

The Impacts of Changing Temperature on Plant Water Use

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Abstract

The movement of water through a plant's parts, out its stomata, and into the atmosphere begins with moisture available in the soil. Soil water availability is determined by rates of evaporation from the Earth's surface, which increases with temperature. Alteration of water content determines the soil's water potential, the tendency of water to move from one area to another due to physical pressure forces. The means by which plants utilize and transport water occurs along a water potential gradient in a soil-plant-atmosphere-continuum. Water eventually exits the plant via transpiration when the leaves' stomata open to release vapor and receive carbon dioxide. Water availability is critical for plants' physiological processes and is determined by a mixture of environmental abiotic factors. Thus, the plots in the Reciprocal Transplant Experiment have been moved to different sites along the Washington Gulch elevation gradient to experience different warming or cooling temperatures. Water potential patterns are mainly studied in woody plant species and the water potential of herbaceous species is heavily understudied. My observational study focused on five different herbaceous species at these turf sites. At each site and their experimental treatment plots, I recorded weather observations, measured the soil moisture of the turfs, and water potential of the individual plants. At the intermediate site that had both cooled and warmed plots, I measured leaf gas exchange for the plant individuals which accounts for their stomatal conductance rates. I hypothesized that plants do not have an acclimated response and rather, as warming temperatures increase, soil becomes drier which leads to more negative water potential values and lower transpiration rates: the inverse for cooling temperatures. Results found that, although water potential did vary along the elevation gradient in the hypothesized way, soil moisture was highest at the lowest elevation site and lowest at the highest site. Moreover, along the warming and cooling treatments, there was no significant difference in plant water stress: there was no significant difference in stomatal

conductance either. These outcomes suggest inter-annual variability in water availability, the plants have an ability to converge with their surroundings, and a complex model that accounts for climatic conditions should occur in the future.

Introduction

Like all living things on Earth, water is essential to plant life. Plant cells function in a special way where their membranes allow for water molecules to pass through easier than other solutes¹. Plant cell walls provide turgidity which allows for the build up of pressure². These cells exist in an osmotic system that relies on water molecules to diffuse pressure within the system and transport water molecules to different parts of the plant³. This general idea of plant pressure is termed water potential: an integrative measure of how much tension there is in the water column of the xylem⁴. Water potential values reflect the ease or difficulty a plant has in transporting water from the soil. Plant water potential operates in the soil-plant-atmosphere-continuum (SPAC): water potential values are highest in soil, lowest in atmosphere, and intermediate values in the plant, which drives water movement upward⁵. Transpiration is one of the many physiological processes that serves as an indicator of plant water status. It is the movement of water from the soil to the plant's stomata which is then released into the atmosphere. This process disperses water to be used for growth, metabolism, and flow of nutrients. The opening of stomata releases the remaining water via transpiration and allows for diffusion of CO₂ gas from air for photosynthesis⁶. Stomatal conductance is a similar idea that is representative of transpiration: it is the measure of the degree of stomatal opening that allows CO₂ to enter and water to exit. The underlying measurements of water potential are

¹ Slatyer, R O. "Plant-water Relationships." Academic Press (1967)

² Ibid.

³ Ibid.

⁴ Ibid.

⁵ Ibid.

⁶ Ibid.

foundational yet have not been thoroughly studied in herbaceous species. Herbaceous species are particularly sensitive to changes in water availability, as compared to woody plants. Herbaceous species innately have a less developed diffusion pressure deficit and so there are excess osmotic pressures which boost the overall osmotic potential by hydrolysis of osmotically inactive substances within the plant⁷. Thus, when water availability is low, the volume of intercellular air spaces in the plant shrinks faster than the whole leaf causing rapid senescence and water loss⁸. Overall, herbaceous plants are much less drought resistant than their woody counterparts.

Increased global temperatures due to anthropogenic climate change are altering the physiology of organisms, the distribution of biodiversity, and the functioning of ecosystems and the biosphere⁹. Plant physiological processes are very temperature-dependent. In particular, many of these processes begin in the soil, whose water content is easily altered by rising temperatures. Evaporation is the loss of water from the soil's surface, which rapidly increases with warming temperatures¹⁰. Excessive evaporation that results from increasing temperatures can disrupt the SPAC, making it more difficult for plants to transport water.

To understand how cooling and warming effects impact plant communities, Lorah Seltzer from Dr. Brian Enquist's lab implemented a Reciprocal Transplant Experiment (2017-present). Three sites, Upper Montane, Pfeiler, and Monument, were established along an elevation gradient in Washington Gulch. Washington Gulch is of particular interest since subalpine ecosystems are especially sensitive to climate change due to its high elevation and latitude. The transplant treatment consisted of moving the turfs up or down the elevation gradient one or two

⁷Kennedy, J., Booth, C. "Water Relations of Leaves from Woody and Herbaceous Plants". *Nature* 181, (1958): 1271–1272. .

⁸ Ibid.

⁹ Gretta T. Pecl et al., "Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being," *Science* 355, no. 6332 (2017).

¹⁰ M.E. Dusinge et al., "Plant carbon metabolism and climate change: elevated CO₂ and temperature impacts on photosynthesis, photorespiration and respiration," *New Phytologist*, 221 (2019)

steps into either warmer, drier, or cooler, wetter environments. There were a total of 6 transplanted turfs and 3 turfs that remained in their respective origin locations. In addition to Seltzer's project, graduate student Jocelyn Navarro of the Enquist Lab specifically investigated how this temperature gradient affects plant-water relations in an alpine environment by measuring water potential of five abundant plant species (2021). Initial conclusions indicated that increased warming led to more water stress, and cooling led to less water stress. Yet, her project did not incorporate soil moisture analysis at the plot level.

This project will investigate the effect of soil moisture on transpiration rates in cooling versus warming environments. I will address this question by measuring plant water potential measurements. I will assess two potential hypotheses relative to the environments.

H0: Plant water status is insensitive to ambient temperature due to potential acclimation responses by plants. Plants can adjust their rates of photosynthesis and stomatal conductance with temperature changes. These physiological shifts (or acclimation) can adjust plant physiology to compensate for changes in temperature. If plant water status does not depend on temperature, changes in temperature will not influence soil water available to plants.

H1: Temperature primarily influences soil water available to plants by influencing soil evaporation rates. In warmer environments, soils will dry out more quickly. Plant water potential will be more negative because there will be less soil water availability, resulting in lower transpiration rates. In cooler environments, soil evaporation will be lower. As a result, plant water potential will be less negative because of greater soil water availability, resulting in higher transpiration rates.

Methods

Turf Transplant Experiment

This project will collect data in three experimental turf sites in Washington Gulch: Upper Montane (elevation 2900m), Pfeiler (elevation 3200m), and Monument (elevation 3300m). The temperature differences between these sites is 1.5 degrees celsius. My study used a pre-existing experimental setup of transplanted alpine plant communities or turfs. Within each site along the elevation gradient, there are three $0.5 \times 2\text{m}$ experimental turfs combined with different treatments. At each elevation site, one turf remains at its origin as a control and two transplants from the other two sites. At the highest site, Monument, there is a turf from the lowest site that was moved up two steps cooler, and one from the middle site that was moved up one step cooler. At the lowest site, Upper Montane, there are (i) experimental turf communities that were moved down in elevation from the highest site (these turfs have been moved down two steps warmer.) and (ii) there are experimental turfs that have been moved (moved down one step warmer) from the middle site. The middle site, Pfeiler, has two turfs experiencing different temperatures: one from Upper Montane moved up one step cooler, and one from Monument moved one step down warmer. Figure 1 provides a visualization of the transplant sites along the gradient and the temperature manipulations of each turf: at each elevation site there is a control and two transplants from the other two sites. Figures 2, 3, and 4 are geological maps of each site along the elevation gradient with the turf plots pointed.

Soil Moisture and Water Potential Measurements

Each of the sites were visited at their respective peak seasons: Upper Montane during June 18 to 21, Pfeiler on July 11 and 15, and Monument on July 25. On each day of data collection at all of the sites, the following was done at each site. Before data collection would commence, I recorded the observed weather conditions, specifically regarding precipitation and humidity in the air. For each of the experimental treatments, I located 3 individuals of each plant

species at different plots. All identified 3 individuals of the 5 plant species are covered with a bag in order to.... Before water potential measurements, I measured the soil moisture of each said plot using the HydroSense II Handheld Soil Moisture Sensor. I snipped the identified bagged species individuals from the plot and measured each of their water potential values using the water potential pump-up chamber. Measurements of water potential range from approximately zero MPa (indicating little tension on the water column and little to no stress on the plant for water) to increasingly more negative MPa values indicating increased tension on the water column indicating decreasing availability of water for plants.

Gas Exchange

Pfeiler was the only site where, in addition to these other measurements, I also measured leaf gas exchange. This is because this is also the site where it had all the standard treatments: control, warmed 1, cooled 1. For each experimental treatment, I collected 3 individuals of each plant species at different plots, just like as in the soil moisture and water potential measurements. I measured their gas exchange using the LiCor 6400. This system measures photosynthesis and conductance which are all representative of transpiration. The measured leaves were collected in coin envelopes and brought back to the lab to have their surface area measured. Since the LiCor system measures all of the area of its mouth clamp, the photosynthesis and conductance values are then divided by their true leaf areas. These corrected photosynthesis and conductance values are then respectively averaged to get the mean amounts for the individuals.

Results

The elevation gradient, as defined by the low, middle, and high study sites, had some unexpected results. In particular, we observed no significant difference ($p = 0.2447$) in soil moisture values along the elevation gradient (Figure 5). Although the differences were

insignificant, Upper Montane had an average soil moisture value of 7.15, while Monument had an average of 6.02. Also along the elevation gradient, we observed variation in water potential values (Figure 6). Across the sites, there was a significant difference in water potential ($p = 0.001$) with Upper Montane having the lowest mean (-0.99) and Monument the highest (-0.052).

In order to get a clearer insight of how cooling and warming temperatures impact water potential, we zoomed in on the experimental turfs at the lowest and highest sites. When observing water potential values at the warmest and lowest site, Upper Montane, we witnessed no significant difference between the controlled plots and experimentally warmed treatments ($p = 0.132$). Yet, there was an accountable difference between the two warmed plots (Figure 7). The plants in the plot warmed 1 step had the highest average water potential value (-0.78). Meanwhile, the plants in the plot warmed 2 steps had a more negative average water potential value (-1.08). At the coolest and highest site, Monument, the results were less variable (Figure 8). There was no significant difference across any of the experimental treatments ($p = 0.462$).

Yet, when observing water potential at the highest and coolest site, Monument, there was no difference. These results are similar to the water potential values observed at Pfeiler (Figure 9). There was no significant variation across any of the experimental treatments at this intermediate site ($p = 0.545$). Yet, all of the average water potential values at Pfeiler's experimental treatment plots were more negative than -0.5 MPa. This was also the only site where stomatal conductance was measured (Figure 10). These stomatal conductance rates did not vary significantly across the treatments either ($p = 0.9926$). To further analyze a relationship across the elevation gradient, we compared water potential in relation to stomatal conductance (Figure 11). There was a strong, negative correlation between the variables ($R = -0.69$).

Meanwhile, when looking at the relationship between water potential and soil moisture (Figure 12), there showed to be a weak, negative relationship between the two factors ($R = -0.2$).

Discussion

Soil Moisture did not vary along the elevation gradient. This finding strays away from the general presumption that the lowest site, Upper Montane, is the driest, and the highest site, Monument, is the coolest. The highest average soil moisture value was actually in Upper Montane. Yet, the weather conditions that I had recorded on days of data collection at Upper Montane and Monument are worth nothing. On June 20th and 21st and July 25th, I recorded weather conditions as cloudy, dewy, and wet from rain the days before. This surely could have altered the data by increasing the water content present in the soil. These unexpected soil conditions could also be attributed to inter-annual variability. As temperatures rise more each year, Washington Gulch may experience earlier and heavier snowmelt, which can increase water content at lower elevations. Moreover, it was a rainy season overall. This may cause fluctuation in critical abiotic factors such as solar radiation, air temperature, wind speed, and relative humidity¹¹. Also, studies also show that the effects of inter-annual variability on soil moisture specifically impact water content at the surface level: this is where the roots of our herbaceous species exist¹². These are all probable, climatic reasons that could prompt inflated soil water availability.

Although soil moisture did not vary across the site along the elevation gradient, water potential did significantly. As predicted, the plants at the lowest and warmest site, Upper Montane, were more water stressed. Meanwhile, the plants at the highest and coolest site,

¹¹ Venkata Radha Akuraju, Dongryeol Ryu, Biju George, Youngryel Ryu, Kithsiri Dassanayake. "Seasonal and inter-annual variability of soil moisture stress function in dryland wheat field". Australia, Agricultural and Forest Meteorology, (2017)

¹² Ibid.

Monument, were the least water stressed. The plants at Pfeiler were intermediate. These results partially support my hypothesis that, with increasing temperatures, water potential values become more negative. Research has shown that for every degree Celsius that Earth's atmospheric temperature rises, according to laws of thermodynamics, the amount of water vapor in the atmosphere can increase by 7%¹³. Additionally, evaporation is the loss of water from the soil's surface, which also increases with warming temperatures. The combined effects that result from warming temperatures disrupt the equilibrium of the soil-plant-atmosphere water potential gradient, making it harder for plants to transport water. Meanwhile, cooler temperatures are associated with higher soil moisture and lower atmospheric water vapor which allows for feasible water movement through the plant according to the soil-plant-atmosphere continuum.

In assessing the effects of explicit warming, there was no difference in the water potential of warmed versus control turfs. But, the plants in the warmed 1 step turfs were much less water stressed than any of the other treatments. This is likely due to the fact that the turfs are experiencing convergence with their environment. After 5 years of transplantation, the plants might be adapting to their new conditions: this supports my null hypothesis that the plants have an acclimated response to their water relations. Studies on *Gossypium barbadense*, a cotton crop bred in hot environments year round, have demonstrated that this herbaceous species has genetic variability for their conductance which has allowed for inadvertent 'heat avoidance' (evaporative cooling) in hot environments. Four generations of cotton in increasingly hotter climates demonstrated that the evolved evaporative cooling method decreases leaf temperature without increasing tissue tolerance by encouraging 'excess' transpiration¹⁴. Yet, this process of

¹³ Buis, Alan, "Steamy Relationships: How Atmospheric Water Vapor Supercharges Earth's Greenhouse Effect". NASA.gov. (2022)

¹⁴ Radin JW, Lu Z, Percy RG, Zeiger E. "Genetic variability for stomatal conductance in Pima cotton and its relation to improvements of heat adaptation". (July 1994)

evaporative cooling requires much water. The opposite reaction occurred at the extreme treatment, warmed 2 steps. The plants at this extreme warming treatment were much more water stressed. It is possible that the change in conditions for these turfs were too drastic and the plants were not able to adapt soon enough: the soil and atmosphere were too dry. This suggests that, as temperatures rapidly warm as a result of climate change, plants will not be able to keep up and survive intense conditions. At the other extreme site, Monument, the treatments were also not statistically significant from each other. With this being the highest site in elevation, Monument is associated with cool temperatures and high moisture content. Over time, the plants' water transportation systems could have adjusted to benefit from Monument's generally favorable conditions¹⁵.

The water potential across the experimental treatments at the middle side, Pfeiler, was insignificant as well. Yet, all of the average water potential values for the treatments were more negative than -0.5 MPa, indicating that the plants were generally water stressed. Similarly, the variation in stomatal conductance rates measured at each Pfeiler treatment were insignificant as well. According to these results, stomatal conductance does not vary when cooled or warmed. These average values, regardless of treatment, were all close to 0. Although soil moisture at Pfeiler was rather high and intermediate to the other sites, the plants at these turfs were still water-stressed and transpiring at low rates. These discrepancies in correlations call for a more complex model that accounts for climatic conditions. Although I meant to include it in my data collection, it would have been very informative to attain the average evaporation rates at each of the sites. Moreover, future direction could involve measuring atmospheric pressure, relative temperature, vapor pressure deficit, photoactive radiation, and soil temperature. The ways in

¹⁵ Slayter, "Plant-water Relationships."

which soil moisture determines water potential is a multifaceted picture that involves various abiotic aspects of the surrounding environment¹⁶. A complex model in the future would require more time, advanced equipment, and collaboration with weather stations. In conclusion, soil moisture is not the only indicator of water stress or low transpiration rates in herbaceous plant species: climatic conditions, which are rapidly changing due to climate change, must be considered. This idea is supported by figure 12, where water potential decreases in negative values despite increases in soil moisture.

Figure 11 is especially interesting as it does not coincide with current literature. This negative relationship between the variables entails that, as plants become more water stressed, their stomata open more. This is unexpected since a plant's physiology aims to conserve as much water as possible, especially when availability is limited. This negative correlation could also be due to the small sample size since stomatal conductance was only measured at Pfeiler. This pattern could also be due to inter-annual variability: water potential and stomatal conductance values were collected on different days. If the days of water potential collection were wetter, and ones of stomatal conductance were drier, this could have also produced a negative relationship. Future directions would include measuring these values on the same day to avoid variation in weather conditions. Moreover, these two variables could be measured for the same individual: stomatal conductance of the leaf and water potential for the stem. In eliminating discrepancies in the methods, hopefully future directions will reveal more accurate patterns of how changing temperature impacts plant water use.

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¹⁶Ibid.

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Tables & figures

High (3300m):

 Cooled 2 steps

 Cooled 1 step

 Control

Middle (3200m):

 Warmed 1 step

 Cooled 1 step

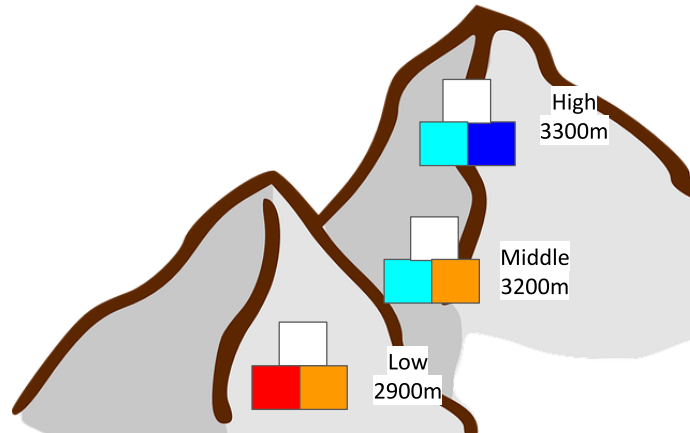
 Control

Low (2900m):

 Warmed 2 steps

 Warmed 1 step

 Control



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Figure 1

Upper Montane Turf Transplant Plots

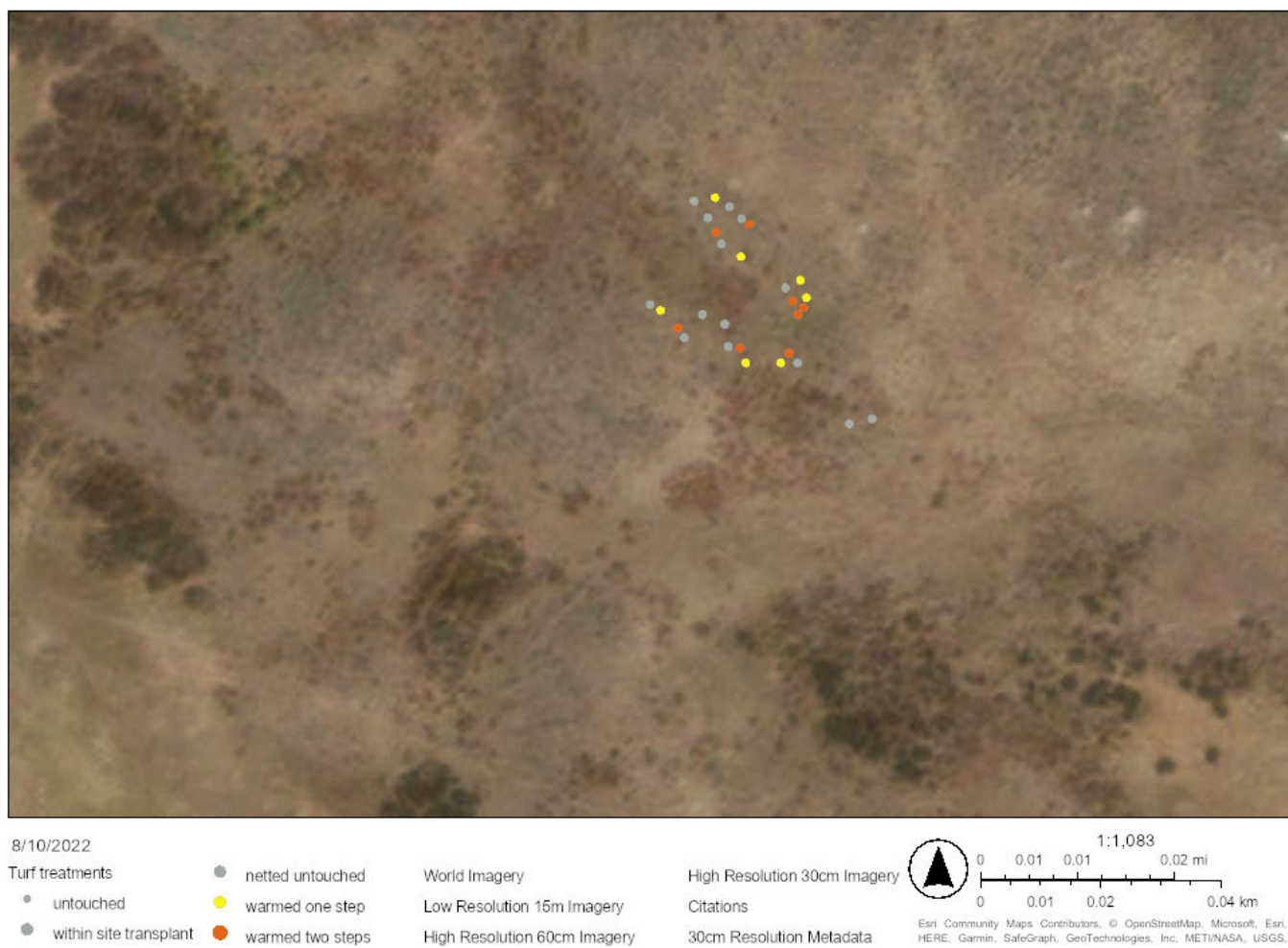


Figure 2

Pfeiler Turf Transplant Plots



Figure 3

Monument Turf Transplant Plots

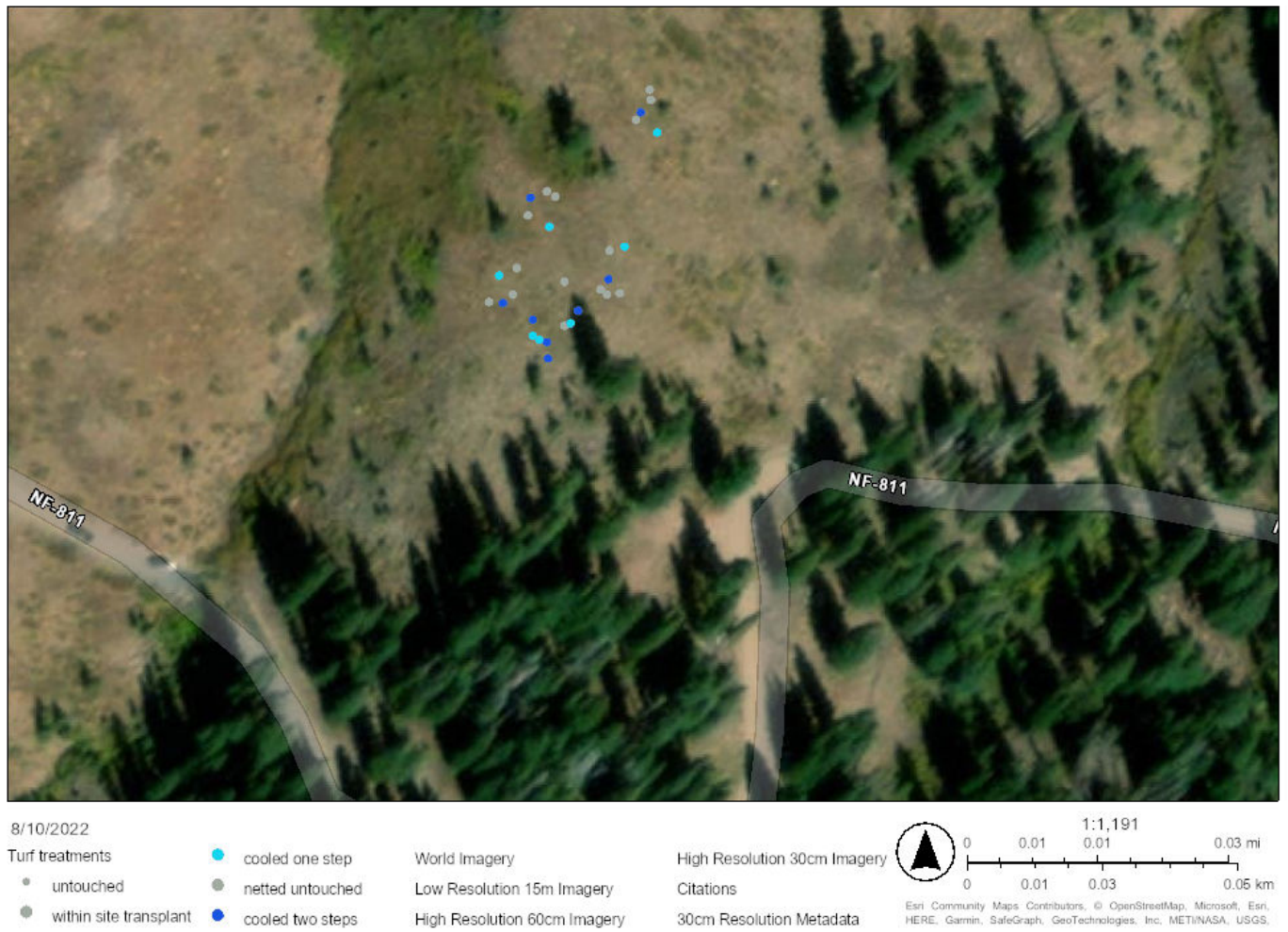


Figure 4

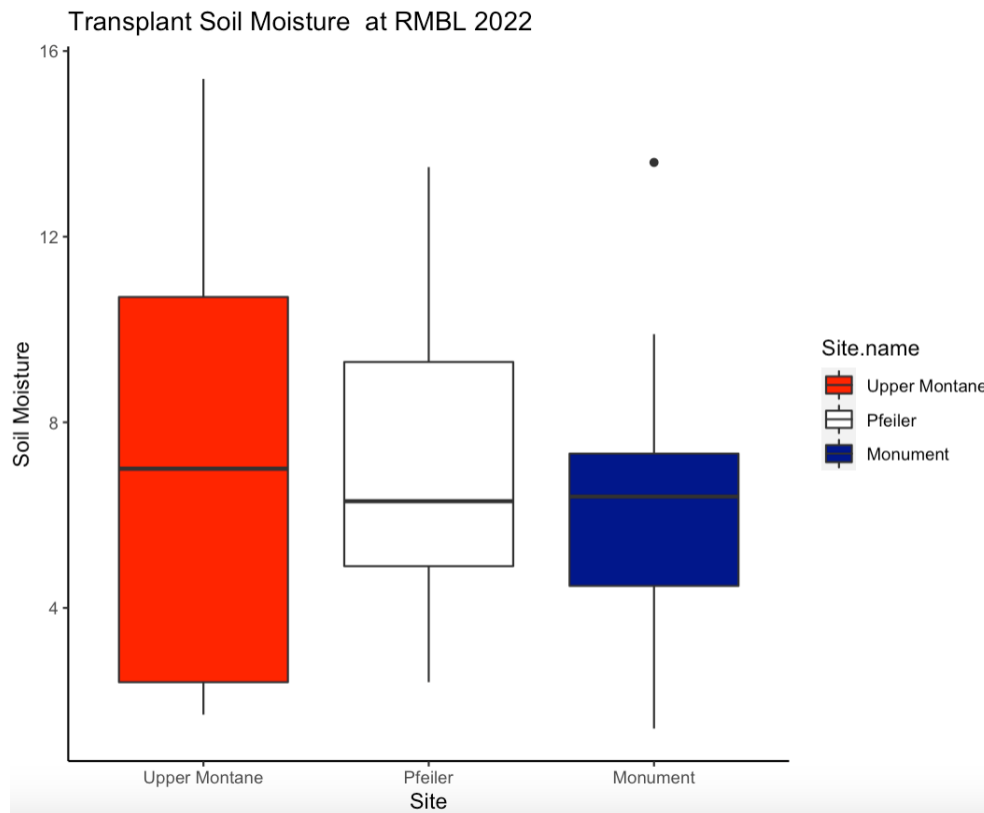


Figure 5

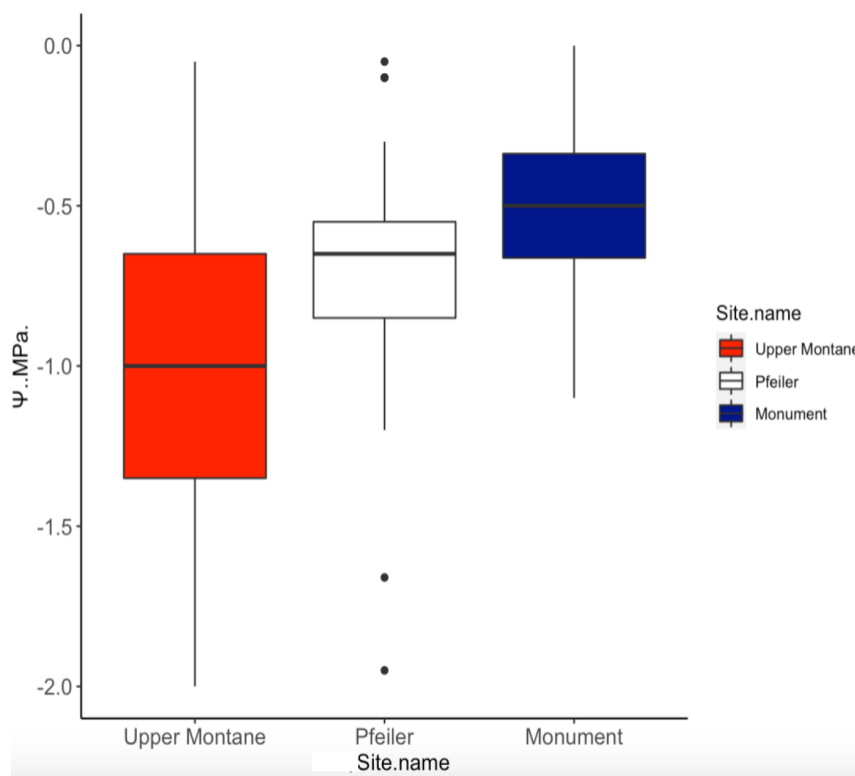


Figure 6

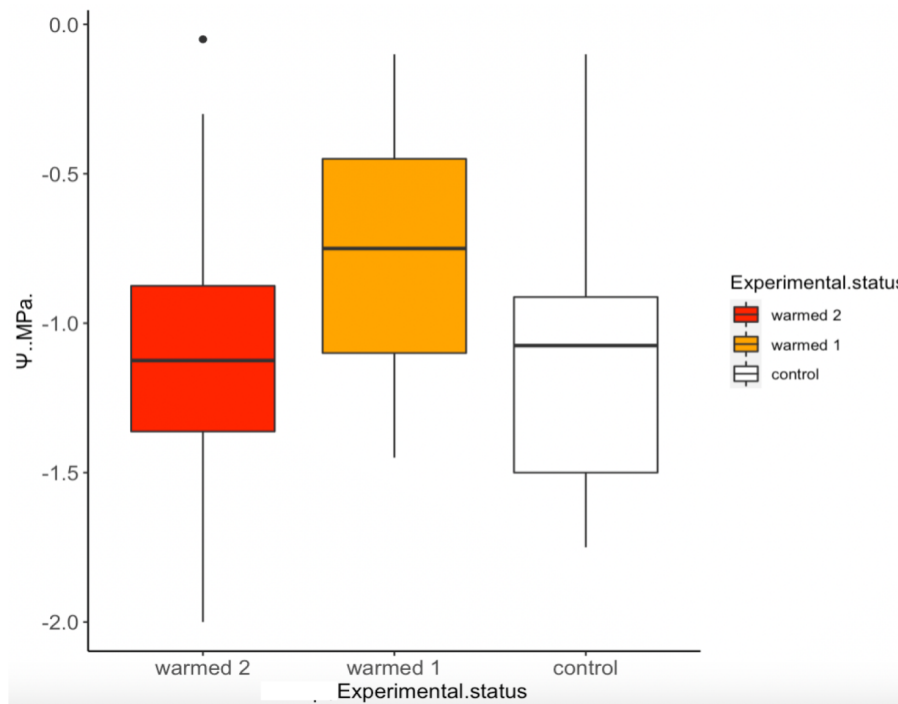


Figure 7

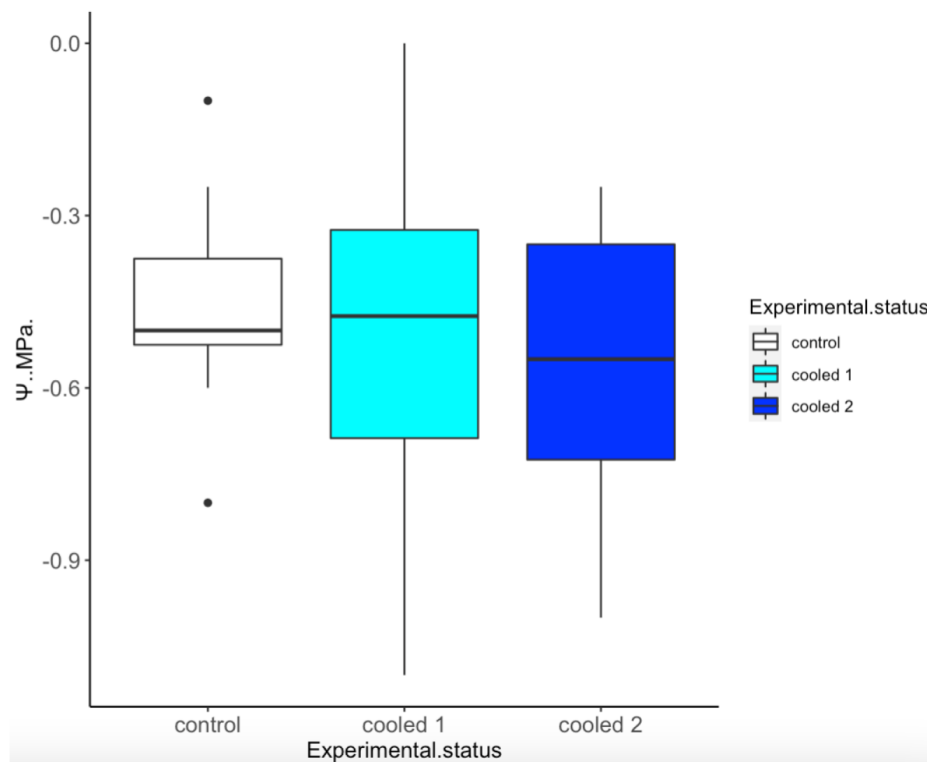


Figure 8

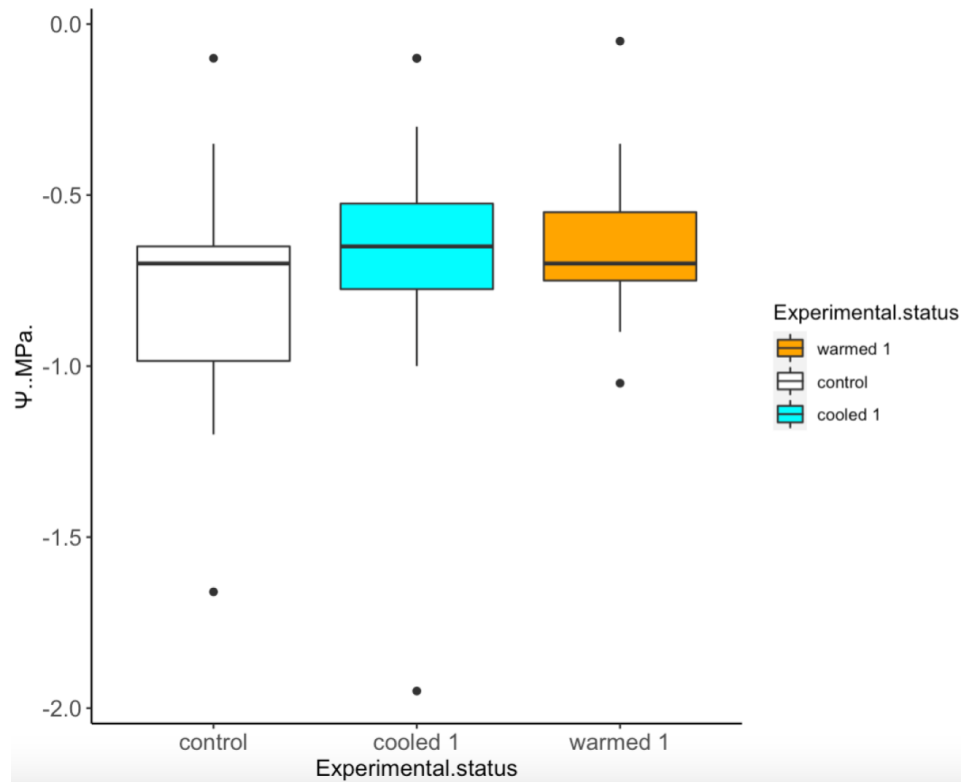


Figure 9

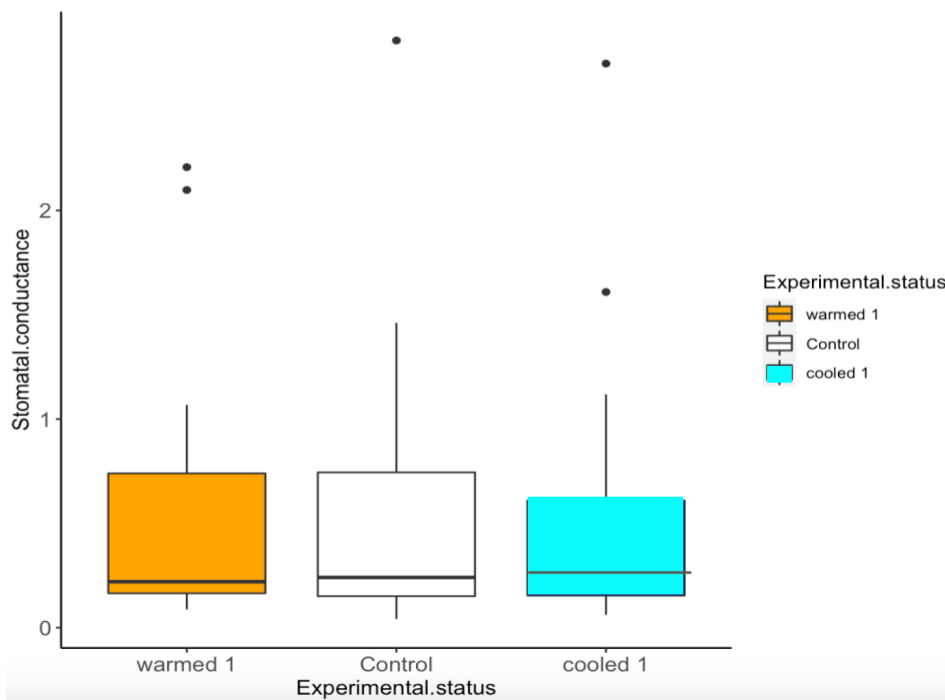


Figure 10

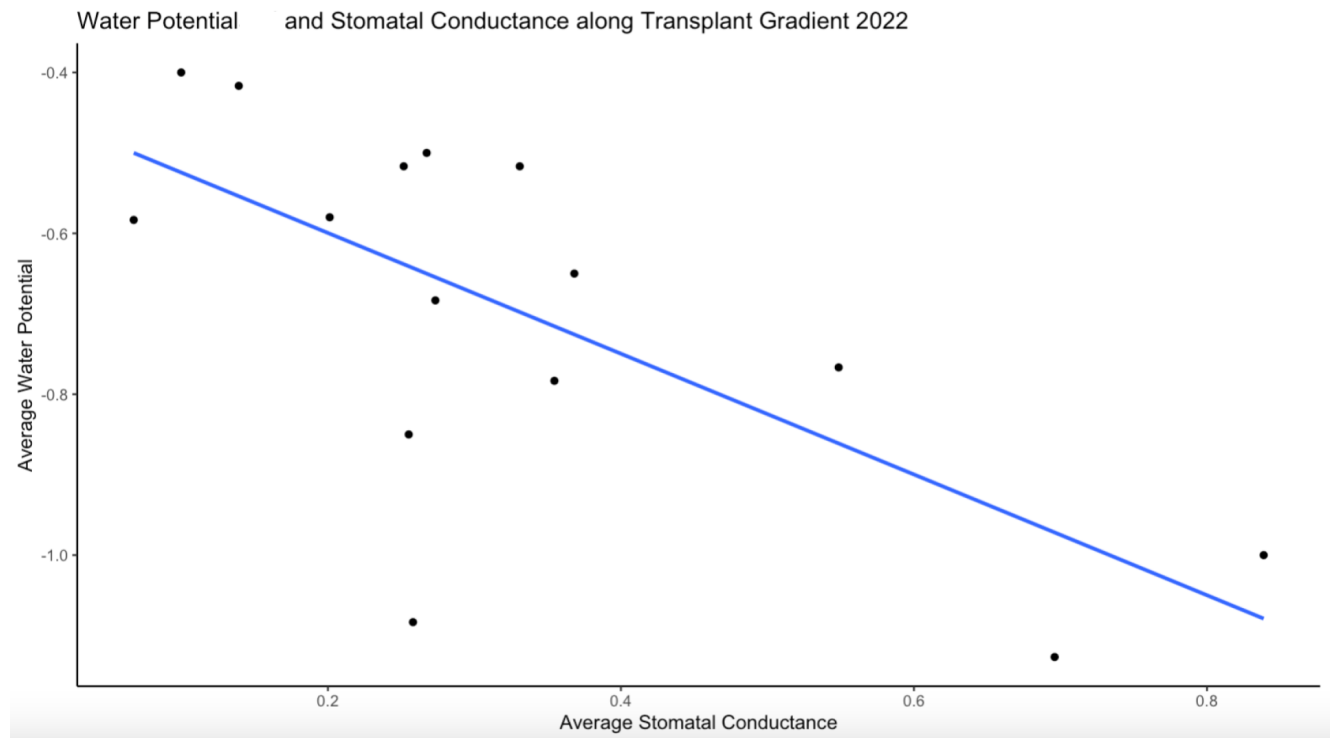


Figure 11

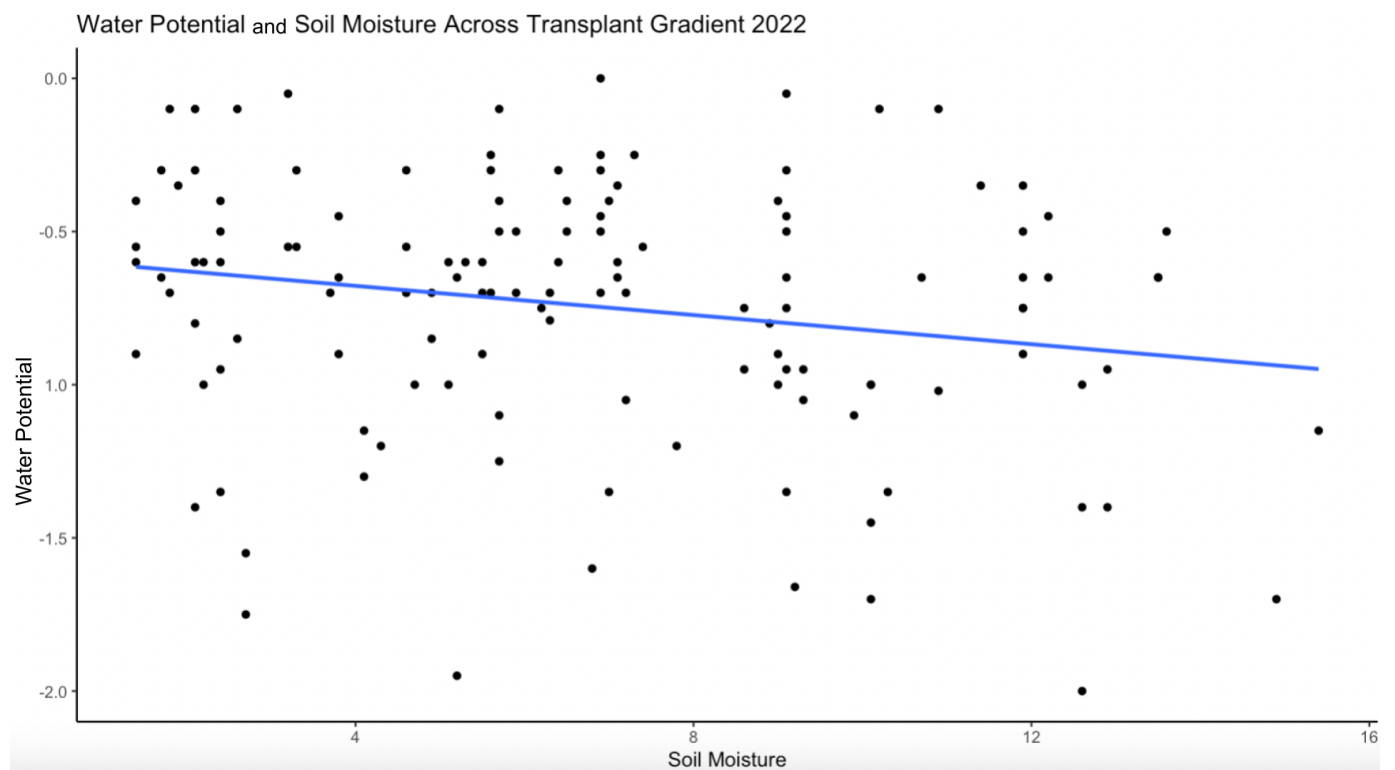


Figure 12