

THESIS

CLIMATE CHANGE IMPACTS ON POPULATION DYNAMICS IN
TALLGRASS PRAIRIE: IMPLICATIONS FOR SPECIES CODOMINANCE

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ABSTRACT

CLIMATE CHANGE IMPACTS ON POPULATION DYNAMICS IN TALLGRASS PRAIRIE: IMPLICATIONS FOR SPECIES CODOMINANCE

Two grass species, *Andropogon gerardii* and *Sorghastrum nutans*, together account for the great majority of individuals, biomass, and possibly genetic diversity in plant communities of the tallgrass prairies of the Great Plains, US. As competitors with similar functional traits and what appears to be overlapping niches, it is not clear what mechanisms facilitate their co-dominance, but it may rely on the high variability of environmental conditions that characterize grassland ecosystems. Because these abundant grasses strongly influence plant community structure and ecosystem function, it is critical that we understand the factors influencing the population dynamics of these species, and how climate change might alter those relationships. We found an asynchrony in population dynamics in which *A. gerardii* begins each growing season at higher tiller densities, with attrition of tillers starting mid-season. Concurrent gains of *S. nutans* tillers results in *A. gerardii* becoming the less abundant by the end of most growing seasons. We hypothesized that this differentiation in tillering strategies causes each species to be vulnerable to unfavorable environmental conditions during different parts of the growing season, thus enabling their coexistence by preventing an inter-annually consistent competitive advantage of either species. We found that greater tiller density asynchrony was associated with higher population densities of *S. nutans* and of aggregate tiller densities of both species. Experimental increases in temperature and rainfall variability reduced population-level asynchrony while exacerbating population declines and overall community productivity, suggesting this mechanism of co-dominance may rely on current levels of environmental variability, and may be vulnerable to projected increases in that variability with climate change.

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DEDICATION

To Fred Montague, who taught me how to find hope within the cracks.

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CHAPTER 1. CLIMATE CHANGE IMPACTS ON POPULATION DYNAMICS IN TALLGRASS PRAIRIE:
IMPLICATIONS FOR SPECIES CODOMINANCE

INTRODUCTION

For more than a century, the factors that promote coexistence have received considerable attention in the ecological literature (Grinnell, 1904; Gause, 1934; MacArthur, 1958; Hutchinson, 1961; Grant, 1972; Chesson, 2000; Adler, et al., 2007; Hubbell, 2008; Tilman, 1990; Angert, et al., 2009). Most investigations have limited their focus to species that are asymmetric in their abundances, often revisiting the question of how rare species avoid competitive exclusion by a dominant species (MacArthur, 1958; Hutchinson, 1961; Chesson, 2000). However, many communities include two or more competing species that are found in similarly high abundances within and between sampling locations, leaving open the question of how species not only coexist, but co-dominate.

One factor used to explain coexistence is temporal niche partitioning, or more specifically temporal asynchrony in resource use (Anten & Hirose, 1999; Chesson, 2000; Silvertown, 2004). In temperate regions where plant growth cannot occur year-round, it is logical to assume that the dominant species will be those that can maximize the length of time during which they are actively photosynthesizing. To do otherwise risks being overtaken by similarly productive species that can take advantage of a greater proportion of the growing season (Carothers & Jaksic, 1984). In mixed grass prairie, C3 grasses partition their growth early and late in the growing season when temperatures and moisture are favorable for growth, whereas C4 grasses are active during the hottest and driest months of the growing season (Williams, 1974; Kemp & Williams, 1980; Singh, et al., 1983). This results in coexistence of both C3 and C4 grasses via partitioning of use of space and other resources in time. Yet, this raises an interesting challenge for species that are concurrently abundant or co-dominant, as their period of resource use overlaps. In this case, it may be that a subtler temporal niche partitioning or asynchrony in resource use may be sufficient for facilitating co-dominance.

In the mesic regions of the Great Plains, the two perennial, rhizomatous C4 grasses, *Andropogon gerardii* (Big Bluestem) and *Sorghastrum nutans* (Yellow Indiangrass), are generally the first and second most abundant species (Freeman, 1998), respectively. Together, they contribute >80% of community aboveground productivity (ANPP) and canopy cover (Smith & Knapp 2003). While *A. gerardii* is regionally more abundant than *S. nutans* (Smith & Knapp, 2003), either species can have greater population densities on a local scale (Brown, 1985; Hartnett, 1996; Smith & Knapp, 2003), and both are consistently found well-mixed within the same local communities. They also have many traits in common, both qualitative (Lauenroth & Adler, 2008; Brown, et al., 2010) and quantitative (Forrestel, et al., 2014), including tall stature (>1 m tall when flowering) and maintaining and recruiting primarily vegetatively from an extensive belowground bud bank (Hartnett & Keeler, 1995; Benson & Hartnett, 2006). In addition, both grasses respond positively to spring fires (Weaver & Rowland, 1952; Knapp & Hulbert, 1986; Silletti & Knapp, 2002; Towne & Kemp, 2003; Benson & Hartnett, 2006; Towne & Kemp, 2008) and nitrogen addition (Berg, 1995; Silletti & Knapp, 2001; Mulkey, et al., 2008), but negatively to shading (Lett & Knapp, 2003; Bowles, et al., 2011) and grazing by large mammals (Hartnett, 1996; Silletti & Knapp, 2002; Forrestel, et al., 2015).

Given their similarities in physiology, morphology, and resource requirements, niche differentiation alone appears not to be sufficient to explain the coexistence of these grasses. The co-dominant relationship of *A. gerardii* and *S. nutans* is therefore enigmatic, but may in part result from relatively subtle differences in temporal niche partitioning facilitated by differing tillering strategies. Under current climate conditions, *A. gerardii* tiller emergence begins and ends during a relatively brief period in Late-April to Early-May (Ott & Hartnett, 2012). In contrast, although most their tillers emerge concurrently with those of *A. gerardii*, *S. nutans* bud activation is maintained at a steady but reduced rate for the remainder of the growing season (Benson & Hartnett, 2006). If these contrasting patterns result in intra-annually asynchronous tiller densities, they may play an important role in co-dominance by generating subtle differences resource use and in vulnerability to growing season environmental variability, while enabling both species to remain photosynthetically active for the entirety of the growing

season. Indeed, the tallgrass prairie is subject to high inter- and intra-annual variation in precipitation (Goudie & Wilkinson, 1977). Within season, precipitation varies because of differences in the size of rainfall events, their pattern and the length of dry periods (Knapp, et al., 2002). The subtly different tillering strategies may therefore promote coexistence of the dominant grasses as climate conditions vary from one year to the next.

The potential asynchronous tillering response of the co-dominant grasses may have other consequences as well. The insurance effect hypothesis states that functionally redundant species stabilize community function, as any decline in function that results from the loss of one species can be offset by a compensatory increase in function of another (Naeem & Li, 1997). However, this stabilizing effect should only occur when those species have asynchronous responses to environmental variability, such that they do not decline in parallel to unfavorable conditions (Chesson, 2000; Loreau & de Mazancourt, 2013). This effect should be most apparent among co-dominant species, as they contribute the most to ecosystem function and are the most capable of replacing lost functionality (Smith & Knapp, 2003; Chang & Smith, 2014; Forrestel, et al., 2015). It may then be that if asynchronous dynamics promote co-dominance between *A. gerardii* and *S. nutans*, those effects may extend beyond the population level to enhancing overall ecosystem function and stability.

Climate change projections indicate that temperatures and variability in intra-annual precipitation in the Great Plains are likely to increase over the next half-century, with the latter leading to both longer periods between rainfall events and larger volumes of rainfall during those events (IPCC, 2012). If coexistence between *A. gerardii* and *S. nutans* relies on asynchronous tillering responses to the current variability in intra-annual precipitation, that relationship may be vulnerable to change particularly if the future conditions are more variable and compounded by warmer temperatures. Because of the importance of these species, we began monitoring their population dynamics in 2005 within an experiment that both increased temperatures and altered intra-annual variability of growing season precipitation, while keeping the total volume of rainfall consistent with that of ambient conditions (Fay, et al., 2000; Fay, et al., 2011). Over the study period, this increased-variability treatment resulted in extended dry periods and larger

rainfall events, with both occurring at times during the growing season differing considerably from ambient conditions (Knapp et al. 2002).

The expectation was that if climate variation plays a role in influencing co-dominance of *A. gerardii* and *S. nutans*, then increased variability in precipitation, when combined with climate warming, may alter population dynamics of these two species with potential consequences for their coexistence. To address this, eight years of measurements of population size, collected as tiller densities, were analyzed to determine (1) if under ambient conditions the two species demonstrated population-level asynchrony intra-annually as a result of different tiller recruitment patterns, (2) whether that asynchrony is muted or amplified when precipitation variability and/or temperatures are increased, (3) if changes in intra-annual population-level asynchrony with altered precipitation and warming are associated with inter-annual changes in population densities of either species or their aggregate density, (4) and if overall community-level function is likewise affected by such changes.

METHODS

STUDY SITE:

This study took place at the Konza Prairie Biological Station, located in northeastern Kansas, USA, within the Rainfall Manipulation Plots (RaMPs) experiment (Fay, et al., 2000). Mean monthly air temperature during mid-growing season (July) is 27°C, and intra- and inter-annual variability in both temperature and precipitation is considerable for the region (Hayden, 1998). The study site encompasses intact, tallgrass prairie dominated by C₄ grasses, particularly *Andropogon gerardii* and *Sorghastrum nutans* (Knapp, et al., 1998; Fay, et al., 2000). The area encompassing the experiment is ungrazed and has been burned annually in mid-March, prior to any sampling, since 1979.

EXPERIMENTAL DESIGN AND SAMPLING METHOD

The RaMPs experiment was begun in 1998 to assess the effects that predicted climate change-induced alterations in rainfall variability (IPCC, 2012) will have on tallgrass prairie plant community

structure and ecosystem function (Fay, et al., 2000). RaMPs consists of 12 rainfall-exclusion structures placed over intact, native tallgrass prairie. Each of these structures includes a 9 x 14m fixed roof that encloses a 6 x 6m experimental area (termed “RaMP”). This area was divided into 4 plots, each measuring 2x2m. Each plot was further divided into four 1x1m subplots. All rainfall incident on the shelter during the growing season was collected and then immediately applied to the six control (ambient) structures. Rainfall incident on the six altered precipitation treatment structures was collected and aggregated from multiple precipitation events prior to application, such that the altered precipitation treatment would have 50% longer periods between rainfall events without changing the total amount of water applied during the full length of the growing season. Through this rainfall event aggregation, treatment plots experienced statistically extreme rainfall patterns that included longer dry periods and rainfall events that were both larger in volume and fewer in number than in ambient patterns (Knapp, et al., 2002; Smith, 2011). This treatment application was limited to the growing season (approx. mid-Apr to early Sept). The altered precipitation treatment resulted in a reduction in average soil moisture and an increase in soil moisture variability, compared to the ambient-precipitation treatment plots over the course of the experiment (Fay, et al., 2011).

In 2003, a warming treatment was added to each of the ambient and altered RaMPs in one of the 2 x 2 m plots to determine if the effects of increased variability in precipitation might interact with the increasing temperatures also expected with climate change within the region (Fay, et al., 2011; IPCC, 2012). Overhead heat lamps provided continual infrared radiation to the heated plots, resulting in an average 1°C increase over ambient temperatures. Dummy lamps were placed over unheated 2 x 2 m plots (ambient temperature treatment) to control for shading effects. The heat treatment was applied continuously, and year-round. Overall, there were six replicates of each of the four treatment combinations, with the two heating treatments nested within the two precipitation variability treatments.

Population densities of all species were monitored using 20 x 50 cm permanent sampling quadrats located in opposite 1 x 1 m subplots within each heated and unheated 2 x 2m plot. The same subplots were sampled twice each growing season from 2005 to 2013, with the exceptions of 2008, when no

sampling took place, and 2011, when sampling took place only in the early season. Early-season surveys took place over 1-5 days between late May and early July. Late-season surveys took place over 1-8 days between late August and early September. Tiller counts from the two survey frames in each plot were averaged to give an average number of tillers per 100cm² (tiller densities).

All collected data were categorized as either early or late season. Early-season measurements included surveys, temperatures, and rain events that occurred on days between the date of the yearly spring burn and the first tiller density survey. Temperatures and rainfall events that occurred on days between the first and second tiller density surveys were considered late-season. Due to weather constraints, the length of defined early- and late-seasons varied somewhat from year to year (early-season range: 73-115 days, average: 92 days; late-season range: 68-88 days, average: 80 days). Aboveground net productivity (ANPP), estimated by clipping, drying, and weighing, was measured only once yearly from areas adjacent to tiller density survey locations, after each growing season, and those measurements were included in both early- and late-season analyses. ANPP sampling locations were moved from year to year to avoid introducing the effects of repeated clippings.

DATA ANALYSIS

All statistical analyses were performed in R version 3.3.1 (R Core Team, 2016). All linear regression models were generated with the base package function `lm()` with weights set to ordinary least squares. Groups were checked for equal variance using Levene's test before using the function `aov()` to perform analysis of variance (ANOVA).

To determine if *A. gerardii* and *S. nutans* demonstrated differential intra-seasonal tiller dynamics (i.e., differences in early season vs. late season tiller densities), and whether tiller dynamics were affected by the altered precipitation and warming treatments, a repeated measures (year), mixed model analysis was performed, with species, season (early vs. late), and the heat treatment nested within the precipitation treatment. Treatment groups were compared for differences in means following a Tukey adjustment.

Asynchrony of population dynamics was assessed by calculating a modified version of Loreau and de Mazancourt's synchrony (φ) (Loreau & de Mazancourt, 2013), that replaces the variances of biomass with the variances in the number of stems, such that

$$\varphi = \frac{\sigma_{DT}^2}{(\sum_i \sigma_{Di})^2}$$

where σ_{DT}^2 is the variance in the aggregate number of *A. gerardii* and *S. nutans* tillers in a plot over the course of the study, and σ_{Di}^2 is the variance in the number of stems of species *i*. If all variance in the aggregate number of tillers is accounted for by variance in the tiller densities of the component species, then the dynamics of those species can be considered to be synchronous. However, if the dynamics of the species counter-balance one another, such that increases in tiller density of one species from each time point to the next is matched by declines in tiller density of another species over the same time periods, the aggregate tiller density should have low variance, and the dynamics can be considered to be asynchronous. Perfect synchrony is indicated when $\varphi = 1$, and perfect asynchrony when $\varphi = 0$. Synchrony was calculated for each plot and averaged across plots within each treatment. An ANOVA was used to determine if there were differences in mean synchrony between treatment groups.

To determine whether plot-level, inter-annual trends in tiller densities for either species, or their aggregate tiller densities, were associated with intra-annual asynchrony, we used the values of synchrony φ , as calculated above, for each plot, as the independent variable in a linear regression model predicting the season-maximum tiller densities observed in the final year of the study, 2013. Season-maximum tiller densities were always those that were recorded in the spring for *A. gerardii*, while the date of maximum tiller density for *S. nutans* depended on both year and plot.

To determine whether increased temperature and/or rainfall variability affected population densities over longer periods, one-way ANOVA was used to test whether the treatment groups had reached a difference in their average year-maximum number of tillers of each species per plot, or of their aggregate number of tillers, by the final year of the study.

To determine if community-level function is affected by changes in population-level, intra-annual asynchrony between *A. gerardii* and *S. nutans*, we looked for associations between plot-level synchrony ϕ , and either plot-level community above-ground net primary productivity (ANPP) averaged over 2005-2013, or plot-level ANPP measured only in 2013, the final year of the study. The former was done to minimize the influence of inter-annual variability in our analysis, while the latter was done to more directly examine whether synchrony might affect long-term trends in community productivity. The same was done for the plot-level coefficient of variability (CV) of ANPP across years of the study to determine if synchrony was associated with the stability of productivity from year-to-year. One-way ANOVAs were also used to determine if productivity averaged across years, or in 2013, differed by treatment, or if the CV of productivity differed by treatment.

RESULTS

TILLER DYNAMICS UNDER CURRENT CONDITIONS

Analysis of average tiller density dynamics using two-way ANOVA indicated that there was significant interactive effect of species and survey date ($p < 0.01$), and post-hoc comparisons found a significant difference between the number of early and late season tillers of *A. gerardii* under ambient conditions (estimated late density – early = -16.24 tillers/0.1m², $p < 0.01$, Fig. 1A). However, no significant difference between the number of early- and late-season tillers of *S. nutans* was found under ambient conditions (estimated late density – early = 5.76 tillers/0.1m², $p=0.66$) after Tukey adjustment. Likewise, while the average number of tillers of *A. gerardii* were significantly lower than those of *S. nutans* by late season (estimated late *S. nutans* density – *A. gerardii* = 14.11 tillers/0.1m², $p = 0.028$), their densities were not significantly different during the early season (estimated early *A. gerardii* density – *S. nutans* = 7.88 tillers/0.1m², $p = 0.40$). Overall, while the number of *A. gerardii* tillers significantly decreased from early to late season, there was only a marginal trend of increase in *S. nutans*. The tiller densities were only marginally different early in the season, but these dynamics resulted in significantly different tiller densities by the late season.

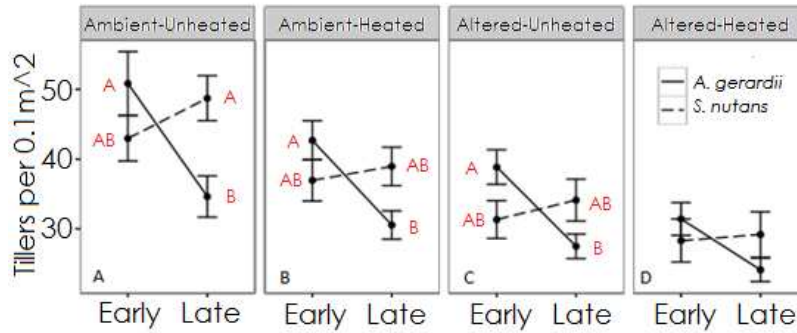


Figure 1: Stem densities at early and late growing seasons. Averaged across both plots within treatments, and across years of the study. While *A. gerardii* typically is the more abundant species in the early season under ambient conditions, it declines in number to become the lower-density species by 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. Under treatment conditions, the amplitude of the dynamics is muted, particularly when both increased temperature and rainfall variability are applied.

IMPACTS OF INCREASED PRECIPITATION AND WARMING ON TILLER DYNAMICS

A one-way ANOVA found a significant difference in synchrony ϕ among treatment groups ($p = 0.045$). Post-hoc comparisons of treatment groups did find a significant difference between the altered-heated (average $\phi = 0.51$) and the ambient-unheated (average $\phi = 0.80$) treatment groups, with an increase in average synchrony in the altered-heated plots of 28% over ambient. No other significant differences in synchrony were found between treatment groups.

Two-way ANOVAs and *post-hoc* comparisons indicated that there were significant differences between early- and late-season tiller densities in ambient-heated plots (estimated 12.2 *A. gerardii* tillers lost / 0.1m² / season, $p < 0.01$, Fig. 1B), and altered-unheated plots (estimated 11.4 *A. gerardii* tillers lost / 0.1m² / season, $p < 0.01$, Fig. 1C), but not in the altered-heated plots (Fig. 1D). No significant differences were detected between sampling periods for either species in either the ambient-heated or altered-unheated treatments. Nor were any significant differences detected between the tiller densities of *A. gerardii* and *S. nutans* within either part of the growing season under the heated and/or altered rainfall treatments. However, two-way ANOVAs using data sets including only the altered-unheated and altered-heated plots did not meet the assumption of equal variance among groups, so it is possible there were differences among some groups that could not be detected.

Linear regression analysis revealed that the association between plot-level synchrony φ and tiller densities in 2013 was species dependent (Fig. 2A). Greater synchrony φ was associated with lower tiller density of *S. nutans* (coeff = -54.38, adj. $R^2 = 0.30$, $p < 0.01$), but no significant association was detected between *A. gerardii* tiller density and synchrony. The aggregate stem density of the two species in 2013 had a significant negative relationship with plot-level synchrony (coeff = -95.26, adj. $R^2 = 0.34$, $p < 0.01$).

Analysis of variance did not find a significant effect of the treatments, and after a Tukey adjustment for multiple comparisons, no significant differences in tiller densities were found between any of the treatments for either species. Non-overlapping standard errors in mean *S. nutans* and aggregate tiller densities were observed when comparing ambient and altered-unheated plots (Fig. 2B).

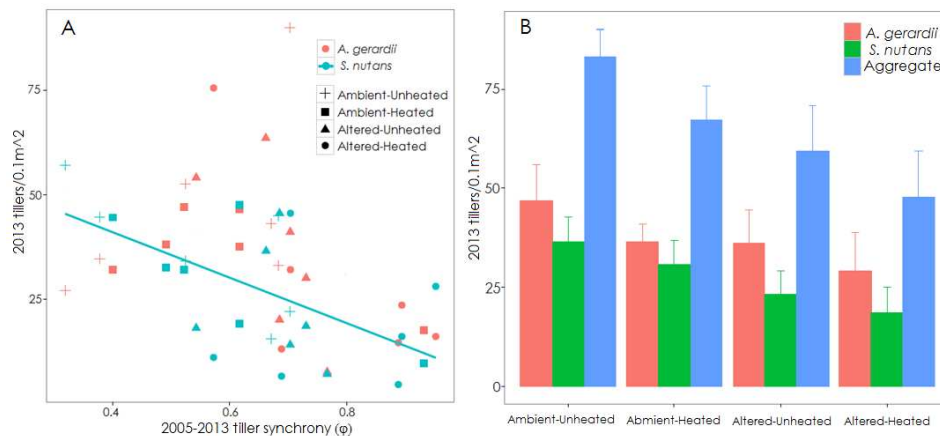


Figure 2A: Plot-level, season-maximum tiller density observed in the final year of the study, 2013, as a function of plot-level synchrony calculated from observations from 2005-2013. As synchrony increases, the variability in aggregate tiller density becomes more similar to the sum of variabilities of the component species. With greater synchrony, the stability of coexistence between the species is expected to decline. The observed negative relationship between synchrony and is statistically significant for *S. nutans*, but not for *A. gerardii*.

Figure 2B: Average plot-level season-maximum tiller densities observed in the final year of the study, 2013, by treatment type. Error bars are standard errors of the means. While standard errors are non-overlapping, after correcting for multiple comparisons, no significant differences were found between treatments for either species, or for their aggregate tiller density.

Linear regression analysis indicated that there were no significant relationships between plot-level average synchrony (φ) and overall average community above-ground net primary productivity

(ANPP), either averaged across years, or in the final year of the study (2013), nor was there a significant relationship with the CV of productivity across years (Fig. 3).

One-way ANOVAs did not find significant differences between treatment groups in either average ANPP, 2013 ANPP, or the CV of productivity.

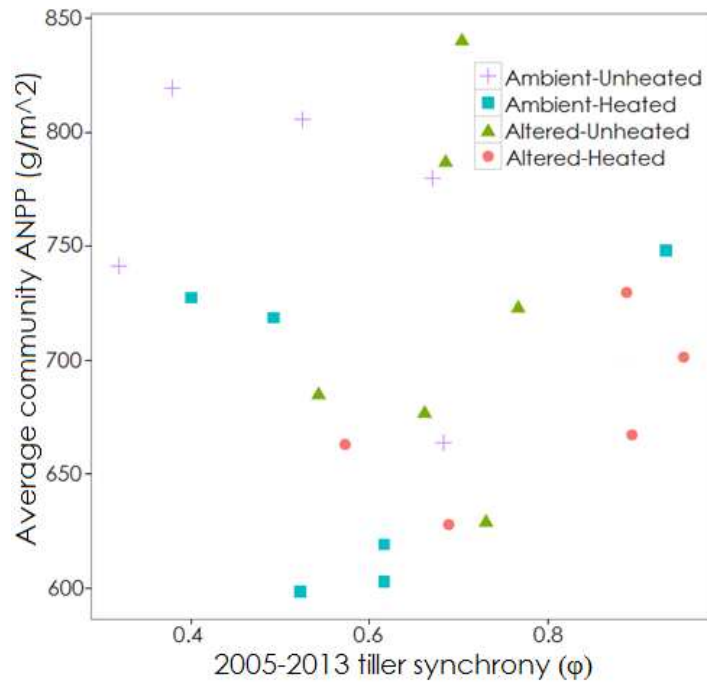


Figure 3: Average whole-community, plot-level productivity (ANPP) as a function of the tiller density dynamic synchrony between *A. gerardii* and *S. nutans* within those plots. No significant relationship was observed between the tiller density dynamic synchrony of the dominant species and community productivity.

DISCUSSION

The factors that control plant population dynamics in the tallgrass prairie have received thorough consideration over the past century (Hartnett & Fay, 1998). Factors that have been associated with variability in the population densities of warm-season grass species like *A. gerardii* and *S. nutans* include variabilities in fire frequency (Knapp & Hulbert, 1986; Hulbert, 1986; Hulbert & Wilson, 1983; Svejcar, 1990), grazing intensity (Vinton & Hartnett, 1992; Hartnett, et al., 1996; Hartnett, 1989), competition (Hartnett, 1993) and climate (Hartnett & Keeler, 1995; Silletti & Knapp, 2002; Knapp, 1984). While

responses to these factors contribute to variability in population densities of dominant C4 grasses, their dynamics are stable relative to those of C3 grasses and forbs (Hartnett & Fay, 1998). It is the nature of this stability that this study sought to address, as the principles provided by modern coexistence theory for explaining the coexistence between dominant and subdominant species do not appear sufficient for describing how functionally redundant, co-dominant species maintain stable coexistence. While long-lived species may appear to have stable population densities on relatively short time scales, and

We found mixed evidence that the population-level intra-annual tiller density dynamics of *Andropogon gerardii* and *Sorghastrum nutans* are asynchronous with one another (Fig. 1A). While the tiller densities of *S. nutans* may increase from early to late season, the trend is not statistically significant. In contrast, a large proportion of *A. gerardii* tillers are consistently lost over the course of the growing season, providing the primary driving force behind the asynchronous relationship with *S. nutans*. It should be noted, however, that the tiller dynamics of *A. gerardii* depend only on mid-season tiller losses, while the dynamics of *S. nutans* represents the net result of mid-season recruitment and loss of tillers, which may mask the degree to which *S. nutans* invests in late-season tiller population growth. On average, there does appear to be an exchange abundance over the course of the growing season, as *A. gerardii* begins at higher tiller density, but ends at lower densities than *S. nutans*, though the difference between the species in the early season is only marginally significant. This suggests that if intra-annual environmental variability results in either early- or late-season conditions unfavorable for growth, the two species may be affected asymmetrically.

The amplitude asynchrony of tiller dynamics was reduced by both the increase of temperature and rainfall variability, and was most severely altered in plots that received both treatments (Fig. 1B-D). While *A. gerardii* tiller densities declined during the growing season under the altered precipitation and heat treatments, they did not tend to do so when both of the treatments were applied. Further, though the intra-annual rise in tiller densities of *S. nutans* was not statistically significant under ambient conditions, that increase was even more doubtful under each of the treatment conditions (Figs. 1B-D). Overall, these analyses suggest that changes in variability in precipitation, particularly under warmer conditions,

destabilized the average asynchrony of tiller population dynamics of *A. gerardii* and *S. nutans*. This trend becomes even more clear when examining the tiller densities of the altered-heated plots during the final 5 years of the experiment, during which, in contrast with other treatments, they apparently became largely synchronous in their dynamics (S. Fig. 1).

We looked for associations between tiller densities in the final year of our study, 2013, and the interspecific asynchrony of their dynamics for the prior 8 years, using linear regression analysis. We also looked for associations between 2013 densities and experimentally increased temperature and rainfall variability treatments using analysis of variance. This was done to determine if change in asynchrony resulting from altered environmental conditions could potentially lead to long-term population trends. In our linear regression models, we found that greater synchrony between the population dynamics of *A. gerardii* and *S. nutans* was associated with a more severe decline in the number of tillers of both species (Fig 2A). The results from the analysis of variance were less clear. After adjusting for multiple comparisons, we did not find a significant difference between treatment groups for either species, or for the sum of their tiller densities, but there appears to be a negative trend in the tiller densities of *S. nutans* under heating and increased rainfall variability, particularly when they are both applied. This appears to also be true of the aggregate tiller densities of the two species (Fig 2B). The partial disagreement between these analyses may indicate that factors other than those experimentally imposed may also result in reductions in plot-level asynchrony, but that lowered asynchrony, regardless of its cause, likely stills result in long-term population destabilizations.

Alternatively, the lack of a clear difference in tiller densities between the treatment groups may have been a result of differential densities among plots within treatments at the onset of the experiment. Unfortunately, tiller density measurements did not begin until 7 years after the altered rainfall variability treatment began, and 2 years after the heat treatment began. As such, we do not know what the tiller densities were before either of the treatments were imposed, nor how or if they changed in the years before observations began. Nevertheless, in a follow-up analysis of tiller density declines from 2005 to 2013, relative to observed densities in 2005, we did find a significant difference between ambient plots

and altered-unheated plots in severity of decline of *S. nutans* (39% more tiller loss estimated in altered/heated, $p = 0.032$). We also found a marginally significant difference in declines between ambient and altered-heated plots and (36% more tiller loss estimated in altered-heated, $p = 0.052$, S. Fig. 2A, B). While there was no such significant difference in declines in *A. gerardii* tiller densities, there was a striking increase in variability among plots within each treatment over that among the ambient treatment plots (S. fig 2A). This increased variability might be accounted for as a result of differences in community composition among plots. In the final years of the experiment, some of the plots experienced a rapid, pathogen-generated decline in an abundant forb (*Solidago canadensis*, personal observation), and part of the lost canopy coverage was recovered by tiller population expansions of *A. gerardii*. This resulted in a tiller population increase in some plots where *S. canadensis* was previously abundant, and a decline elsewhere.

This difference among plots may have also been a result of the spatial heterogeneity in genotypes and phenotypes described by Avolio et al. (2013). If this was the case, it would suggest that *A. gerardii* populations in this experiment were less susceptible to the treatment conditions compared to the more uniformly-declining *S. nutans*, not only because of characteristics intrinsic to the species, but also as a result of variability in those characteristics among genets.

Our analyses to determine whether variability in plot-level tiller dynamic synchrony, or our treatment conditions, were associated with differences in community function and/or stability were not indicative of such. Linear regressions did not find a significant relationship between tiller dynamic synchrony in either community productivity (ANPP), or year-to-year variability in productivity, and analysis of variance did not detect any differences in productivity between treatments. Given the high proportion of annual community biomass production accounted for by the productivity of *A. gerardii* and *S. nutans*, and the lower aggregate tiller densities associated with greater synchrony in their tiller density dynamics, we found this to be a surprising result. Three possible explanations may account for this inconsistency.

Firstly, it may be that forbs and other grasses within the communities increased their productivity in response to population declines of the dominants. To examine this possibility, we examined community productivity trends from 2005 to 2013, averaged across plots within each treatment, and compared those to the trends in relative productivity of the dominant species. While average productivity was variable from year to year, there was no long-term trend in any of the treatments (Fig. S4A). Within the altered-heated treatment, however, there was a strong decline in the average relative productivity of *S. nutans* ($-0.13\text{g/g/m}^2/\text{year}$, adj. $R^2 = 0.53$, $p = 0.038$), but not of *A. gerardii* during that time (Fig. S4B). This suggests that at least the decline in *S. nutans* productivity in altered-heated plots was compensated for by increases in productivity of other species, but not increases in *A. gerardii* productivity.

Secondly, because tiller sizes can vary, there may not be as strong a correlation between tiller density and species-specific ANPP as might be assumed. Variability in flowering rates from year-to-year would also contribute to the noise in such a correlation (La Pierre, et al., 2011). Lastly, because tiller densities and biomass were measured in nearby, but non-overlapping subplots, any spatial heterogeneity in either measure would blur signals of association between them. To test for both possibilities, we looked for correlations between plot-level biomass and season-maximum tiller densities for each species across all years and treatments. While there was considerable variability in the relationships, they were significant for both *A. gerardii* ($p < 0.01$, $R^2 = 0.05$) and *S. nutans* ($p < 0.001$, $R^2 = 0.17$). This suggests that there might be a relationship between loss of tillers and a loss in species-specific biomass, and that spatial heterogeneity is not fine enough to preclude detection of that association, but that relationship may be too weak to detect higher scale associations between tiller dynamic synchrony and community ANPP using our methodology and level of replication. Given that plant population densities are maintained mainly by highly localized regeneration from belowground bud banks (Hartnett & Keeler, 1995; Ott & Hartnett, 2012), and those population densities have long been considered more important than tiller sizes in driving ANPP (Hartnett & Fay, 1998; Dalgleish & Hartnett, 2009), spatial heterogeneity in ANPP between subplots seems a more likely explanation for a lack of correlation between tiller dynamic

asynchrony, but direct testing using ANPP measured from the same plots as tiller densities should be conducted.

Overall, we found that *A. gerardii* and *S. nutans* tiller densities shift asynchronously, relative to one another, over the average course of a growing season. Those asynchronous dynamics appear to partially rely on the current average temperatures and level of variability in precipitation that are typical of the region, and they may become muted when these climatic conditions are altered. If the dynamics do become less asynchronous, our results suggest that the populations of *A. gerardii*, and of *S. nutans* in particular, could decline and because these two species are co-dominant and highly productive, those declines can have broader impacts on community function. Moreover, the loss of either species would represent a severe reduction in functional redundancy, negating an insurance effect (Smith & Knapp, 2003). Moreover, as Fay et al. (2011) concluded from their study of the RaMPs experiment, increased intra-annual variability in precipitation results in longer periods of water limitation, and that this shift may cause tallgrass prairie ecosystems to become more sensitive to inter-annual precipitation variability. Our findings indicate that this interaction between increases in intra- and inter-annual precipitation variability may also be manifest through more synchronous population dynamics of the dominant species. If their dynamics occur more in parallel intra-annually, they may be more vulnerable to inter-annual variability, particularly if both species population nadirs occur in tandem during a drought year.

Codominance among competitors implies that the species involved do not evade exclusion through temporal or spatial avoidance, but instead co-occur in a proximity that necessitates sharing of resource pools during periods that are both favorable and unfavorable for growth. Our results suggest a possible mechanism through which this could occur, an asynchrony that does not preclude exploitation of the full length of a limited growing season. Such a dynamic could represent a partitioning of environmental vulnerabilities, such that stable coexistence becomes a result of non-coinciding peaks in asset-leveraging and natural intra-annual environmental variability. This would allow each species to be less exposed to some of the periods of unfavorable conditions, while also benefiting asymmetrically from some of the periods of favorable conditions. Provided these types of conditions do not always occur

during the same part of the growing season from year to year, neither species would consistently have the advantage over the other, and therefore neither would be able to exclude the other.

Alternatively, asynchrony could promote coexistence between dominant species by reducing the aggregate tiller densities that occurs during any isolated part of the growing season, and through that reduction assuage the intensity of competition between the two species at all times. For example, if both species had peak tiller densities at the outset of the growing season, the sum of their tiller densities during that time would be greater than what we observe at any point in the growing season under ambient conditions. Such a pattern would result in enhanced resource demand compared to a pattern in which the peak tiller densities of the dominant species are temporally offset. If altered rainfall variability results in more synchronous tiller density dynamics, we might expect to see the dominant species reach peak tiller densities simultaneously, resulting in enhanced competition under the altered rainfall treatment.

To account for this possibility, we examined the relationship between relative tiller densities of *A. gerardii* and *S. nutans* within plots across the years of the experiment. If more synchronous tiller density dynamics resulted in harsher competition, we would expect that the relationship between the relative tiller densities of competing species to become more strongly negative, as each exerts a more deleterious effect on the other. If, on the other hand, less favorable conditions resulted in greater facilitation between the two species, as has been shown by others (Callaway, 1995; Stachowicz, 2001), we would instead expect a shift to a positive relationship between relative tiller densities. We used Spearman's tests for significant within-plot correlations between early-season relative tiller densities of *A. gerardii* and *S. nutans* for each of the treatment conditions (Fig. 4). However, we found that while their relative tiller densities were highly negatively correlated under current precipitation patterns (ambient-unheated $R^2 = -0.91$, $p < 0.001$; ambient-heated $R^2 = -0.73$, $p < 0.001$), there was no significant correlation between relative tiller densities under the altered rainfall pattern (altered-heated or altered-unheated) (Fig. 4). These results were similar for late-season measures of relative tiller densities. This suggests that while competition is likely playing a major role in structuring communities under ambient rainfall patterns, under altered precipitation variability, which we have shown to be associated with more synchronous tiller density

dynamics (Fig. 2), competition was not a driving force in determining relative tiller densities. In our view, this leaves vulnerability partitioning the more likely explanation for stable co-dominance between *A. gerardii* and *S. nutans* in this region.

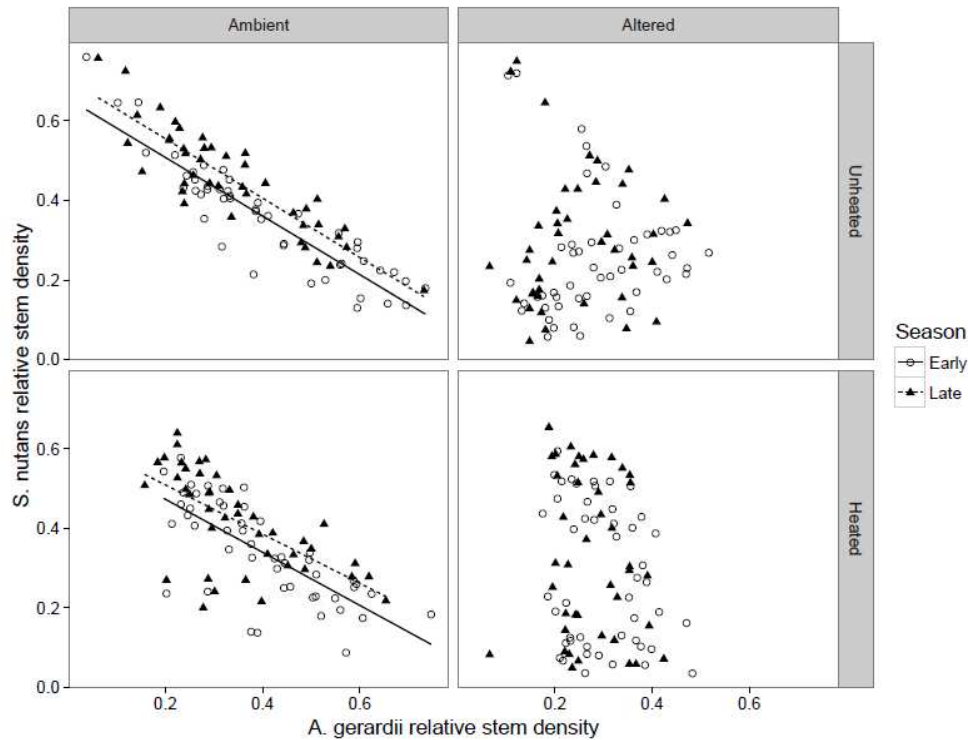


Figure 4: Tiller densities of *S. nutans*, relative to whole-community tiller densities, as a function of *A. gerardii* relative tiller densities. If negatively correlated, a higher densities of *A. gerardii* are associated with lower densities of *S. nutans*, implying that competition between the two species is playing a role in shaping community composition within plots. Under increased-rainfall variability treatments, where interspecific tiller dynamic asynchrony is lower, there is no significant relationship between relative tiller densities, indicating that competition between *A. gerardii* and *S. nutans* within these plots is not determining species composition.

CONCLUSION

Codominance between *A. gerardii* and *S. nutans* appears to be facilitated by their intra-annually asynchronous tiller dynamics. We believe this pattern enables both species to capture resources for the entirety of the growing season, but partially isolates their vulnerabilities to unfavorable growing conditions to only a portion of that season. Because those vulnerabilities occur at different times of the season for each species, and the climate in the region is characterized by both inter- and intra-annual

climatic variability, neither species can enjoy a consistent advantage over the other. If this mechanism is functioning to facilitate co-dominance, it appears to rely on current levels of climatic variability, and breaks down when that variability is increased in the way that is projected to occur under climate change. This population-level destabilization likely has negative implications for overall ecosystem productivity.

CHAPTER 2. FUTURE DIRECTIONS: TESTING GENERALITY OF OBSERVATIONS AND VALIDITY OF THE
PROPOSED MECHANISM OF CO-DOMINANCE

This experiment was situated within an ungrazed, lowland site that had been burned annually since 1979. However, the grazing pressure, topography and the fire frequencies in the Flint Hills and other regions surrounding the Konza Prairie vary. While the infrastructure of the RaMPs experiment was considerable, and cannot be replicated elsewhere within the Konza Prairie Biological Station, it will be important to establish whether the tiller dynamics we observed under current climatic conditions are consistent across these other variables. This will help to establish whether asynchronous tiller density dynamics operate under the range of conditions that the dominant species of this region experience, and therefore whether it is possible that those dynamics play a role in coexistence and/or codominance across that range. To accomplish this objective, we will propose to establish semi-permanent 0.1m² plots at sites with differing grazing histories, topographies, and fire frequencies, with levels of replication at each site resembling that in the RaMPs experiment. These plots will be surveyed for tiller densities twice each season, at times within the range of those of this study, for at least two consecutive growing seasons. At the end of the second growing season, biomass will be clipped and weighed for estimates of productivity, facilitating a more direct comparison of synchrony and community productivity than was possible in the RaMPs experiment.

In this study, we also observed a decline in aggregate tiller densities, and of one of the two dominant species, with increasing synchrony, and there were indications that density declines may have been greatest in the plots with increased heat and rainfall variability. It will be important to know the nature of those declines. We see 3 possibilities, 1) that the amount of rhizome tissue is declining, 2) that the density of meristems on rhizomes is declining, or 3) that the proportion of available meristems that are being activated during the growing season is declining. Some combination of these possibilities may also be occurring. Because each of these scenarios offers different long-term implications, we will propose to obtain standard-volume soil core samples surrounding individual tillers of *A. gerardii* and *S. nutans* from each plot in the RaMPs experiment at time points both before and after early-season bud break. From each sample, we will

measure total rhizome mass, bud density relative to rhizome mass, and proportion of buds that have been activated. We will then compare the observations between the RaMPs treatments.

While Silletti and Knapp demonstrated an asymmetric competitive relationship between *A. gerardii* and *S. nutans* using plant removals from natural tallgrass prairie (Silletti, et al., 2004), it remains to be seen whether and if either species would outcompete and exclude the other given consistently ideal conditions. Because eventual exclusion under such a scenario represents an important assumption of the mechanism of codominance proposed here, I will use a greenhouse to test whether exclusion occurs when ideal conditions are provided only early in the season, late in the season, or over the full growing season, when starting from equal proportions of both species.

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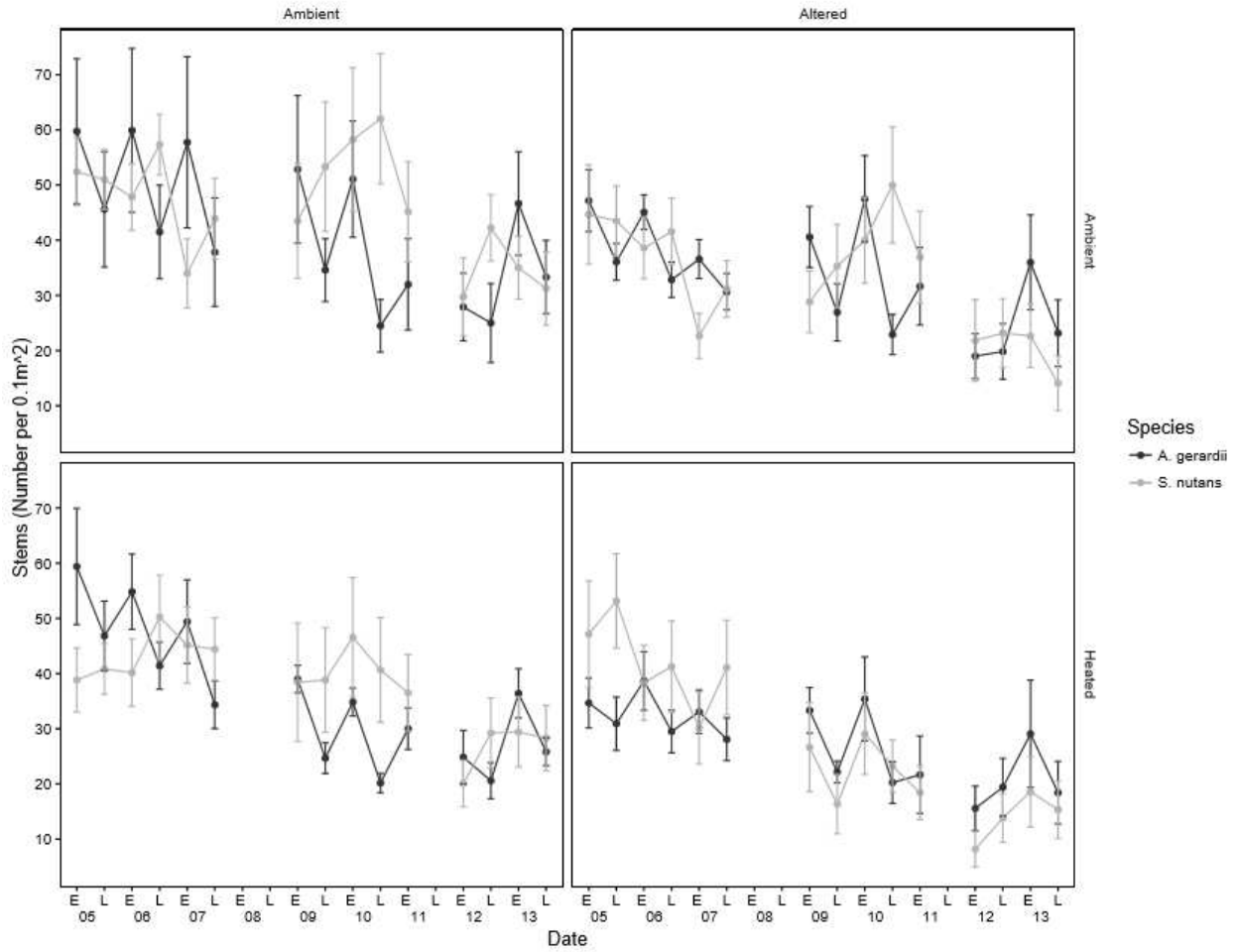
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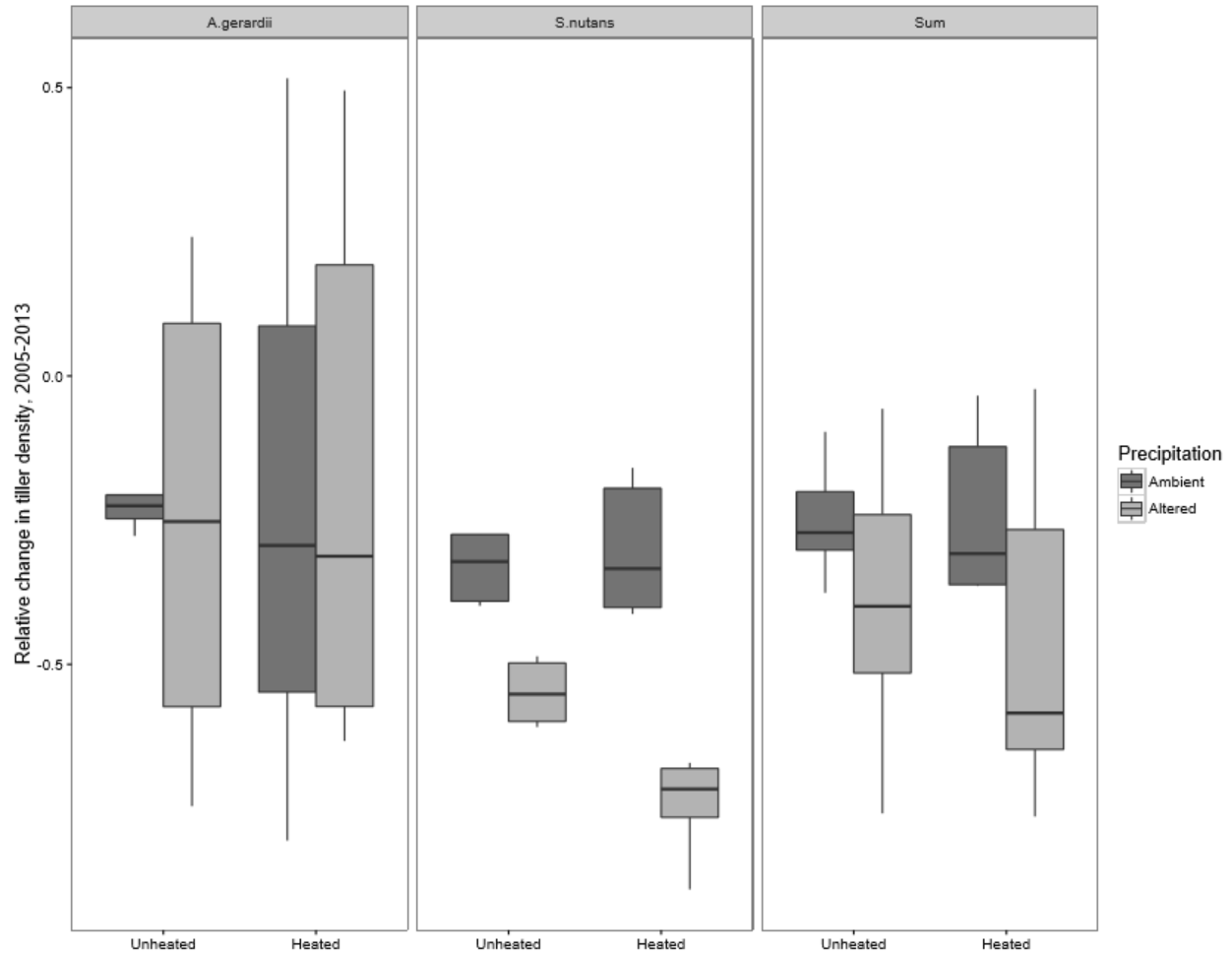
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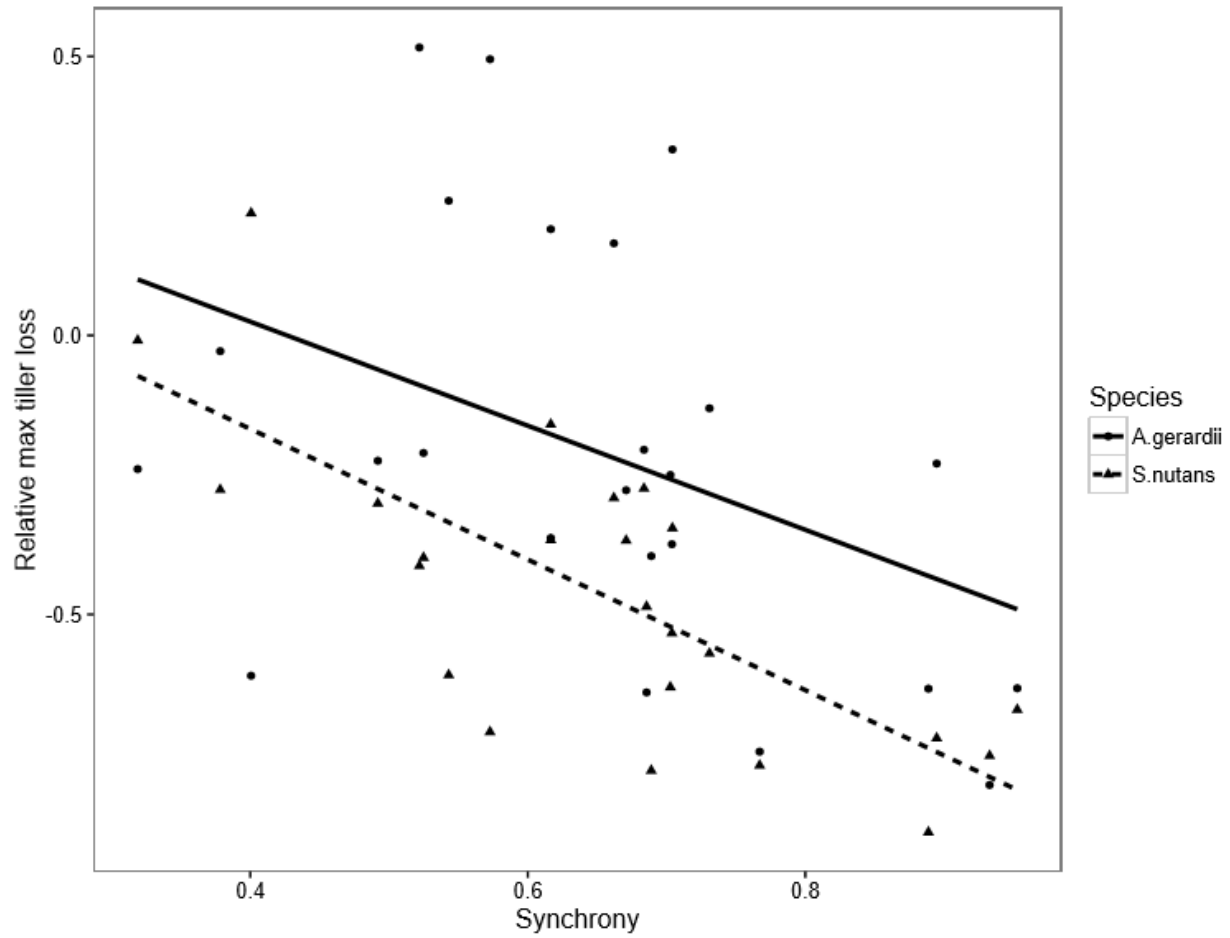
APPENDIX: SUPPLEMENTAL FIGURES



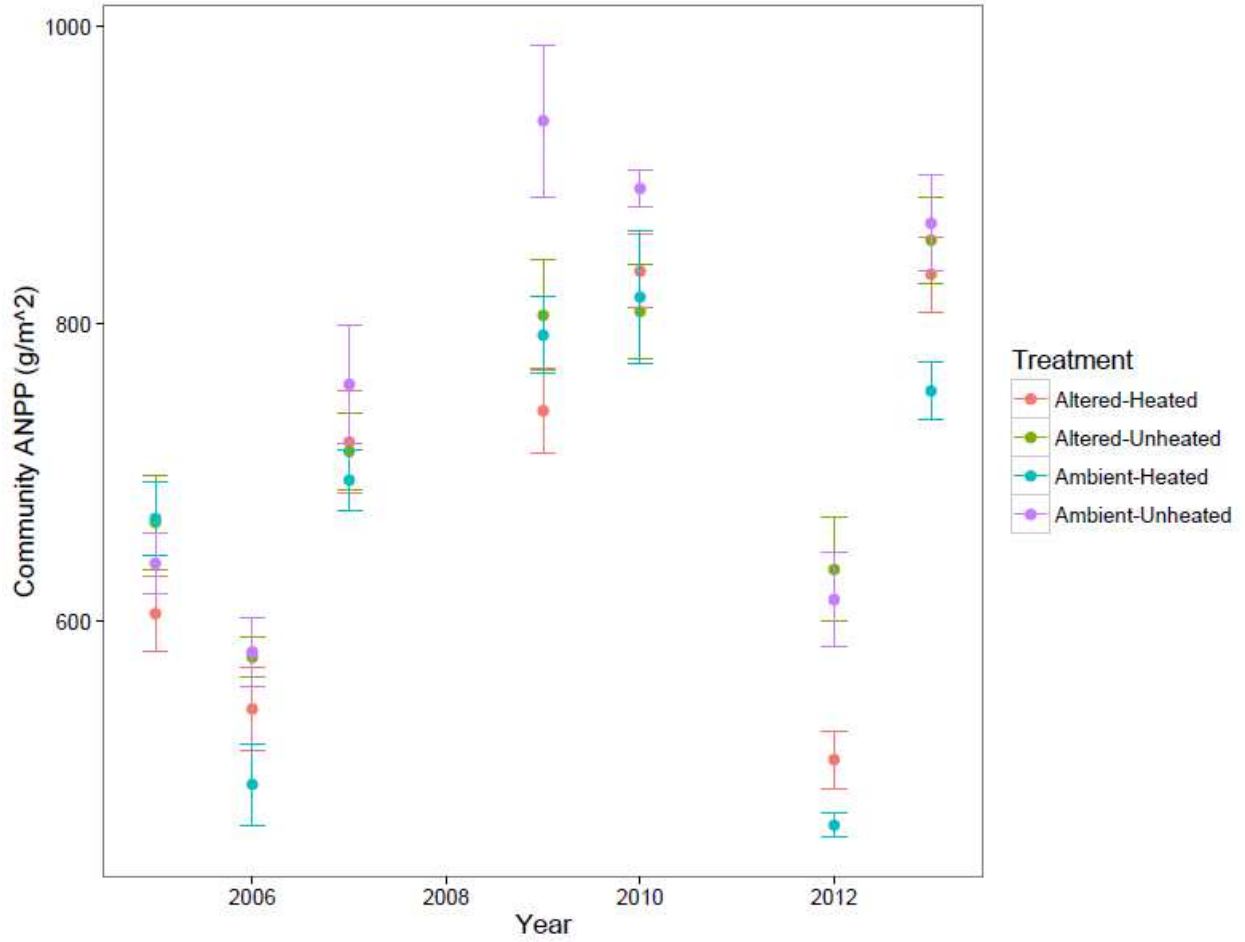
Supplemental Figure 1: Tiller density dynamics, averaged over plots, for each of the experimental treatments. *A. gerardii* demonstrates a consistent decline from early- to late season each year under current conditions. That pattern becomes less consistent under increased temperatures and rainfall variability, losing amplitude, and in some cases, direction. In the altered-heated plots, the two species dynamics became completely synchronous, increasing and decreasing in parallel, for the last 5 years of the study.



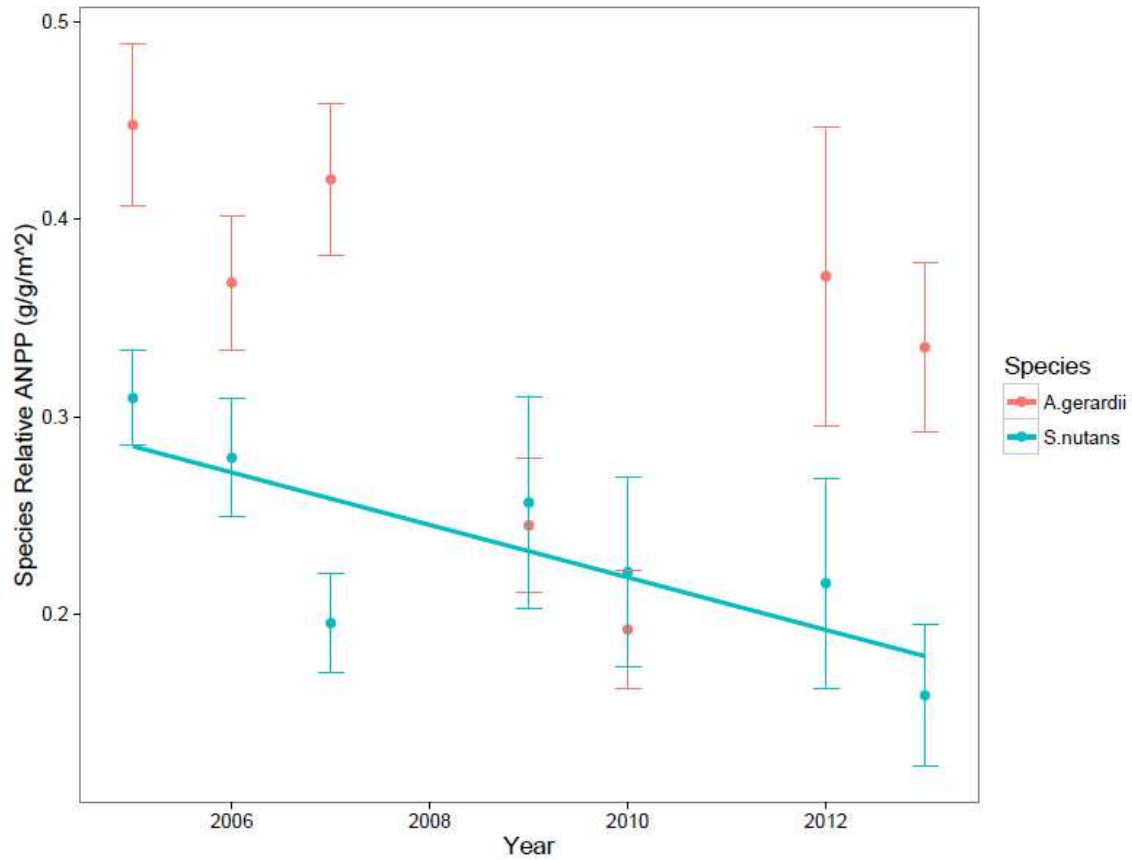
Supplemental Figure 2A: Changes in tiller densities from 2005 to 2013, relative to tiller densities observed in 2005. *S. nutans* consistently experienced sharper declines under increased rainfall variability, and those declines were more severe when also heated. *A. nutans* responded variably to both treatments, as density increased in some plots and declined in others within the same treatment. A confounding factor of a decline in an abundant forb in some plots, and its replacement with *A. gerardii* possibly accounts for this variability.



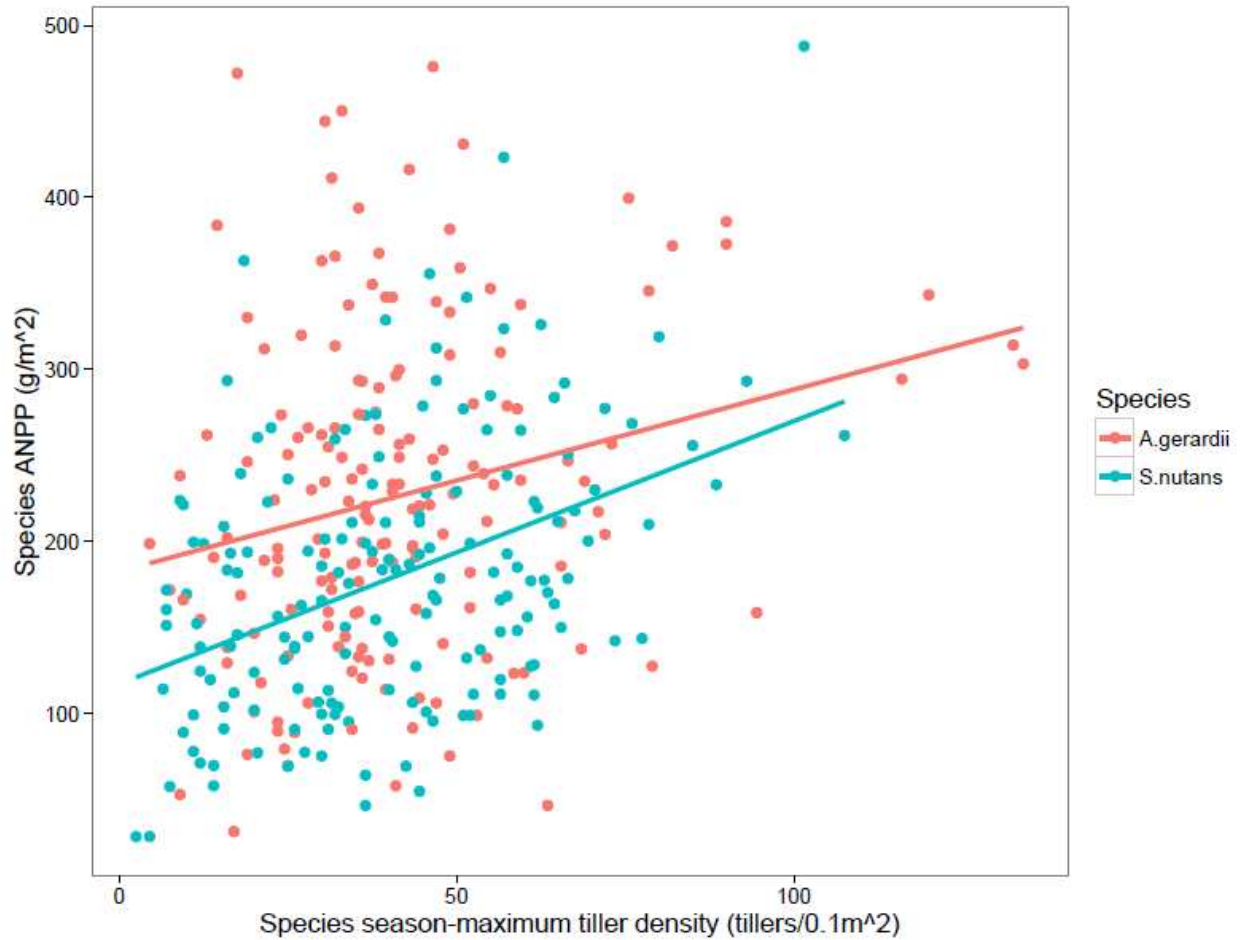
Supplemental Figure 2B: Decline in season-maximum tiller densities from 2005 to 2013, relative to maximum tiller densities observed in 2013, as a function of synchrony ϕ . Each data point represents a species' tiller density decline within a single plot. Declines of both species were significantly related to plot-level synchrony from 2005-2013.



Supplemental figure 3A: Community above-ground net primary productivity over time, averaged across plots within each treatment. No long-term trend is apparent in the amount of biomass produced by the plant communities under any of the experimental treatments.



Supplemental figure 3B: While no long-term trend in ANPP occurred in any of the treatments (S. Fig. 3A), in the altered-heated treatment there was a decline over time in the proportion of that ANPP represented by *S. nutans*. No trend was observed in the proportional ANPP of *A. gerardii*. This suggests that the decline in productivity of *S. nutans* was compensated by increases in productivity of other species within the same communities, but not by *A. gerardii*.



Supplemental Figure 4: Species-specific above-ground net primary productivity (ANPP) of *A. gerardii* and *S. nutans* as a function of their respective tiller densities. While the ANPP of both species were significantly and positively related to their tiller densities, those relationships were quite variable. The weak relationship may be result of both variabilities in the mass of individual tillers, and the distance between subplots from which tiller density and productivity measurements were taken.