Mechanisms of plant species codominance in a tallgrass prairie: Progress report 2018

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Background:

Much has been learned about the mechanisms of coexistence of dissimilar species through niche partitioning (e.g., (Hutchinson, 1959; Hutchinson, 1961; MacArthur, 1958; MacArthur, 1967)), and of the role of longevity and other neutral processes in the delay of competitive exclusion (Hubbell, 2008). While these processes may facilitate some types of codominance (e.g., savanna and forest, respectively), they may not be responsible for the codominant relationships of highly similar, but temporally dynamic populations. The storage effect ((Chesson, 1985; Chesson, 2000)) may provide some insight into how two functionally equivalent species can avoid competitive exclusion in the long term. This mechanism is expected to play a role in coexistence when two competitive, but self-limiting species are affected differently by environmental variability, such that conditions that are favorable for growth in one species are less favorable to the other, while at another time (or place) those roles are switched. During periods when conditions are favorable, the benefactor population grows or stores a surplus of resources that can sustain its population during the less favorable periods. If the environmental variability pattern is such that periods of favorable conditions are sufficient to bolster against the spans of unfavorable conditions, then each species population may be either sustaining, storing, or growing more often than declining, facilitating stably dynamic coexistence. However, as with many other coexistence mechanisms, the storage effect has often been invoked as one by which rare species have avoided exclusion by competitively superior species (e.g., (Chesson, et al., 2004).

In my previous work, I uncovered a possible variation of the storage effect in which both species of a functionally-similar, codominant pair are similarly affected by environmental variability. Both warm-season grasses, *Andropogon gerardii* and *Sorghastrum nutans*, appear to respond much in parallel to some aspects of environmental variability of a tallgrass prairie region of the Great Plains, including demographically negative responses to grazing (Hartnett, et al., 1996) and shading (Lett & Knapp, 2003), and positive responses to increased fire frequency (Hartnett, et al., 1996) and increased nutrient and water availability (Silletti & Knapp, 2001). This would directly contradict one of the requirements of storage effect - that the coexisting species must respond differently to environmental variability - but these two grasses appear to be temporally partitioning their risk to unfavorable conditions via subtle differences in their tillering patterns. *A. gerardii* is rhizomatous grass with determinantly activated, annual tillers that are recruited within a relatively brief period from late April to early May and are thinned afterwards (McKendrick, et al., 1975; Ott & Hartnett, 2012). *S. nutans* is also a rhizomatous grass, however it has indeterminantly activated, biennial tillers, with the previous year's cohort of tillers re-emerging during the same period as *A. gerardii* tillering and a second set for first year tillers recruited during the remainder of the growing season (McKendrick, et al., 1975). This difference results in temporally asynchronous tiller density dynamics, wherein *A. gerardii* tiller reach a peak density early in the growing season and decline afterwards, and *S. nutans* tillers are at peak density late in the growing season (Gray and Smith, in preparation). This asynchrony appears to temporally partition each species' peak risk towards unfavorable conditions to time during which they achieve their peak densities, while also facilitating parallel, but density-proportionate responses to favorable conditions without requiring dormancy in either species at any point in the growing season.

Climate change projections indicate that both intra- and inter-annual climate variability in the tallgrass prairie region of the Great Plains will increase (IPCC, 2012). Intra-annual variation is expected to increase as dry periods become more prolonged and rainfall events more intense. Indeed, there is already evidence for the latter occurring in the region (Easterling, et al., 2000). Since the stabilizing effect of risk partitioning likely depends on the historic range of environmental variability, changes in intra- and inter-annual variation in rainfall regimes may have effects on the codominant relationship between *A. gerardii* and *S. nutans*. For instance, if intra-annual variability shifts such that favorable conditions occur more often early in the growing season, and/or less favorable conditions occur more often later in the growing season, then *A. gerardii* with its annual tillering and early season emergence is expected to consistently benefit disproportionately from the former, and by not actively tillering later in the growing season this species could avoid less favorable conditions during this time. In contrast, these conditions are expected to be unfavorable for the later tillering *S. nutans*. If intra- or inter-annual variability were increased such that periods of favorable conditions were insufficient to promote population growth or resource storage for enduring through periods of unfavorable conditions, then both species may be expected to decline to some degree.

In my previous work, I found evidence that the degree to which interspecific tiller dynamics were asynchronous was muted when intra-annual variability in soil moisture was increased, particularly when this increased variability was accompanied by warmer canopy temperatures, a condition also predicted under climate change (Gray & Smith, in preparation). Because of the regular inter- and intra-annual dynamics of *A. gerardii,* the degree of asynchrony was primarily driven by the relatively more variable dynamics of *S. nutans* tiller densities. For example, when *S. nutans* tiller densities rose less over the course of the growing season, its numerical advantages by the end of the growing seasons were diminished. If its densities remained constant, because of conditions unfavorable for activation of previous year's buds, early senescence of previous year's tillers, or failure of current year's tillers to emerge, there may not have been an exchange of rankings at all. In cases where *S. nutans* tiller densities declined, the dynamics of the two species became synchronous, declining in parallel over the growing season (Figure 1). Plots that were observed to have diminished asynchrony also tended to have reduced tiller density of one of the two species, *S. nutans*, and there was a trend towards lower tiller densities of both species with more variable precipitation and warming. While suggestive of the importance of asynchrony in stabilizing codominance, however, this research was conducted in an area where interannual variability in growing conditions was not controlled, and important environmental variables such as fire frequency and topography (Collins & Calabrese, 2012; Briggs & Knapp, 1995) were held constant among plots, relative to the variability in those factors found regionally (Fay, et al., 2000). As such, it could not demonstrate that risk partitioning was a causal factor of stable codominance, and if it was, whether it would have a stabilizing role in other locations where codominance occurs, but important environmental variables differ. This previous work therefore represents context for improved understanding of mechanisms of codominance. Moreover, as codominant species, *A. gerardii* and *S. nutans* play important roles in ecosystem function, and the degree to which their populations are stable is reflected in the stability of the tallgrass prairie (Smith & Knapp, 2003). A greater understanding of the factors that influence their population dynamics, and of the strategies they wield to exploit or allay these factors, will enhance our knowledge of the tallgrass prairie ecosystem and how its functioning may differ under climate change.

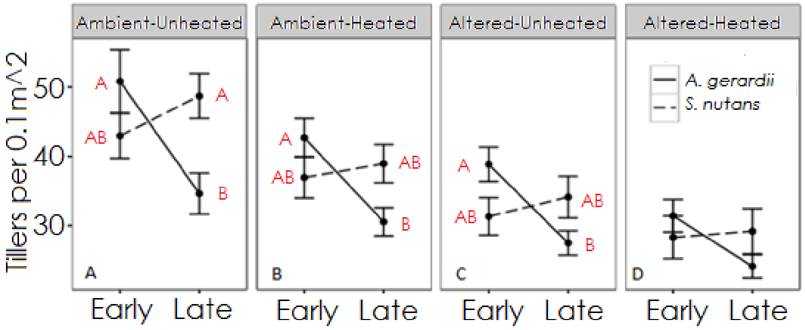

Figure 1: Tiller densities at early and late growing seasons. Averaged across both plots within treatments, and across years of the study. While *A. gerardii* typically is the more abundant species in the early season under ambient conditions, it declines in number to become the lower-density species by season's end. *Sorghastrum nutans* typically increases in density over the growing season, despite the loss of some tillers that were recruited during the early season. The amplitude of the dynamics is muted, particularly when both increased temperature and rainfall variability are combined.

As a corollary to determining whether asynchronous tiller dynamics occur over a range of conditions where *A. gerardii* and *S. nutans* are dominant, I sought to determine whether these species demonstrate similar dynamics under alternate climate conditions where they are not codominant, as this would suggest whether those dynamics could be responses to competition with one another where they are, or whether they may be environmentally driven. I conducted tiller density surveys both in mesic locations in Kansas where the species are codominant and xeric locations in northern Colorado, where neither species is considered dominant and populations are smaller and more isolated. The purpose of these surveys was to determine the degree to which the tiller density dynamics observed in Kansas populations occur independently of the competitive matrix found there. If there is variability in the dynamics, it would begin to suggest that that either populations have locally adapted tillering patterns, or that the trait is plastic and environmentally driven. Such an observation would remain inconclusive due to the environmental differences between sites, but it would represent substantial motivation for a future common garden experiment to explore genetically-based geographical differences in tillering strategies.

Summary of 2017 findings:

Early-season sampling:

Early-season sampling took place concurrently with site establishment. Stems and tillers were counted by hand in each subplot, with each stem or tiller categorized as either *A. gerardii*, *S. nutans*, other late-season tall grasses (LSTG), other grasses (OG), or forbs. Species classified as LSTG included *Panicum virgatum, Bouteloua curtipendula, Schizachyrium scoparium,* and *Sporobolus spp*. Species classified as OG included *Bromus inermis, Bromus tectorum, Bouteloua gracilis, Poa pratensis, Pascopyrum smithii, Carex spp., Buchloe dactyloides, Koeleria macrantha*, and unidentified grass species.

Results:

On average, both *A. gerardii* and *S. nutans* were the most numerous single species in their respective survey sites, but those species collectively categorized as OG made up the most numerous overall. Those categorized as LSTG were the least numerous (Figure 2) in both site types, while forbs had similar densities. While subplots were selected for the presence of either *A. gerardii* or *S. nutans*, and not the other, some of the *S. nutans* subplots did not fully exclude *A. gerardii*, owing to similarity of appearance and the latter's occasionally high local abundance. No *S. nutans* individuals were found in any *A. gerardii* subplots. Because these plots were selected based on species presence, these results are biased towards the respective species and do not reflect actual site abundances.

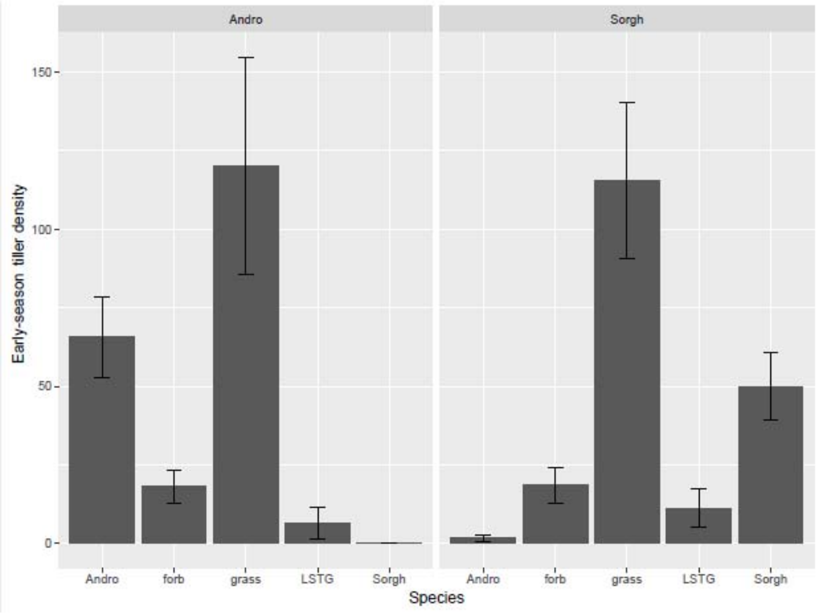

Figure 2: Average early-season tiller densities (tillers/0.1m^2) in *A. gerardii* subplots (left) and *S. nutans* subplots (right). Does not represent regional densities.

Late-season sampling:

In August and September, each of the sites was surveyed again to determine the changes in density in each category over the growing season. In general, the subplots proved more difficult to find than anticipated, resulting in a longer re-sampling period than was ideal. Additionally, some of the roofing nails used as subplot markers were discovered to have been removed and relocated, presumably by rodents. In these instances, I used my best guess to approximate the exact location and orientation of the subplots.

Results:

Tiller densities in the late season were not significantly different from those in the early season, when comparing across all plots (Figure 3). However, when plots are split by soil moisture class estimations including dry (JP, upland SBC, unirrigated SCC, and upland Reservoir Ridge in Fort Collins), moderate (lowland SBC, Pineridge in Fort Collins, Maxwell in Fort Collins, lowland Reservoir Ridge in Fort Collins) and wet (irrigated SCC, marshy hillside SBC, VVN, and Coyote Ridge in Fort Collins, and Poudre Canyon), some dynamics emerge. These plot types were designated based on factors such as topography, community composition, and biomass estimation.

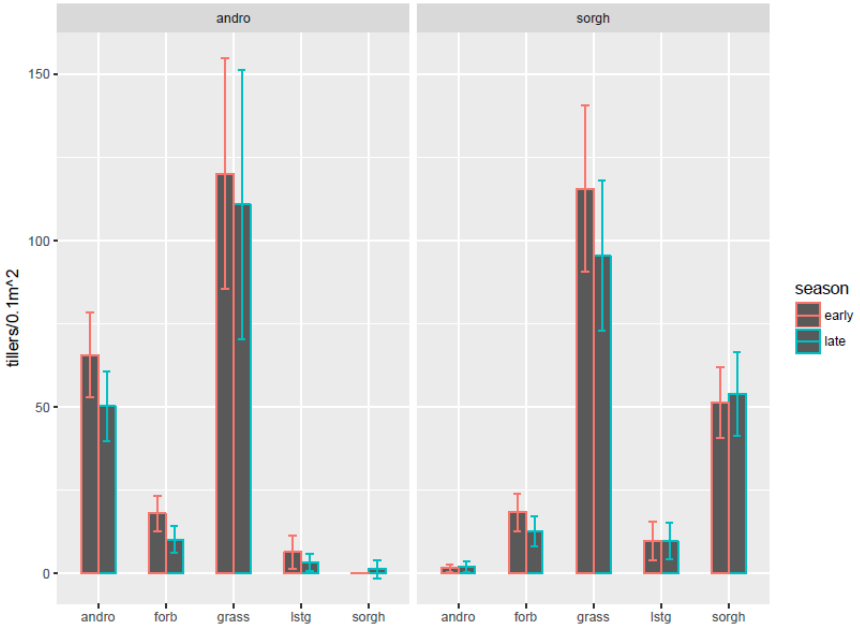

Figure 3: Comparison of early and late season tiller densities in 2017, averaged over all soil types.

While the densities remained statistically similar within soil moisture types and between seasons, the change in tiller density was positive for *S. nutans* in wet plots but remained stable in moderate and dry plots after correcting for differences among plots in early-season tiller densities (Figure 4). Tiller densities of *A. gerardii* declined in all soil moisture types except wet, where they remained stable. Other dynamics included a decline in forb density in dry and moderate plots, a decline in OG densities in moderate plots and in the dry plots of *S. nutans* sites, and a decline in LSTG densities in the moderate plots of *A. gerardii* sites.

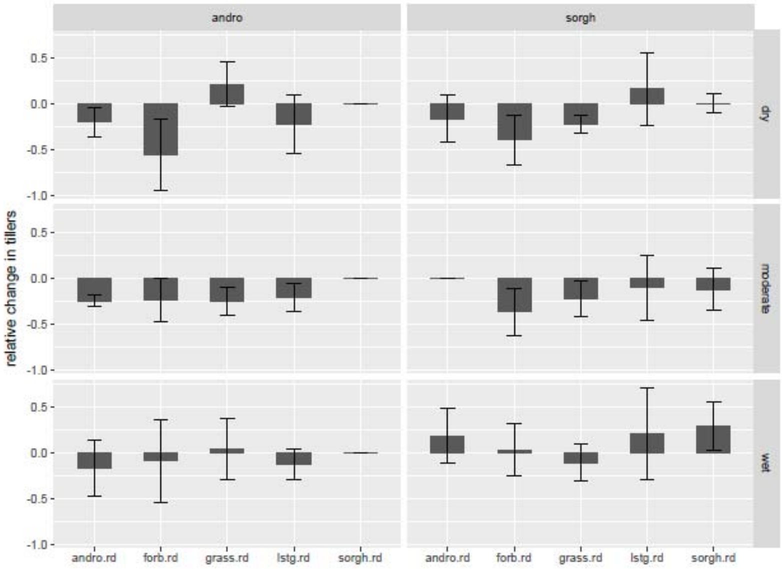

Figure 4: Seasonal tiller density dynamics, separated by perceived average soil type (dry, moderately wet, and wet) in 2017.

Summary of 2018 findings:

In 2018 this study was expanded and altered in several ways. While in 2017 we observed that *S. nutans* density increased during the growing season only in the subjectively-grouped wet plots, and *A. gerardii* densities declined in all plots except the wet plots, we sought in 2018 to establish causality in the relationships between precipitation and these dynamics. With the financial support of City of Boulder Open Space and the OSMP Funded Research Program, we added late-season water additions to one subplot out of two in each of the 40 plots. This consisted of weekly application of 8.8in. water per 20x50cm subplot beginning on July 13th and ending on August 24th, one week prior to the late-season density measurements. In all, 7 water applications were made to each treatment subplot, adding a total of 62in. of rainfall above ambient (8.59in).

Because ambient-level soil moisture was expected to vary considerably between plots, these additions were supplemented with soil-moisture monitoring. While we had intended to make this monitoring continuous in a subset of plots with the installation of below-ground soil-moisture sensors and dataloggers, the units unfortunately could not be made functional in time to test and install them before the water additions needed to begin. Instead, soil moisture measurements were taken using a portable sensor in two locations of each subplot prior to early-season sampling (April 12th), during early-season density sampling (June 6th-11th), once per week during the water addition treatment period (July 13th-August 24th), and during the late-season density sampling (August 31st – September 3rd).

Finally, two of the sampling sites (each with 2 plots) were relocated in 2018, due to the discovery of an unfortunate misplacement of the sites in a designated bird nesting area. These plots were referred to as Boulder Creek G and Boulder Creek H in 2017. One of the replacements (now Boulder Creek I) was located further west along the Boulder Creek Trail, at 39.947033, - 105.25721. The second replacement site was selected at the Van Vleet property (now Van Vleet North B) in a lowland area located at 39.969014, 105.218979. Both sites were reestablished for measuring *S. nutans* density dynamics. Additionally, a subplot in a site outside of the City of Boulder Open Space properties, located at Coyote Ridge Natural Area south of Fort Collins ("Coyote", plot 2, subplot 2) was burned without notice in 2017 and the ramets of *A. gerardii* within the subplot did not recover. An alternative subplot was established within the plot ("Coyote", plot 2, subplot 3) for both early and late season 2018 sampling. While the remaining Coyote Ridge plots and subplots were burned as well, the *A. gerardii* ramets within them tillered successfully.

Results:

We compared the climate patterns of 2017 and 2018 and found striking similarity between the two years. Total growing season (designated as March-August) precipitation volumes were both below long term average (1981-2010), with 2017's volume at 64% (8.71in) and 2018's at 63% (8.59in). Both growing seasons had only 4 days with precipitation above 0.5in, two in their early seasons (March-May) and two in the late seasons (June-August). Most of the precipitation deficit occurred in the late seasons of both years, with the 2017 volume at 32% and the 2018 volume at 53% of the late-season long-term average. The average maximum temperatures for the growing seasons were also quite similar and were just slightly below long-term average (99%, 89.7°F in 2017, 88.17°F in 2018). Both early seasons were slightly cooler than average, and both late seasons were slightly warmer than average. Given the remarkable similarity in climate between years, we did not anticipate much of a difference in the tiller density patterns of the study species. Further, we did not expect *S. nutans* tiller densities to increase significantly in any but the wettest plots, given dryer than average conditions in both late seasons.

We found that in control subplots (figures 5 & 6, left columns) there were no significant within-species differences in early or late tiller densities of either *A gerardii* (figure 5), or *S. nutans* (figure 6) between 2017 and 2018. We also did not see any increases in *S. nutans* tiller densities from early to late season in any but the wettest plots in 2017, and in no plots in 2018. These findings confirm our expectations given the similarity of the climate patterns between years and the below average precipitation in the late-seasons of each.

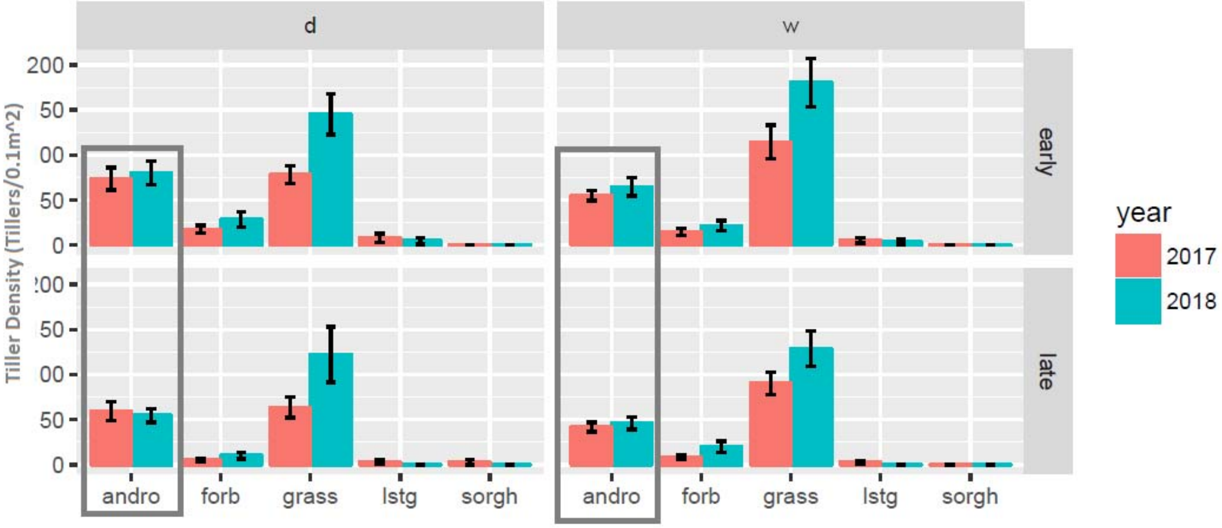

Figure 5: Early and late tiller densities in *A. gerardii* observation plots in 2017 and 2018. The left column represents control subplots, and the right column represents watered subplots, though these plots were only watered in 2018. We do not see any significant differences between the 2017 and 2018 early- or late-season tiller densities of *A. gerardii* (andro) in either the control or watered treatments.

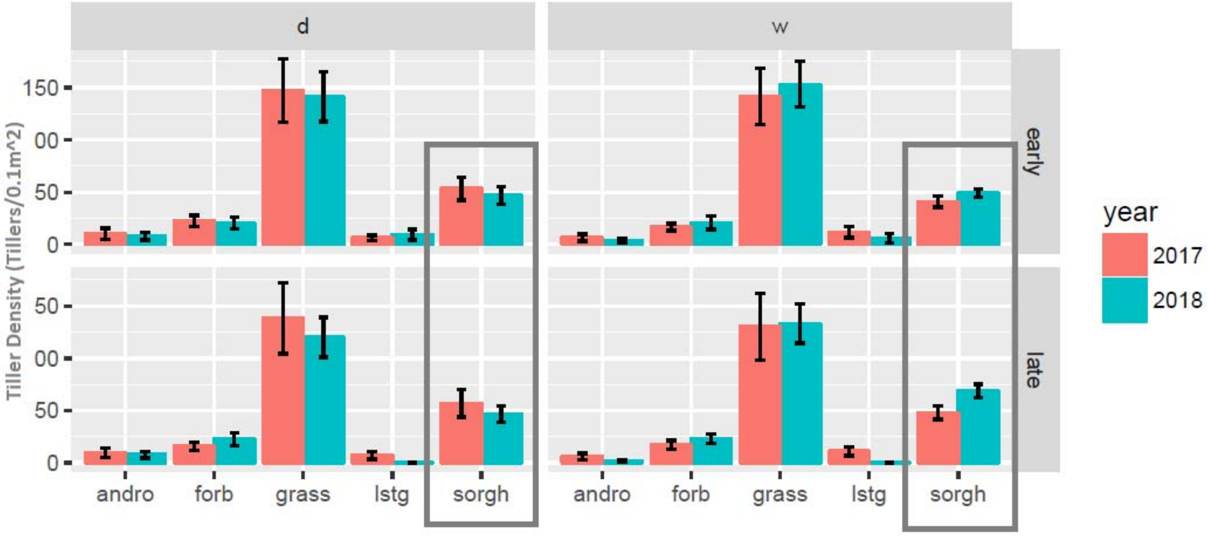

Figure 6: Early and Late tiller densities in *S. nutans* observation subplots in 2017 and 2018. The left column represents control subplots, and the right column represents watered subplots, though these plots were only watered in 2018. Plots were originally designed to contain only either *A. gerardii* or *S. nutans*, but the difficulty of finding *S. nutans* populations necessitated the inclusion of a small number of *A. gerardii* tillers in some subplots. In the control subplots, we see no significant difference in the early or late season *S. nutans* tiller densities (sorgh). However, we see a substantial increase in late-season tiller densities of *S. nutans* in 2018 compared to that in 2017, in the watered subplots.

In 2017, prior to the application of the watering treatment, watered subplots in the ambiently dry and moderate plots did not show any seasonal increase in *S. nutans* tiller densities in 2017 (figures 5 & 6, right columns), though there was an increase in *S. nutans* tiller densities in the wetter plots (those near water sources, or at the bases of hillsides). However, after the application of the water treatments in 2018 we saw increases in tiller densities of *S. nutans* in all three plot types, though there was not a significant difference in the dynamics in the wet plots compared to 2017.

In contrast, we did not observe differences between 2017 or 2018 *A. gerardii* early- or late-season densities, regardless of watering treatment. Further, we did not see significant differences in the seasonal dynamics between years, regardless of treatment. This suggests that the late-season watering treatment had no effect on the tillering dynamics of *A. gerardii*, neither causing new tillering, nor preventing tiller mortality. When grouped by the subjectively classified plot types, however, we did see a larger seasonal decline in the wetter control plots in 2018 than in 2017. This may be a result of the somewhat dryer early season in 2017 (though both early seasons were well below average) and *A. gerardii's* greater early-season investment relative to *S. nutans.* Alternatively, this may be evidence of a cumulative negative effect of dry conditions occurring over sequential seasons, as the late season in 2017 was dryer than in 2018.

While we did observe a significant effect of the watering treatment on *S. nutans* tiller density dynamics, we were surprised to find that the relationship between those dynamics and the average of the late-season soil moisture measurements taken after watering were only marginally significant. We analyzed a simple linear regression model with the change in *S. nutans* tiller densities from the early to the late-season measurements (DensityChange, Late Density – Early Density) as the dependent variable and the average late-season soil moisture percentage (avgVWC), along with the average percent increase in soil moisture immediately after the application of water (IncAvg) and the percent decline in soil moisture that had occurred 5 minutes after watering (DecAvg) as the independent variables (model: DensityChange = avgVWC x IncAvg x DecAvg). We found that IncAvg and DecAvg were not associated with DensityChange, while avgVWC was only marginally associated ($p = 0.0723$). This was quite surprising given the effect of the treatment on DensityChange ($p = 0.0012$, adjusted $R2 = 0.224$, estimated average increase of 20.1 tillers per subplot in watered treatment), and we believe that the discrepancy of these observations may be owed to the crudeness and punctuated nature of our soil water measurements. The soil types in the subplots ranged from sandy to clayey, and we expect that the ability of different subplots to retain and supply added water to the tillers varied likewise. Additionally, some of the sites had surprisingly low soil moisture measurements, particularly those near bodies of water (e.g. Poudre Canyon, Van Vleet North 1). We suspect that plants in these sites are obtaining most of their water from groundwater, resulting in the soil moisture measurements taken at 10cm depth to have little association with density dynamics at these sites.

Despite the failure to capture an association between average late-season soil moisture measurements and the amplitude of tiller density dynamics, we feel confident that the addition of water to *S. nutans* populations in the late season results in enhanced tillering, while the same treatment has no effect on the tillering or thinning of *A. gerardii* populations. This supports our hypothesis that these species are differentially sensitive to environmental variability occurring at specific times of the growing season, and that this may offset negative effects of competition between them and stabilize their populations in regions where climatic conditions are variable both intra- and interannually.

Based on these findings, we believe that the *S. nutans* populations in the Front Range are more vulnerable to dry conditions than those of *A. gerardii*. If these populations of *S. nutans* are dry-adapted ecotypes relative to populations further east (e.g., eastern Kansas), they may be valuable in restoration efforts in those locations should their climates become dryer through climate change. However, if the climate along the Front Range also becomes dryer, populations of these ecotypes may be overwhelmed *in situ*. We believe it may be of considerable interest to collect propagules of the Front Range *S. nutans* populations for the development of drought-resistant cultivars that can be used for restoration, before local extinction through climate change has the chance to occur. On the other hand, the robust perseverance of *A. gerardii* in both the watered and control treatments suggests that they are in less danger of extinction from more severe or prolonged dry conditions. For these populations, we instead recommend continued conservation efforts aimed at minimizing disturbance from foot traffic and encroachment of invasive species such as *Bromus inermis*.

Discussion and Outlook:

This project was originally designed as a comparison between the dynamics of the focal species in two contrasting environments, the mesic tallgrass prairie of eastern Kansas, and the xeric tallgrass prairie of central Colorado, to see if the dynamics observed in Kansas, where they are codominant, could be observed in Colorado, where they are not. We were surprised in 2017 to find that while the dynamics of *A. gerardii* were largely consistent, those of *S. nutans* depended greatly on precipitation (indirectly) and soil moisture content (directly). This led to a change to the study in 2018 in which we added water to half of the subplots, which confirmed that *S. nutans* density dynamics were largely dependent on late-season water availability, while those of *A. gerardii* were not. Unfortunately, we couldn't establish a more direct link between water availability and these dynamics do to failures to build a functional continuous monitoring system in a timely fashion. However, having already obtained the materials to do so, and having made nearly all the progress required in assembling the monitoring units, we would like to extend the study for a 3rd growing season in 2019. The study would proceed similarly to the 2018 design, with only a switch in which subplot within each plot receives the late-season watering treatment. This would also afford the opportunity to more firmly establish the causality of the watering-tillering relationship, as we would expect the subplots that were watered in 2018, but not watered in 2019 to have lower tillering rates of *S. nutans* than the subplots to be watered in 2019.