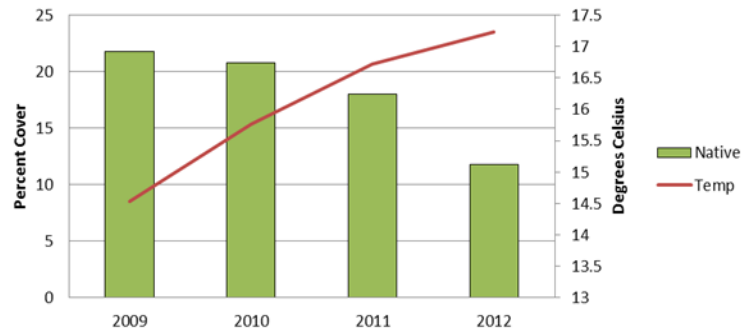
Based on these data one observation is that it is becoming increasingly apparent that specific species (PFT or species origin) matter in terms of a community response to fluctuations in resources. If composition is more  $C_3$  rather than  $C_4$  or if there are natives or non-natives present is of importance, but even more important is the specific species of  $C_3$ ,  $C_4$ , native, non-native, perennial, annual, etc. If this relationship with resources is strongly positive one year and negative the next then it might mean resource availability is not important to establishment or growth of the general community of species, but of a specific species individually based on its resource needs. With an increasingly variable climate and related soil conditions presented for species this relationship may be more of a concern in the future.

#### **3.4.5. Plant-Soil relationships**

Finally, to further emphasize the influence that microsite has on the vegetation cover at these sites, average seasonal temperature and moisture at both sites were compared to percent cover of all PFTs and species origin designations (Figures 3.11.-13.).  $C_4$  species and forbs both show an increase in percent cover with soil temperature (Figure 3.11.D. and E.). In the summer season at Shanahan Ridge there is a positive relationship between soil temperature, native species and perennial species (Figure 3.11.B. and F.). Unlike spring at Shanahan Ridge, there were no relationships in the spring season in terms of soil temperature at White Ranch. Interestingly during the summer season at White Ranch there are two relationships with summer soil temperature to note.  $C_4$  and native species both show negative growth in percent cover with increased average temperature from 2009 to 2012 (Figure 3.9.A. and C.).

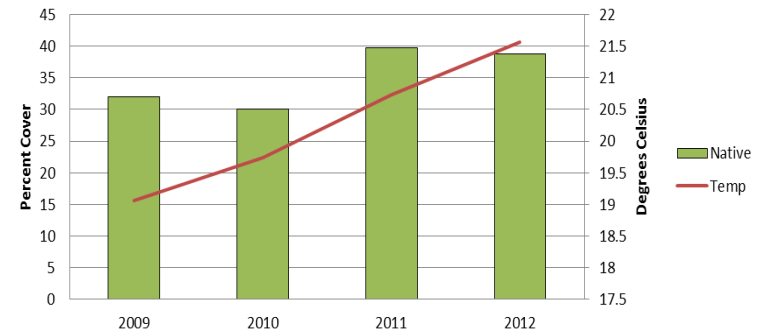
At Shanahan Ridge in relation to soil moisture there is an increase in percent cover of forb species during the spring season (Figure 3.12.G.). Additionally during the summer,  $C_4$  species are correlated with soil moisture (Figure 3.12.D.). In terms of spring soil moisture at White Ranch a decrease in the average from 2010 to 2012 (Table 3.2.) correlates with a reduction in percent cover of  $C_4$ , forb, and native species (Figure 3.12.A., C., and E.). Summer soil moisture at White Ranch, while not strongly related in 2009, show a slow decline in percent cover of native and forb species as soil moisture declines from 2010 to 2012 (Figure 3.12.B. and F.).

Native Species Cover vs Summer Soil Temperature at White Ranch, CO

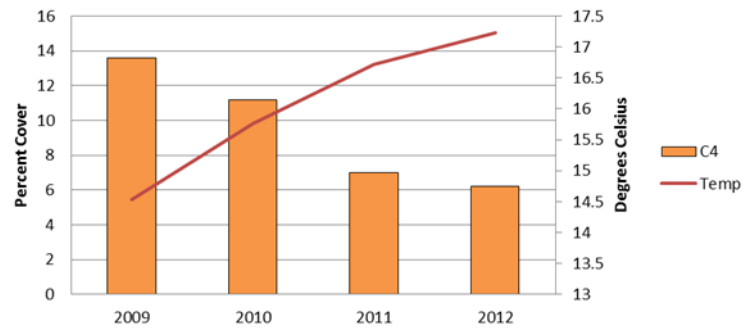


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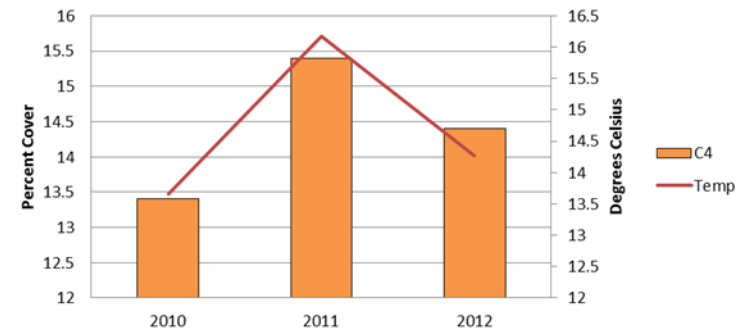
Native Species Cover vs Summer Soil Temperature at Shanahan Ridge, CO



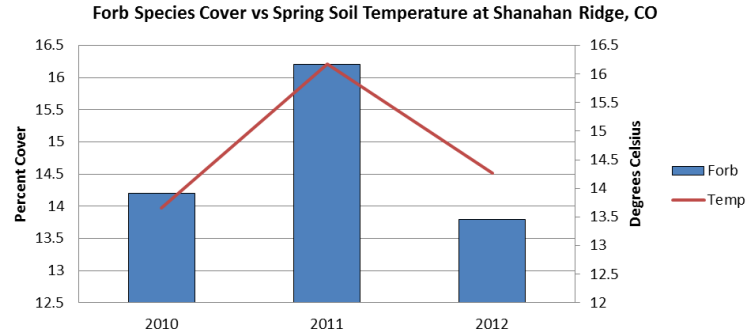
B.

C<sub>4</sub> Species Cover vs Summer Soil Temperature at White Ranch, CO

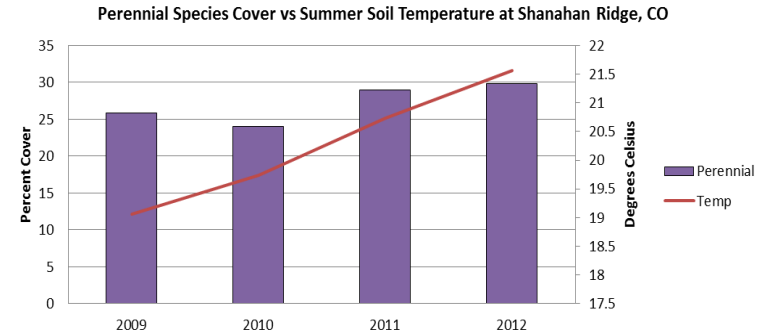
C.

C<sub>4</sub> Species Cover vs Spring Soil Temperature at Shanahan Ridge, Co

D.

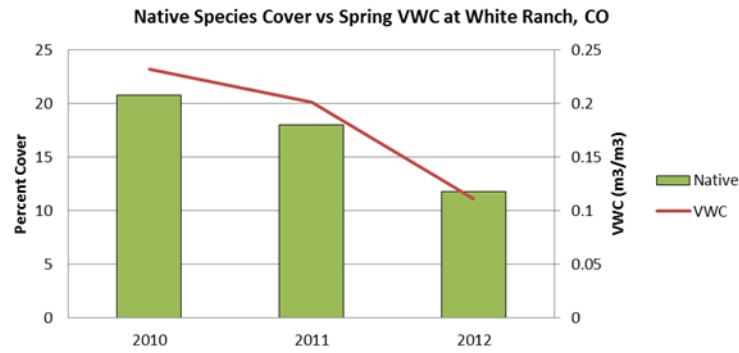


E.

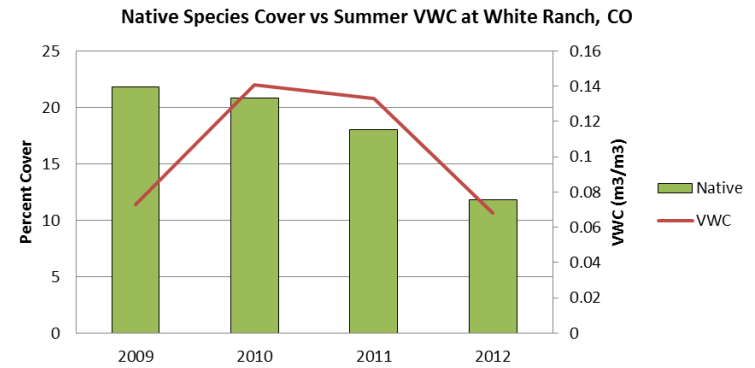


F.

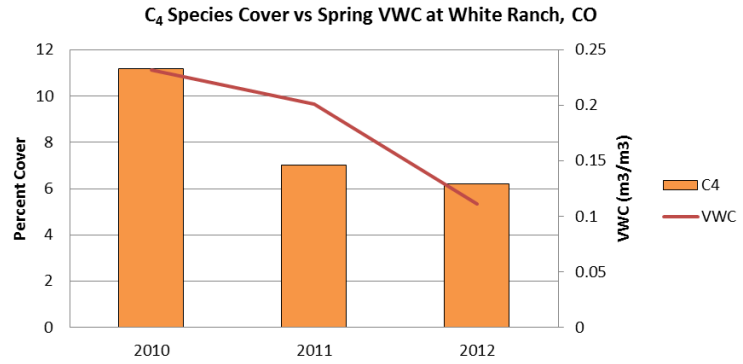
**Figure 3.11.** Average spring and summer soil temperature relationships with PFTs and species origins. Regional climate data obtained from the Western Regional Climate Center for Evergreen, CO and Boulder, CO. A. and B., native species correlations with soil temperature. C. and D.,  $C_4$  species correlations with soil temperature. E., forb species correlations with soil temperature. F., perennial species correlations with soil temperature.



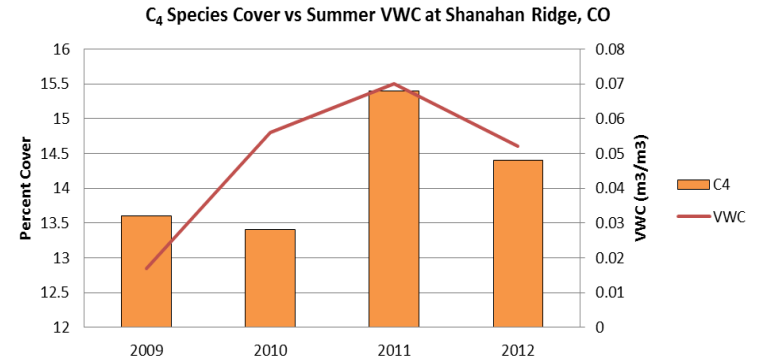
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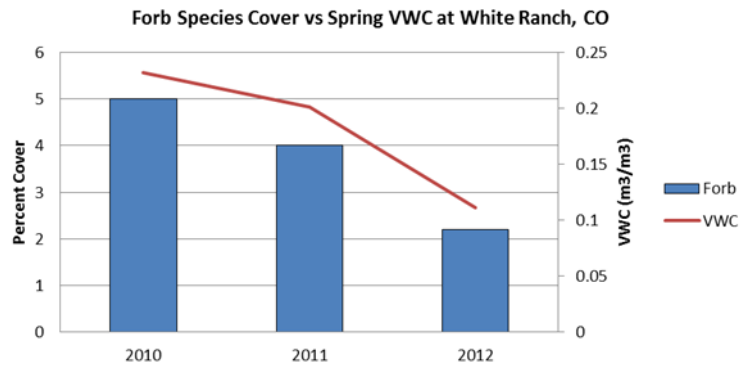
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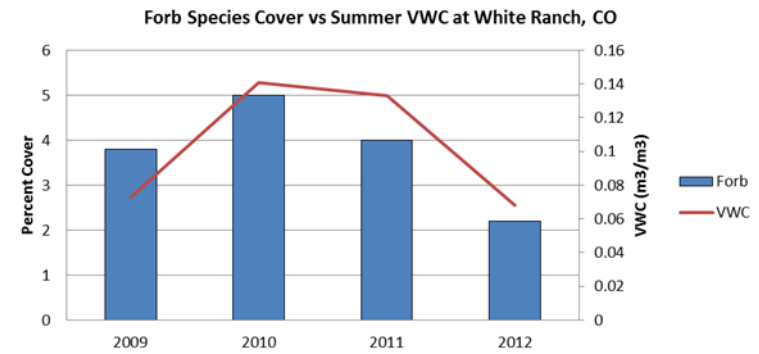
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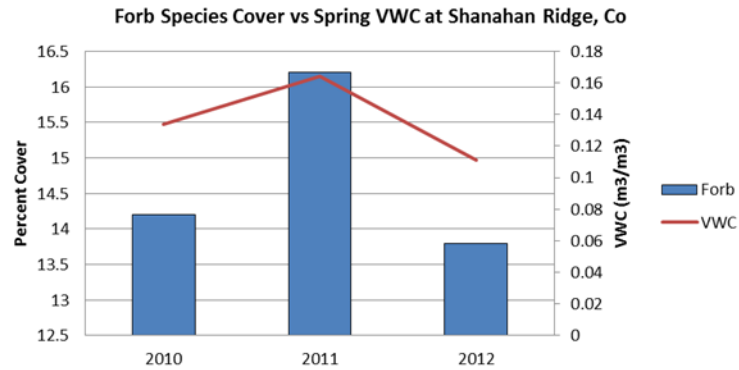
D.



E.



F.



G.

**Figure 3.12.** Average spring and summer volumetric water content (VWC in  $\text{m}^3/\text{m}^3$ ) relationships with PFTs and species origins. Regional climate data obtained from the Western Regional Climate Center for Evergreen, CO and Boulder, CO. A. and B., native species correlations with VWC. C. and D.,  $C_4$  species correlations with VWC. E., F., and G., forb species correlations with VWC.



Throughout the analysis one species group in particular stands out, C<sub>3</sub> and C<sub>4</sub> species. The differentiation between C<sub>3</sub> and C<sub>4</sub> plants is important in the framework of global change because their responses to CO<sub>2</sub> and climate change are different (Ehleringer 1978, Carson & Bazzaz 1982, Carter & Peterson 1983, Pearcy & Ehleringer 1984, Curtis et al. 1990, Polley et al. 1992, 1993, Kimball et al. 1993). Paruelo and Lauenroth (1996) found that the regional distribution of the relative cover of C<sub>4</sub> grasses was positively related with mean annual temperature (25%) and mean precipitation and its timing (75%). Additionally, they found that C<sub>3</sub> grass cover decreased with mean annual temperature and increased with the proportion of precipitation falling during winter, which correlates well with the outcomes here as well.

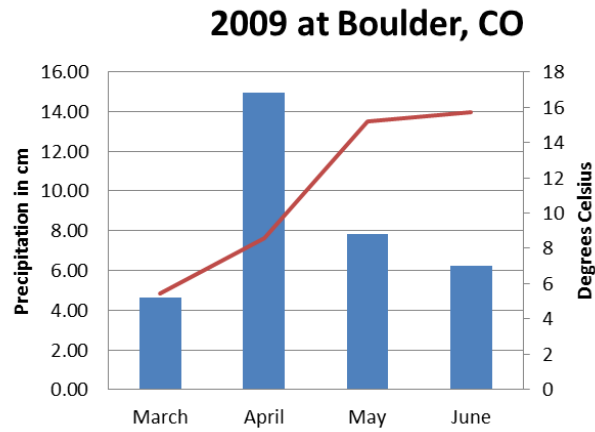
It has been said that shifts in precipitation regimes may have an even greater impact on ecosystem dynamics than the singular or combined effects of rising CO<sub>2</sub> and temperature, especially in arid and semiarid environments (Weltzin et al. 2003). For example, precipitation substantially influenced plant and ecosystem response to elevated CO<sub>2</sub> in an arid ecosystem (Smith et al. 2000). In the current study, spring season has emerged as the most important season for determining percent cover of both annual and perennial species. If air temperature and precipitation at each site are compared and subsequently compared to percent cover per year, the months of March and April are significantly important at both sites at an even finer scale. For example, at the Shanahan Ridge site, percent cover of non-native species rose from 2009 to 2010 (28% cover to 42% cover) and then gradually declined after that (16% in 2011 and 7% in 2012). With that there is a similar relationship between the amount of precipitation and the temperatures associated with them during that same period (Figure 3.13. A-D). The year

2009 saw an average (4.6 cm) amount of precipitation in March with more than double the average (6.6 cm) amount in April along with a 5-9°C temperature (Figure 3.13.A.), which is the average temperature for these two months at this site. The year 2010 has similar moisture in March and much closer to average in April with slightly warmer temperatures 7-9°C (Figure 3.13.B.). The years 2011 and 2012 show significant drops in precipitation to near zero for March and much lower than normal in April (6 and 1.3 cm respectively) (Figure 3.13.C. and D.).

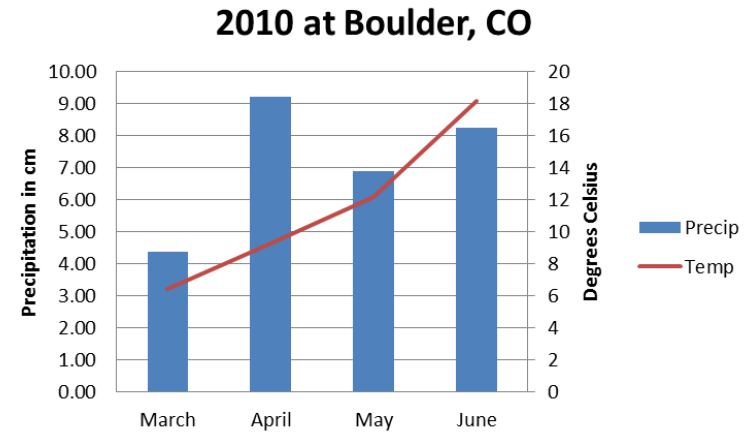
Not only was the precipitation much below average, but much higher temperatures in 2012 (10-12.5°C) set the area up for a much lower cover of all species groups. As was discussed earlier the amount of winter precipitation may affect many perennial species, but many grasses with shallower roots require soil moisture in the upper layers to assist in new growth in the spring. If the temperature is high enough, but the needed precipitation is absent then these species will not thrive as usual.

Average air temperature for White Ranch in March and April are 1.5°C and 5.3°C respectively, while precipitation ranges from 4 to 5.5 cm. White Ranch shows a much similar trend with 2009 being slightly lower in soil moisture in March, but rebounding to more than double the average in April with associated slightly warmer temperatures and 2010 being average in soil moisture with slightly lower temperatures which may affect the ability of certain species to emerge (Figure 3.14.A. and B.). Native species cover went from 22.4% in 2009 to 24% in 2010 showing that this variability may have had no effect on species. However, non-native species declined from 50% to 40% in one season. Whether this is the only cause is hard to determine from this analysis alone. Native species in 2011 remained around the 23% cover,

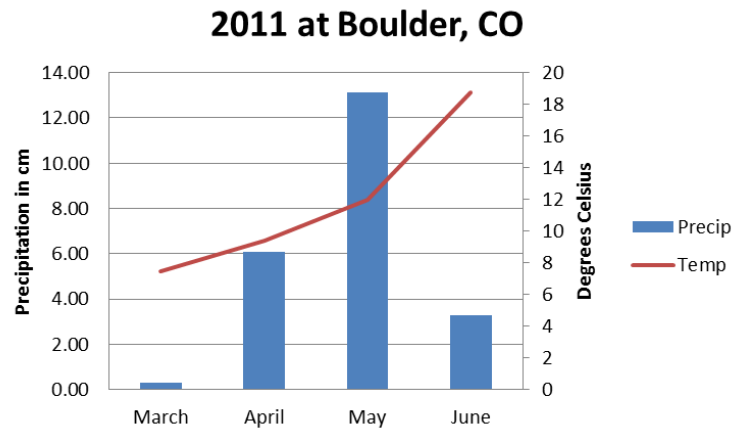
while non-native species rose to 45%. Interestingly, the amount of precipitation was below normal for both months while temperature was closer to average (Figure 3.14.C.). There may be a threshold that may have not been met or a residual from earlier precipitation events not noticed in this relationship. The year 2012, as with Shanahan Ridge shows a decline in both native and non-native cover (14.5 and 39% respectively) to their lowest of the study period. Related to this is the 0.06 cm of precipitation in March of that year and subsequent nearly 1.75 cm below average precipitation in April and associated 5-6°C above average temperatures (Figure 3.14.D.).



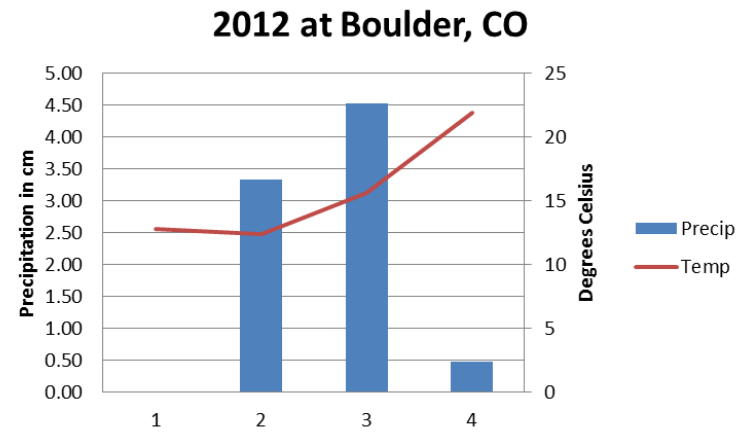
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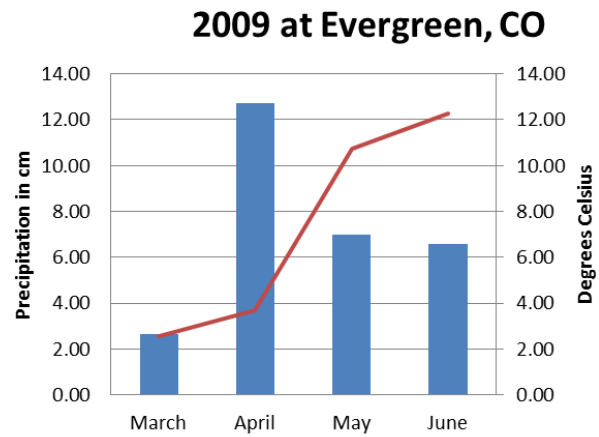


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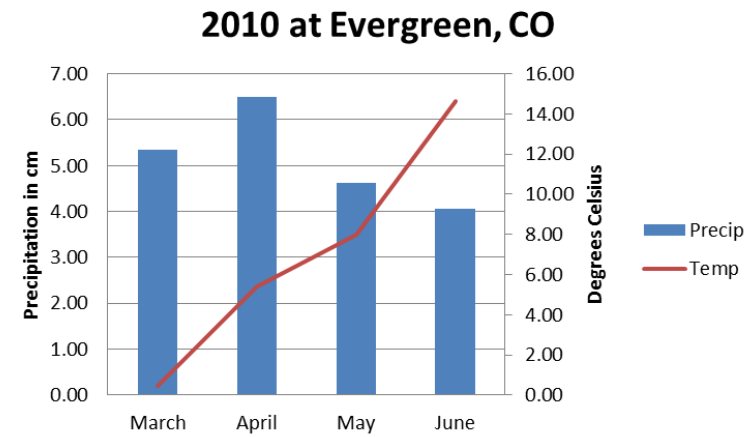


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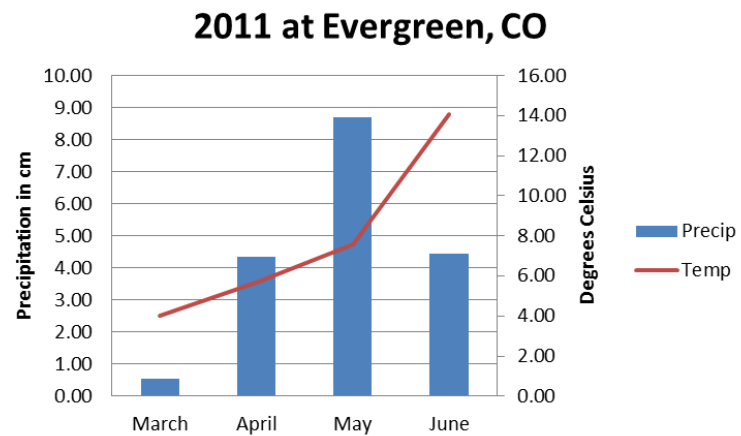
**Figure 3.13.** Relationship between spring precipitation and air temperature at Boulder, CO. Regional climate data obtained from the Western Regional Climate Center.



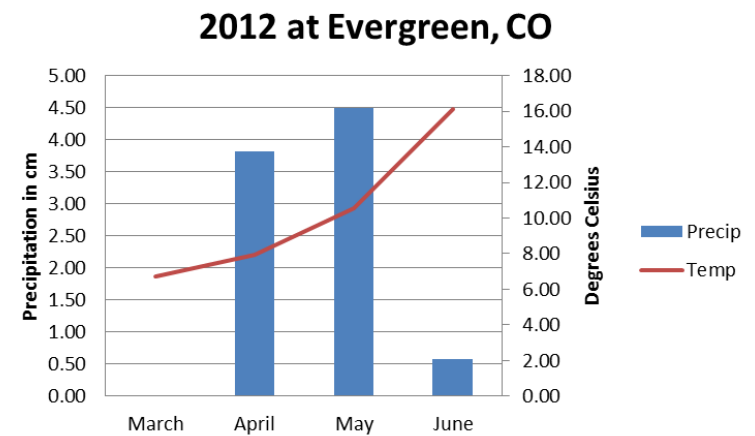
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**Figure 3.14.** Relationship between spring precipitation and air temperature at Evergreen, CO. Regional climate data obtained from the Western Regional Climate Center.

While current climate models seem unable to make reliable predictions about the magnitude or even the direction of precipitation change on smaller, biologically meaningful scales, they do indicate that many regions of the world will experience alterations in precipitation regimes over the next 100 years (Weltzin et al. 2003). The current study provides several indications that the timing of precipitation and its connections to several varying plant functional types and species origins (native and non-native) dictates the species composition of these sites.

### **3.5. Conclusions**

Grasslands cover over 40% of the terrestrial land surface, and their response to changes in rainfall patterns will have significant consequences for global patterns of diversity under future climate scenarios (Knapp et al. 1993, Fay et al. 2003). Functional traits provide a mechanistic linkage between ecosystem structure and function that can be used to predict the ecological impacts of climate change (McGill et al. 2006, Suding et al. 2008).

This study provides some evidence for the theory that a more diverse community can provide some sort of resistance to change with future climate change, which will alter the microclimate that these species must persist in. The important management implications are for establishing, maintaining, and restoring diverse plant communities. Grasslands high in species diversity are important for providing the range of ecosystem services or plasticity necessary to resist an ever changing climate with resilience each season. Maintaining increased species group diversity should be a primary objective of land managers because it could be related to increased productivity and stability. In the face of an ever changing environment and

invasion of non-native species that are able to utilize resources better than natives and are more adapted to opportunism, the diversity of native PFT members may help in invasion resistance as well.

Quantitative models of the relationships between PFTs and geographic and climatic variables provide new insights into the fine-scale distribution of vegetation along a gradient of soil temperature and moisture at the ecotone between grassland and forest. Temperature has been recognized as an important control on the distribution of numbers of species, but our results suggest that when percent cover is considered, precipitation and the seasonal distribution of it are also important controls.

A proper description of the spatial distribution of the percent cover of species groups is critical in relation with some aspects of global change research at all scales. Species composition affects the exchange of energy, matter, and momentum between the surface and the atmosphere and changes in the percent cover of grasses and shrubs will affect ecosystem processes such as nutrient availability (Berendse et al. 1987, 1994, Pastor et al. 1993, soil water dynamics (Sala et al. 1989, Paruelo & Sala 1995), primary productivity (Sala et al. 1989), soil carbon accumulation (Archer et al. 1988, Schlesinger et al. 2000), and horizontal and vertical resource patterning (Belsky 1994).

## **Chapter 4. General findings and conclusions**

### **4.1. Evaluation of soil properties and their relationship to microclimatic variability**

This research provides information on the connections between regional, local, and soil microclimatic conditions and vegetation percent cover along the forest-steppe ecotone of the Front Range of Colorado near Boulder and Golden, CO. The first objective of this research was to illustrate the use of autocorrelograms as tools to identify the degree of dependency of soil temperature and moisture on the distance and time between pairs of measurements and how to take advantage of this dependency along several line-transects that cross this ecotone. The second objective was to use *in situ* measurements to determine the effects of changes in soil temperature and moisture on plant functional types and species origin.

Autocorrelation analysis of spatial and temporal soil temperature and moisture determined that there are significant correlations in both space and time (Chapter 2). Depending on the season spatial variability shows a strong clustering of points along the transect at the one meter level with decreased clustering when the resolution is increased to two meter interval. Temporal variability in soil temperature and moisture becomes more variable and unpredictable in this continental, semi-arid region. Soil temperature becomes insignificantly autocorrelated within a few hours up to three days or more in the spring season and almost never autocorrelated in the summer. Temporal autocorrelation of soil moisture extends much further into the season due to the variable nature of precipitation events in this region. Significance can be achieved for up to two weeks in the spring, two weeks to a month in the summer, and a week and a half up to two weeks in the fall.



When these measurements are taken along the line-transect to determine a minimum value of sampling interval both spatially and temporally the results show that in the spring season a two hour interval can capture the resolution of the variability in the grassland temporally, three hours along the ecotone, and four hours in the forest. The summer season sees slightly lower values with hourly in the grassland, two hours along the ecotone and in the forest. The fall, being the most regulated by higher soil moisture and declining temperature values shows that a five hour interval is needed in the grassland and six hours in both the ecotone and forest. Soil moisture, with its variability and higher interval between events shows that in the spring season, daily recordings would be necessary in the grassland and ecotone, with twelve hour intervals in the forest. During the summer daily recordings in the grassland, ecotone, and forest would capture the variability. The fall season would need 36 hour intervals in the grassland, daily at the ecotone and the forest.

The relationship between soil variables, plant functional types (PFTs), and species origin (native/non-native) show that there are significant species groups in these locations that are particularly sensitive to a variable microclimate (Chapter 3). It has been noted that non-native species are generally more adept at invading a site because of their ability to adapt and take advantage of conditions present. These invaders are more opportunistic to utilize unrealized niches that native species are unable to utilize. With this in mind, this research shows that the two dominant non-native species (*Bromus tectorum* and *Bromus inermis*) not only do not take advantage of this variation with quite extreme temperatures and precipitation events over the

course of the study, but they actually decline in percent cover along with native species present.

This portion of the study provides some evidence for the theory that a more diverse community can provide some sort of resistance to change with future climate change. Grasslands high in species diversity are important for providing the range of ecosystem services or plasticity necessary to resist an ever changing climate with resilience each season. At both sites native,  $C_4$ , and forb species respond positively to the fluctuations in soil temperature and moisture that has been observed over the course of the study period. Due to the high percent cover of perennial species at both sites the influx of winter moisture elucidates the utilization by non-native species for early and continual growth through the early parts of the spring and into summer.

At both sites the timing of precipitation events in the spring correlated with favorable temperatures may be an indication of percent cover later in the year. Although temperatures have increased at both sites during the spring season soil moisture has slowly declined. Therefore, even though soil temperatures have been preferable for increased growth the moisture has been insufficient for these species to take advantage of this. The steady decline in percent cover and subsequent increase in bare ground (or nothing growing at all) overall at both locations may indicate that these species are unable to respond to continually higher temperatures and lower moisture availability.

#### **4.2. Future research directions**

The City of Boulder Open Space and Mountain Parks has recently given permission to continue the monitoring of the Shanahan Ridge site past the current dissertation research timespan. This provides the opportunity to continue the current research into a more significant time period with regards to sub-decadal and decadal climate variability. Many questions emerge when discussing the effects of climate on vegetation. One is the time needed to see significant changes in community composition and structure. By extending this research to ten to twenty years, I hope to see these changes and contribute more to the knowledge base for vegetation species reactions to fine-scale microclimatic variability.

The immense dataset resulting from data collected in this research can be exploited for further research in microclimate variability (Chapter 2) as well as the continual relationship between this variability and the ever changing plant communities present (Chapter 3). Additionally, because these line-transects cross the forest-steppe ecotone the possibility of utilizing this information to establish a method for determining a vegetation and microclimate boundary based on vegetation and fine-scale soil properties exists. By determining breaks in boundary distance in either direction extending into the forest and into the grassland community may add to the discussion of forest expansion with future climate change or contraction with soil moisture limitations.

Also, the findings of correlations with certain PFTs and species origin and soil conditions (Chapter 3) suggest the opportunity to extend this work to other grassland and forest-grassland

communities throughout the western United States and interior of British Columbia. I will be extending this type of work into a post-doctoral position at the University of British Columbia that I will begin in July of 2013 to determine the effects of topography and soil conditions on PFTs and native/non-native species at various elevations in the southern interior of British Columbia (Lac du Bois Provincial Park and surrounding areas). This work extends current research on this topic.

#### **4.3. Prescribed burning effects on a forest-steppe ecotone community**

Much research focused on the forest-steppe community boundary in this area is focused on the effects of disturbance such as grazing or fire and how these communities respond. Disturbances play an important role in shaping forest communities and creating variability in forest structure (Pickett et al. 1987), and can increase the potential invasion by non-native species (Hobbs & Huenneke 1992, Christensen & Burrows 1986). Fire disturbance can stimulate or maintain high primary productivity, by enhancing the removal of litter and altering the microclimate and nutrients (Knapp & Seastedt 1986). Some studies imply that through exceeding or reducing these disturbances by frequency, spatial patterns, scale, or intensity, the dominance of non-native species will increase (Fox & Fox 1986, Hobbs & Huenneke 1992). The lack of experimental tests to clarify the role of disturbance in plant invasions is a problem in invasion ecology with very few exceptions (Burke & Grime 1996). What is urgently needed is the study of the invasion ecology and the microclimatic differences across the gradient of available resources where these non-native species may invade in order to determine the potential for controlling future invasions via management planning.

Increased light availability, bare ground, and decreased total soil nutrients and competition are all characteristic of the post-fire environment and all have been shown to coincide with an increase in non-native species (Rejmanek 1989, Crawford et al. 2001, Keeley et al. 2003, Freeman et al. 2007) The response of natives to disturbances may indirectly affect the invader by enhancing or depleting nutrient pools as a function of the fuels present and ecological effects of species litter when it accumulates without fire (Gundale et al. 2008). Consequently, grass invasion could initiate a grass/fire cycle whereby invading grasses promote fire, which in turn favors alien grasses over native species (Hughes et al. 1991). In addition the rapid depletion of nutrients by the non-native species may further inhibit the colonization of the less competitive native species (Melgoza 1990).

Studies have shown that biomass and seed production of non-native species increase after prescribed burns (Jacobs & Sheley 2003). Therefore, the potential for invasion of non-natives will most likely increase. The immediate post fire sites are devoid of non-natives because of a lack of seed bank due to the closed canopy before invasion (Keeley et al. 2003). As the duration of the time between fire and canopy closure increases, the susceptibility of invasion increases (Keeley et al. 2003). Selecting an appropriate temporal scale to evaluate invasion, establishment and persistence by non-native species into burnt areas is critical. Studies by Turner et al. (1997), Crawford et al. (2001) and Keeley et al. (2003) were done within 5 years of burning, and not surprisingly all found that non-native species increased in cover after the fire and/or were more abundant in burned than in unburned sites. In contrast, Fornwalt et al. (2003) found no relationship between time since fire and richness or cover of

non-native species, but this was likely due to the fact that most sites they analyzed had burned > 20 years previously, with some being centuries old.

Currently both sites are slated for prescribed burn. Although the White Ranch site was removed after the summer of 2012, the City of Boulder Open Space and Mountain Parks has given approval for maintaining the Shanahan Ridge site indefinitely. This long term monitoring will not only allow the continual monitoring of microclimatic conditions and the relationship with natural vegetation, but will also provide the opportunity to observe the effects of prescribed burning on this system.

Several research questions will be associated with this future research:

- Are there significant differences in the biotic (vegetation attributes) and abiotic microsite conditions (soil moisture, temperature, nutrients) across the ponderosa pine/grassland ecotone of the Colorado Front Range following low severity fire, which would make the site more invasible?
- In the post-fire landscape, following low severity fire, how are non-native plant species colonization patterns affected by the microsite patterns?

#### **4.4. Non-native species invasion**

Resistance to climate change, defined as the ability of a community to maintain its composition and biomass in response to environmental stress, could be explained by reference to the functional composition and successional status of sensitive areas such as the two studied here. One aspect of resistance is in terms of invasion of non-native species. Invasion by some

non-native species can result in rapid displacement of native communities (D'Antonio and Vitousek 1992), a reduction in species diversity, alteration of resource availability and soil stability, promotion of erosion, accumulation of litter, an increase in allelopathy, the alteration of natural fire regimes and trophic structures, and an alteration of forage quality for native herbivores (Vitousek 1990, Gordon 1998, Richardson et al. 2000, Mack et al. 2001, Brooks et al. 2004, Wolfe and Klironomos 2005, Freeman et al. 2007). These species can also alter ecosystem processes, such as disturbance frequency and intensity, nutrient cycling, and net primary productivity (Vitousek 1990, Reichard 1996, Schlesinger et al. 1996). Early detection and rapid response to new invasions may be effective tools for protecting habitats most at risk (Peterson and Vieglais 2001, D'Antonio et al. 2004).

Many studies of invasions discuss the fact that invasive species and their target communities cannot be studied independently of each other (Moulton and Pimm 1986, D'Antonio 1993). As a community, non-natives cannot be viewed as a group that would respond to a disturbance in a similar way. Each individual has a varying autecology, which would limit their invasion potential. If climatic variability, as has been discussed here, is significant enough to make these sites susceptible to further invasion, or in the near term the expansion of current non-native species, will the native species that have been adapted to live in an already stressed community be able to resist invasion.

Non-native species may be poised to take advantage of emerging opportunities for colonization and population growth created by climate change. By definition, non-native species have, given their presence in introduced habitats, already succeeded in colonizing new

environments. As a result, many non-native species have traits that are useful for coping with environmental change (Dukes and Mooney 1999, Theoharides and Dukes 2007, Vila et al. 2007), including relatively strong dispersal abilities (Rejmanek and Richardson 1996), minimal reliance on specialized mutualists (van Kleunen et al. 2008), rapid growth rates (Grotkopp et al. 2010), broad environmental tolerances (Zerebecki and Sorte 2011) and high phenotypic plasticity (Daehler 2003, Davidson et al. 2011). In addition, some climatic changes are increasing resource availability and fluctuations in resource availability (e.g. linked to extreme climatic events; Diez et al. 2012), which could facilitate the establishment and spread of fast-growing species, including many of non-native origin (Davis et al. 2000, Daehler 2003, Blumenthal et al. 2008, Dukes et al. 2011).

With a 1°C increase in average temperature already noticeable and higher fluctuations of precipitation in one of the most important months, March, in terms of germination and emergence are we to believe that climate can be expected to become a persistent and possibly compounding disturbance event over the next 10-15 years? Research has been conducted on possible effects of climate change. Simulations of temperature regimes expected at the end of this century had immediate and persisting effects on community composition and structure in arctic (Arft et al. 1999, Walker et al. 2006) and alpine communities (Harte and Shaw 1995, Harte et al. 2006) and have altered ecosystem processes such as carbon storage (Perfors et al. 2006). Short-term experimental shifts in precipitation regimes altered the diversity, productivity, and trophic relationships of seasonally water-limited systems such as Mediterranean grasslands (Zavaleta et al. 2003b, Dukes et al. 2005, Suttle et al. 2007).



Maintaining or increasing plant species diversity is an important goal of habitat managers in semi-arid environments (West 1993, Fulbright 1996). Disturbance is considered to be one of the main factors influencing species richness in plant communities (Collins et al. 1995, Mackey & Currey 2001). Management practices should be based on sound theory on which predictions about the outcome of practices are based (Joyce 1993). Vegetation change on semi-arid rangeland may correspond to state-and-transition models of succession rather than the traditional model of sequential community replacement leading to a climax community upon which the intermediate disturbance hypothesis is based (Laycock 1991). Disturbance may simply result in a new, relatively stable plant community rather than in the traditional succession from a pioneer to a climax community.

The future of management of invasive species will involve new tools developed from research that integrates invasion and climate-change biology. Increased monitoring and more interagency and interstate coordination will also be necessary (Bierwagen et al. 2008). Risk assessments over a broader geographic area than have traditionally been performed will be essential. It will be considerably easier to prevent the introduction of harmful non-native species than to project their impact in novel and changing environments. Many problems with invasive species are immediate and severe. Climate change, in contrast, is more subtle and long term, and resource managers have a difficult time knowing when to start addressing it. It will take more research to understand how specific invasive species may behave under an altered climate and which new species will emerge as invasive. Unfortunately, the timescale for pursuing this type of research and using it to inform novel management techniques is short.

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## Appendix A. Plot vegetation measurement data (Shanahan Ridge, CO)

Tables of yearly percent species cover measurements at Shanahan Ridge. Genus and species are in the upper left cell with each meter listed below. The years are along the top with 2011 and 2012 having the added transects listed as well. This data was discussed in Chapters 3 and 4. All data is stored digitally and can be edited as future seasons are added.

<i>Ambrosia psilostachya</i>	2009	2010	2011	2	3	2012	2	3	<i>Andropogon gerardii</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	20	0	0	10	0	20	20	10	80	30	20	60	0
1	0	0	0	0	20	0	0	20	1	15	5	5	70	30	10	30	30
2	0	0	0	0	20	0	0	10	2	0	0	0	40	50	0	40	30
3	0	0	0	0	0	0	0	0	3	0	0	0	30	0	0	20	0
4	0	0	0	0	20	0	0	15	4	40	40	40	30	0	50	20	0
5	0	0	0	10	0	0	10	0	5	65	65	65	0	0	50	0	0
6	0	0	0	25	10	0	10	0	6	70	70	100	0	10	70	10	15
7	0	0	0	0	0	0	0	0	7	80	80	90	0	70	85	0	60
8	0	0	0	10	0	0	10	0	8	40	40	75	0	50	75	0	30
9	0	5	0	0	0	0	0	0	9	0	10	0	0	10	0	0	20
10	10	10	10	0	0	10	0	0	10	10	5	0	0	0	0	0	0
11	0	10	0	0	0	20	0	0	11	0	0	0	0	0	0	0	0
12	20	20	20	15	0	20	0	0	12	0	0	0	0	0	0	0	0
13	0	0	10	25	0	0	15	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	5	0	0	5	0	0	15	0	0	0	0	0	0	0	0
16	0	0	20	0	0	15	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	10	5	15	0	0	10	0	0	18	0	0	0	0	0	0	0	0
19	30	10	20	0	0	30	0	0	19	0	0	0	0	0	0	0	0
20	0	0	20	0	10	15	0	10	20	0	0	0	0	0	0	0	0
21	20	30	30	0	0	25	0	10	21	0	0	0	0	0	0	0	0
22	40	50	50	0	0	40	10	0	22	0	0	0	0	10	0	0	10
23	15	15	30	10	10	20	25	10	23	0	0	0	0	0	0	0	0
24	10	20	40	30	0	15	30	0	24	0	0	0	0	0	0	0	0

<i>Artemisia ludoviciana</i>	2009	2010	2011	2	3	2012	2	3	<i>Bromus tectorum</i>	2009	2010	2011	2	3	2012	2	3
0	10	10	10	10	0	20	10	0	0	20	20	0	0	0	0	0	30
1	15	20	20	0	0	15	0	0	1	15	40	0	10	20	0	0	0
2	0	0	0	0	0	0	0	0	2	30	40	20	15	0	0	0	0
3	0	0	0	0	0	0	0	0	3	20	30	20	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	15	20	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	10	15	10	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	15	0	0	0	0
7	0	0	0	0	0	0	0	0	7	10	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	50	30	15	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	45	40	70	0	0	50	0	0
10	0	0	0	0	0	0	0	0	10	50	65	80	0	0	60	0	0
11	0	0	0	0	0	0	0	0	11	30	40	40	0	0	10	0	0
12	0	0	0	0	0	0	0	0	12	20	35	15	0	0	5	0	0
13	20	0	20	0	0	20	0	0	13	25	75	5	0	0	0	0	0
14	10	10	5	0	0	5	0	0	14	10	40	15	0	0	5	0	0
15	0	0	0	0	0	0	0	0	15	50	60	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	30	15	15	0	0	15	0	0
17	0	0	0	0	30	0	0	25	17	20	70	15	0	0	5	0	0
18	0	0	0	0	80	0	0	60	18	20	95	25	0	0	0	0	0
19	0	0	0	0	35	0	0	20	19	40	80	15	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	20	30	5	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	10	35	0	0	0	0	0	0
22	0	0	0	0	10	0	0	10	22	20	15	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	10	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	10	0	0	15	0	0	0
<i>Carex heliophila</i>	2009	2010	2011	2	3	2012	2	3	<i>Crataegus mollis</i>	2009	2010	2011	2	3	2012	2	3
0	10	10	20	0	30	20	0	30	0	0	0	0	0	0	0	0	0
1	5	10	35	0	30	25	0	40	1	0	0	0	0	0	0	0	0
2	15	15	20	0	30	20	0	40	2	0	0	0	0	0	0	0	0
3	20	20	30	40	50	40	30	60	3	0	0	0	0	0	0	0	0
4	15	20	40	20	70	30	40	65	4	0	0	0	0	0	0	0	0
5	15	10	15	80	80	15	80	90	5	0	0	0	0	0	0	0	0
6	10	10	0	60	80	0	80	70	6	0	0	0	0	0	0	0	0
7	10	10	5	80	30	15	80	40	7	0	0	0	0	0	0	0	0
8	0	0	0	40	20	0	30	20	8	0	0	0	0	0	0	0	0
9	0	0	0	0	70	0	0	65	9	0	0	0	100	0	0	100	0
10	0	0	0	0	70	0	0	70	10	0	0	0	100	0	0	100	0
11	0	0	0	0	0	0	0	0	11	0	0	0	50	20	0	50	20
12	5	5	5	0	0	5	0	0	12	0	0	0	0	20	0	0	30
13	0	0	10	0	0	15	0	0	13	0	0	0	0	50	0	0	50
14	0	0	0	0	0	0	0	0	14	0	0	0	0	50	0	0	50
15	0	0	0	0	0	0	0	0	15	0	0	0	0	80	0	0	80
16	0	0	0	0	0	0	0	0	16	0	0	0	0	30	0	0	30
17	0	0	0	20	10	0	15	10	17	0	0	0	30	0	0	50	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	15	0	0	20	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	20	0	0	20	0
21	0	0	0	0	10	0	0	20	21	0	0	0	0	0	0	0	0
22	0	0	0	5	25	0	10	25	22	0	0	0	0	0	0	0	0
23	0	0	0	0	35	0	0	30	23	0	0	0	0	0	0	0	0
24	0	0	0	0	15	0	0	15	24	0	0	0	0	0	0	0	0

<i>Elymus elymus</i>	2009	2010	2011	2	3	2012	2	3	<i>Erigeron sp.</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	20	15	30	0	0	30	0	0
3	0	0	0	0	0	0	0	0	3	5	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	5	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	10	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	20	0	0	0	0	20	0	15	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	10	10	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0
<i>Heterostipa comata</i>	2009	2010	2011	2	3	2012	2	3	Open	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	15	15	45	10	10	25	30	20
1	0	0	0	0	0	0	0	0	1	5	5	10	20	0	20	50	0
2	0	0	0	0	0	0	0	0	2	20	20	30	45	0	50	40	0
3	5	5	0	0	0	0	0	0	3	0	0	40	20	50	60	15	40
4	0	0	0	0	0	0	0	0	4	0	0	15	20	10	20	10	20
5	0	0	0	0	0	0	0	0	5	0	0	0	10	20	0	10	10
6	0	0	0	0	0	0	0	0	6	10	10	0	0	0	30	0	15
7	0	0	0	0	0	0	0	0	7	0	10	0	20	0	0	20	0
8	0	0	0	0	0	0	0	0	8	0	10	10	20	30	15	10	50
9	0	0	0	0	0	0	0	0	9	15	10	0	0	20	35	0	15
10	0	0	0	0	0	0	0	0	10	20	10	10	0	10	30	0	0
11	0	0	0	0	0	0	0	0	11	40	30	30	50	40	50	50	50
12	0	0	0	0	0	0	0	0	12	15	0	50	85	80	40	100	60
13	0	0	0	0	0	0	0	0	13	50	20	55	75	50	65	85	50
14	0	0	0	0	0	0	0	0	14	50	20	50	70	50	50	40	50
15	0	0	0	0	0	0	0	0	15	15	10	70	45	20	70	45	20
16	0	0	0	0	0	0	0	0	16	50	60	40	100	30	40	100	30
17	0	0	0	0	0	0	0	0	17	50	10	55	80	60	65	85	65
18	0	0	0	0	0	0	0	0	18	70	0	60	65	20	90	65	40
19	0	0	0	0	0	0	0	0	19	30	10	65	85	50	70	85	60
20	0	0	0	0	0	0	0	0	20	40	30	35	80	90	85	80	90
21	0	0	0	0	0	0	0	0	21	45	10	45	100	90	50	100	70
22	0	0	0	0	0	0	0	0	22	40	35	50	95	55	60	80	55
23	0	0	0	0	0	0	0	0	23	85	70	70	65	55	80	50	60
24	0	0	0	0	0	0	0	0	24	80	60	40	70	50	85	70	65



<i>Opuntia macrorhiza</i>	2009	2010	2011	2	3	2012	2	3	<i>Poa compressa</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	20	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	25	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	25	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	15	10	10	0	0	10	0	0	12	0	0	0	0	0	0	0	0
13	5	5	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	5	5	5	0	0	15	0	0	14	0	0	0	0	0	0	0	0
15	20	10	10	0	0	10	0	0	15	0	0	0	0	0	0	0	0
16	20	25	25	0	0	30	0	0	16	0	0	0	0	0	0	0	0
17	0	0	5	0	0	5	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0
<i>Psoralegium tenuiflorum</i>	2009	2010	2011	2	3	2012	2	3	<i>Ribes cereum</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	10	0	10	0	0	10	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	15	0	0	10	0
14	0	0	0	0	0	0	0	0	14	0	0	0	40	0	0	50	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	20	0	0	20	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	15	0	0	15	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0

Rock	2009	2010	2011	2	3	2012	2	3	<i>Rosa woodsii</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	30	30	30	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	20	20	20	0	0	20	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	15	15	15	0	0	15	0	0	14	10	10	10	0	0	0	0	0
15	15	15	15	0	0	15	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	40	0	0	40	16	0	0	0	0	0	0	0	0
17	30	20	25	0	0	25	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	40	40	40	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	25	25	25	0	0	25	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	10	0	0	10	0
24	10	10	10	0	0	0	0	0	24	0	0	0	0	20	0	0	20
<i>Senecio spartioides</i>	2009	2010	2011	2	3	2012	2	3	<i>Silene antirrhina</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	15	5	0	0	0	0	0	0
4	0	0	0	30	0	0	30	0	4	10	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0

Stick	2009	2010	2011	2	3	2012	2	3	<i>Symphocarpus occidentalis</i>	2009	2010	2011	2	3	2012	2	3
0	15	15	15	0	0	15	0	0	0	0	0	0	0	0	0	0	0
1	20	20	20	0	0	20	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	10	0	0	10	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	10	10	10	0	0	10	0	0	5	0	0	0	0	0	0	0	0
6	10	10	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	5	5	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	15	0	0	40	0
15	0	0	0	0	0	0	0	0	15	0	0	0	15	0	0	5	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	15	0	0	15	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0
<i>Thlaspi arvense</i>	2009	2010	2011	2	3	2012	2	3	<i>Tragapogon dubius</i>	2009	2010	2011	2	3	2012	2	3
0	10	10	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0
1	15	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	15	10	0	0	0	0	0	0	2	0	0	0	0	0	0	0	20
3	15	10	0	0	0	0	0	0	3	20	30	10	0	0	0	0	0
4	10	0	5	0	0	0	0	0	4	10	15	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	5	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	10	20	0	0	0	10	0	0
9	0	0	0	0	0	0	0	0	9	10	5	0	0	0	10	0	0
10	0	0	0	0	0	0	0	0	10	0	5	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	10	0	10	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	5	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	5	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	10	0	0	0	0	0

<i>Yucca glauca</i>	2009	2010	2011	2	3	2012	2	3									
0	0	0	0	0	0	0	0	0									
1	0	0	0	0	0	0	0	0									
2	0	0	0	0	0	0	0	0									
3	0	0	0	0	0	0	0	0									
4	0	0	0	0	0	0	0	0									
5	0	0	0	0	0	0	0	0									
6	0	0	0	0	0	0	0	0									
7	0	0	0	0	0	0	0	0									
8	0	0	0	0	0	0	0	0									
9	0	0	0	0	0	0	0	0									
10	0	0	0	0	20	0	0	30									
11	0	0	0	0	40	0	0	30									
12	0	0	0	0	0	0	0	0									
13	0	0	0	0	0	0	0	0									
14	0	0	0	0	0	0	0	0									
15	0	0	0	0	0	0	0	0									
16	0	0	0	0	0	0	0	0									
17	0	0	0	0	0	0	0	0									
18	0	0	0	0	0	0	0	0									
19	0	0	0	0	0	0	0	0									
20	0	0	0	0	0	0	0	0									
21	0	0	0	0	0	0	0	0									
22	0	0	0	0	0	0	0	0									
23	0	0	0	0	0	0	0	0									
24	0	0	0	0	0	0	0	0									

## Appendix B. Plot vegetation measurement data (White Ranch, CO)

Tables of yearly percent species cover measurements at White Ranch. Genus and species are in the upper left cell with each meter listed below. The years are along the top with 2011 and 2012 having the added line-transects listed as well. This data was discussed in Chapters 3 and 4. All data is stored digitally and can be edited as future seasons are added.

<i>Achillia lanulosa</i>	2009	2010	2011	2	3	2012	2	3	<i>Agropyron intermedium</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	10	10	0	10	5	0	0	0	0	0	0	0	0	0
1	0	5	5	0	15	0	0	10	1	0	0	0	0	0	0	0	0
2	0	0	0	0	15	0	0	5	2	0	0	0	0	0	0	0	0
3	0	0	0	0	10	0	0	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	30	0	0	15	4	0	0	0	0	0	0	0	0
5	0	0	0	0	20	0	0	10	5	0	0	0	0	0	0	0	0
6	0	0	0	0	10	0	0	10	6	10	0	0	0	0	0	0	0
7	0	10	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	15	5	0	0	5	0	0	8	0	0	0	0	0	0	0	0
9	5	5	0	0	0	0	15	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	10	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0

<i>Allium cernuum</i>	2009	2010	2011	2	3	2012	2	3	<i>Artemisia ludoviciana</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	15	15	0	10	10
2	0	0	0	0	0	0	0	0	2	0	0	0	10	30	0	10	15
3	0	0	0	10	0	0	10	0	3	0	0	0	0	10	0	0	10
4	0	0	0	0	0	0	0	0	4	0	0	0	0	10	0	0	5
5	0	0	0	0	0	0	0	0	5	0	0	0	15	0	0	5	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	25	0	0	15	0
8	0	0	0	0	0	0	0	0	8	0	0	0	15	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	5	0	0	10	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	20	10	10	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	5	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	15	5	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	5	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	10	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	5	10	0	0	15	0	0
24	0	0	0	0	0	0	0	0	24	0	5	15	0	0	5	0	0
<i>Aster porterii</i>	2009	2010	2011	2	3	2012	2	3	<i>Astragalus flexuosus</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	10	0	0	0	6	0	0	0	0	0	0	0	0
7	5	5	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	20	0	5	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0

<i>Bouteloua gracilis</i>	2009	2010	2011	2	3	2012	2	3	<i>Bromus inermis</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	100	30	50	50	70	30	20	85
1	0	0	0	0	0	0	0	0	1	100	75	60	75	70	30	40	65
2	0	0	0	0	0	0	0	0	2	80	60	40	70	35	40	50	65
3	0	0	0	0	0	0	0	0	3	30	15	15	50	30	30	50	55
4	0	0	0	0	0	0	0	0	4	25	5	15	20	50	20	25	50
5	0	0	0	0	0	0	0	0	5	40	40	70	20	60	10	25	50
6	0	0	0	0	0	0	0	0	6	70	75	80	15	80	50	25	80
7	0	0	0	0	0	0	0	0	7	20	20	20	5	100	20	0	90
8	0	0	0	0	0	0	0	0	8	15	5	30	15	90	20	5	90
9	0	0	0	0	0	0	0	0	9	30	20	30	10	85	15	25	80
10	0	0	0	0	0	0	0	0	10	70	50	50	55	100	35	30	90
11	0	0	0	0	0	0	0	0	11	50	30	35	50	100	50	45	100
12	0	0	0	0	0	0	0	0	12	85	60	60	90	90	60	80	90
13	0	0	0	0	0	0	0	0	13	10	15	25	10	100	20	70	85
14	0	0	0	0	0	0	0	0	14	60	50	50	95	100	50	50	100
15	0	0	0	0	0	0	0	0	15	55	75	70	95	100	70	60	100
16	0	0	0	0	0	0	0	0	16	80	100	90	85	80	90	50	70
17	0	0	0	0	0	0	0	0	17	70	90	85	95	80	95	80	50
18	0	0	0	0	0	0	0	0	18	90	75	85	85	75	90	60	80
19	45	30	15	0	0	0	0	0	19	20	10	30	95	90	70	95	50
20	30	20	10	0	0	15	0	0	20	20	20	10	90	100	20	90	80
21	50	40	20	0	0	25	0	0	21	0	0	0	90	85	0	70	80
22	80	80	70	0	0	50	0	0	22	0	0	0	90	80	0	50	60
23	90	75	40	0	0	45	0	0	23	0	0	0	100	90	0	90	70
24	45	35	20	0	0	20	0	0	24	0	0	15	100	100	25	90	80
<i>Campanula rotundifolia</i>	2009	2010	2011	2	3	2012	2	3	<i>Carex heliophila</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	10	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	0	15	10	0	0	5	0	10
4	0	0	0	0	0	0	0	0	4	25	25	25	15	0	15	5	15
5	0	0	0	0	0	0	0	0	5	0	0	10	20	0	10	10	15
6	0	0	0	0	0	0	0	0	6	0	0	0	50	0	0	25	0
7	0	0	0	0	0	0	0	0	7	0	0	0	75	0	0	55	0
8	0	0	0	0	0	0	0	0	8	0	0	0	30	0	0	20	0
9	0	0	0	0	0	0	0	0	9	0	0	0	65	0	0	25	0
10	0	0	0	0	0	0	0	0	10	0	0	0	30	0	0	20	0
11	0	0	0	0	0	0	0	0	11	0	0	0	50	0	0	45	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	20	10	0	0	10	0	0
20	0	0	0	0	0	0	0	0	20	0	15	15	0	0	10	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	20	0	0	20	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0

<i>Chenopodium album</i>	2009	2010	2011	2	3	2012	2	3	<i>Erigonum sp.</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	5	0	0	10	0
9	0	0	0	0	0	0	0	0	9	0	0	0	10	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	10	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0
<i>Geranium caespitosum</i>	2009	2010	2011	2	3	2012	2	3	<i>Heterotheca villosa</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	10	10	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	15	0	0	15	2	0	0	0	0	10	0	0	10
3	0	0	0	0	0	0	0	0	3	0	0	0	10	0	0	5	0
4	0	0	0	0	0	0	0	0	4	0	0	0	10	0	0	5	0
5	0	0	0	0	0	0	0	0	5	0	0	0	5	0	0	10	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	15	0	0	5	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	15	0	0	0	18	0	5	5	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	30	30	15	0	0	0	5	0
20	0	0	0	0	0	0	0	0	20	20	20	30	0	0	5	0	0
21	0	0	0	0	0	0	0	0	21	20	10	20	0	0	20	0	0
22	0	0	0	0	0	0	0	0	22	0	5	20	0	0	20	0	0
23	0	0	0	0	0	0	0	0	23	10	10	15	0	0	15	0	0
24	0	0	0	0	0	0	0	0	24	15	0	15	0	0	10	0	0



<i>Koeleria macrantha</i>	2009	2010	2011	2	3	2012	2	3	Open	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	70	50	20	10	70	50	10
1	0	0	0	0	0	0	0	0	1	0	20	35	20	0	70	60	10
2	0	0	0	0	0	0	0	0	2	20	40	60	15	0	60	40	10
3	0	0	0	0	0	0	0	0	3	70	70	75	30	20	65	35	10
4	0	0	0	0	0	0	0	0	4	50	70	60	55	10	65	65	10
5	0	0	0	0	0	0	0	0	5	60	60	20	45	0	80	45	10
6	0	0	0	0	0	0	0	0	6	20	25	20	35	0	50	50	10
7	0	0	0	0	0	0	0	0	7	75	65	80	5	0	80	35	10
8	0	0	0	0	0	0	0	0	8	85	80	66	10	10	75	45	10
9	0	0	0	0	0	0	0	0	9	65	75	70	0	15	85	35	20
10	0	0	0	0	0	0	0	0	10	30	50	50	10	0	65	40	10
11	0	0	0	0	0	0	0	0	11	10	30	25	0	0	50	10	0
12	0	0	0	0	0	0	0	0	12	15	40	40	10	10	40	20	10
13	0	0	0	0	0	0	0	0	13	80	85	70	90	0	80	30	15
14	0	0	0	0	0	0	0	0	14	40	50	50	5	0	50	50	0
15	0	0	0	0	0	0	0	0	15	15	15	20	5	0	30	40	0
16	0	0	0	0	0	0	0	0	16	0	0	0	15	10	10	50	30
17	0	0	0	0	0	0	0	0	17	0	0	0	5	20	5	20	50
18	0	0	0	0	0	0	0	0	18	0	10	0	5	15	10	40	20
19	5	10	20	0	0	0	0	0	19	0	0	0	5	10	20	0	50
20	15	10	15	0	0	15	0	0	20	0	0	0	10	0	25	10	20
21	0	15	25	0	0	0	0	0	21	0	0	0	10	15	20	30	20
22	0	0	0	0	0	0	0	0	22	0	0	0	10	20	20	50	40
23	0	0	0	0	0	0	0	0	23	0	0	0	0	10	0	10	30
24	0	0	0	0	0	0	0	0	24	0	0	15	0	0	25	10	20
<i>Penstemon strictus</i>	2009	2010	2011	2	3	2012	2	3	<i>Poa compressa</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	0	0	0	10	0	0	10	10	5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	5	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	10	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	10	0	10	0	0	0	0	0
17	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	10	5	10	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	15	0	15	0	0	10	0	0
21	10	15	15	0	0	15	0	0	21	20	15	20	0	0	20	0	0
22	20	15	10	0	0	10	0	0	22	0	0	0	0	0	0	0	0
23	0	0	15	0	0	5	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	40	60	20	0	0	15	0	0

Stick	2009	2010	2011	2	3	2012	2	3	<i>Tragopogon dubius</i>	2009	2010	2011	2	3	2012	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	5	0	0	0	0	10	0	0	0
6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
11	40	40	40	0	0	40	0	0	11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	13	5	0	5	0	0	0	0	0
14	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
17	10	10	10	0	0	0	0	0	17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0

## Appendix C. Plot soil measurement data

Tables of soil condition measurements at Shanahan Ridge and White Ranch, CO. This data was discussed in Chapters 3 and 4. All data is stored digitally and can be edited as future samples are analyzed.

Meter	Org	Sand	Silt	Clay	pH
0	2.63	82.00	7.00	11.00	4.92
1	3.84	77.00	10.00	13.00	5.23
2	3.90	74.00	11.00	15.00	5.38
3	4.24	74.00	11.00	15.00	5.33
4	4.13	74.00	12.00	14.00	5.41
5	4.44	73.50	11.50	15.00	5.54
6	4.30	76.00	11.00	13.00	5.50
7	3.87	73.00	12.00	15.00	5.35
8	3.65	79.00	7.50	13.50	5.32
9	4.60	76.50	9.50	14.00	5.25
10	5.89	76.50	9.50	14.00	4.86
11	5.67	76.50	9.50	14.00	4.65
12	7.39	76.00	9.50	14.50	4.82
13	3.96	80.00	7.00	13.00	4.51
14	6.60	77.00	10.00	13.00	4.21
15	10.06	76.00	10.50	13.50	4.75
16	5.87	75.00	11.50	13.50	4.57
17	5.14	73.50	12.00	14.50	4.45
18	5.24	79.00	8.00	13.00	4.40
19	4.37	81.00	6.00	13.00	4.50
20	5.23	76.00	10.00	14.00	4.33
21	5.53	77.50	9.00	13.50	4.31
22	4.08	76.50	10.50	13.00	3.85
23	6.38	76.50	9.50	14.00	4.35
24	5.92	78.00	8.50	13.50	4.37
25	5.67	74.00	11.00	15.00	4.45

Meter	Org	Sand	Silt	Clay	pH
0	4.05	74.00	17.00	9.00	5.73
1	3.20	73.00	16.00	11.00	5.88
2	3.59	75.00	15.00	10.00	5.78
3	4.94	84.00	8.00	8.00	5.72
4	5.78	75.00	17.00	8.00	5.72
5	4.51	73.00	18.00	9.00	5.70
6	6.38	75.00	16.00	9.00	5.59
7	3.54	77.00	14.00	9.00	5.69
8	4.13	73.00	16.00	11.00	5.32
9	3.64	76.00	15.00	9.00	4.72
10	3.34	78.00	12.00	10.00	4.88
11	3.96	74.00	17.00	9.00	5.70
12	3.65	80.00	11.00	9.00	6.63
13	7.43	77.00	14.00	9.00	5.06
14	4.99	75.00	16.00	9.00	5.75
15	8.32	73.00	19.00	8.00	5.72
16	8.79	76.00	15.50	8.50	5.71
17	6.76	77.00	14.00	9.00	5.70
18	8.36	80.00	12.00	8.00	5.33
19	3.45	78.00	13.00	9.00	5.79
20	5.68	79.00	12.00	9.00	5.67
21	5.84	77.00	15.00	8.00	5.17
22	5.54	79.00	13.00	8.00	5.21
23	4.48	79.00	12.50	8.50	5.74
24	4.91	77.00	16.00	7.00	5.72
25	3.65	76.00	14.00	10.00	6.12