

Effects of species composition change under experimental warming on soil microclimate in a montane meadow

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Abstract:

The results of a long-term experimental warming study, in a montane meadow in the Rocky Mountains of Colorado, have shown that *Artemisia tridentata* (Common Sagebrush) is likely to increase in abundance under climate change, as perennial forb species decrease in abundance. This change in species composition in the ecosystem could have a feedback effect on microclimate conditions. In this study we examined the potential effects on soil microclimate, by measuring various temperature variables in the soil around selected forb species and *A. tridentata*, as well as soil moisture among the two vegetation types. Results showed significant, and sometimes dramatic, differences in soil temperature between *A. tridentata* and the forbs. Soil moisture appeared to be higher surrounding *A. tridentata*, compared to forb species, but this result was not significant. Thus, the change in species composition towards *A. tridentata* seems to act as a local negative feedback to an external heat forcing, in this one respect. Implications for this effect on soil microclimate could be important for ecosystem processes such as litter decomposition and seed germination.

Introduction:

The effects of global warming on biological systems are becoming increasingly apparent (IPCC, 2007). Evidence documenting these diverse changes is accumulating, as studies use projections of climate change to examine the responses in ecosystems (Shaver et al., 2000). Some types of ecosystems are predicted to be more vulnerable to changes in climate than others. Specifically, montane and high-latitude systems could be particularly sensitive, due to the dominant influence of the snow-albedo feedback and growing season length in these locations (Harte & Shaw, 1995; Harte et al., 1995). Thus, it is of particular interest and importance to understand the direct and indirect effects of warming on montane ecosystems, as well as potential feedbacks to the climate system from the biotic community.

An ongoing, long-term warming experiment, conducted in a montane meadow of the Rocky Mountains in western Colorado, has provided an abundance of data on changes in community structure and function (De Valpine & Harte, 2001; Harte et al., 1995; Harte & Shaw, 1995; Loik & Harte, 1996; Perfors et al., 2003). This experiment, at the Rocky Mountain Biological Laboratory, directly simulated the effect of a doubling of atmospheric carbon dioxide, by using infrared radiators to add an additional flux of 22 W/m² to the soil surface (Harte & Shaw, 1995). One of major results to arise from this site showed that experimental warming had significant effects on abundance and biomass of various plant species. Most noteworthy was the increasing dominance of *Artemisia tridentata*, and decreasing biomass of various perennial forb species, in response to warming (Harte & Shaw, 1995). The shift in dominance from forbs to *A. tridentata* (common Sagebrush) could have widespread importance across much of the western United States, since *A. tridentata* has a broad range, and is often limited at its upper elevational boundary by temperature restriction (Loik & Redar, 2003). Furthermore, there is evidence of past migration of *Artemisia* spp., in response to climate change (Nowak et al., 1994).

Other studies on the same experimental system have also examined the functional characteristics of the ecosystem. Under heated conditions, snowmelt date was found to advance by an average of about 2 weeks, soil temperature increased by an average of 2° C, and soil moisture content was reduced up to 25% during the summer season, compared to controls (Harte

et al., 1995; J. Harte, personal communication). Furthermore, the increased aboveground biomass (AGB) of *A. tridentata* has been shown to correspond, causally, to these changes in physical characteristics of the ecosystem. For example, *A. tridentata* was found to respond positively to the longer growing season, with an increased biomass growth rate, due to earlier snowmelt (Perfors et al., 2003). Also, while a species of forb, *Erigeron speciosus*, displayed a decrease in water potential as well as permanent shutdown of Photosystem II under experimental warming, *A. tridentata* did not. (Loik et al., 2000). In addition, prominent forb species such as *Erigeron speciosus* and *Helianthella quinquenervis*, were found to be limited by water or nitrogen deficiencies, both of which are consequences of heating (De Valpine & Harte, 2001). It is not yet clear, however, whether the increase in *A. tridentata* AGB and decrease in forb AGB were both independent results of heating, or whether heating also caused the *A. tridentata* to become a better competitor (J. Harte, personal communication). It is clear, though, that the changes in soil microclimate brought about by experimental heating resulted in significant species composition change.

The purpose of this study, then, was to examine the possible feedbacks from the observed shift in the vegetation community to the abiotic factors which caused this shift. More specifically, we analyzed whether the local soil temperature and soil moisture was affected differently by *A. tridentata* than by the forb community. The mechanisms for these potentially different vegetation effects on soil microclimate could act through differences in plant albedo, water-use efficiency, litter quantity, growth form, or a combination of these factors; higher albedo, higher water-use efficiency, higher concentrations of soil organic matter, and canopy shading would be expected to correlate with lower soil surface temperatures and greater moisture concentrations (J. Harte, personal communication). A previous study has shown that water-use efficiency differs between *A. tridentata* and another shrub species at the study site, and suggests plausibility for a water-use efficiency mechanism (Shaw et al., 2000). Thus, we sought to quantify the effects on soil microclimate which potentially arise from the difference in plant community; we hypothesized that characteristics associated with *A. tridentata* such as higher water use efficiency, and canopy shading, could lead to comparatively cooler and more mesic conditions, thereby dampening the effect of an external heat forcing on the soil microclimate.

Many important ecosystem processes, such as seed germination, plant establishment, and litter decomposition, depend critically on soil microclimate conditions (Flerchinger & Pierson, 1997; Shaw & Harte, 2001). Thus, changes in soil temperature or moisture, brought about by species composition change, could affect these processes and have implications for community structure and function into the future. Furthermore, our current understanding of ecosystem-climate feedbacks is centered around greenhouse gas feedbacks, while other types of feedback processes have not received as much attention (Shaver et al., 2000). Thus, it has been recommended that the kinds of feedbacks that function through changes in surface energy balance and water balance should be high priorities of research (Shaver et al., 2000). This study examined one such potential feedback.

Methods:

The study took place at the Rocky Mountain Biological Laboratory in Gunnison County, Colorado, in two ungrazed montane meadows, one at 2900 m elevation (latitude 38°57'25" N, longitude 106°59'08" W) and another at 2930 m elevation (latitude 38°57'42" N, longitude 106°59'24" W) about 0.7 kilometer apart. At the lower site, 4 plots, each 2m x 2m, were established within about 20 meters of each other, with varying slope and aspect. These plots were studied observationally, without manipulation. At the upper site, 4 plots, each 1.5m x 3m, were established on a West-facing, moderate slope, each about 10 meters apart. Each of these plots was divided in two, and manipulated using aboveground plant removals to create one half exclusively *Artemisia tridentata*, and one half exclusively forbs and graminoids. This manipulation was implemented in order to establish the direction of causation, ensuring that the measured soil microclimate conditions were a result of the species composition, and not vice versa.

The forb species selected for study, because of documented changes in biomass under experimental warming, were *Helianthella quinequenervis*, *Potentilla gracilis*, and *Erigeron speciosus* (Harte & Shaw, 1995; De Valpine & Harte, 2001). These forb species, representing the montane meadow community, were compared to the most prominent members of the sagebrush community, *Artemisia tridentata* and *Festuca thuberi* (J. Harte, personal communication).

The temperature variables sampled from each species were: foliage temperature, soil surface temperature at the base of the stem, soil surface temperature 20 cm away from the base of the stem, and soil temperature 10 cm deep at the base of the stem. Foliage temperature was measured near the top of the leafage, and soil surface temperature at 20 cm distance was measured in the direction of the plant's shadows, depending on the time of day. All foliage and surface temperatures were measured using a handheld infrared thermometer (Everest Agri-Therm III, Everest Interscience Inc., Tuscon, AZ), while soil temperature at depth was measured using 10 cm-long temperature probes (DeltaTRAK, PTC Instruments, Los Angeles, CA). The infrared thermometer was calibrated to measure an area with a radius of 2 mm on the desired surface.

Temperature sampling was performed on species within all 8 of the plots, manipulated and unmanipulated, over the course of 5 weeks at the peak of summer, from early July through early August. Within each plot, all four temperature variables were sampled from one individual of each species. Data for each variable were averaged from 3 measurements, in order to reduce inherent noise in temperature variation. The time of day, percentage cloud cover, and ambient temperature was also recorded before the sampling of a plot, each of which averaged about 20 minutes in duration. Due to practical considerations, and the limitations of instruments used, no sampling was done under precipitation conditions. The plots at the lower site were each sampled 11 times over the course of the study, while the plots at the upper site were sampled 8 times. Samplings took place between 9:00 a.m. and 6:00 p.m., and were concentrated around the hottest part of the day, during mid-afternoon. Thus, there were 8 replicate plots for the temperature component of the study.

In addition, soil moisture sampling was done at the 4 plots of the upper site. These manipulation plots were divided into exclusively *A. tridentata* and exclusively forb subplots, so that soil moisture could be compared between these two different vegetation types. Data for the soil moisture content of each subplot was averaged from 4 measurements, one in each quadrant, using a time-domain-reflectometer probe at 10 cm depth (Hydrosense, Campbell Scientific, Australia). Time of day, percentage cloud cover, and ambient air temperature were also recorded for each sampling time. Each of these 4 replicate plots were sampled for soil moisture 15 times over the course of the study.

Data were recorded using spreadsheet software (Microsoft Excel, Microsoft Corp., Redmond, WA) and analyzed in the statistical program, R (R programming, www.r-project.org). Differences in temperature were calculated between species within a given plot at a given sampling time, to avoid confounding geographical and weather effects. Welch t-tests were used to look for: differences in foliage temperature, differences in soil surface temperature at two distances from the stem, and differences in soil temperature at depth, between each pair of plant species. Additionally, soil moisture data were compared between the manipulated *A. tridentata* subplots and forb subplots.

Results:

Over the course of 5 weeks and 76 samplings of temperature data within the plots, a wide range of climatic conditions were captured. Between the hours of 09:00 and 18:00, ambient air temperature ranged from 16 °C to 32 °C, and cloud cover percentage ranged from 0 % to 95 %. The mean temperature at the time of sampling was 25.8 °C.

Preliminary analysis of the temperature data revealed that species effects on microclimate were similar between observational and manipulated plots. This confirmed the direction of causality in the effect, ruling out the possibility that the observed microclimates led to the species associated with them. It also allowed further analyses of these species-level temperature measurements to consider all the data, from all plots, together.

In order to compare our data between species using a Welch t-test, it was necessary to first examine whether each sampling could be treated as independent, since an assumption of independence underlies the t-test. Because the data were repeatedly collected from the same group of eight plots, there was a possibility of spatial auto-correlation between samplings within a plot. To determine whether spatial auto-correlation existed among our data, we compared the variance of all samples within a given plot to the variance of the same number of samples randomly selected from any of the plots. In all cases, the variance of the spatially-specific group was as large or slightly larger than the variance of the spatially-random group of samples. These results showed that samples taken from within a given plot were no more closely related to each

other than samples taken from random plots. This implies that there was no spatial autocorrelation in our experimental design, and each sample could be treated as independent.

The results of comparison between foliage temperatures, using Welch two-sample t-tests, are shown in Table 1 in the Appendix. Figures 1 and 2 illustrate the data graphically, with a barplot and boxplot, respectively. Among the six comparisons between each of the three forb species with *A. tridentata* and *F. thurberi*, two comparisons showed significant differences; *P. gracilis* foliage was 2.8 °C warmer than *A. tridentata* foliage ($p = 1.7 \times 10^{-4}$), and *E. speciosus* foliage was 2.9 °C warmer than *A. tridentata* ($p = 1.2 \times 10^{-4}$).

The results of comparison between soil surface temperatures at the base of the stem, using Welch two-sample t-tests, are shown in Table 2 in the Appendix. Figures 3 and 4 illustrate the data graphically, with a barplot and boxplot, respectively. At this location, all three of the forb species differed significantly with *A. tridentata*, but none differed significantly with *F. thurberi*. The base of *H. quinquenervis* was 2.5 °C warmer ($p = 1.6 \times 10^{-2}$), the base of *P. gracilis* was 3.9 °C warmer ($p = 6.9 \times 10^{-5}$), and the base of *E. speciosus* was 3.4 °C warmer ($p = 3.0 \times 10^{-3}$) than the base of *A. tridentata*.

The results of comparison between soil surface temperatures at 20 cm from the stem, using Welch two-sample t-tests, are shown in Table 3 in the Appendix. Figures 5 and 6 illustrate the data graphically, with a barplot and boxplot, respectively. As with the soil surface temperature at the base of the stem, each of the forb species differed significantly with *A. tridentata*, but not with *F. thurberi*. These differences were the most pronounced of any comparisons in the study, with the forbs averaging 8.8 °C warmer soil surface temperatures at distance, than the Sagebrush ($p < 1.0 \times 10^{-5}$). Specifically, *H. quinquenervis* was 7.2 °C warmer ($p = 6.3 \times 10^{-6}$), *P. gracilis* was 9.8 °C warmer ($p = 6.1 \times 10^{-10}$), and *E. speciosus* was 9.3 °C warmer ($p = 1.3 \times 10^{-7}$).

The results of comparison between soil temperature at 10 cm depth, using Welch two-sample t-tests, are shown in Table 4 in the Appendix. Figures 7 and 8 illustrate the data graphically, with a barplot and boxplot, respectively. Similarly to the other temperature variables, all forb species differed significantly from *A. tridentata* with regard to soil temperature at depth, but none differ significantly with *F. thurberi*. The increased temperatures for *H. quinquenervis*, *P.*

gracilis, and *E. speciosus*, compared to *A. tridentata*, respectively, were 1.3 °C ($p = 1.2 \times 10^{-2}$), 2.1 °C ($p = 1.9 \times 10^{-4}$), and 1.8 °C ($p = 2.2 \times 10^{-3}$). In total, it is of note that 11 of the 12 forb-Sagebrush comparisons yielded significant differences while none of the forb-*F. thurberi* comparisons did. Also of note is the fact that the data range of *A. tridentata* is smaller than that of the other species, for nearly all the measured variables (See Figures 2, 4, 6, 8).

For the soil moisture component of the study, all the data from the control, or forb plots, were compared to all the data from manipulated, or *A. tridentata* plots (See Figures 8 and 9). A Welch two-sample t-test between these groups revealed a nearly-significant difference, with the volumetric water content in the Sagebrush plots 0.94 percent higher than that in the forb plots ($p = 6.9 \times 10^{-2}$). However, due to a very shallow bedrock layer under one of the control plots, probe depth between the control and manipulation was uneven there, and these data were excluded for a subsequent t-test. This revealed that without the imprecise data included in the analysis, the difference between controlled and manipulated plots was only 0.56 percent volumetric water content, and highly insignificant ($p = 0.34$).

Discussion:

The purpose of this experiment was to investigate the potential feedbacks of changing species composition on soil microclimate. We found that *A. tridentata*, or common sagebrush, affected soil temperature significantly differently than the selected forb species, keeping its surrounding soil cooler in comparison to the soil surrounding forbs. Sagebrush vegetation also appeared to keep the soil more moist than forb vegetation, but these differences were not significant, and therefore our soil moisture results were inconclusive. Thus, these results strongly supported our hypothesis that increasing *A. tridentata* abundance would lead to lower soil temperatures, but neither supported nor refuted our hypothesis that it would also lead to wetter soil.

While this study was not designed specifically to evaluate the potential mechanisms through which an observed effect may be acting, it is possible to critically examine these mechanisms with respect to the data. Of the mechanisms which may have contributed to this vegetation effect on soil microclimate, two seem to be best supported by the data; albedo

differences and differences in growth form appeared to be most influential. Differences in water use efficiency apparently did not have any significant effect, because no difference in the soil moisture content was detected. Furthermore, litter quality and quantity would be unlikely to change significantly at the timescale of the manipulation, so it is unlikely to have contributed to the observed effect. Instead, the significantly lower foliage temperature of *A. tridentata* compared to the forb species suggests that a lower albedo among Sagebrush may have led to cooler soil conditions. Similarly, the canopy shading of *A. tridentata* seems to be important, which is supported by the fact that temperature differences were greatest at 20 cm distance from the stem, where shading is the most influential factor.

The primary difficulty with this study is the limited scope of its timescale. Sampling was intentionally focussed on the peak of summer, and the hottest part of each day, because these were expected to be the times with the greatest temperature differences between species. Indeed, plotting the temperature differences versus the time of day supported this assumption, by showing a peaking trend near mid-afternoon. However, the potential ecological importance of these results are heavily timescale dependent. For example, seed germination, which could be affected by changes in soil microclimate, tends to peak during the spring season, for which this study has no data. Also, diurnal variation in soil temperature was not measured in this study. In other words, a better understanding of the temperature differences integrated over time would lead to a fuller understanding of potential ecological significance.

Nevertheless, the results of this study do suggest that there could be cascading effects from a change in species composition, which act through changes in soil microclimate. For instance, it has been shown in a pasture meadow that different species composition mediated differential tree seedling establishment, through microclimate effects (Balandier et al., 2009). Also, seed dormancy and germination among North American grasses have been shown to be a function of incubation temperatures (Qi & Upadhyaya, 1993). Furthermore, soil microbes have varying temperature optima, which can affect their rates of metabolism (Sylvia et al., 2004). These examples illustrate the potential for downstream ecological effects from changes in soil microclimate.

We found that *Artemisia tridentata*, which is expected to become more abundant in montane meadows under climate warming, affects the soil microclimate differently than the forb species that it may replace. Specifically, soil conditions around *A. tridentata* tend to be cooler than around forb species, so that *A. tridentata* acts as a negative feedback to the heat forcing, in this one respect. The ecosystem changes associated with climate warming, and particularly changes in species composition, are sure to be complex, but this study documents one possible effect of the biotic community on the physical environment.

Appendix:

Table 1:

Foliage comparison	Difference in mean	P-value for no difference
<i>H. quinquenervis</i> foliage - <i>A. tridentata</i> foliage	+0.2 °C	0.73
<i>P. gracilis</i> foliage - <i>A. tridentata</i> foliage	+2.8 °C	0.00017***
<i>E. speciosus</i> foliage - <i>A. tridentata</i> foliage	+2.9 °C	0.00012***
<i>H. quinquenervis</i> foliage - <i>F. thurberi</i> foliage	-1.8 °C	0.066
<i>P. gracilis</i> foliage - <i>F. thurberi</i> foliage	+0.2 °C	0.87
<i>E. speciosus</i> foliage - <i>F. thurberi</i> foliage	-0.1 °C	0.93

Figure 1:

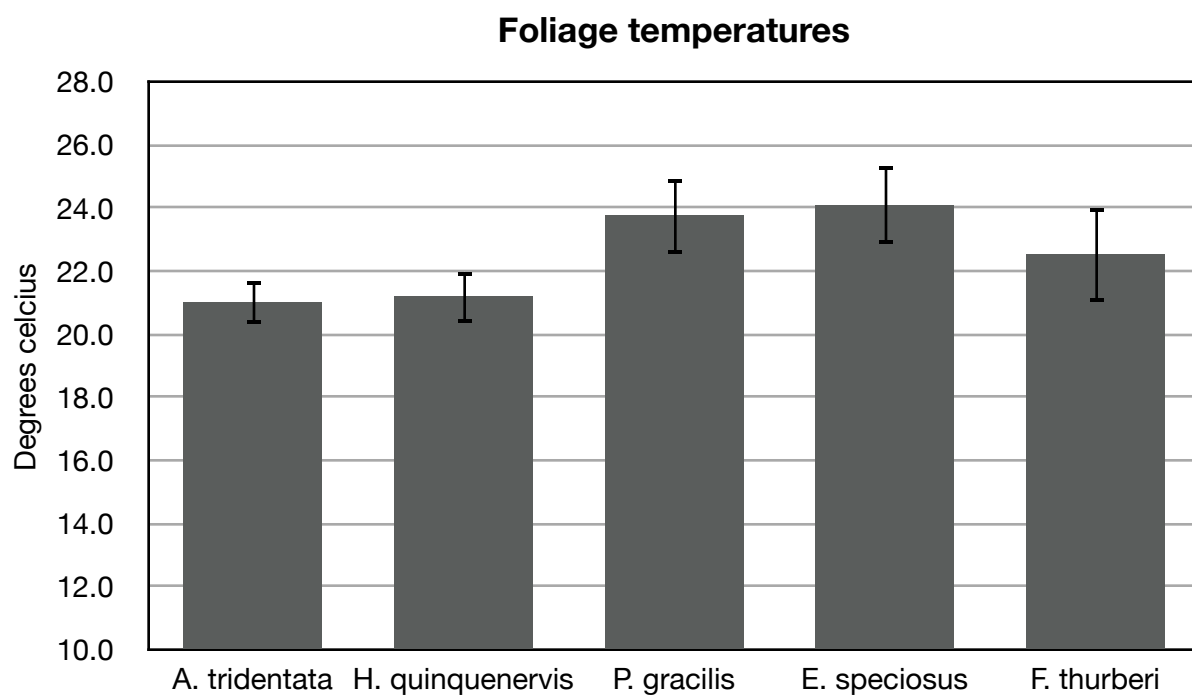


Figure 2: (boxes represent interquartile range, and whiskers represent total range)

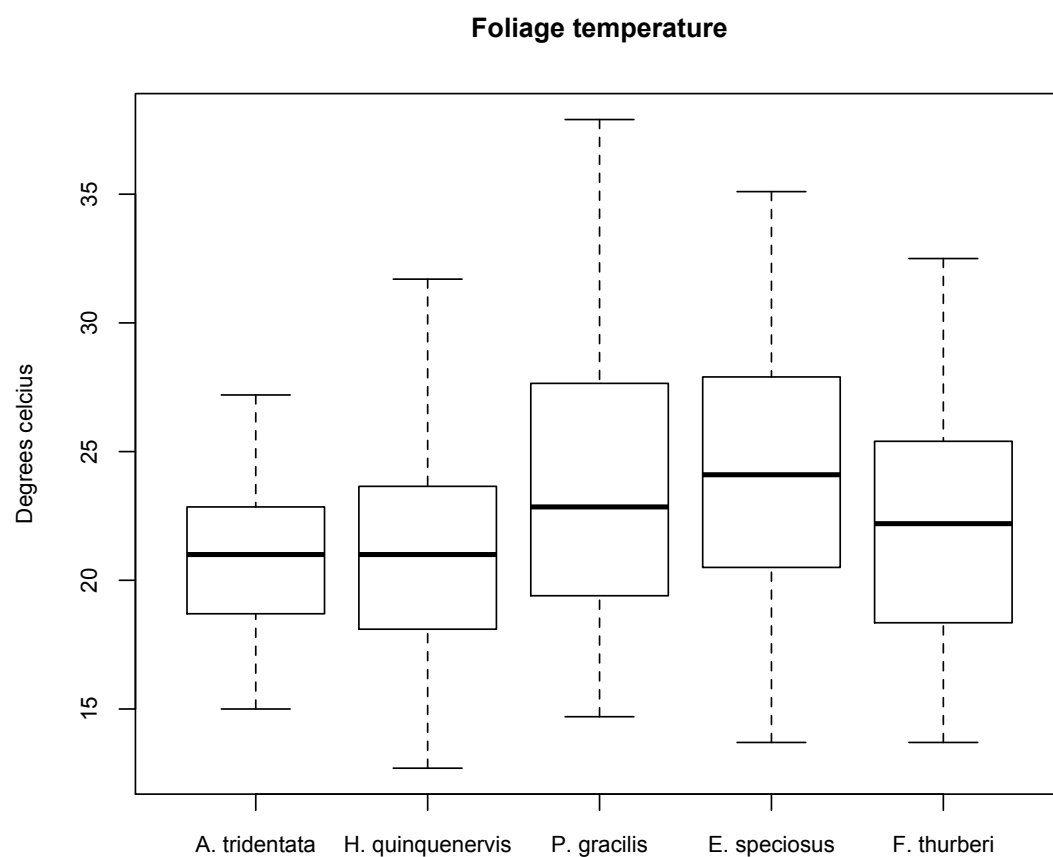


Table 2:

Base comparison	Difference in mean	P-value for no difference
<i>H. quinquenervis</i> base - <i>A. tridentata</i> base	+2.5 °C	0.016*
<i>P. gracilis</i> base - <i>A. tridentata</i> base	+3.9 °C	0.000069****
<i>E. speciosus</i> base - <i>A. tridentata</i> base	+3.4 °C	0.0030**
<i>H. quinquenervis</i> base - <i>F. thurberi</i> base	+0.9 °C	0.58
<i>P. gracilis</i> base - <i>F. thurberi</i> base	+1.5 °C	0.32
<i>E. speciosus</i> base - <i>F. thurberi</i> base	+0.1 °C	0.96

Figure 3:

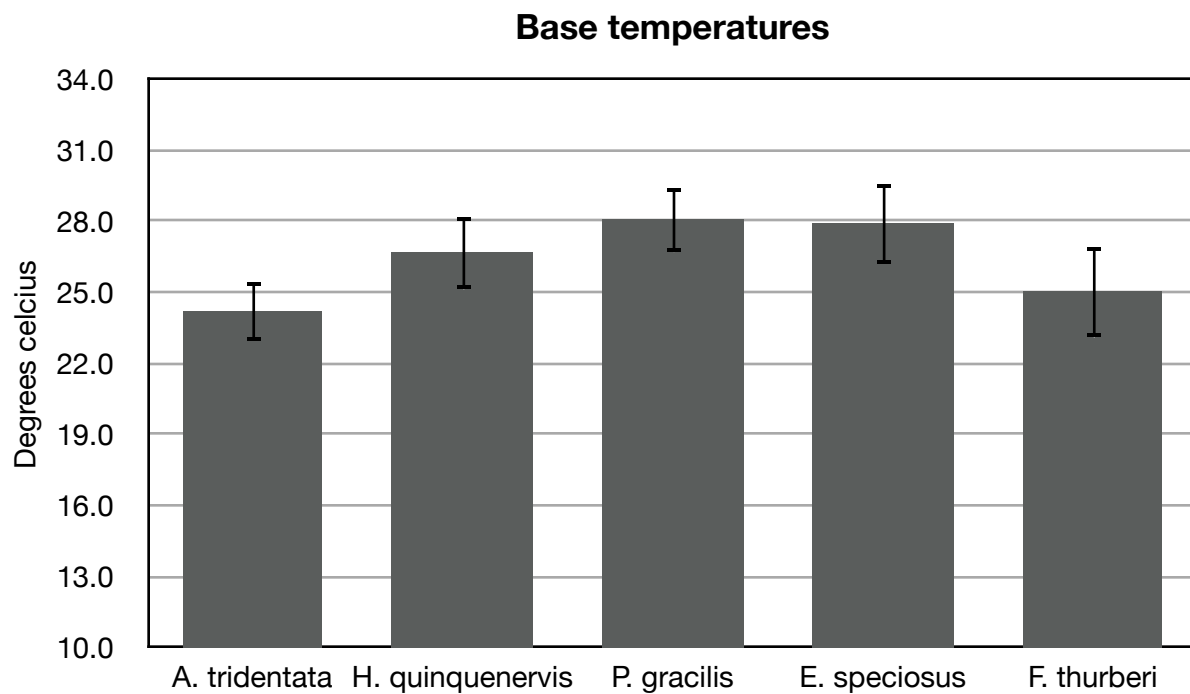


Figure 4: (boxes represent interquartile range, and whiskers represent total range)

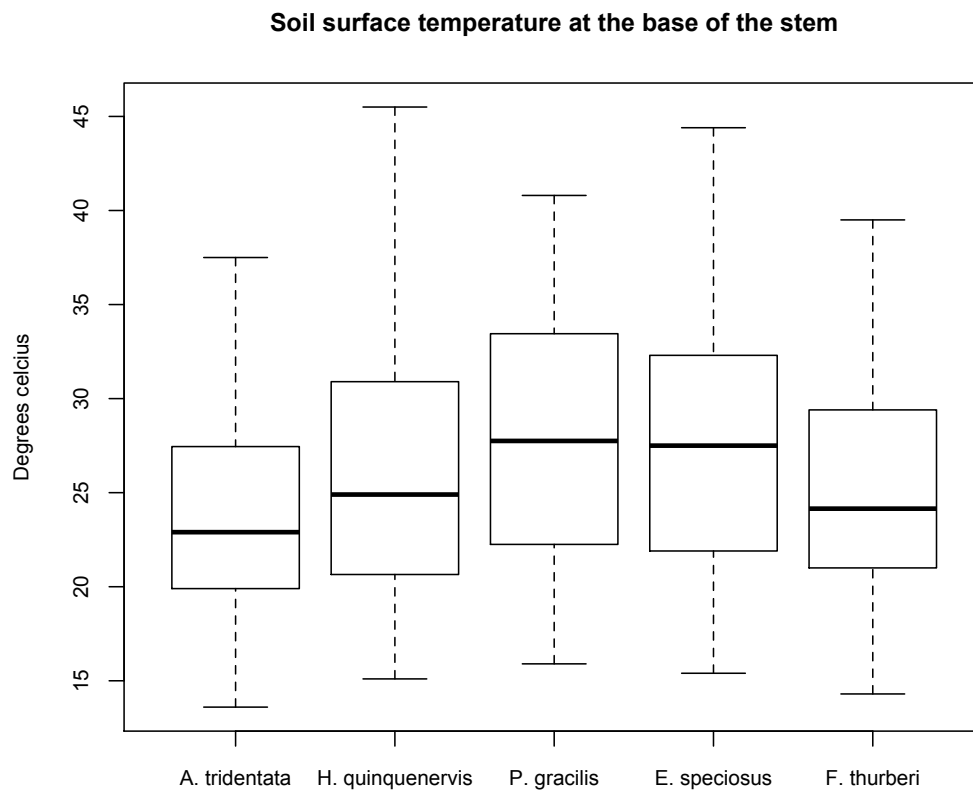


Table 3:

Distance comparison	Difference in mean	P-value for no difference
<i>H. quinquenervis</i> distance - <i>A. tridentata</i> distance	+7.2 °C	0.0000063****
<i>P. gracilis</i> distance - <i>A. tridentata</i> distance	+9.8 °C	0.00000000061****
<i>E. speciosus</i> distance - <i>A. tridentata</i> distance	+9.3 °C	0.00000013****
<i>H. quinquenervis</i> distance - <i>F. thurberi</i> distance	+2.4 °C	0.36
<i>P. gracilis</i> distance - <i>F. thurberi</i> distance	+4.3 °C	0.11
<i>E. speciosus</i> distance - <i>F. thurberi</i> distance	+4.1 °C	0.21

Figure 5:

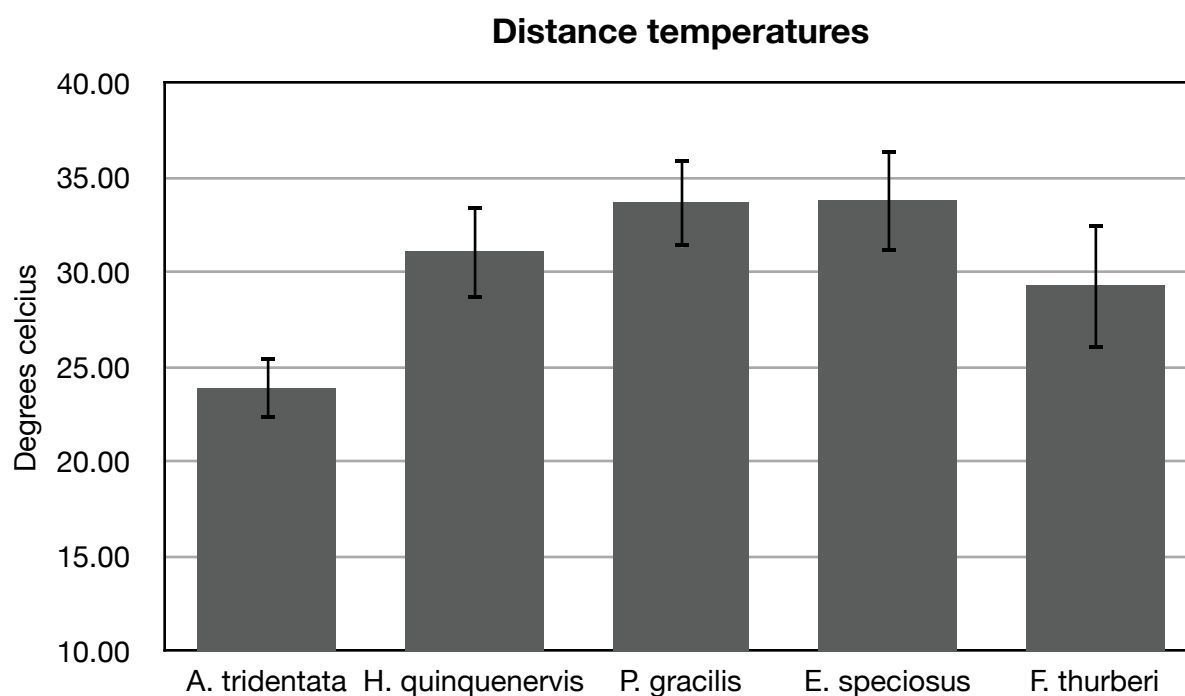


Figure 6: (boxes represent interquartile range, and whiskers represent total range)

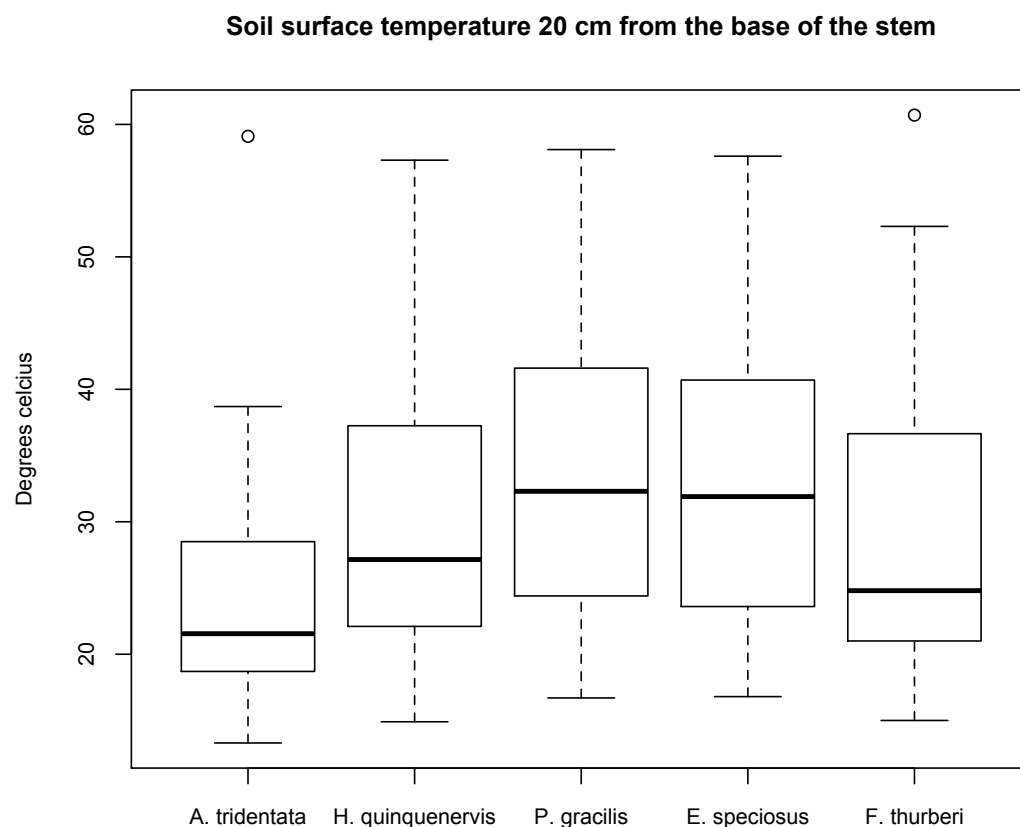


Table 4:

Depth comparison	Difference in mean	P-value for no difference
<i>H. quinquenervis</i> depth - <i>A. tridentata</i> depth	+1.3 °C	0.012*
<i>P. gracilis</i> depth - <i>A. tridentata</i> depth	+2.1 °C	0.00019***
<i>E. speciosus</i> depth - <i>A. tridentata</i> depth	+1.8 °C	0.0022**
<i>H. quinquenervis</i> depth - <i>F. thurberi</i> depth	+0.5 °C	0.47
<i>P. gracilis</i> depth - <i>F. thurberi</i> depth	+0.7 °C	0.32
<i>E. speciosus</i> depth - <i>F. thurberi</i> depth	+0.1 °C	0.83

Figure 7:

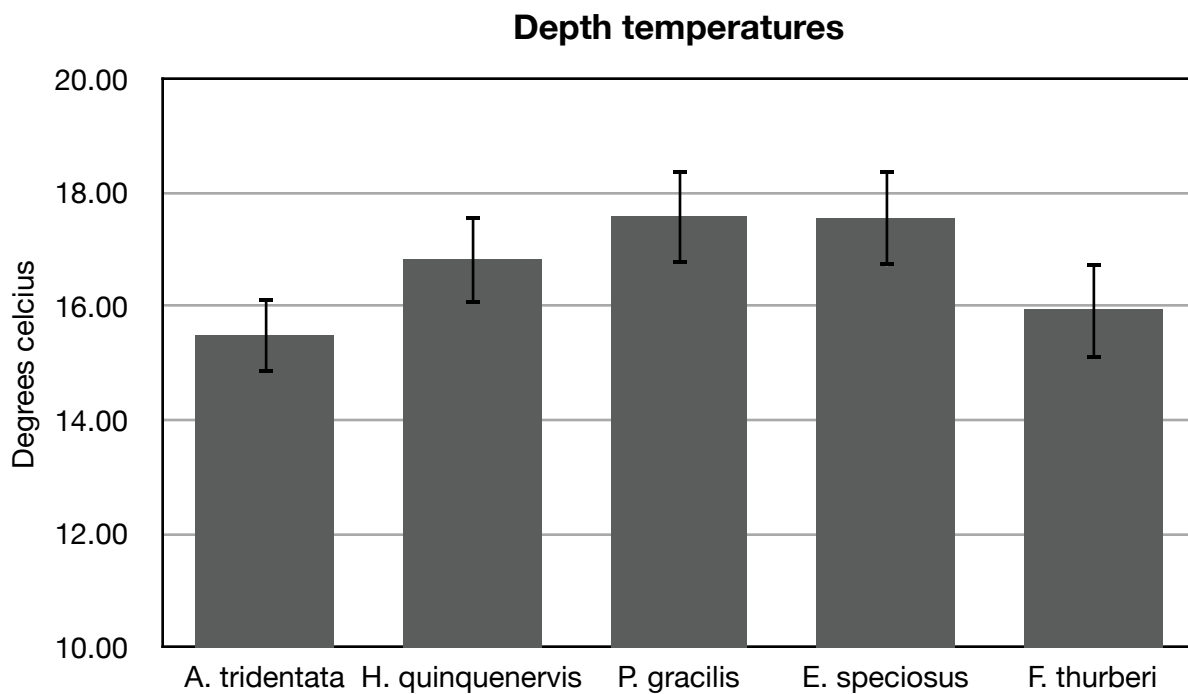


Figure 8: (boxes represent interquartile range, and whiskers represent total range)

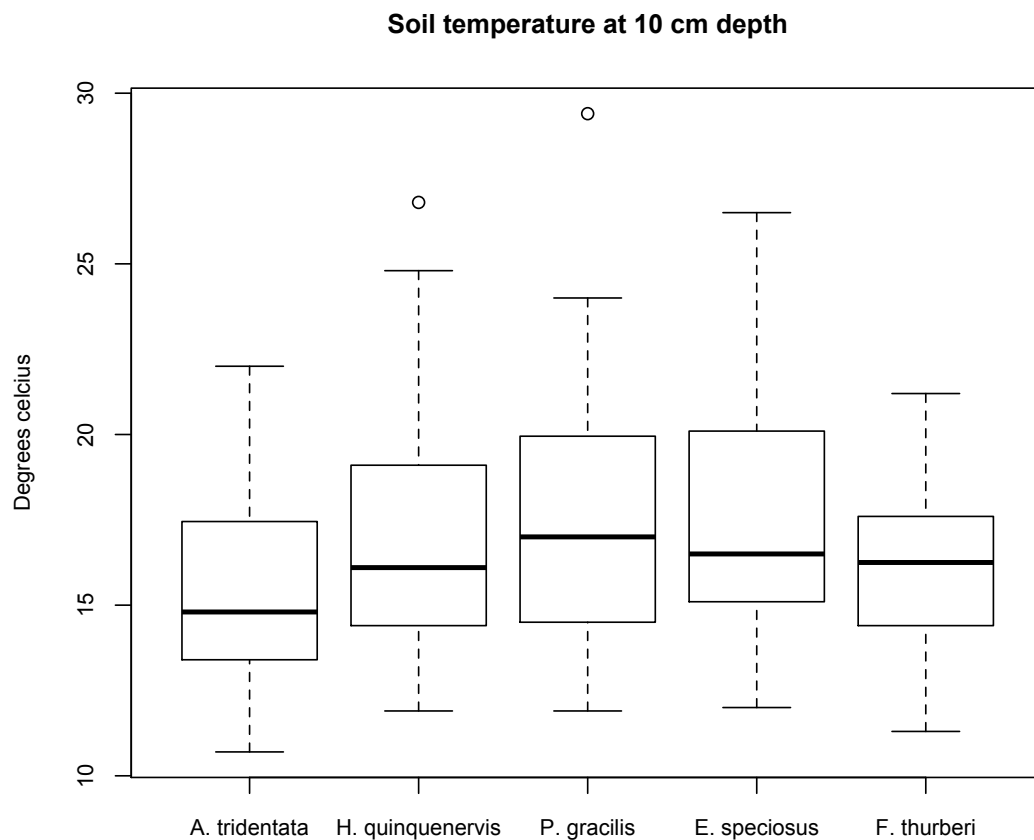


Figure 9:

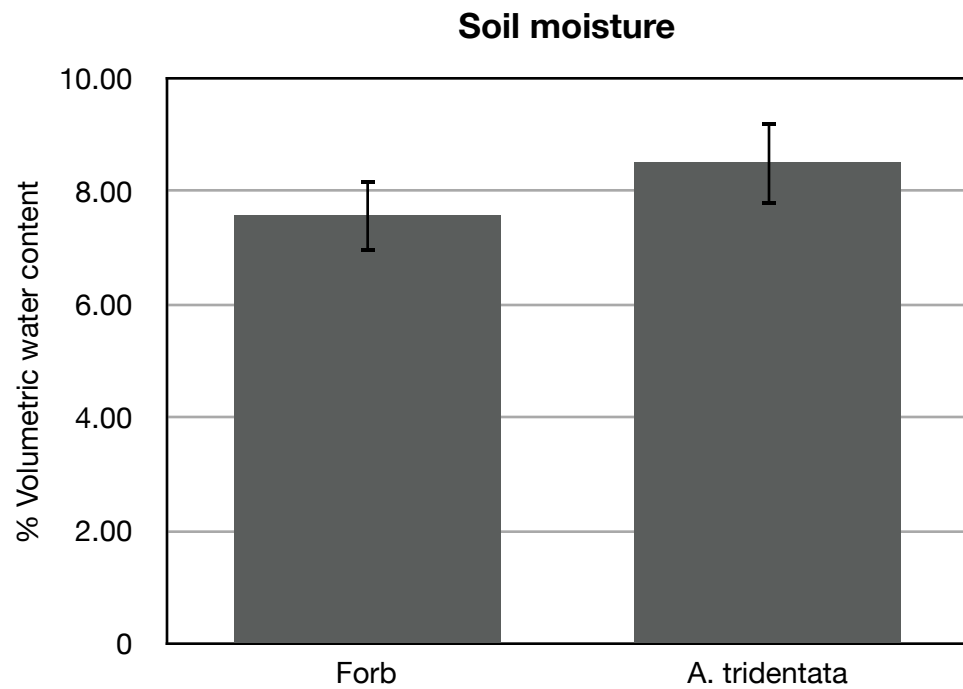
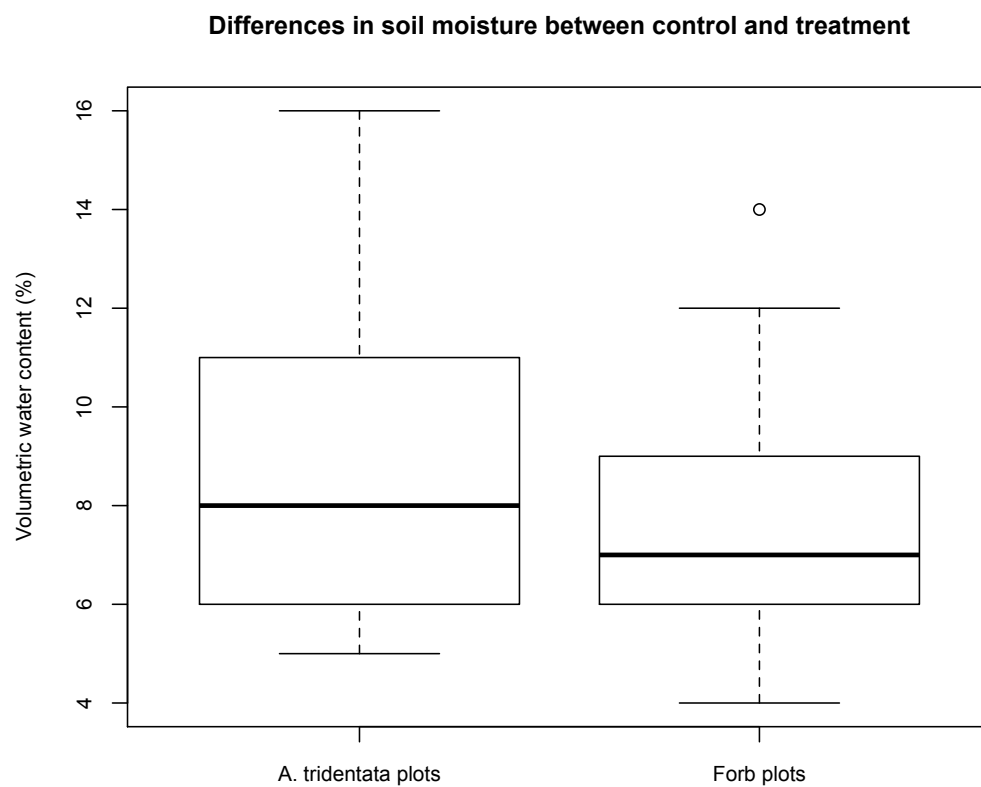


Figure 10: (boxes represent interquartile range, and whiskers represent total range)



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