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RESEARCH ARTICLE

# Contrasting intra-annual population dynamics of two codominant species are consistent across spatial and temporal scales

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## Abstract

1. Despite asymmetric competition and a wide array of functional similarities, two ecologically important $C_4$ perennial grasses, *Andropogon gerardii* and *Sorghastrum nutans*, frequently codominate areas of the mesic tallgrass prairie of the US Great Plains. A subtle difference in their vegetative reproduction strategies may play a role in preventing the exclusion of *S. nutans*, the presumed weaker competitor in such regions.
2. While *A. gerardii* vegetative tiller densities peak in the early growing season and decline thereafter (determinate recruitment), those of *S. nutans* may continue to increase throughout the growing season (indeterminate recruitment), providing a potential avenue for recovery from more intensive early season competition. However, until now these patterns have only been informally observed in the field.
3. We examined the year-to-year consistency of growing season vegetative tiller dynamics (measured as seasonal change in tiller densities) of each grass species from an intact tallgrass prairie in Kansas – a site within the core of both species' distributions – over a period of 8 years. Then, to investigate environmental effects on these dynamics, we examined whether they differ across a Kansas landscape varying in topography, fire management regimes, and the abundances of the study species. Finally, we expanded the investigation of environmental effects on growing season tiller dynamics by observing them at the periphery of the species' distributions in central Colorado, where climatic conditions are dryer and the study species' abundances are reduced.
4. *Synthesis*. We found that the tiller densities of *A. gerardii* decline within seasons with striking consistency regardless of spatio-temporal scale or environmental factors (topography and fire regimes). In contrast, we found the seasonal dynamics of *S. nutans* tiller densities were dependent on environmental factors, with seasonal tiller density increases occurring only within the Kansas populations but not consistent between years. These observations lay the groundwork

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for establishing differences in tiller recruitment determinacy as a potentially important yet underappreciated mechanism for promoting coexistence and co-dominance among perennial plant species.

**KEYWORDS**
codominance, coexistence, environmental variability, growth determinacy, life history traits, species distributions, stabilizing mechanisms, warm-season grass

## 1 | INTRODUCTION

The determinacy of growth and reproduction among plants, while historically important in the context of agricultural applications (e.g. Hauggaard-Nielsen & Jensen, 2001; Huyghe, 1998), has with few exceptions (e.g. Hinman & Fridley, 2018; McKendrick et al., 1975; Seiwa, 2000) received little attention in the study of native plant communities. Determinate behaviour is exhibited when processes such as plant growth, flowering or vegetative reproduction begin and end on a genetically predetermined schedule, for example, recruitment within only the first weeks of a growing season. This characteristic is desirable in industrial crop species as it enables efficient harvesting of synchronously generated agricultural products, such as fruits and grains. While this feature can be artificially selected for (Tian et al., 2010), it also exists among uncultivated species (e.g. C4 grasses, McKendrick et al., 1975) and is, therefore, likely to play a role in certain life history strategies. Indeed, determinacy of growth has been suggested as an adaptation among conservative species that encounter predictable patterns of resource availability (Boke, 1979; Fischer & Turner, 1978; Shishkova et al., 2013; White et al., 1992).

Although growth determinacy trait data is not often collected in native plant communities, determinately growing species coexist with those that have indeterminate growth forms (e.g. tallgrass prairie, McKendrick et al., 1975). Indeterminately growing species have growth and recruitment processes that can persist or be initiated any time environmental conditions are suitable and necessary resources are available. We posit that variation in determinacy within a community is more than coincidental, and may enable or enhance coexistence, even among otherwise functionally similar and competitive species. Because environmental conditions suitable for growth may persist after processes in determinate species reach their predetermined conclusion, indeterminately growing species may be able to gain late-season advantages or recover from asymmetric competition (sensu Freckleton & Watkinson, 2001) suffered earlier in the growing season. Similarly, indeterminate growth has been suggested as beneficial for recovery from stress or herbivory in agricultural settings (Cichy et al., 2009; Mekbib, 2003). Thus, when multiple competitive species exhibit differences in determinacy, codominance may result and ultimately may enhance ecosystem stability.

Differences in growth determinacies could enable individuals of strongly competing species to have broadly or entirely overlapping periods of activity. This contrasts with well-known examples of seasonal differences in growth, such as winter versus summer annuals (Guo & Brown, 1997) or cool- versus warm-season grasses (Monson et al., 1983). In these two scenarios, growth is segregated to different times during the growing season, minimizing direct competition. In contrast, if a difference in growth determinacy allows two species to maintain activity simultaneously, this could mean that species that have very similar niche requirements and functions can avoid competitive exclusion and coexist at relatively high abundances. In such a scenario, two species could respond asynchronously to environmental variability, not through differences in physiological or morphological characteristics, but because one species has ceased a key process or processes regardless of the favorability of growth conditions, while the other continues to gather resources, grow, and/or recruit new individuals. Yet, despite the potentially important role that growth determinacy may play in coexistence, studies in natural systems of differences in growth determinacy are rare.

Two grass species are frequently codominant (sensu Gray et al., 2021) in the tallgrass prairie of the Great Plains, US: *Andropogon gerardii* (Vitman) and *Sorghastrum nutans* L. (Nash) (L. Brown, 1985; Duralia & Reader, 1993; Freeman, 1998; Hartnett et al., 1996; Smith & Knapp, 2003). Both species reproduce primarily through the asexual production of tillers (Benson & Hartnett, 2006), genetically identical individuals originating as underground stems from the parent plant, that can later separate from the parent and mature to produce tillers of their own. This growth form contributes to the dominance of many perennial grasses in the tallgrass prairie by enabling extended parental support of young tillers, shielding the primary reproductive process underground and away from fire and herbivory, and modularly expanding the lifespan and spatial extent of successful genotypes. The more competitive of the two in this region, *A. gerardii* (Silletti et al., 2004), is a determinately growing perennial warm-season ($C_4$) grass that vegetatively produces annual tillers (senescing before the next season) within a limited period from mid- to late April (Benson & Hartnett, 2006; McKendrick et al., 1975). Its codominant, *S. nutans*, indeterminately produces biennial (overwintering) or potentially longer-lived tillers, a process that begins in the same weeks as *A. gerardii* but continues throughout the growing season until water becomes too limiting or temperatures become too cold (Benson & Hartnett, 2006; McKendrick et al., 1975). Despite this difference in recruitment determinacy, these two species are very similar in their morphologies, functional traits and their responses to various environmental variables, including herbivory and fire (Bowles et al., 2011; Forrestel et al., 2014, 2015; Hadley & Kieckhefer, 1963; Polley et al., 1992; Towne &

Kemp, 2003; Weaver, 1931; Weaver & Fitzpatrick, 1932), and the availabilities of key resources—light, water and nitrogen (Berg, 1995; Hoffman et al., 2018; Lett & Knapp, 2003; Mulkey et al., 2008; Silletti & Knapp, 2001, 2002; Swemmer et al., 2006; Weaver & Rowland, 1952). Given these broadly overlapping ecological niches, and the expectation for competitive exclusion entailed, the determinate growth form of *A. gerardii* may play an important, but cryptic role in enabling the less competitive species, *S. nutans*, to maintain its codominant status.

Importantly, while *A. gerardii* and *S. nutans* are frequently codominant in tallgrass prairie, their abundances vary considerably across such landscapes. Specifically, their population densities and biomass production rates are higher in lowland areas than in uplands, and higher under annual compared to quadrennial fire frequencies. Lowland areas are typically wetter because they have relatively poorly draining soils and receive supplemental inputs via runoff and drainage from upland areas. This prolongs the availability of water to plants both after each rain event and later into the growing season (Nippert & Knapp, 2007; Oviatt, 1998). Meanwhile, infrequently burned areas accumulate litter, which can also prolong the availability of soil moisture by creating a humid microclimate but also reduce the penetration of sunlight to the soil surface, and lower light availability to newly emerging and diminutive tillers throughout the growing season. Both of these factors may interact with the temporal recruitment patterns of *A. gerardii* and *S. nutans*, potentially affecting their abundances. For instance, late-season *S. nutans* tiller recruitment may be stifled by insufficient light in infrequently burned areas, and by insufficient water in upland areas if late seasons are dry in a given year. Furthermore, since plant litter in infrequently burned areas is present throughout the growing season, it may also negatively affect the recruitment rate of *A. gerardii* tillers, gradually resulting in lower abundances and the subordinate ranking of both species.

To lay the groundwork for establishing determinacy of tiller growth as a niche axis that contributes to coexistence and/or codominance, we studied the seasonal population (tiller) dynamics of *A. gerardii* and *S. nutans* in the field. We would expect that where plant species are persistently codominant, differences in the patterns of intra-seasonal tiller density dynamics provide a more responsive, but less competitive species periodic opportunities to recover from early-season competitive disadvantages, but only if late-season conditions (water and light availability) permit. We observed the intra-seasonal tiller density dynamics of each species, and how they vary from year to year and spatially across their east–west geographic distribution from mesic to xeric sites in the Central United States. We also observed how the intra-seasonal density dynamics of the two species vary with topographical position, and frequency of fire, a common and influential disturbance in the tallgrass prairie (Blair, 1997; Briggs et al., 2002; Briggs & Knapp, 1995; Ojima et al., 1994; Wan et al., 2001). We hypothesized that *A. gerardii* tiller densities would decline in the latter weeks of the growing season *regardless of growing conditions* due to its determinant growth strategy, but tiller densities of *S. nutans* should either remain stable or increase, *depending on growing conditions* due to its indeterminant growth strategy. This would result in intra-seasonally diverging trajectories of tiller densities (i.e. losses vs. gains). Given that *A. gerardii* exhibits determinate growth, we expected that although its intra-seasonal dynamics could be muted or amplified, they would remain consistently negative at the local scale over time, at a landscape scale varying in topographic position (soil type and depth) and fire frequency, and at a regional scale among sites differing in humidity and average annual rainfall. In contrast, given the indeterminate growth of *S. nutans*, we expected that its intra-seasonal dynamics would be more sensitive to environmental changes over time, topographic position, and fire frequency, as well as regionally in mesic versus xeric sites, with tiller densities varying not only in magnitude but also in direction (increase, neutral or decrease). While this study was not controlled and cannot show that codominance results causally from variability in determinacy, we found that these prerequisites were typically met. That is, an otherwise dominant species failed to respond to a temporally limited, variably available resource, while the reproductive rate of its codominant species was increased when that resource was more available.

## 2 | MATERIALS AND METHODS

We focused on tiller densities and their dynamics as our measures of determinacy in this study for four key reasons. First, since tillers represent clonally-generated individuals, this measure is directly associated with these species' demographic patterns. Second, while seed production and germination are also typically integral aspects of population dynamics, and both species produce viable seeds in sufficiently wet years, these seeds rarely establish in intact tallgrass prairie (Benson & Hartnett, 2006), and vegetative (clonal) reproduction accounts for more than 99% of all yearly recruitment in such sites. Third, while proportional canopy cover is often measured in populations of our study species to estimate productivity and community influence, these species are abundant to the point of codominance in mesic tallgrass prairie, so their cover in the canopy maximizes relatively early in the season and changes little throughout the season. Thus, proportional canopy cover does not represent as sensitive a measure of abundance as tiller densities. Lastly, direct aboveground productivity measurements are destructive, and we intended to monitor the demographics of our species within the same plots over multiple years. Moreover, if measured at the end of the season, tiller mass cannot reveal species-specific variabilities in productivity over time within that season, only their cumulative outcomes. As such, the most intra-seasonally variable and measurable demographic aspect of these species is tiller density. We, therefore, conducted tiller density censuses twice each growing season (late Spring, late Summer) at mesic tallgrass prairie sites in Kansas and xeric grassland sites in Colorado. Each of the censuses (described below) followed a similar protocol for measurement wherein each stem (or tiller leaf bundle) of any forb or graminoid emerging from single points along the soil surface was identified and tallied by species (or functional group in some cases).

Both the temporal and spatial censuses in Kansas were conducted within the Konza Prairie Biological Station (KPBS; 39.107, −96.609, Kansas State University fieldwork permit number: 446, Figure S1A), a 3487-ha mesic tallgrass prairie in the Flint Hills near Manhattan and part of the Long-Term Ecological Research network (lternet.edu). The climate at KPBS is temperate mid-continental (mesic). Long-term mean annual precipitation is 835 mm and ~70% of which falls during the growing season (Table S1, Figure S2, Hayden, 1998). Because the study species are both highly abundant at KPBS, every plot (and nearly every subplot) in both the temporal and spatial censuses included individuals of both *A. gerardii* and *S. nutans*.

## 2.1 | Kansas temporal census

The temporal census in Kansas took place from 2005 to 2013 in the control plots of a precipitation manipulation experiment: the Rainfall Manipulation Plots (RaMPs, see Fay et al., 2000, 2011), which was conducted in an annually burned and ungrazed lowland site at KPBS. In each 6 × 6 m plot ($n = 6$ control plots), growing season rainfall was intercepted from each precipitation event and then immediately added to the control plots through an overhead sprinkler system. Precipitation over these 8 years was highly variable, and slightly lower in volume compared to the 25-year precipitation average for this area (Table S1). Censuses were conducted in two 20 × 50 cm subplots situated permanently at opposite corners of a 2 × 2 m plot within each control plot. Due to unforeseen circumstances, we were unable to collect temporal census data in 2008 and 2011.

## 2.2 | Kansas spatial census

The Kansas spatial census was conducted across four watersheds within KPBS (Figure S1B). Twenty 2 × 2 m plots were established in each watershed, ten in upland sections with shallow Florence soils and ten in poorly drained lowland sections with deep Tully soils, for a total of 80 plots. All four of the watersheds were ungrazed by cattle or bison but differed in prescribed fire frequency regimes, with two watersheds receiving the fire application annually in the spring (mid-April; watersheds 1B and 1D), and the remaining two receiving fire only once every 4 years, also in the spring (watersheds 4A and 4F). Neither of these latter watersheds was burned in 2017, but 4A was burned in the Spring of 2018. Both *A. gerardii* and *S. nutans* are, with some spatial and temporal variation, more common in the annually burned watersheds, particularly in the lowlands (Hartnett et al., 1996; Silletti & Knapp, 2002; Towne & Kemp, 2008). As with the temporal census, two 20 × 50 cm subplots were permanently established in opposite corners of each plot. The late spring censuses were conducted from May 26 to June 5 in 2017 and from May 18 to May 23 in 2018. The late summer censuses were conducted from August 5 to August 19 in 2017 and from August 9 to August 16 in 2018. Growing season precipitation was lower than average in both years, and 2018 was dryer than 2017, particularly in the early season (April–June, Table S1).

## 2.3 | Colorado spatial census

A second spatial census was conducted in Colorado in 2017 and 2018. We established 20 2 × 2 m plots at sites along the Front Range (Figure S1), which is the eastern edge of the Rocky Mountains and largely represents the western range limit of both species (Bock & Bock, 1998; Keeler, 2004; USDA, 2021a, 2021b; Weaver, 1931; Weaver & Fitzpatrick, 1932). Census sites were split between locations near southern Boulder (City of Boulder Open Space and Mountain Parks fieldwork permit granted without number assignment) and northern Fort Collins (Fort Collins Natural Areas fieldwork permit numbers: 887 and 1046, Figure S1A, Table S2). Plots varied in topographical position, soil moisture availability, community composition and grazing regimes, but fire was excluded from all, and all could be considered lowland sites relative to nearby foothills. However, with one exception, all plots were observed to have much lower soil moisture content than plots in both the upland and lowland areas of KPBS (data not shown). This region has a semi-arid climate, with highly variable annual precipitation averaging 406 mm near Fort Collins and 486 mm near Boulder (Hansen et al., 1978). Neither of the study species is as abundant in this region as they are in mesic prairies (Bock & Bock, 1998; Keeler, 2004), so plots were non-randomly established at the centers of isolated patches of either *A. gerardii* or *S. nutans* (10 plots for each species). The emergence of tillers of these species occurs later than in Kansas, so each measurement (two 20 × 50 cm permanently established subplots per plot) was taken following its respective Kansas census. The late spring censuses were conducted from June 11 to June 27 in 2017 and from June 6 to June 16 in 2018. The late summer censuses were conducted from August 27 to September 5 in 2017 and from August 30 to September 3 in 2018. Due to unforeseen factors that prevented their resampling, four of the plots required nearby re-establishment in 2018 (details in Supplementary Table 2). Growing season precipitation resembled the 25-year average in both years (Figure S2).

## 2.4 | Statistical analysis

Because data were collected from different sets of years and regions, we analysed the Kansas temporal censuses, Kansas spatial censuses, and the Colorado spatial censuses independently, focusing on whether intra-seasonal tiller density dynamics depend on species within each. For the Kansas census analyses (spatial and temporal), we first averaged the densities measured in the two subplots for each plot. Because four of the Colorado subplots could not be censused twice, we analysed the Colorado spatial censuses at the subplot level, rather than averaging beforehand. To examine the effect of species identity on intra-seasonal tiller density dynamics in the spatial censuses (Tables S3 and S4), we analysed both absolute and relative changes in density (ratio of absolute change in density to early season absolute density):

$$\text{Relative Change}_i = \frac{\text{Late Density}_i - \text{Early Density}_i}{\text{Early Density}_i}.$$

While the measure of absolute change in density gives a direct indication of the number of tillers gained or lost in a season, it is not indicative of the severity of this change within a population. For instance, if a population loses many tillers but from an exceedingly high initial density, the importance of this loss may be overestimated. On the other hand, while relative change can provide such context, large relative changes may involve few real additions or losses of tillers in small populations. We, therefore, included both analyses to provide a more complete picture of seasonal dynamics.

For the Colorado spatial census (Table S3), we used unpaired Wilcoxon rank sum tests for differences by species in their relative changes in tiller densities. These tests were not paired because the two species were censused from separate plots. However, we used paired Wilcoxon rank-sum tests for the Kansas spatial census, as each plot was censused for both *A. gerardii* and *S. nutans*, and as such, they could not be considered independent samples. These analyses were performed independently for 2017 and 2018 and Bonferroni adjustments were made for the four comparisons (2 years, absolute and relative dynamics, adjusted alpha = 0.0125).

For the Konza temporal surveys, we used analysis of variance of repeated measure mixed models of the absolute and relative tiller density changes to determine the effects of species identity (*A. gerardii* or *S. nutans*) on intra-seasonal tiller density dynamics (Table S5). Species identities were treated as fixed effects, and both plot and year were treated as random effects.

We examined the effects of topography and fire frequency on relative tiller density dynamics in the Kansas spatial censuses separately, using Wilcoxon rank-sum tests (Tables S6 and S7) to determine whether each species' tiller density dynamics differed either by upland or lowland environments (irrespective of fire frequency) or by the frequency of fire disturbance: annual or quadrennial (irrespective of topographical position). This was done independently for the 2017 and 2018 censuses, and Bonferroni adjustments were used to correct for four comparisons (two species, 2 years, adjusted alpha = 0.0125).

## 3 | RESULTS

### 3.1 | Differences in tiller density dynamics by species

We found that *A. gerardii* consistently exhibited tiller losses following peak early-season densities in both years of the Colorado and Kansas spatial censuses, as well as on average in the Kansas temporal censuses (Figures 1 and 2). The tillering and senescence behaviours of *S. nutans* were less consistent, with aggregate seasonal losses occurring in both years of the Colorado censuses and in the 2018 Kansas spatial census, while recruitment outpaced senescence in the 2017 Kansas census and on average in the Kansas temporal census (Figures 1 and 2).

While the seasonal dynamics of *S. nutans* tiller densities depended on both region and year, we found that they consistently diverged from those of *A. gerardii* (Figure 2). The relative dynamics of *A. gerardii* were significantly more negative than those of *S. nutans* during both years of the Kansas (Table S4) and Colorado spatial censuses (Table S3). The average absolute and relative dynamics in the temporal census also significantly differed between species (Figure 2, Table S5), with consistent intra-seasonal declines of *A. gerardii* and *S. nutans* dynamics depending on the year (Figure S3).

### 3.2 | Topography and fire frequency effects on seasonal dynamics

The effects of fire frequency (Table S6) and topographic position (Table S7) on seasonal density dynamics of the two grasses were species-dependent (Figure 3). The absolute density dynamics of *A. gerardii* were negative in all cases, but more tillers were lost in the annually burned than in quadrennially burned watersheds in both

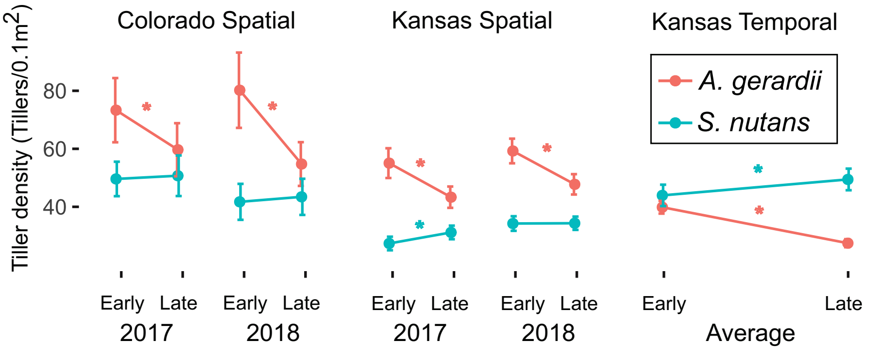

FIGURE 1 Absolute densities (average number of tillers per $0.1\text{m}^2$ subplot) of *Andropogon gerardii* and *Sorghastrum nutans* in the Colorado spatial censuses, Kansas spatial censuses, and Kansas temporal census (averaged across measurements taken from years 2005–2013). Asterisks indicate significant differences between early and late-season absolute densities. Error bars indicate standard error estimates.

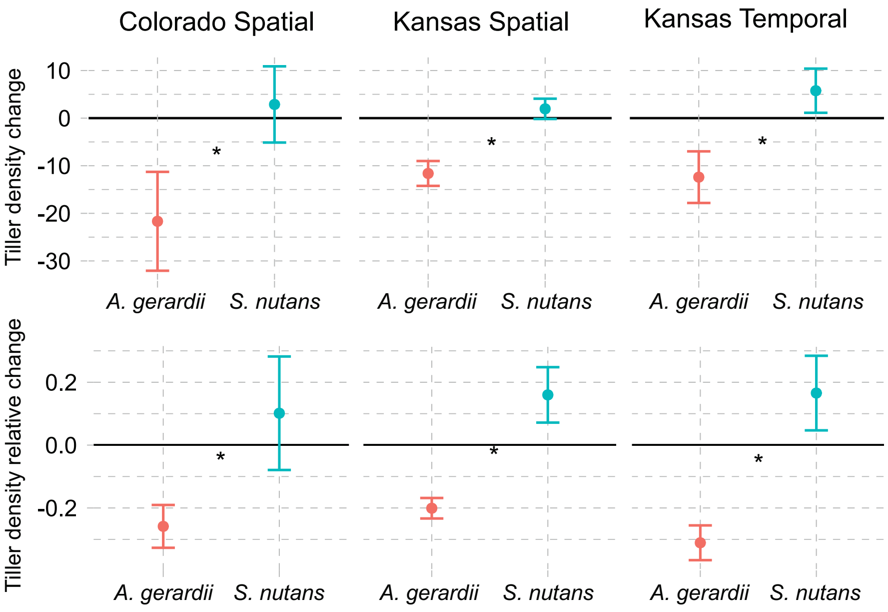

**FIGURE 2** Average absolute (top row) and relative (bottom row) changes in tiller densities in the three surveys: Colorado spatial (averaged across 2017 and 2018), Kansas spatial (averaged across 2017 and 2018), and Kansas temporal (averaged across 2005–2013). Error bars indicate estimates of standard error. Asterisks indicate significant differences between the two species. Values greater than 0 (highlighted by the solid horizontal grid lines) indicate that the species' tiller densities increased seasonally on average. Absolute change was calculated as late season density—Early season density. Relative change was calculated as each species' absolute changes divided by their respective early season densities.

2017 and 2018. No differences were observed in *A. gerardii* relative density dynamics between fire frequencies in either year. The absolute and relative dynamics of *S. nutans* were positive in both annually and quadrennially burned watersheds in 2017 (Figure 3). In 2018, there was an increase in *S. nutans* tiller densities in the quadrennially burned watersheds, but a decline in the annually burned watersheds.

The absolute dynamics of *A. gerardii* differed by topographic position in 2017 (Figure 3), with greater tiller density declines in the lowland areas. However, these effects were not observed in 2018. No differences in relative dynamics between upland and lowland positions were observed for *A. gerardii* in either year. For *S. nutans*, neither absolute nor relative density dynamics differed between upland and lowland sites in 2017 (Figure 3). However, more positive relative dynamics were observed in lowlands in 2018 along with a correspondingly higher average increase in absolute density, although this difference was non-significant.

## 4 | DISCUSSION

We found that the tiller densities of *A. gerardii*, a determinately recruiting grass species, consistently declined from early to late growing seasons across our observations spanning xeric and mesic regions, upland and lowland positions, annual and quadrennial fire frequencies, and on average over 8 years in a mesic tallgrass prairie. In contrast, we found that the tiller density dynamics of the codominant and indeterminately recruiting grass species, *S. nutans*, were dependent on both region and yearly conditions, although they were always less negative than those of *A. gerardii*. We consider these species characteristics to be the foundational requirements for the hypothesis that differences in determinacy promote coexistence and codominance between these two native grass species: One species maximizes investment during the period of the growing season most frequently favourable for growth but sacrifices the ability to respond to favourable conditions outside of this period, while a second species retains continual responsiveness at the expense of more optimized investment timing. In an environment where the favorability of growth conditions varies within and between seasons, neither of the species has a continuous advantage, enabling occasional recoveries from previous periods of asymmetric competition.

We recognize that other factors must also be playing their roles in the high abundances of *A. gerardii* and *S. nutans* observed in eastern Kansas, regardless of whether the mechanism discussed above is important. For instance, several studies have reported greater drought tolerance in *A. gerardii* populations and greater heat tolerance and more opportunistic growth in *S. nutans*, indicating some niche differentiation between the species exists along these axes (Hoover et al., 2014; Silletti et al., 2004; Silletti & Knapp, 2001, 2002; Swemmer et al., 2006). Moreover, the consistency of the pattern of intra-seasonal decline in *A. gerardii* and the stability of *S. nutans* in the Colorado populations has not resulted in their widespread codominance in this region. This may instead indicate that the morphological and physiological traits held in common by these two species enable them to compete with other plant species more effectively in the mesic regions of the Great Plains and thrive within the range

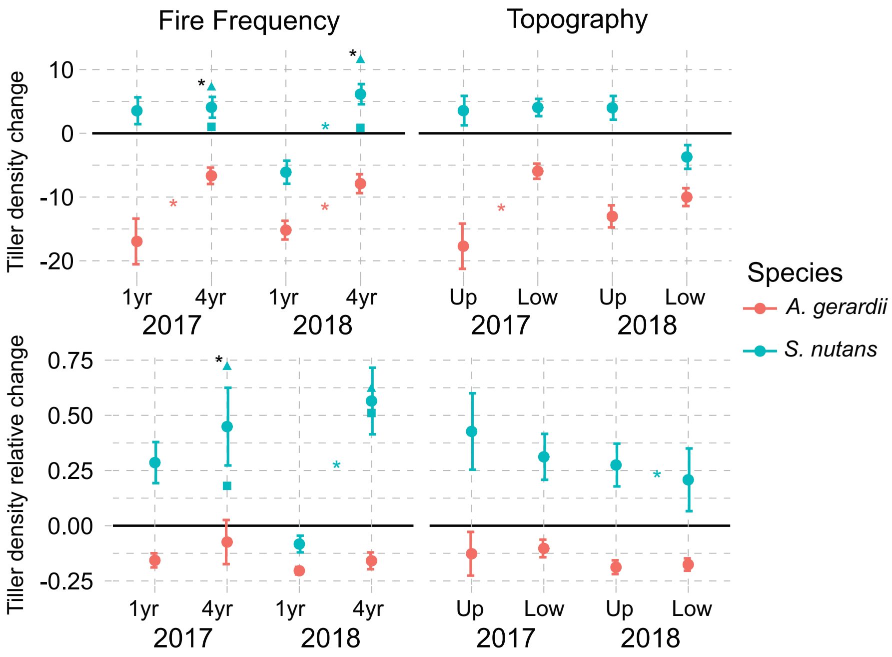

**FIGURE 3** Effects of fire frequency (1-year or 4-year fire return, left) and topographic position (drier upland or wetter lowland, right) on absolute seasonal changes in tiller density (tillers 0.1 $m^{-2}$) in the Kansas spatial census, calculated as early season density minus late season density, for *Andropogon gerardii* and *Sorghastrum nutans* (top row). The bottom row shows seasonal changes in tiller densities within populations of *A. gerardii* and *S. nutans*, relative to their respective early-season tiller abundances (calculated as each species' absolute seasonal changes divided by their respective early-season densities). Blue and red asterisks indicate significant differences between the seasonal dynamics of a species under different fire regimes or topographies. Triangles indicate *S. nutans* tiller density dynamic values from the 4A watershed only (burned in 2018, but not in 2017), and squares indicate those from 4F (not burned in 2017 or 2018). Black asterisks indicate significant differences between the 4A and 4F watersheds in the dynamics of *S. nutans* within each year.

of environmental conditions found there. This continental trend in abundance extends as increasing relative abundances of both species with greater water availability (Weaver & Fitzpatrick, 1932), particularly for *S. nutans* in the warmer southeastern United States where it is often dominant (Brown, 1993; Epstein et al., 1998) and for *A. gerardii* in cooler northern central Great Plains (Grman et al., 2013). Together, niche differences and a high degree of adaptation to mesic environments may explain much about the codominance of *A. gerardii* and *S. nutans*. However, we believe our findings may begin to address gaps in this picture, namely that the differences between the two species are relatively subtle (Forrestel et al., 2014, 2015) and that the more competitive species is also the more drought-tolerant (Silletti et al., 2004), which limits the fluctuation-based opportunities for *S. nutans* expansion described in modern coexistence theory (Chesson, 2000).

While plant growth and recruitment determinacy research has largely been confined to crop and forestry science for their agricultural applications, there have been a few efforts examining how determinacy might affect plant communities. For instance, expanding on their earlier coexistence models by easing assumptions of continual (indeterminate) growth, Armstrong concluded that, following disturbance, communities with determinate growth patterns should more easily accommodate multiple species than communities that exhibited only indeterminate growth (Armstrong, 1976, 1989). Although our study system consisted of a mix of recruitment determinacies, we find some agreement with these conclusions: Being the more competitive and drought-resistant species, if *A. gerardii* also exhibited indeterminate growth, we would expect its accommodation of *S. nutans* codominance would be less probable.

Although seldom investigated, reported, or featured within species trait databases (e.g. TRY, 2021; Fraser, 2020; Kattge et al., 2020), growth and reproductive determinacy traits potentially represent additional niche axes along which species may be differentiated, adding to the list of more recognized differences among species (e.g. those related to competition-colonization and competition-stress tolerance tradeoffs) that underly environmental fluctuation-dependent coexistence mechanisms like relative nonlinearity and the storage effect (Chesson, 2000; Grime, 1988). In association with other trait axes (Blonder, 2018; Hutchinson, 1957), growth determinacy may also uniquely contribute to coexistence stability at the community scale. In contrast to the limitations imposed by strict temporal niche partitioning (e.g. Kindscher & Wells, 1995; Silvertown et al., 2015; Sweet & Holt, 2015; Wilsey et al., 2011), differences in determinacy do not necessarily preclude the active periods of photosynthesis of competing species from overlapping to any degree other than through variations in population densities. As such, these traits may be an important factor in plant species codominance, not just coexistence, since individuals of both species can be fully and similarly active throughout the growing season and may share similar responses to stress, disturbance and variabilities in resource availabilities. Instead, niche differences in resource acquisition would be evident not between individuals of different species, but in the number of individuals that are present at different periods within the growing season.

If this mechanism of coexistence and/or codominance does play a role in the stability of existing plant communities, it could have important implications for ecological restoration and conservation. Restoring disturbed areas with perennial plant species that have a diversity of growth determinacies may lead to more species-rich community establishment and longer-term stability in variable environments. Likewise, the dependence of this mechanism on suitable growth conditions following the programmed decline of the more competitive species may represent an overlooked vulnerability for conservation under climate change. Because the general pattern we observed in the Kansas temporal census was for *S. nutans* tiller densities to increase through the growing season and then begin the next season at a lower tiller density (Figure 1), consecutive years lacking in late-season precipitation may be especially problematic for this species. For example, the tiller densities of *S. nutans* remained stable during each of the growing seasons of the Colorado spatial censuses, but the 2018 early season tiller density was lower than the early season density of the year prior. Such downward ratcheting would be expected to result in local population loss if the pattern continues. It may be noted as well that our method of surveying tiller densities with a census of individuals both early and late in the season likely underestimates tiller mortality rates, as some tillers that are lost may be replaced without our knowledge by newly recruited tillers that, in the short term, are less capable of resource capture. This suggests that for late-season tiller rates to exceed those of senescence, *S. nutans* requires more favourable conditions (e.g. larger precipitation totals) than were present in Colorado during these years. In contrast, after an intra-seasonal density increase in eastern Kansas in 2017, *S. nutans* began 2018 at a higher density than was observed in early 2017. However, with only 2 years of such observations in Colorado and Kansas, these findings are limited and longer-term research into the stability of this species under future climate scenarios will be necessary.

In conclusion, the consistency of the seasonal dynamics of tiller densities observed in our study species across space, over time, in contrasting climates, and despite varying management regimes and environmental conditions suggests the strong possibility that differing seasonal tiller dynamics play an important role in the success of these ecologically important $C_4$ grass species and the stability of their codominance over time. These patterns rely firstly on differences in the growth determinacy of the two species, a cryptic form of diversity that may be quite common and consequential in plant communities. For instance, during our study, we observed several other perennial plant species within their communities that declined during the growing season (e.g. *Panicum virgatum*, *Carex heliophila*, *Carex meadii*, *Poa pratensis*, *Sporobolus asper* and forb species in aggregate) and others that either increased in density or remained stable (e.g. *Bouteloua curtipendula*, *Schizachyrium scoparium*). This suggests that the mechanism we have described for stabilizing tiller densities of competing perennial plant species may be widespread and diffusely operating. Secondly, the proposed determinacy mechanism for coexistence is reliant on inter-annual and intra-annual environmental variability such that neither the determinately nor the indeterminately growing species have a consistent advantage. Such a mechanism may be vulnerable to changes in seasonal environmental conditions, particularly if these changes extend a consistent advantage to one species over another. Such issues should be considered in the context of climate change, conservation and restoration, yet the concept of growth determinacy and its potential variation within perennial species has been almost entirely unexplored in plant community ecology. However, because this study was not a controlled experiment, we cannot yet make strong inferences regarding a causal relationship between growth determinacy and codominance. More rigorous study through controlled greenhouse and field experiments involving (1) varying patterns of environmental conditions and (2) artificial communities composed of plant species with differing growth determinacies, will shed additional light on the effects of determinism diversity. Furthermore, greater inclusion of determinism in plant trait data collections will be necessary to assess how widespread and important its variability in natural communities can be.

## AUTHOR CONTRIBUTIONS

Jesse E. Gray and Melinda D. Smith conceived and designed the study. Jesse E. Gray collected and analysed the data. Jesse E. Gray and Melinda D. Smith wrote the manuscript.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.8w9ghx3r3 (Gray & Smith, 2022).

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