DISSERTATION

DEFINING, DESCRIBING, AND ASSESSING GROWTH DETERMINACY AS A MECHANISM OF PLANT SPECIES CODOMINANCE

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ABSTRACT

DEFINING, DESCRIBING, AND ASSESSING GROWTH DETERMINACY AS A MECHANISM OF PLANT SPECIES CODOMINANCE

The associations of both dominant species and species diversity with the functioning and stability of ecosystems are well established in plant community ecology theory. Despite this, there remains substantial debate regarding which driver is more important in determining rates of productivity, nutrient cycling, and other functions, as well as their resistance and resilience to disturbance. Both sides make compelling arguments. For example, common species, by definition, contribute the most to functions like productivity, but champions of species diversity can counter that resource use efficiency declines as dominance increases since a single species is limited in the resources it can access. What has seemingly been overlooked in this debate, however, and what may ultimately resolve some of its controversies, is a community structure that merges these two attributes: codominance. Codominant plant species, which I define as those that comparably share abundance that aggregately comprises the majority of the total abundance of a spatially and temporally specified community, can also be thought of as those species that represent *dominant* species diversity. For example, like dominant species, codominants directly contribute more to the productivity of an ecosystem than other members of the community, but they can also provide biodiversity-related enhancements to the ecosystem such as greater efficiency of resource capture and stabilizing features such as compensation for the loss of a codominant species with another, and asynchronous responses to environmental variability. Despite this, little progress has been made in linking the occurrence of codominance to its driving factors and their vulnerabilities, nor in exploring its effects, and how and why they vary.

I performed a literature review of ecological papers containing mentions of plant species codominance, and emblematic of the concept's appeal to intuition, found the term codominance is often used. However, this is most often done only in passing, typically limited to the abstract or introduction,

and is rarely considered *per se*, or even defined. Synthesizing the available and compatible definitions found in the review, I devised a more general definition (summarized above) that provides thresholds for inclusion under it. In addition, I provide a novel metric for measuring codominance, C_{max}, that can be used to complement other community structure measurements such as Simpson's dominance, Pielou's evenness, and Shannon-Wiener diversity. I demonstrate the calculation and application of C_{max} using synthesized and real-world data and show that is it readily capable of differentiating between communities and is particularly adept at discriminating between communities that are dominated by a single species from those that are codominated, despite sharing similar measures of Simpson's dominance. I am hopeful that this more general definition and the C_{max} metric will be used to advance our understanding of codominance, the mechanisms that underlie it, and what measures we must take to preserve and restore it.

In the remainder of this dissertation, I focus on a pair of species that have been recognized as supremely important codominant contributors to ecosystem structure and function in the mesic tallgrass prairies of the Great Plains, *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indiangrass). Of the two species, *A. gerardii* is the stronger competitor and the more drought-tolerant, making it the species that is better adapted to nearly the entire spectrum of climatic conditions occurring in this region. Moreover, the two species share many morphological and physiological characteristics in common, and both respond to water limitation by increasing their water conservancy. How the perennially inferior competitor in the region has not just coexisted, but remained codominant with *A. gerardii* is an enduring, but essential question, given their important roles in ecosystem function and stability and the possibility that climate change could alter their relationship. A subtle difference in the clonal recruitment patterns of the species was described nearly 50 years ago but has since been overlooked. While *A. gerardii* recruits new individuals only within a limited period in late Spring (determinate recruitment), *S. nutans* is capable of recruiting throughout the growing season (indeterminate recruitment). The inability of *A. gerardii* to respond concurrently to favorable late-season growing conditions may enable *S. nutans* to bolster population densities and recover from early season competitive asymmetry. If late-season conditions are not favorable for growth, this latter strategy would result in lost resource investment. I hypothesized that since the region is notably variable in both the total volume and timing of precipitation received during growing seasons, neither species has a consistent advantage from year to year, resulting in a dynamically stable codominant relationship. In this dissertation, I describe my observations of these patterns, and how they varied in both the center of their codominance in eastern Kansas and at the outskirts of their range in central Colorado, finding that *A. gerardii* densities unfailingly decline during each growing season, while those of *S. nutans* either increase or remain stable, depending on the region and growing season precipitation.

Having established this foundation for this proposed mechanism of codominance, I performed a greenhouse experiment that manipulated water availability, the timing of variations in water availability within growing seasons, and the consistency of that timing between growing seasons, to determine whether these patterns can affect the outcome of competition between *A. gerardii* and *S. nutans.* I compared the outcomes of competition between communities receiving no variation in water availability (either always wet or always dry) to those with intra-seasonal variability only, those with inter-annual variability only, and those with both intra-seasonal and inter-annual variability. I found that without any variations in water availability, one species comes to dominate (*A. gerardii* in dry, *S. nutans* in wet). The same occurs if variations only occur within seasons (*A. gerardii* if late seasons are always dry, *S. nutans* if late seasons are always wet). When inter-annual variation occurs, the two species have more similar population densities, and when both inter-annual and inter-seasonal variation in water availability occurs, this stabilizing effect is enhanced. The proposed mechanism is supported by these findings, but unexpected mortality rates of *S. nutans* receiving late-season dry conditions implores further experimentation, as does the necessity for study within field settings.

An alternative hypothesis for codominance between *A. gerardii* and *S. nutans* was also tested. In many ecosystems with varying environmental conditions, it has been observed that species interactions can become more facilitative as growth conditions deteriorate. The theory related to this phenomenon has been termed the stress gradient hypothesis (SGH). I hypothesized that during dry late seasons, the stronger competitor, *A. gerardii*, facilitates the recruitment, growth, and/or survival of newly recruited *S. nutans* individuals. If such were the case, the presence of *A. gerardii*, though a competitor, would be more beneficial to *S. nutans* than an equal density of intra-specific competitors. Using a similar experimental format as described above, but varying only late-season water availability, controlling community density, and comparing performance against monocultures, I tested whether the SGS could explain codominance between these species. However, I found that while increasing community density reduced recruitment, survival, and/or aboveground biomass production, the performance of both species was profoundly unaffected by the species identity of their neighbors. That is, each species behaved the same under dry late-season conditions whether in high-density monocultures or in mixed communities with matching total densities. Given the similarities between these species and their strategies of increasing water conservation during water stress, this suggests that the shifts in interaction outcomes could be limited by functional similarities between the interacting species. This result also lends deeper inference in support of the hypothesis that differences in determinacy enhance the stability of codominance between *A. gerardii* and *S. nutans*, though other feasible mechanisms remain to be tested.

Differences in determinacy may be common among closely-neighboring plant species and widespread across ecosystems. As such, the findings presented here are relevant not only to this single, though important, pair of species. More generally, it is essential to determine how frequently codominance occurs, when and how important codominance is for driving and stabilizing ecosystem function, what threats its different forms might face, and what we can do to preserve and restore codominant relationships. I hope that this dissertation, and the metrics described within, will serve as both an inspiration and a framework for these endeavors.

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DEDICATION

To Kit, who is not as lucky as I am.

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CHAPTER 1: INTRODUCTION

1.1 BACKGROUND

Topics considered: plant species codominance – defining, why they matter, measuring, mechanisms underlying, prevalence, effects on ecosystem function and stability, vulnerability, targets for conservation, strategies for restoration, insights for coexistence theory

In the coming years and decades, the effects of climate change and the increasing prevalence of drought on the functioning of ecosystems of every type will be an increasingly prevalent concern (Chapin et al., 2000; Cramer et al., 2001; Weltzin et al., 2003; Zhai et al., 2021). Important functions for plant species that may be affected include plant productivity (e.g., food, livestock and game forage, building materials (Chen et al., 2012; Cramer et al., 2001; Fay et al., 2003; Frank et al., 2015; Hoover et al., 2014b; Olesen & Bindi, 2002; Piao et al., 2013; Susan Moran et al., 2014)), soil stability (i.e., root-derived erosion resistance (Allen & Breshears, 1998; Lee & Gill, 2015; Slette et al., 2021; X. Zhang & Wang, 2015)), freshwater storage and flood mitigation (Baron et al., 2002; Novick et al., 2016; Sala et al., 2015), filtration of pollutants from water (Tzilivakis et al., 2019), nutrient cycling (Larsen et al., 2011; Mora-Gómez et al., 2020), atmospheric carbon removal and storage (Chen et al., 2012; Frank et al., 2015; Novick et al., 2016; Piao et al., 2013; Sitch et al., 2008; Slette et al., 2021; R. Zhang et al., 2020), and even climate regulation (D’Odorico et al., 2013; Novick et al., 2016; Ramankutty et al., 2006; Serna-Chavez et al., 2017; Stuenzi et al., 2021; Wu et al., 2021). In addition to these, wildlife species also depend on ecosystem functions that are at risk from climate change such as habitat and shelter provision (Bhattacharyya et al., 2014; A. C. Brown & McLachlan, 2002; Butler, 2012; Caddy-Retalic et al., 2019; Matthews et al., 2010; Orimoloye et al., 2020; Roy & Thomas, 2003; van Beest et al., 2012), stable predator-prey dynamics (Parmesan, 2006; Tscholl et al., 2021; Tylianakis et al., 2010; L. H. Yang & Rudolf, 2010), and habitat connectivity (Kang et al., 2016; Liang et al., 2021). While these functions affect every aspect of the lives of humans and wildlife, it is clear that they are not all similarly affected by factors associated with climate change such as acutely or chronically altered precipitation patterns and temperatures (Emmett et al., 2004; Hanson & Weltzin, 2000; Lemoine & Smith, 2019; Wilcox, Shi, et al., 2017). For example, in their meta-analysis of field experiments manipulating precipitation patterns, Wilcox et al. (2017) found that belowground plant productivity was relatively unaffected by precipitation additions or reductions in grassland ecosystems, while aboveground plant productivity was more sensitive to these manipulations. Moreover, specific functions are not necessarily affected similarly by climate change factors across different ecosystem types (Al-Yaari et al., 2020; Felton & Smith, 2017; Heisler-White et al., 2009; Knapp, Carroll, Denton, la Pierre, et al., 2015; Knapp et al., 2006, 2017; la Pierre et al., 2016; G. E. Maurer et al., 2020; Stuart-Haëntjens et al., 2018; Susan Moran et al., 2014; Wilcox et al., 2015; Wilcox, Shi, et al., 2017). For example, Wilcox et al. (Wilcox et al., 2015; Wilcox, Shi, et al., 2017) also found that the sensitivity of aboveground plant productivity to precipitation manipulations was dependent on the grassland type in question, with semi-arid shortgrass prairies having greater sensitivity than tallgrass prairies. Further, in an observational study comparing grasslands on different continents, Knapp et al. (2006) found that, despite similarities in mean annual precipitation and average aboveground plant productivity, productivity was more sensitive to precipitation variability in South Africa than in North America, but only if that variability occurred in the early portions of the growing season. To better prevent and/or adapt to changes and losses of vital ecosystem functions, it will be important to fully understand not just the responses of ecosystems to factors associated with climate change, but the causes of variability in these responses among different ecosystems.

Differences in plant species compositions between ecosystems, including those that have significant functional similarities (Knapp et al., 2006), has been suggested as an important factor underlying variabilities among ecosystems' responses to environmental changes (Al-Yaari et al., 2020; Byrne et al., 2017; Felton & Smith, 2017; Grime et al., 2000; Knapp et al., 2006; la Pierre et al., 2016; C. Li et al., 2021; Shi et al., 2018; Stuart-Haëntjens et al., 2018; Susan Moran et al., 2014). For example, the presence of a species that is more slow-growing and drought-tolerant may buffer the productivity of an ecosystem as changes in precipitation occur, producing less biomass in wetter years than a rapidly growing, drought-intolerant species, but comparatively more biomass in the drier years (Grime, 2001). It has also been argued that how much of an effect on ecosystem function a species has depends critically upon its relative abundance within that ecosystem (Grime, 1998a; Hillebrand et al., 2008; Smith et al., 2020), and – depending on the function in question and the measure of abundance – a highly abundant (i.e., dominant) species can be expected to exert a proportionally greater influence than subordinate species (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Gaston, 2010a, 2011a; Grime, 1998a; Smith et al., 2020; Smith & Knapp, 2003). As such, the identity of the dominant species and its traits can be the primary determinant of an ecosystem function's response to environmental change (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Bardgett et al., 1999; Fay et al., 2003; Grime et al., 2000; Hoover et al., 2014b; Knapp, Carroll, Denton, la Pierre, et al., 2015; Smith & Knapp, 2003). However, many others have argued that biodiversity is the key factor in driving ecosystem function (Clavel et al., 2011; Hooper et al., 2005; Hou et al., 2021; Isbell et al., 2011; S. Li et al., 2021; Liang et al., 2016; Loreau et al., 2001; Maestre et al., 2012; Tilman et al., 1996a, 2012) and stability (Lyons et al., 2005; Pérez-Ramos et al., 2017; Walker et al., 1999; Wilcox, Tredennick, et al., 2017). Greater biodiversity is purported to result in more efficient resource use, as some resources are available or useful to some species that aren't to others, leading to enhanced functions, such as productivity (niche complementarity (Berendse, 1983; Naeem et al., 1994; Tilman et al., 1996b, 1997, 2001)). For example, tap-rooting plants may be able to access water that is deeper in the soil than more fibrous-rooted species can reach (Sala et al., 1989; Ward et al., 2013). When both species are present, their aggregate biomass production is expected to be greater compared to monocultures of either species, as less of the water resource is wasted (Sala et al., 1989; Ward et al., 2013). In turn, this more efficient use of available resources may reduce the invasibility of ecosystems (Fargione et al., 2003; Kennedy et al., 2002).

In addition to enhancing mean function values, greater biodiversity can contribute to ecosystem stability through its more emergent properties, including greater asynchrony of responses to temporal variations in environmental factors, which imparts those ecosystem functions that species jointly contribute to with reduced variability (Pérez-Ramos et al., 2017; Tilman & Downing, 1994; Wilcox, Tredennick, et al., 2017; Yachi & Loreau, 1999). For example, communities containing both drought-tolerant (but slow-growing) and fast-growing (but drought-sensitive) species should have greater productivity over periods during which both wet and dry conditions occur compared to communities composed only of either one type of species or the other. Similarly, with greater biodiversity, an ecosystem may have increased redundancy. For example, it may have multiple species that can contribute similarly to an ecosystem function. In such cases, if one species is lost through catastrophic, stochastic events such as species-specific pathogen spread that another is resistant to, the latter may be able to compensate and ensure the function is continued (Lyons et al., 2005; Naeem & Li, 1997; Tilman, 1996; Walker et al., 1999; Yachi & Loreau, 1999), albeit with newly reduced redundancy and stability (Ehrlich & Ehrlich, 1981; Nippert et al., 2009; Smith & Knapp, 2003).

The relative importance of these two aspects of community composition – dominance and biodiversity – in driving ecosystem function and regulating the sensitivity of functions to environmental change is of considerable debate. There is some indication from studies that considered both factors in parallel that they can play key, simultaneous roles in determining ecosystem function (Chapin et al., 1997; Grime, 1998a; Hooper & Vitousek, 1997; Jiang et al., 2021; Orwin et al., 2014; Wilsey & Potvin, 2000; Z. Yang et al., 2017). Even this more nuanced determination is inconsistent, however (S. Li et al., 2021; Ma et al., 2021; Smith et al., 2004a; Smith & Knapp, 2003; Wilsey & Potvin, 2000; Z. Yang et al., 2017). In sum, increases in many of the ecosystem functions that have been studied, and their stabilities, have been attributed to increased dominance, decreased dominance (greater biodiversity), a combination of the two, and strictly one of the two. It is surprising then that far less has been said about what could be considered the intersection of dominance and biodiversity: *codominance* (Chapter 2). Though definitions in ecological literature are rare and inconsistent, codominant species are those that, like dominant species, have a much greater share of abundance than subordinate species, but also contribute more to biodiversity than dominants by sharing that abundance with another or several other codominant species (Chapter 2). As such, codominants may drive ecosystem function both by being the leading direct contributors to those functions (e.g., biomass production), and more indirectly through biodiversity-associated effects such as niche complementarity, asynchronous responses to environmental variability, and ecological redundancy. This makes codominant species uniquely suited for fine-tuning our understanding of these drivers. For instance, by varying the abundances of codominant species, both relative to one another and their remaining community, the strength of the effects of abundance and biodiversity may be teased apart under a variety of environmental conditions. Moreover, given that plant communities have long been characterized as having a few common species and many rare species (MacArthur, 1960; Preston, 1948a; Whittaker, 1965a), codominance may be more common than either monodominance or high evenness. Despite this, though the term codominance has often been attached to plant species within ecological literature, codominance *per se*, its prevalence, its underlying mechanisms, and its consequences have not been rigorously examined (Chapter 2). Therefore, the goal of this dissertation is to serve as a starting point and a framework for addressing the gaps in our understanding of codominance. I believe that narrowing these gaps will provide new targets for effective conservation, strategies for resilient restoration, insights for coexistence theory, and considerations for climate change adaptation.

1.2 DISSERTATION OVERVIEW

The goal of this dissertation, and the research involved, was to generate a holistic re-framing of the concept of plant species codominance that standardizes the way the scientific community converses about codominant species, highlights their unique importance to ecosystem function, and explores the mechanisms through which species might come to assume such roles, as well as potential vulnerabilities of those mechanisms. This work has involved synthesizing the various conceptualizations of codominance reported within the fields of coexistence and ecosystem function theory, identifying commonalities among them, developing a metric that can be used to determine degrees of codominance and facilitate comparisons across ecosystems, experimental treatments, and time, and then using these tools to explore various possible mechanisms behind the unexplained stability of codominance of two ecologically, economically, and culturally important tallgrass plant species. In pursuit of these objectives, I performed a review of the literature involving codominant plant species, conducted observational field studies of population dynamics and aboveground primary productivity, and performed experiments within greenhouse settings that manipulated mesocosm species composition and resource availability patterns. The details of these efforts are outlined in greater detail below.

Study system

One of the clear findings of my literature review was that researchers studying codominant species most frequently attribute the stability of their relationships to fluctuations in environmental conditions that alternately favor one species over the other and which occur at a frequency that is rapid enough to prevent overall trends towards competitive exclusion (Duan et al., 2015; Hartvigsen, 2000; Mori & Komiyama, 2008; Ribichich & Protomastro, 1998; Witwicki et al., 2016; Zedler & West, 2008). This insight helped inform my approach to investigating the unexplained dynamically stable relationship between *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indiangrass), two codominant grass species in the mesic prairies of the central Great Plains, US (L. Brown, 1985; Duralia & Reader, 1993; Freeman, 1998; Hartnett et al., 1996; Smith & Knapp, 2003).

At first glance, these species may seem like unsuitable candidates for stabilization *via* differential responses to environmental variability, as they bear many functional similarities (Forrestel et al., 2014, 2015) and respond similarly to all previously investigated environmental factors (Berg, 1995; Bowles et al., 2011; Forrestel et al., 2014, 2015; Hadley & Kieckhefer, 1963; Lett & Knapp, 2003; Mulkey et al., 2008; Polley et al., 1992; A. M. Silletti & Knapp, 2001a; Towne & Kemp, 2003, 2008; Weaver, 1931; Weaver & Fitzpatrick, 1932; Weaver & Rowland, 1952). Moreover, *A. gerardii* is believed to be more competitive in the central Great Plains (A. M. Silletti et al., 2004a), as well as more drought tolerant

(Hoffman et al., 2018a; Hoffman & Smith, 2018a; A. Silletti & Knapp, 2002; Swemmer et al., 2006c), suggesting an advantage over *S. nutans* across much of the precipitation gradient that characterizes the region. However, other mechanisms attributed to codominance (outlined in Chapter 2) are also questionable:

Partial and complete spatial niche partitioning

Codominance through spatial niche partitioning (e.g., Breshears et al., 1997; Dias & Melo, 2010; Cohn et al., 2011; Ward et al., 2013) seems unlikely in this case, as these species are well-mixed throughout the Konza Prairie (personal observation), where they are codominant (L. Brown, 1985; Duralia & Reader, 1993; Freeman, 1998; Hartnett et al., 1996; Smith & Knapp, 2003), and both obtain most of their water and nutrients from the same shallow soils (Nippert et al., 2012; Nippert & Knapp, 2007).

Spatially attenuated dominance

This mechanism can be likened to spatial niche partitioning but acts not to favor a less competitive species, but to negatively affect an otherwise dominant species (e.g., Káplová et al., 2011; Rebele, 2013). As such, it is unlikely to explain codominance between *A. gerardii* and *S. nutans* for the same reasons, unless there is an environmental factor that asymmetrically reduces the fitness of *A. gerardii* throughout the Konza Prairie.

Successional Circumstance

The chance observation of an intermediate successional stage (e.g., Simard et al., 1998; Sefidi et al., 2011) is possible (though difficult to test for), but *A. gerardii* and *S. nutans* have been considered codominant in the central Great Plains for nearly a century or longer (Weaver, 1931; Weaver & Fitzpatrick, 1932), and abundances of both species are frequently observed to both rise and decline over 1 to 3-year intervals (Craine et al., 2010; A. Silletti & Knapp, 2002; Towne & Kemp, 2003, 2008), indicating that there are environmental controls that can override any successional process that might be occurring.

Consumer control

Both species are similarly targeted by native and domestic grazers (Gillen et al., 1998), making it unlikely that preferential herbivory of an otherwise dominant species drives their codominance (e.g., Goheen et al., 2007; Augustine et al., 2017). However, preferential grazing of *A. gerardii* has been implicated in increased biomass of other species, and the evidence for effects of grazers on both species is quite mixed (e.g., Vinton et al., 1993; Silletti & Knapp, 2002).

Allelopathy

Neither species is known to be allelopathic to the other (Greer et al., 2014; Parker, 2000), though there is a regionally invasive, allelopathic species closely related to *A. gerardii*. However, the reported mechanism requires the less competitive species to have this ability so that it can impede the performance of the species that would otherwise overtake it (e.g., Meier et al., 2009). Moreover, root extracts of *S. nutans* have been shown not to inhibit, but to increase shoot growth of *A. gerardii* (Parker, 2000). However, it has not been ruled out that *S. nutans*, the less competitive species in the region (A. M. Silletti & Knapp, 2001a), is capable of allelopathically reducing the performance of *A. gerardii* at other growth stages, and this may be worth further investigation. It is also possible that *S. nutans* can allelopathically control subordinate species, as has been shown with the forb *Asclepias tuberosa* while having no effect on *A gerardii.* If so, this could bolster the relative abundance of the two codominants, thus making them more likely to be observed as codominant, but it would not account for the stability of *S. nutans* populations under asymmetric competition from *A. gerardii* (Chesson, 2000).

Mutualist intervention

A third-party mutualist may favor one species over the other (e.g., Petanidou et al., 1995), and both species form positive, obligate relationships with mycorrhizal fungi (Hartnett et al., 1994; Hetrick et al., 1988, 2011). This mechanism was not investigated in developing this dissertation but doing so may be a valuable next step.

Mutual spatial attenuation

This mechanism would imply that one species is monodominant at one end of an environmental gradient, the other species is monodominant at the other end, and there is codominance in the intermediate part of the gradient (e.g., Meentemeyer & Moody, 2002; Balzotti & Asner, 2017). On a continental scale, this would appear to apply, as *S. nutans* is more dominant in the more humid eastern and southeastern parts of the US (D. A. Brown, 1993; Epstein et al., 1998a; USDA, 2021b), and *A. gerardii* is more dominant in the Midwest and northern Great Plains (Keeler, 1990; USDA, 2021a), with codominance occurring where these regions intersect in the central Great Plains. As such, mutual attenuation of dominance could be considered a contributor to *A. gerardii / S. nutans* codominance. However, for the purposes of this dissertation, I am more interested in the maintenance of codominance at scales wherein direct interactions between the species involved can occur, and these species often do have mutually high abundances in well-mixed communities at the Konza Prairie (Hartnett et al., 1996; A. Silletti & Knapp, 2002).

A similar degree of adaptation

Given the functional similarities of the two study species and their abundance in the central Great Plains, it is very likely that similarity in their fitnesses within this region plays an important part in their codominance, particularly relative to their subordinate species. However, while equalizing mechanisms - those that reduce fitness differences between species – can make the process of competitive exclusion slow enough to be unobservable (e.g., Drenovsky & Richards, 2006; Bai et al., 2015), they cannot prevent exclusion indefinitely (Chesson, 2000). Although equalizing mechanisms have likely played an important role in *A. gerardii* and *S. nutans* codominance, population densities of both species are highly dynamic from year to year and are regularly observed to asynchronously increase and decline in abundance (Craine et al., 2010; A. Silletti & Knapp, 2002; Towne & Kemp, 2003, 2008) This suggests that random, slow drifts toward the fixation of either species are not occurring and that a stabilizing mechanism must be operating to alternate advantage between them (Chesson, 2000; Vellend, 2010).

Direct facilitation

The facilitation of one codominant species by the other (e.g., Kikvidze et al., 2006; Pueyo et al., 2016) was one mechanism I considered a strong candidate for explaining *A. gerardii – S. nutans* codominance. I hypothesized that the less drought-tolerant species, *S. nutans* might be facilitated by the presence of *A. gerardii* during the recruitment of vulnerable new tillers under drought conditions. This hypothesis was supported by observations that *A. gerardii* facilitates subordinate species and invasions (Smith et al., 2004a; Smith & Knapp, 2003). I used a greenhouse experiment to test for this effect, and the details are discussed in Chapter 3 of this dissertation.

Indirect facilitation

As mentioned in the previous section, *A. gerardii* removal has been observed to result in declines in productivity in subordinate species, suggesting facilitation of subordinate species rather than suppression. Moreover, this mechanism, as it has been described (e.g., Souza et al., 2011), excludes suppression of the codominant species, but *A. gerardii* and *S. nutans* have repeatedly shown signs of negative interactions, especially under competitive conditions (A. M. Silletti et al., 2004a).

Differential response to temporal environmental heterogeneity

Ultimately, I chose to focus my research on a mechanism of codominance that was not mentioned in the literature I reviewed. Instead, I proposed and investigated a mechanism unknown to be reported previously that relies on differences among the species in their recruitment strategies and temporal heterogeneity in growing conditions, though this latter requirement may warrant further investigation. To illustrate the mechanism with my study species as an example, *A. gerardii* is clonal and determinately recruits new ramets from existing genets during the early weeks of each growing season (McKendrick et al., 1975), after which no new ramets are produced until the following year (unless ramets are damaged through herbivory or fire (Ott & Hartnett, 2012)). While recruitment is paused, ramets grow leaves, produce underground buds, and may ultimately flower, but a substantial portion of the ramets senesce before the end of the growing season (Benson & Hartnett, 2006; Mitchell et al., 1998) and the severity of this self-thinning is exacerbated when late-season precipitation is more limited (Chapter 4) (Mitchell et al., 1998). In contrast, *S. nutans* clonally recruits new ramets indeterminately (McKendrick et al., 1975). While they tend to begin each season at lower densities than they ended the previous season with, they continue to vegetatively add new individuals to their populations throughout the season until growing conditions become limiting (i.e., insufficient water and/or light availability, cold) (Benson & Hartnett, 2006; McKendrick et al., 1975). I propose that in the late seasons where conditions are favorable for recruitment, *A. gerardii* remains programmatically incapable of doing so while also losing population density through senescence and thereby making light (and possibly water) more available to the community. This in turn enables *S. nutans* to take disproportionate advantage of this late-season recruitment favorability to recover from the early-season asymmetric competition by adding new ramets under a state of somewhat relaxed competition. However, if late-season conditions were consistently favorable for recruitment, *S. nutans* might be expected to become the dominant species, suggesting the requirement for temporal heterogeneity in growing conditions to maintain codominance. In the region where they are codominant, precipitation does vary considerably both within and between growing seasons (Craine et al., 2012; Hayden, 1998). I, therefore, tested for the effects of intra- and interannual precipitation variability on competitive outcomes in a greenhouse experiment, the results of which are detailed in Chapter 5.

While the proposed mechanism resembles a tradeoff between stress tolerance and competition/colonization ability (a type of differential response to environmental heterogeneity), it differs in some subtle ways. First, *A. gerardii* is typically the more competitive species in the region of codominance (A. M. Silletti et al., 2004a), but as a determinately tillering species, it is unable to capitalize on that advantage in the latter months of growing seasons. Second, while *S. nutans* may be relatively more opportunistic (A. Silletti & Knapp, 2002; A. M. Silletti & Knapp, 2001a), this mechanism does not rely on metapopulation dynamics (Hanski, 1998; Hanski & Gilpin, 1991; Hooper et al., 2005), but rather on periodic, vegetative recruitment from already-established populations. Thirdly, while the proposed mechanism requires differences in demographic-level dynamics, it does not require that the two species respond differently to environmental heterogeneity at the level of the individual. Ramets of both are theoretically free to have identical physiological responses to environmental conditions and changes if differences in their recruitment strategies cause them to encounter those conditions with varying population-scale capacities for resource capture and/or investment.

There are several important considerations implied by the proposals presented in this dissertation that should be kept in mind by the reader. First, codominant species are common (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Gaston, 2010a, 2011a; Gaston & Fuller, 2008; Limpert et al., 2001a; Preston, 1948a; Sugihara, 1980a), perhaps much more common than we realize, and through their abundance and interactions are of vital importance to ecosystem functions and their stabilities and their adaptabilities (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Avolio & Smith, 2013a; Bailey et al., 2009a; Bangert et al., 2008a; Crawford & Rudgers, 2012a; Crutsinger et al., 2008a; Gaston, 2010a, 2011a; Grime, 1998a; Hughes et al., 2008; Smith et al., 2004a, 2020; Whitham et al., 2006a). Second, variability in the determinacy of recruitment is present in more than just the study species used here (Chapter 4 discussion, Ott & Hartnett, 2012) and may also be quite common. As such, the novel mechanism of codominance stabilization might be widespread, diffuse, and cryptically important for maintaining species codominance. Lastly, if this mechanism indeed relies on current environmental conditions and variabilities, and those factors are likely to be altered by climate change, we must seek a more complete understanding of its prevalence, importance relative to simultaneously operating mechanisms, vulnerabilities to likely aspects of climate change, consequences of its failure, and ways to conserve and restore its functioning.

1.3 SUMMARY OF CHAPTERS

This dissertation is composed of six chapters including this introduction, a literature review of plant ecology research related to codominance, three chapters describing original research, and concluding remarks. The literature review in chapter 2 describes issues encountered when attempting to synthesize previously published conceptualizations of codominance, namely that definitions have mostly not been provided when authors have described their study species as codominant (often only doing so in the abstracts of papers) and when they have, their definitions have often been inconsistent with one another's. Moreover, data provided in these papers show strikingly different relative abundances among species labeled as codominant. The review presents a qualitative definition of codominance that synthesizes the definitions of others I considered conceptually consistent, as well as a novel metric of codominance that combines the abundances of the purported species and their distinctiveness relative to their subordinate species. I demonstrate the behavior of this metric in distinguishing between communities using exaggerated community data, simulated data generated from lognormal distributions with varying standard distributions, and real-world data collected from contrasting grassland ecosystems. This chapter also discusses mechanisms of codominance reported in the literature and offers future directions for research into this relatively unexplored concept.

In the third chapter, I discuss a greenhouse experiment I performed to determine whether *A. gerardii* facilitates the late-season recruitment of *S. nutans* tillers under drought conditions, one of the mechanisms I considered to be a viable explanation for their codominance in the central Great Plains (direct facilitation). The stress gradient hypothesis, for which there is strong but inconsistent evidence (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Callaway & Walker, 1997; Olofsson et al., 1999; Ploughe et al., 2018), holds that as abiotic stress increases, the sum of interspecific interactions between plants become less negative, and may result in overall positive (facilitative) interactions. I hypothesized that *A. gerardii*, being more drought tolerant (Hoover et al., 2014a; A. Silletti & Knapp, 2002; Swemmer et al., 2006c), may facilitate *S. nutans* by reducing subcanopy/soil moisture loss when water addition frequency was halved in the latter half of a growing season. Since *S. nutans* can continue to recruit new ramets (which may be more vulnerable to drought than mature ramets) throughout the growing season, this effect of *A. gerardii* neighbors was expected to result in better *S. nutans* recruitment rates compared to monocultures. In turn, the presence of *A. gerardii* would be a benefit to *S. nutans* average fitness, helping to explain their codominance. However, I did not find support for this hypothesis, as both *S. nutans* and *A. gerardii* recruitment rates were roughly similar whether in monocultures or mixtures. The same was the case for other measures of plant performance: ramet survival rate and aboveground primary production of biomass. While there may be other scenarios in which one species facilitates the other, variability in precipitation is a common source of stress in the region where these species are codominant (Craine et al., 2012; Hayden, 1998). These observations suggest that the shift to facilitative interactions between competing plant species may be limited by the functional similarities between the plants involved. This limitation could be an important consideration in conservation and restoration efforts, as it may explain why some communities are less successful in resisting environmental stress than others.

In the fourth chapter I describe the results of an observational study that sought to establish the foundational elements of the proposed mechanism underlying codominance between *A. gerardii* and *S. nutans*, that differences in their recruitment determinacies enable them to respond differently to environmental heterogeneity at a demographic level, despite similarities between them in their physiologies, morphologies, and their *per capita* responses to a wide variety of environmental factors. This study consisted of population density monitoring (stem density counts) both within and between seasons to concretely establish firstly whether *A. gerardii* densities were consistently insensitive to late-season precipitation and declined (or remained constant) after their initial recruitment events in April. Secondly, the study examined whether *S. nutans* population densities were sensitive to late-season water availability, increasing from early-season densities in years when late-season water availability is high, and declining or remaining unchanged when late-season precipitation is more limited. To determine the consistency of these patterns, population dynamics were monitored at three spatio-temporal scales: 1) across a varying landscape with plots placed across the Konza Prairie Biological Station (a mesic tallgrass prairie in the central Great Plains) and varying in topographical position and fire frequency; 2) across eight years at a single location at the Konza Prairie; and 3) across regions with surveys conducted on the western edge of the Great Pains (and of the species' ranges (Keeler, 1990; USDA, 2021b, 2021a)) in central Colorado. In agreement with my hypotheses, there was remarkable consistency of *A. gerardii* seasonal decline or stasis across all scales, regardless of any encountered environmental factors. In contrast, *S. nutans* densities were far more sensitive to late-season environmental conditions, and were observed to rise, decline, and remain stable across all scales, presumably in response to water availability. However, this dependency was not tested explicitly in this study.

In the fifth chapter, I describe a greenhouse experiment designed to establish the association more firmly between *S. nutans* population dynamics, their dependency on late-season water availability, and their role in maintaining stable populations in communities with *A. gerardii*. This experiment consisted of two seasons during which the availability of water was manipulated both intra- and inter-seasonally. Comparisons were made between communities with intra-seasonal variations in water availability, inter-seasonal variations in water availability, both intra- and inter-seasonal variations in water availability, and neither intra- nor inter-seasonal variations in water availability. I hypothesized that communities receiving only intra-seasonal variation would favor a single species, resulting in trends toward monodominance of

A. gerardii when wet conditions were isolated to early seasons, and of *S. nutans* when wet conditions were isolated to late seasons. Communities receiving no variation in water availability were hypothesized to also favor a single species, leading to trends toward *A. gerardii* dominance if always dry and toward *S. nutans* dominance if always wet. Communities receiving inter-annual variation were expected to result in co-dominance, as the species that was given an advantage in the first season was expected to have a disadvantage in the second, and those communities receiving both intra- and inter-seasonal variation in water availability were expected to be codominant, but with reduced inter-seasonal variance in population densities. We found evidence in support of these hypotheses – and of the codominance mechanism they imply – with densities of the two species' populations averaged over time most similar in treatments including inter-specific variability in water availability, and lower variance in population densities in those treatments that also included intra-specific variability in water availability. However, the late-season dry conditions were surprisingly deleterious for *S. nutans*, particularly in communities that received early-season wet conditions. This caused those *S. nutans* populations receiving late-season dry conditions in the first season to fail to re-emerge in the second season and making the set of comparisons among the treatments incomplete.

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Chapter 2: DEFINING CODOMINANCE IN PLANT COMMUNITIES

2.1 OVERVIEW

Species dominance and biodiversity in plant communities have received considerable attention and characterization. However, species codominance, while often alleged, is seldom defined or quantified. Codominance is a common phenomenon and likely an important driver of community structure, ecosystem function, and the stability of both. Here we review the use of the term 'codominance' and find inconsistencies in its use, suggesting that the scientific community currently lacks a universal understanding of codominance. We address this issue by 1) qualitatively defining codominance as mostly shared abundance that is distinctively isolated within a subset of a community, and 2) presenting a novel metric for quantifying the degree to which relative abundances are shared among a codominant subset of plant species, while also accounting for the remaining species within a plant community. Using both simulated and real-world data, we then demonstrate the process of applying the codominance metric to compare communities and to generate a quantitatively defensible subset of species to consider codominant within a community. We show that our metric effectively distinguishes the degree of codominance between four types of grassland ecosystems as well as simulated ecosystems with varying degrees of abundance sharing among community members. Overall, we make the case that increased research focus on the conditions under which codominance occurs and the consequences for species coexistence, community structure, and ecosystem function would considerably advance the fields of community and ecosystem ecology.

2.2 INTRODUCTION

Conservation research is often focused on biodiversity and rare species (Gaston, 2010b, 2011b), but frequently overlooks the common species that drive many ecosystem functions and services (Avolio, Forrestel, Chang, La Pierre, et al., 2019; Gaston, 2011a; Grime, 1998b). Rare species are certainly threatened by human activities (Ohlemüller et al., 2008; Schatz et al., 2014; Vitousek et al., 1997) and can play important roles in ecosystem function directly, and through their contributions to biodiversity (Gross et al., 2014; Jain et al., 2014; Loreau & de Mazancourt, 2013; McCann, 2000). Yet, common species largely control ecosystem function, often proportional to their greater abundance and biomass in the system (Grime, 1998). They also exert strong influences over community structure, including the potential facilitation of rare species (Smith et al., 2004b). Moreover, because by definition the plurality, or even majority of individuals in many ecosystems belong to a common species, the phenotypic plasticity and genetic diversity associated with these highly abundant species can have ecosystem-level effects in excess of those related to species diversity (Bailey et al., 2009b; Bangert et al., 2008b; Crawford & Rudgers, 2012b, 2013; Crutsinger et al., 2008b; Hughes et al., 2008; Whitham et al., 2006b). Accordingly, long-term ecosystem sensitivity to environmental change may also be principally determined by the population-level responses of common species (Avolio & Smith, 2013b). For these reasons, recent reviews have argued in favor of increasing consideration of common species in conservation programs and research, with recommendations for a shift in focus primarily towards common species over biodiversity for better understanding and management of ecosystem function (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Gaston, 2010a, 2011a; O'Loughlin et al., 2018).

In plant communities, the effect of a common species can easily be determined when a community is highly uneven, meaning when there is a single common species with the remaining species in low abundance (Fig. 2.1). In such instances, these plant species are often referred to as dominant or dominating in the community (*sensu* Avolio *et al*. 2019), and there is ample evidence that the loss of these species can have large consequences for ecosystem function and stability (Gaston & Fuller, 2008; Sasaki & Lauenroth, 2011a; Smith et al., 2020; Smith & Knapp, 2003). However, there are instances where there are more than one common species in a plant community (Fig. 2.1); these are often referred to as *codominant* species (Danin, 1978; Kuebbing et al., 2015; Woods, 1979). Where they occur, codominant plant species are distinct from uncommon (or subordinate, Grime 1998) species, in that they also can control a large proportion of ecosystem function (Ma et al., 2020; A. Silletti & Knapp, 2002; Valencia et al., 2020). The often-observed pattern that ecosystems are frequently characterized by a few abundant and many rare species (Preston, 1948; MacArthur, 1960; Whittaker, 1965) suggests that codominated ecosystems may be as (or even more) common than communities dominated by a single species (i.e., mono-dominated communities). Even if there is a single regionally common species, such dominant species are likely to be locally codominant with other species within portions of their ranges. As such, studies focusing on the characteristics of only the most abundant plant species may fail to capture important aspects of local ecosystem function and stability (Grime, 1998a; Smith et al., 2020; Smith & Knapp, 2003). For instance, the influence of a single common species on ecosystem function will be overestimated if its abundance is correlated with both the measure of that function and the abundance of another common species. Moreover, greater temporal stability in ecosystem function may occur in communities with more than one common species, for example, if changing environmental conditions favor one common species one year, and the other common species in another. Collectively, variance in ecosystem function would be expected to be lower for the codominated community than one that is mono-dominated (Wilcox, Tredennick, et al., 2017).

Given the potential for plant communities to contain more than one common species and the implications of codominance for community and ecosystem functioning and stability, it is surprising that, to our knowledge, no synthesis of ecological literature on codominance has yet been presented. Moreover, based on our review of the literature, the concept of what qualifies as codominance has depended largely upon the author, with species comprising between 5 and 83% (Gilbert et al., 2009; Toft & Elliott-Fisk, 2002) of total abundance having been described as codominant. We assert that this overly broad range of abundances has made the term “codominant” practically meaningless. Additionally, some authors have instead relied on frequencies, rather than abundances in their delineations of codominance (Costa et al., 2009; El-Keblawy et al., 2015; Lawesson, 2000; Lisa & Renato, 2006), which can reflect strong dispersal abilities of species that otherwise bear little ecological influence. To illustrate, a species with low abundance that appears in all samples would appear equivalent in frequency to a species that also appears in all samples but at high abundances. We acknowledge that frequency can be a valuable component of codominance but suggest that it can be misleading when reported in the absence of other abundance metrics. In contrast, others have used the term to refer to indicator species that are unique in their localized abundance and coincident *lack* of frequency across a study area (Dias & Melo, 2010). Such labels are valuable for floristically distinguishing between ecologically dissimilar areas within a region, and we would agree that such species may be codominant within those limited areas. However, this use of the term "32cology32ntt" to refer to a species' distribution throughout an entire region where it is distinctly uncommon is confusing in its incongruity with the more common understanding of the term. Similarly, numerous (especially earlier) papers used the term codominant to classify species with abundances immediately inferior to those of coexisting dominant species (Bazzaz, 1968; Busch, 1995; Day & Monk, 1974). Lastly, though less problematic, many authors have reported only absolute abundances of their codominant species, without referencing the abundances of the remaining species in their communities for comparison (Hamerlynck et al., 2002; Kürschner, 2004). Without a consensus in defining codominance, or a standardized method for quantifying codominance (in line with metrics of dominance), progress towards a better understanding of the mechanisms that lead to such relationships and the consequences of codominance for community structure and ecosystem function and stability will be hindered by ambiguity.

Here, we aim to facilitate more clear communication and generate a deeper discussion of codominance in three ways. First, we delve deeper into the importance of codominant species. Second, we conduct a literature review to synthesize existing definitions or implied meanings of codominance and characterize the mechanisms that have been used to explain the stability of codominant relationships. Based on this synthesis, we provide a qualitative definition of codominance and summarize the proposed mechanisms underlying codominance included in the reviewed papers. Third, we provide a novel metric of codominance that can be used to identify the occurrence of codominance and to quantitatively compare ecosystems, experimental treatments, and community states in space and time. We then present examples of the utility of this metric using synthetic and real data. Finally, we provide an overview of the implications of codominance and future directions of codominance research. We believe a clear qualitative definition and a metric to quantify codominance will garner a greater mutual understanding of this underappreciated community characteristic, fostering a more complete conception of plant communities and the roles their most important members play in them.

2.3 WHY CODOMINANCE MATTERS

The usage of the term 'codominance' is common in plant ecology but often not explicitly defined (see next section). As such, we contend that its importance in plant communities has been overlooked and understudied. Below we describe three ecological topics for which the study of codominance may provide important insights.

1. Coexistence theory

The history of community ecology may be said to embody our lengthy endeavor to better understand how species coexist (Loreau, 2010). Current frameworks around this fundamental question rest on two foundations: niche differences and relative fitness differences among coexisting species. However, the relative importance of the roles that these aspects play are imperfectly understood (Carroll et al., 2011; HilleRisLambers et al., 2012; Kraft et al., 2015; Levine & HilleRisLambers, 2009; Valencia et al., 2020) and are likely variable (Chase & Myers, 2011; HilleRisLambers et al., 2012). For instance, sets of codominant species that exhibit similar degrees of shared abundance but contrasting degrees of functional similarity (Kikvidze et al., 2006; Kuebbing et al., 2015) suggest that the degree of niche partitioning can vary greatly across sets of codominant species. Moreover, while relative fitness differences can cause better competitors to capture greater shares of abundance within their communities, this property must be tempered to enable codominance. As such, species exhibiting stable codominance, particularly in variable environments, present ideal model systems for exploring the relative importance of niche vs. fitness differences in determining the outcomes of species interactions.

2. Ecosystem function and stability

When an ecosystem is overwhelmingly dominated by a single species, many of its functions (e.g., annual net primary productivity) will be controlled primarily by the dominant species in direct proportion to its relative abundance (Grime, 1998; Smith et al., 2020). In turn, the stability of such functions will be a consequence of the population dynamics of that single dominant species and its responses to changing environmental conditions (Gaston & Fuller, 2008; Smith & Knapp, 2003). In contrast, when an ecosystem is codominated, control over its ecosystem functions will frequently depend on the mechanism(s) underling codominance (Mouquet et al., 2002; Tylianakis et al., 2008) and may be more evenly distributed across the co-dominating species in proportion with their shared abundances (Grime, 1998a). In addition to sharing in the control of the magnitude of expression of ecosystem function, codominant species can affect the spatial and temporal variability in ecosystem function when they differ in their responses to changing environmental conditions, (Loreau et al., 2003; Shanafelt et al., 2015). This, in turn, can result in enhanced temporal stability of those functions (Valencia et al., 2020). For instance, if in one year environmental conditions favor biomass production of one species more so than its codominant, and the next year favors the latter over the former, variance in community biomass productivity over those two years will be lower than in an ecosystem that experiences the same environmental variability but is mono-dominated by either one of the two species (Wilcox, Tredennick, et al., 2017). Thus, codominance is likely an important, yet under-recognized, feature of plant communities that influences ecosystem functioning and stability in ways that differ from the most common (dominant) species or species diversity.

3. Global Change

Although common species carry a relatively low probability of extirpation, such events have occurred arising from introduced invasive plants, species-specific pathogens, and uncontrolled preferential herbivory (Anagnostakis, 1987; Ash et al., 1997; Condon et al., 2011; Dillemuth et al., 2009; Fernandez-Winzer et al., 2020; Mal et al., 1997; Nuzzo, 1999; Vinton et al., 1993; M. A. White, 2012), often with dramatic ecosystem consequences. Future losses of common species are anticipated to occur at a greater rate as a result of changing abiotic conditions such as warming (Bokhorst et al., 2008; Llorens et al., 2004), drought (Llorens et al., 2004; Visser et al., 2002a), and altered nutrient availabilities (Cantarel et al., 2013; Isbell et al., 2013). Such issues can be expected to be particularly problematic in cases where codominance is a direct result of interactions between the traits of codominant species and historic climatic conditions and patterns. Interactions between changing abiotic and biotic factors are also likely (Bale et al., 2002a; Kelly & Goulden, 2008; Theoharides & Dukes, 2007). However, if codominant species differ in their responses to environmental change and are redundant in their effects on ecosystem functions, the negative impacts of changing biotic and abiotic factors may be greatly mitigated relative to mono-dominated ecosystems (Mori et al., 2013). This potential should be at the forefront of restoration planning and greater knowledge of the traits of codominant species could be critical for success in these efforts (Laughlin et al., 2018). Likewise, conservation science (Kareiva & Marvier, 2012), a field currently oriented towards crisis mitigation (Geldmann et al., 2020), could be well served through increased consideration of codominant species. Because of the visibility of codominant species and their proportionally greater control over ecosystem functions and services (Grime, 1998a; Smith et al., 2020), arguments for their conservation may be more persuasive among stakeholders than those made for charismatic, but seldom seen species (O'Loughlin et al. 2018). Moreover, because codominant species can have positive effects on biodiversity and function by facilitating rarer species (Smith & Knapp, 2003), investments in their conservation may be required for long-term success. On the other hand, when species are more complementary or mutually facilitative in their effects, or if they respond to certain environmental changes in synchrony, the regions where they co-dominate may be particularly vulnerable to such changes through positive feedbacks (Traveset & Richardson, 2014; Valencia et al., 2020). It will be increasingly important to understand the contributions that various codominant species make to their ecosystems and whether the characteristics of their responses to abiotic and biotic changes will buffer those systems or place them at greater risk of collapse.

2.4 DEFINING CODOMINANCE

1. Literature Search

To determine how codominance is used and defined in the literature, we conducted a literature review. We based our literature search on the criteria that: 1) authors mention some form of the terms "codominance" or "codominant", 2) the usage of the term references abundance or degree of ecosystem function determined by cohabiting species, and 3) the focal species were plants. To ensure repeatability, our primary literature search, conducted in March 2020, used Web of Science and the topic terms "plant", "36cology*", and either "co-domin*" or "codomin*". This returned 83 and 46 articles, respectively (S. Table 1). These were further filtered to remove uses of the term that were not compatible, including references to gene interactions, tree canopy structure, and non-plant focal species. A second search was performed in Web of Science using only the topic terms "co-domin*" or "codomin*". Results were refined using the Web of Science "categories" filter set to "ecology", returning 331 and 315 results, respectively. These returns were then subjected to the same manual filtering described above. In total, 165 research papers were found to match all our criteria. We performed a supplemental, but less replicable search using Google Scholar and the terms "codominant", "ecology", and "plants". This resulted in a return of over 17,000 matches. However, as we reviewed these matches in order from best match to worst, we found they had rapidly decreasing relevance (more frequently incompatible uses of the term and fewer focal species that were plants) and more replicate entries. In addition, a lower proportion of papers from the Google Scholar search provided definitions of, relative abundance data related to, and mechanisms explaining codominance. We, therefore, limited this supplementary inclusion to our core set of literature to the best-matching 100 papers uniquely returned in Google Scholar. In total, we reviewed 265 papers (Supp. Table 1). Importantly, no review or meta-analysis articles of codominance were returned using any of these methods.

2. A qualitative definition of codominant species

To define codominant species, we sought to inclusively synthesize conceptualizations presented in the literature as much as was feasible. Most (77%) of the reviewed papers did not include an explicit definition of codominance, and species were referred to as codominant only in passing (Supp. Table 1). Of those that included definitions, ten papers defined codominant species in aggregate terms (i.e., the sum of relative abundances), without explicitly stating the individual contributions of the component codominant species. Qualitative definitions that explicitly stated the relationship between the codominant species were provided in only nine papers. Quantitative definitions were included in ten of the papers, but all but one of these were based on an arbitrarily set threshold of abundance with no criteria described for their relationship with subordinate species. Species described as codominant included those with 1) the highest individual or aggregate measures of abundance, 2) more than a threshold abundance; or 3) were individually or aggregately major components of the vegetation (without reference to relative abundance), 4) had greater than average species importance value, and 5) exerted more control over an aspect of ecosystem function and/or diversity than other species in the community. Some also defined codominant species as those that were subordinate to dominant species, or those that serve as indicator species where dominant species are ubiquitous. Because the latter uses of the term codominance are limited to specialized fields such as phytosociology and contradict the broader usages, they were not considered when formulating our definition. Though referring to their focal species as codominant, 15 of the papers provided definitions for dominance only, most notably in terms of Simpson’s D (Almazán-Núñez et al., 2016; Hart, 2001; Taft et al., 2011). Because Simpson's D is a description of the community rather than of its component species, we also did not consider these uses of the term in defining codominant species.

Overall, our review suggests that definitions of codominance vary substantially, but most authors have not found it necessary to provide their interpretation of "codominant" or "codominated", despite an intuitive impulse to describe species or ecosystems using these terms. This might be acceptable if the intuitions of the authors were dependably similar. However, data gleaned from the reviewed papers revealed a wide range of abundances among the species that were described as codominant, both relative to one another, and relative to the remainder of species in their communities. For example, in some cases, the first and second-ranked species had an equal share of relative abundance, while in others the first-ranked species had as much as 19 times more abundance than the second (Quartile 1: 1.13x, Q2: 1.33x, Q3: 2.20x, Fig. 2.2A). Aggregate relative abundances of the two most abundant species ranged from 0.07 to 1 (Quartile 1: 0.41, Q2: 0.67, Q3: 0.89), indicating that these species collectively accounted for as little as 7% to as much as 100% of their total communities (Fig. 2.2B). These broad ranges indicate that investigators frequently have very different interpretations of codominance. We, therefore, sought in qualitatively defining codominance to synthesize its various but compatible uses to be as general as is reasonable and to set intuitive thresholds for inclusion under the classification. **We, accordingly, define *codominants* as species that have a 'mostly shared' abundance relative to one another, and at least double the abundance of any subordinate species. 'Mostly shared' abundance occurs when no codominant species has more than triple the abundance of any other codominant species.** We chose the first threshold as it is more than halfway between entirely unshared (where species 1 has 100% and species 2 has 0%) and evenly shared (50%:50%). In other words, if the ratio between one species and another has no more than a 3:1 ratio in abundance, they may be considered codominant. If three or more species are considered, the 'mostly shared' ratio would apply between the most abundant and each of the other species within that group. To illustrate, if one species had 30% of the community abundance, a second had 21%, and a third had 9.9%, the first two species should be considered codominant, but the third should not. These cutoffs are admittedly arbitrary, but they are based on reasonably intuitive notions and there is demonstrable value in setting such limits to avoid the degree of discrepancy revealed among reported communities. However, to address the arbitrary nature of these thresholds, we introduce a more general, quantitative means of comparing communities in a later section.

Because many of the reviewed articles did not include abundance data for subordinate species, we can, for the purposes of illustration, modify the second threshold to state that the aggregate abundance of the codominant species should exceed a certain share of the total abundance of the community. A share exceeding 50% would provide an intuitive example, as having more than half would imply that the codominant species contribute the majority of abundance of their community. Of the 167 pairs of first and second-ranked species reported with relative abundance data in our literature review (Fig 2.2A), 91 met both of these criteria, while 25 had uneven sharing of abundance and 53 pairs contributed less than a majority (<50%) of their community abundances. This is an imperfect compromise, however, as some communities that meet the criteria set in the above definition may be excluded under this alternative formula. For example, if two species each have 24% of the total community abundance, and the subordinates all have less than 5%, the former would be considered codominant, but their aggregate abundance narrowly falls short of the 50% criterion. This illustrates the value of including abundance data for each species when describing community structure.

Our definition is conceptually similar to the definition of dominance in that codominant species have higher relative abundance than others in their community (Avolio, Forrestel, Chang, la Pierre, et al., 2019), but with caveats that reflect the complications of multi-species dominance, namely that the species must be abundant, but not so abundant that others do not also capture a substantial share of the total community abundance. However, unlike Avolio et al. (2019), we do not (yet) include the relative influence of the species on ecosystem function for classification as codominant, not because we do not think this is an unimportant qualification, but because we did not find data of this nature sufficiently reported in the literature we reviewed. Until such data is more readily available (e.g., through multi-species removal experiments), it would be difficult to label any species sets as codominant under this criterion. Some species may be codominant using one type of abundance measurement (e.g., stem density of a bunchgrass), but not in another (e.g., canopy cover of a bunchgrass). As such, the measure by which codominance is determined should always be reported. Moreover, the types of measures of relative abundance should be consistent across the species considered but may be one of a variety of measures such as densities, biomass productivity, canopy cover, or basal area. Combinations of the above (i.e., importance values), can be useful in comparing across plant functional groups. Frequency may also be considered when combined with other measures (see Avolio et al. 2019). Our definition also maintains that for the species to be considered codominant, they should be present in the same space and at the same time, within the scale considered. Investigators should be specific about the temporal and spatial scales within which they consider their species to be codominant. Otherwise, dominance should be considered complementary and temporary/isolated rather than shared.

3. Potential mechanisms for codominance

Differences in the degrees of codominance between communities offer opportunities to gain a greater understanding of the various factors that determine interaction outcomes between highly abundant species. Of the 265 papers that met our criteria and were accessible, 132 had explicitly stated assumptions or findings regarding the cause(s) of codominance (Suppl. Table 1). An additional 37 out of the 265 studies lacked explicitly proposed mechanisms but were interpreted as having inferred mechanisms of codominance based on context (Suppl. Table 1). For example, if a study involved measuring species traits related to drought tolerance in conjunction with a spatial soil moisture gradient, we would assume the authors were testing for spatial niche partitioning. Six of the studies tested for specified mechanisms but did not find evidence for them, and in the remaining 96 studies, we could not detect either explicit or inferred mechanisms. In Table 1, we summarize the explanations for codominance found in our literature search and highlight the frequencies of those explanations. These explanations vary widely in their purported driving mechanisms, including bottom-up and top-down controls, abiotic and biotic influences, and relatively stable and dynamic environments. In general, however, the explanations share the common thread of interactions between a pervasive environmental driver and unique traits possessed among the codominant species. While our comparison of mechanism frequencies may be a suitable starting point for linking coexistence mechanisms to patterns of codominant species abundance, it should not be interpreted as a reliable reflection of the strength of the factors in determining codominance. Multiple factors may be responsible for biases in the frequency by which particular mechanisms are reported, including the potential inaccuracy of our interpretations of implied mechanisms, the inability to infer mechanisms from many of the reviewed studies, the current under-recognition of the codominance phenomenon within coexistence literature, and the potential for observing only a subset of the types of mechanisms driving codominance within systems in which multiple mechanisms operate concurrently.

Furthermore, our review found no efforts to compare the strengths or relative importance of these mechanisms, nor the conditions under which they are more likely to be detected. Aside from a universally understood codominance concept, a metric of codominance could further enable comparative research, allowing for the quantification of differences between ecosystems, communities over time, and community responses to experimental treatments. In the following sections, we describe such a metric and demonstrate its uses and statistical characteristics.

2.5 QUANTIFYING CODOMINANCE

1. A codominance metric – C_{max}

To enable more systematic, quantitative, and unbiased characterizations of codominance among communities, we developed a metric that can be readily used to mathematically compare systems of interest and be included in large data sets for broader analyses. Such a metric also will aid in the search for patterns among the mechanisms of codominance. This metric relies on measures of abundance that are relativized to those from the community aggregate, and as such is adaptable to many types of abundance measurements and a diversity of ecosystems. However, similarity in measurement types used will facilitate greater confidence in such comparisons.

Our approach begins by selecting the number of species to be considered codominant, hereafter termed the *codominant subset*. The number of codominant species can range from including only the two most abundant species to including all but the single, most uncommon species, and comparisons can be made between calculations using different putative codominant subsets to make decisions on which number of codominants is most appropriate to the question and ecosystem.

The harmonic mean of the relativized measures of abundance (or their relative aggregate measures, *e.g.,* importance values) for each codominant subset is calculated as below:

$$\text{Shared Abundance, } A_n = \frac{n}{\sum_{i=1}^{n} \frac{1}{x_i}}$$

Where n is the number of species in a given codominant subset and has a domain of $\{2, \ldots, R - 1\}$, where R is the total species richness of the community. The relative abundance of each species i within the codominant subset is given as x_i. A harmonic rather than an arithmetic mean of relative abundance values is used to distinguish between codominant subsets composed of species having disparate abundance values from subsets that have species with more similar abundances. To illustrate, if species a and b had relativized abundance measures of 0.4 and 0.4, both their arithmetic and harmonic means would be 0.4 (Fig. 2.1). On the other hand, if species w and z had values of 0.1 and 0.7, their arithmetic mean would also be 0.4, but their harmonic mean would be 0.175. The bias towards lower values in the harmonic mean can be used to indicate that species w and z share less of their abundance than do a and b.

The value of A_n alone can be useful to investigators interested in only a particular codominant subset, but it is limited in that it does not account for the remaining community. If two species have the same measure of relative importance as a third, there will be no difference in the values of A_n whether considering codominant subsets with two or three species and thus we would be incorrect in saying that two of the species are dominant over the third. The remainder of the approach proceeds iteratively to consider all possible codominant subsets while optimizing for the subset with the largest combination of shared abundance among codominants and disparity between them and their subordinates. The relative abundance of the next most abundant species, j (S_j, where $j = n + 1$, hereafter referred to as the primary subordinate) is subtracted from the shared abundances of its associated codominant subset to arrive at its Codominance Index:

$$C_n = A_n - S_j$$

The difference of A_n and S_j is a metric that increases both as a function of the similarity between the abundances of species within the codominant subset (A_n) and the degree to which the shared abundance within the codominant subset differs from the abundance of the primary subordinate. This index is calculated for all values of n, and the largest of these index values is considered $\boldsymbol{C_{max}}$, the community's optimized codominance value:

$$C_{max} = maximum\ (C_2, \ldots, C_{R-1})$$

Only species j is considered for each iteration as it represents the most conservative approach to drawing distinctions between the codominants and the subordinates. If instead a mean of the subordinates were subtracted from the shared abundance of the codominants, a larger distinction would necessarily be drawn, but it would reduce the clarity of whether species j (and others) should also be considered codominant. Moreover, if species j is dominated by the codominant subset, the remainder of the community is necessarily more so.

To first assess the efficacy of the codominance index, C_{max}, we simulated 19 different communities that differed in relative abundances of seven species, and thus the degree of dominance or evenness. With this set of communities, we found that the codominance index performs well in ranking different communities in both increasing order of average abundance of the codominant subset and decreasing abundance of the primary subordinate (Box 1).

2. Applying $\mathrm{C}_{\mathrm{max}}$ to simulated data

To better understand the behavior of C_{max} under less extreme contrasts than those included in Box 1, we generated a set of simulated communities, each consisting of 10 species with abundances that were randomly selected from a lognormal distribution with a mean of 2 and standard deviations of either 0.5, 1, or 2. These deviations result in different community types: those with similar, disparate, and widely disparate abundances among community members, respectively (Box 2, Figure). These artificial communities represent proxies for communities having either relatively low abundances of all species in the community (e.g., an old-growth rainforest tree community (Villa et al., 2019)), codominance among a small set of species (e.g., a temperate forest tree community (Greene et al., 2004)), or clear dominance of a single species (e.g., a shortgrass prairie herbaceous community (Munson & Lauenroth, 2009a)), respectively. The lognormal distribution has frequently been observed for species abundances across a wide variety of ecosystems (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Limpert et al., 2001b; Preston, 1948b; Sugihara, 1980b). Five thousand communities were generated for each of the abundance distributions, giving 15,000 total communities. We first examined the distribution of C_{max} values to determine how they varied by the numbers of species within their codominant subsets. Since the highest possible shared abundances (A_n) occur when only two species are in the codominant subset, we expected sets of this size to include the highest values of C_{max}. Then, Pearson's tests of correlations between C_{max} and its component factors, A_l, and S_s were examined (where l and s refer to the values of n and j, respectively, that result in the highest value of C_n). This was done to determine which factor tends to drive C_{max} the most: 1) the degree of shared abundance among species in the codominant subset, or 2) the disparity between the codominant subset and the remaining community. Overall, we found that C_{max} tended to increase and become more strongly correlated with A_l with smaller codominant subsets across each of the community types (Box 2).

3. Assessment of $\mathrm{C_{max}}$ using real-world data

To assess the applicability of the codominance metric on real-world data, we examined canopy cover from the control plots of an experiment conducted at four North American grassland sites: the Extreme Drought in Grassland Experiment (EDGE; (Knapp, Carroll, Denton, La Pierre, et al., 2015). These sites included a cold mixed-grass prairie (near Cheyenne, Wyoming, CHY), a warm mixed-grass prairie (near Hays, Kansas, HYS), a warm shortgrass prairie (near Nunn, Colorado, SGS), and a warm tallgrass prairie (near Manhattan, Kansas, KNZ). Canopy cover was measured with 1% to 5% precision as a percentage of 2 x 2m plots at the beginning and end of the growing season in 2013 (taking the maximum cover of each species over the growing season), with 10 replicates per treatment.

Our objective for this analysis was to determine whether C_{max} could distinguish between an ecosystem that has often been described as both codominated (KNZ (Fay et al., 2011a; Heisler et al., 2004; Hoffman et al., 2018b; Hoffman & Smith, 2018b; A. Silletti & Knapp, 2002; A. M. Silletti & Knapp, 2001b; Swemmer et al., 2006c) and mono-dominated (Smith and Knapp 2003, Smith et al. 2004), from one that is more frequently considered mono-dominated (SGS (Augustine et al., 2017; Munson & Lauenroth, 2009b; Sala et al., 1992)). We sought further to characterize the codominance of the two mixed-grass prairies (HYS and CHY), which were expected to be codominated, in relation to KNZ and SGS.

As expected, site-level dominance (Simpson's D, calculated from average species abundances across the 10 plots) was greatest at SGS (Fig. 2.3), with each of the other sites having distinctly lower measures. While we expected C_{max} to be greatest at KNZ, we were surprised to find that CHY was the most codominated, having the largest C_{max} despite having an intermediate value of D. While the two most common species at KNZ shared similarly high abundances, there was less of a distinction between their harmonic mean and the abundance of their primary subordinate in comparison to the distribution found at CHY. The lowest degree of dominance resulted in HYS having the lowest value of C_{max}. A similarly low value of C_{max} was found at SGS. This was expected, as SGS is typically considered to be highly mono-dominated (Lauenroth & Burke, 2008).

Our results were similar at the plot level (D and C_{max} calculated for each plot before averaging), with the pattern of D at the plot-level mirroring that for the site level. Similarly, the highest mean plot C_{max} was found at CHY, followed by HYS, SGS, and KNZ. The mean plot-level C_{max} was higher than the site-scale C_{max} at all sites, but differed more at HYS and SGS, suggesting that the identities of the species contributing most to codominance at KNZ and CHY were more consistent across plots than they were at the other sites. To further explore the effects of scale on C_{max}, we used pre-treatment data from the same experiment and calculated C_{max} at four different spatial scales (Fig. 2.4). This analysis showed that C_{max}, while fairly scale-invariant, tends to decrease in magnitude with increasing scale at a rate that is characteristic of the site investigated (Fig. 2.4). Overall, we found that site-level C_{max} matched our expectations of the community structure differences between the sites often described as codominated and mono-dominated, and comparisons with plot-level C_{max} exposed site-dependent heterogeneities in community structure.

2.6 SUMMARY AND FUTURE DIRECTIONS

Codominance is an intuitively alluring concept, but it has not been rigorously explored, perhaps owing to the lack of a common definition or a common metric for its quantification. The stable codominance of ecologically important species represents a novel inroad to a greater understanding of coexistence and ecosystem functioning and may prove especially important from the perspectives of restoration and conservation under climate change. We provide a qualitative definition of codominance, reviewed the mechanisms commonly invoked to explain codominance, and developed a metric (C_{max}) to quantify the degree of codominance. We found that our codominance metric ably facilitates comparisons among ecosystems. Moreover, it is easily interpretable, adaptable to different forms of abundance (e.g., density, productivity, cover, importance values), and can be used for a variety of organizational levels (e.g., species, genus, functional groups). However, comparisons made using different abundance metrics or across organizational levels will be of diminished value. As with other biodiversity metrics, authors must determine which measures of abundance and organizational level are most appropriate to their questions. For instance, a savanna codominated by a tree species and a grass species would be better represented with C_{max} calculated in terms of cover than of density in questions relating to contributions to ecosystem function, but may be better represented by measures of density when approaching other topics, such as genetic diversity and its relationship to community adaptability under changing environmental conditions. When appropriate measures or combinations of measures are used in its calculation, the codominance metric will be a useful complement to other frequently used metrics of biodiversity and should serve to inspire further development and interest in the codominance concept.

With greater understanding and standardization of the codominance concept, we can begin addressing new questions. Experiments involving factorial removals of one or more codominant species, or interruptions of the mechanisms purported to determine codominance under a variety of environmental contexts are well warranted. Codominant species have greater influence over ecosystem function than subordinate species, in proportion to their greater share of abundance, making such experiments increasingly essential as land use and climate change alter the conditions that resulted in their mutual success. A greater understanding of ecosystem stability could also be gained through the integrated consideration of codominant species. By virtue of the relatively high availabilities of meristems and propagules associated with their higher abundances, one codominant species potentially represents the most likely driver (or inhibitor) of functional recovery (or compensation (Adler & Bradford, 2002a)) after the loss of Ir codominant species (e.g., due to a specialist pathogen or an Idiosyncratic sensitivity to climate change). However, such an outcome likely depends on multiple factors, including environmental context and rates of dispersal and establishment. A codominant species with a rapid dispersal rate could drive rapid functional compensation, but one that spreads slowly could result in protracted degradation through their competitive effects on less-common species that might otherwise drive compensation. By studying the dispersal properties of all common species, the rate of ecosystem function recovery following extirpation of a codominant partner could be better predicted, while knowing the functional properties of those species could generate a clearer picture of how those ecosystems would behave following recovery.

It is in our interest, therefore, to better understand the relationships between the abundance of codominant species and the processes that resulted in those patterns. The degrees of codominance may vary by the type of stabilizing mechanisms involved, as well as the characteristics of the ecosystems where the patterns are observed. For example, the mechanisms resulting in greater codominance in climatically-variable systems such as grasslands and deserts may differ considerably from those in more stable environments, such as forests and peatlands. Similarly, the growth forms, functional groups, and functional traits of species may determine the degree to which they are capable of codominance, as well as the mechanisms that facilitate those relationships. Discerning these patterns may prove integral for successfully strategizing conservation and restoration efforts aimed at stabilizing or recreating codominance and affecting associated ecosystem properties.

2.7 TABLES

Table 2.1: Summary of reviewed codominance forms and mechanisms, with examples of each. See Supplementary Table 1 for the complete list of citations.

Type of Codominance	Specific Mechanism	Details	Examples
Fluctuation-Dependent Niche Partitioning (61 instances): Recurrent changes in the environment alternately benefit the growth of some species over others. Competition strength varies with the fluctuations of the environment and can be strong. Results in a storage effect when in combination with reduced competition at low population densities and generation of long-lived surplus adults or propagules (Chesson, 2000).	Competition/Colonization Tradeoff	A rapid colonizer achieves high abundance in disturbed sites and is gradually replaced by stronger competitors	(Zedler & West, 2008); (Duan et al., 2015)
	Competition or Colonization/Tolerance Tradeoff	Stress-tolerant species remains at relatively constant abundance while competitive/ colonizing species abundance oscillates with environmental variability	(Ribichich & Protomastro, 1998); (Hartvigsen, 2000)
	Life Stage Mortality Differences	Similar to the above, but differences are limited to certain growth stages, allowing broad similarities between species at mature stages	(Mori & Komiyama, 2008); (Witwicki et al., 2016)
Spatial Niche Partitioning (52 instances): Environmental heterogeneity over space alternately favoring codominant species. Relaxed interspecific competition between the codominants is typical. Contributes to the storage effect in combination with other factors (Chesson, 2000).	Partial Spatial Niche Partitioning	Sharing of some resources (*e.g.*, light), while others (*e.g.*, nutrients and water) are obtained from different soil depths	(Breshears et al., 1997); (Ward et al., 2013)
	Complete Spatial Niche Partitioning	Species separated into adjacent areas that are more suited to their respective requirements and tolerances	(Dias & Melo, 2010a); (Cohn et al., 2011)
Attenuated dominance (55 instances): The abundance of a species	Successional circumstance	Codominance circumstantially observed at a	(Simard et al., 1998); (Sefidi et al., 2011)

that would otherwise be mono-dominant is negatively impacted by a factor resulting in codominance. Interspecific competition may be strong, particularly in cases of successional circumstance, but may be reduced or mitigated by the factors attenuating dominance.	(Temporally attenuated dominance)	midpoint in the decline of one species and rise of another	
	Spatially attenuated dominance	A factor occurring in a region of codominance (*e.g.*, soil toxicity) reduces the growth rate of a highly competitive species	(Rebele, 2013); (Káplová et al., 2011)
	Consumer control	An herbivore or pathogen selectively reduces the growth rate of a highly competitive species	(Goheen et al., 2007); (Augustine et al., 2017)
	Allelopathy	The growth rate of a competitive species is reduced by secondary compounds released by its codominant partner.	(Meier et al., 2009)
	Mutualist intervention	The growth rate of an otherwise subordinate species is selectively benefited by a third-party mutualism	(Petanidou et al., 1995)
	Mutual attenuation	Similar to spatially-attenuated dominance, but occurring for both species, which may dominate at polar ends of an environmental gradient	(Meentemeyer & Moody, 2002); (Balzotti & Asner, 2017)
Equalizing Factors (6 instances): Reductions in fitness differentials between the codominant species. Delays competitive exclusion but cannot independently and indefinitely prevent it. Competition may (or may not) be strong, but because fitness	Similarity degree of adaptation	A similarity in fitness can operate either through convergent traits and strategies or through differential traits and strategies that nevertheless are equally successful and do not confer meaningful advantages	(Drenovsky & Richards, 2006); (Bai et al., 2015)

differences are minimal, exclusionary outcomes are close to random.			
Facilitation (14 instances): The presence of one codominant species increases the population growth rate of another. This benefit may be mutual.	Direct facilitation	One of the codominant species alters the environment to make it more favorable for the other	(Kikvidze et al., 2006); (Pueyo et al., 2016)
	Indirect facilitation	One of the codominant species alters the environment to make it less favorable for all other species except the codominant	(Souza et al., 2011)

2.8 FIGURES

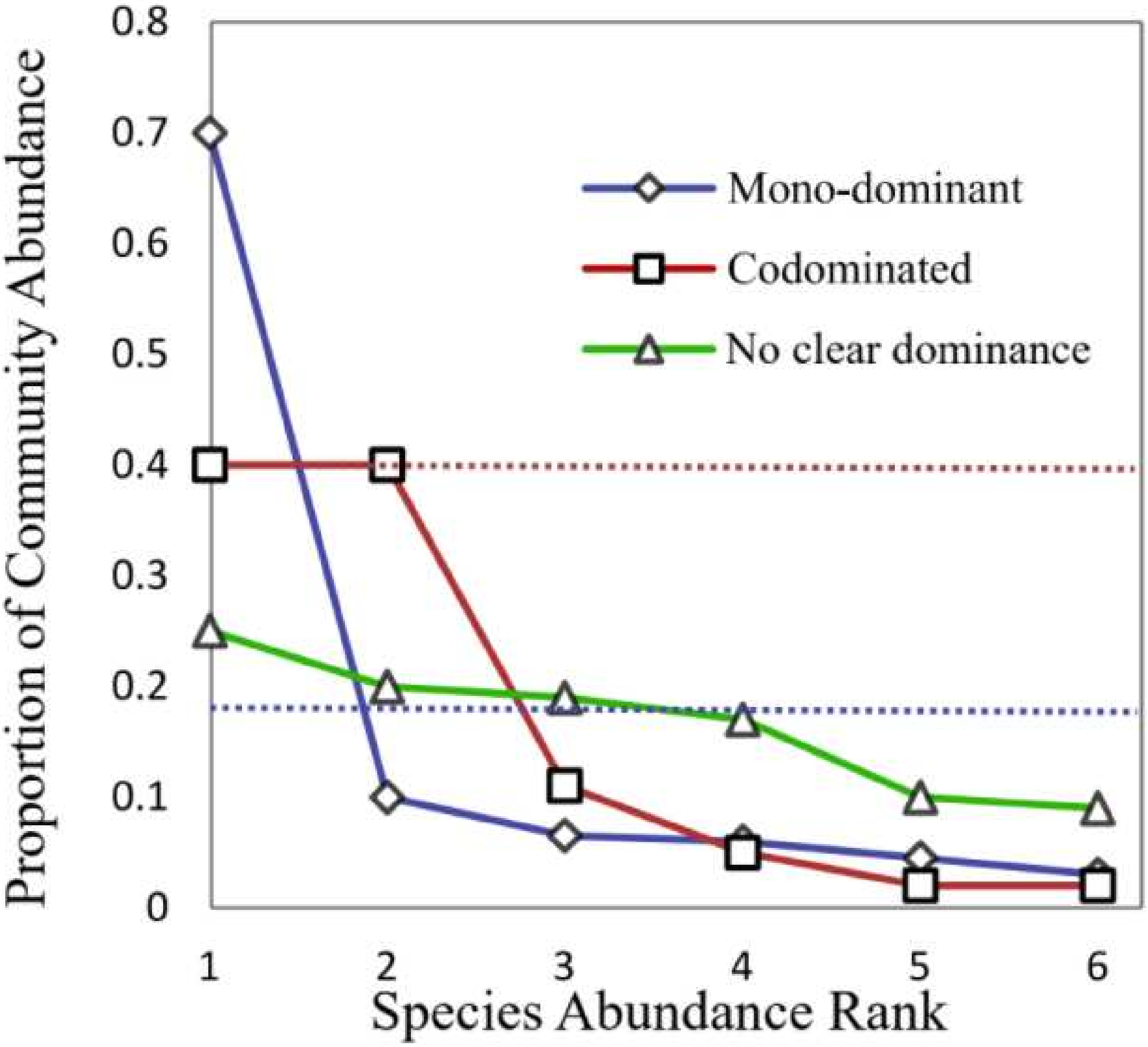
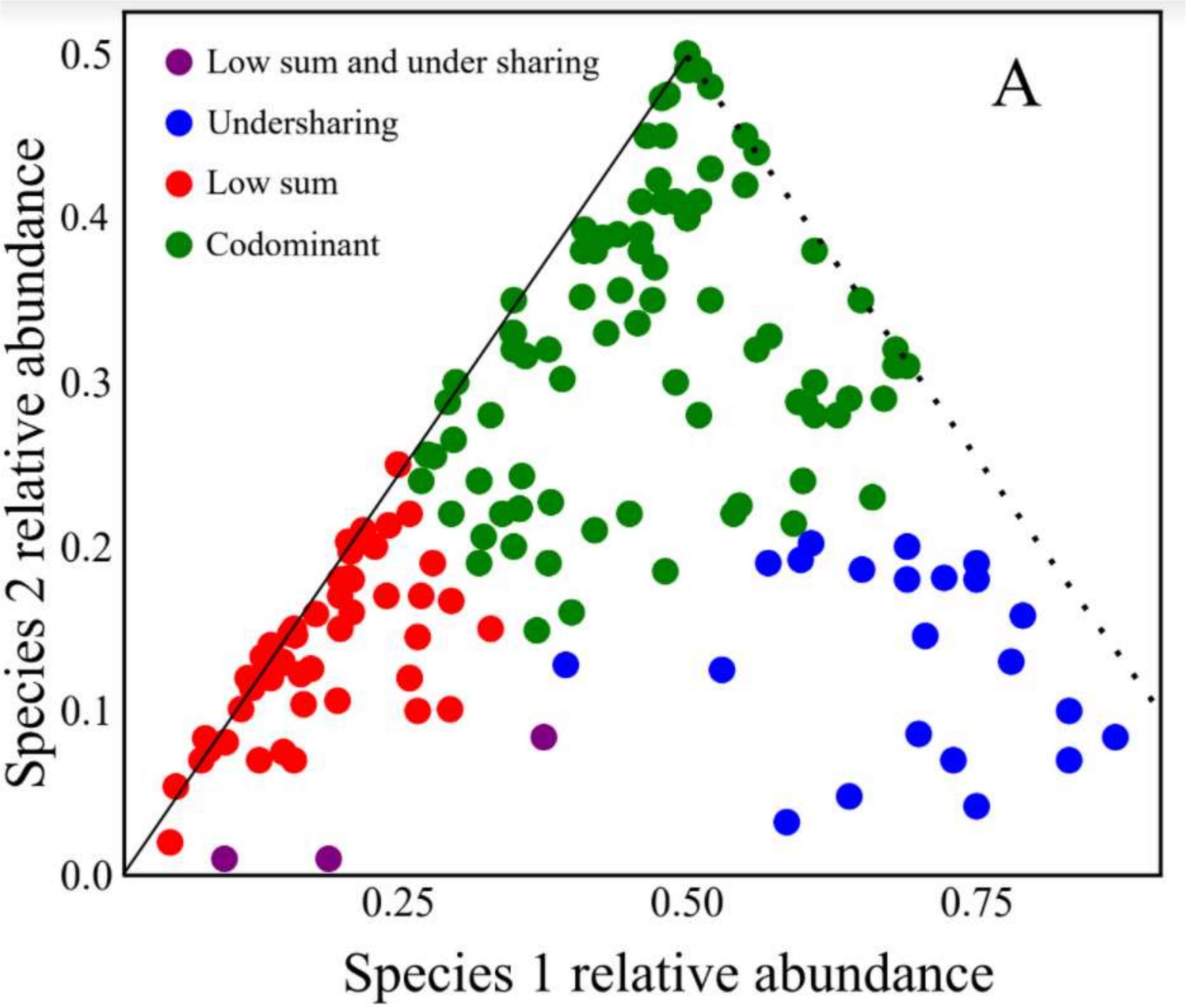


Figure 2.1: Rank-abundance curves of hypothetical communities with contrasting species assemblages. Mono-dominated communities have a single species with a markedly greater abundance than that of any other species in the community. In codominated communities, 2 or more species share a similar degree of abundance that is distinctly greater than that of any other species in the community. In contrast to these, some communities have much smaller differences in abundance among any of their species (no clear dominance). Dotted horizontal lines show harmonic means of the two most abundant species of codominated (= 0.4, red) and mono-dominated (= 0.175, blue) communities. Both have arithmetic means = 0.4.



● Low sum and under sharing
● Undersharing
● Low sum
● Codominant
A
0.5
0.4
0.3
0.2
0.1
0.0
0.25
0.50
0.75
Species 2 relative abundance
Species 1 relative abundance

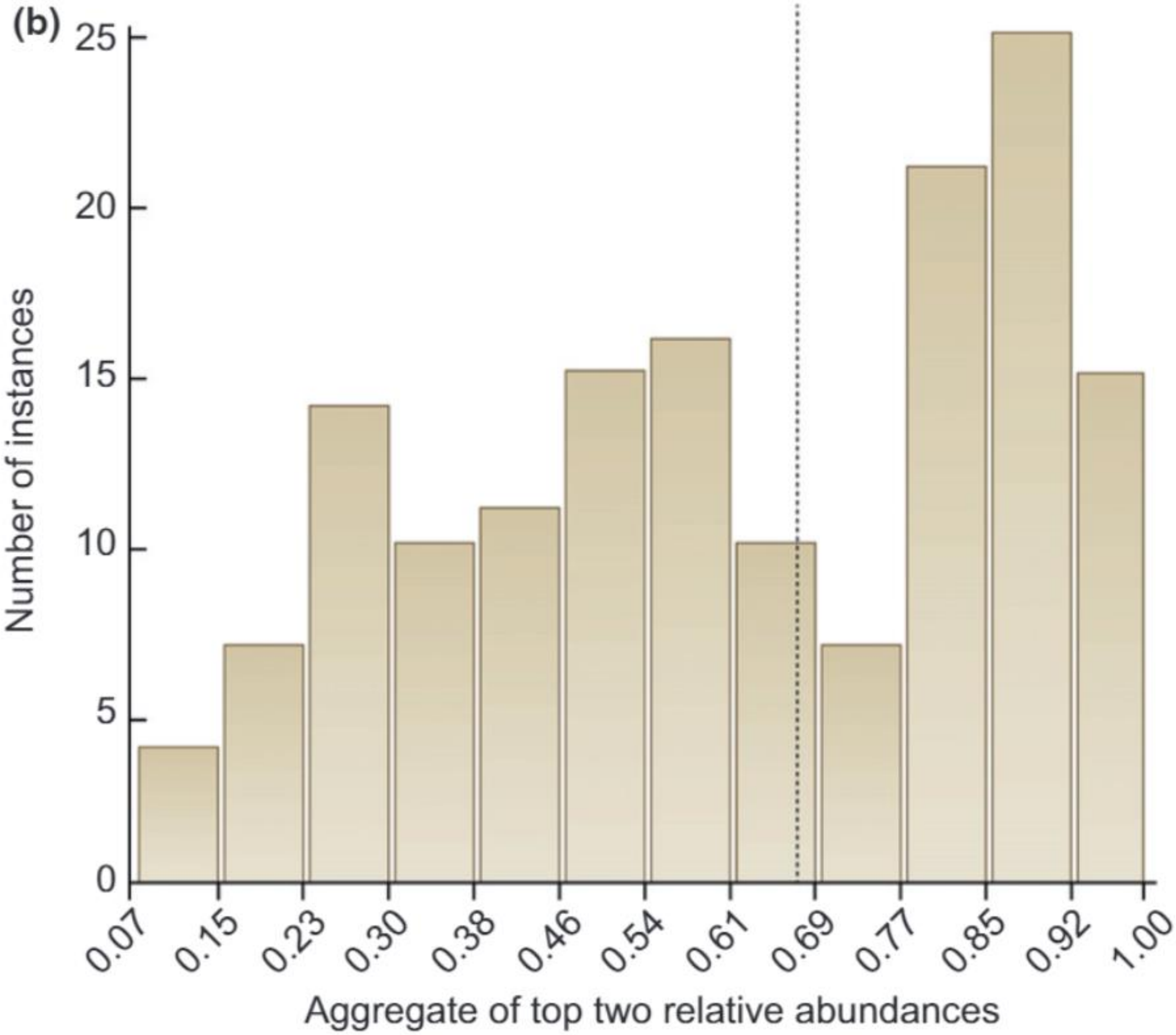


Figure 2.2: (**A**) Relationship between the relative abundances of 167 pairs of first and second-ranked species reported in the literature we reviewed. The solid diagonal line indicates a 1:1 relationship between the two most abundant species at a site. Most species pairs lie near the diagonal, but a large portion shows much greater abundance in the first-ranked species than in the second. The degree of abundance sharing reported within the reviewed literature spans a broad range and was not sufficient in 25 of the 167 species pairs to meet our criteria of codominance as outlined in the text (green and violet points). The dotted diagonal line indicates the limit of the relationships (sums cannot exceed 1). (**B**) The frequency distribution of aggregate relative abundances of 167 pairs of first and second-ranked species is shown as a histogram. The median aggregate relative abundance is indicated by the dashed line, but many species pairs constitute only a small portion of their community total abundances. 53 of the 167 species pairs did not contribute at least 50% of the total community abundance (red and violet points in A).

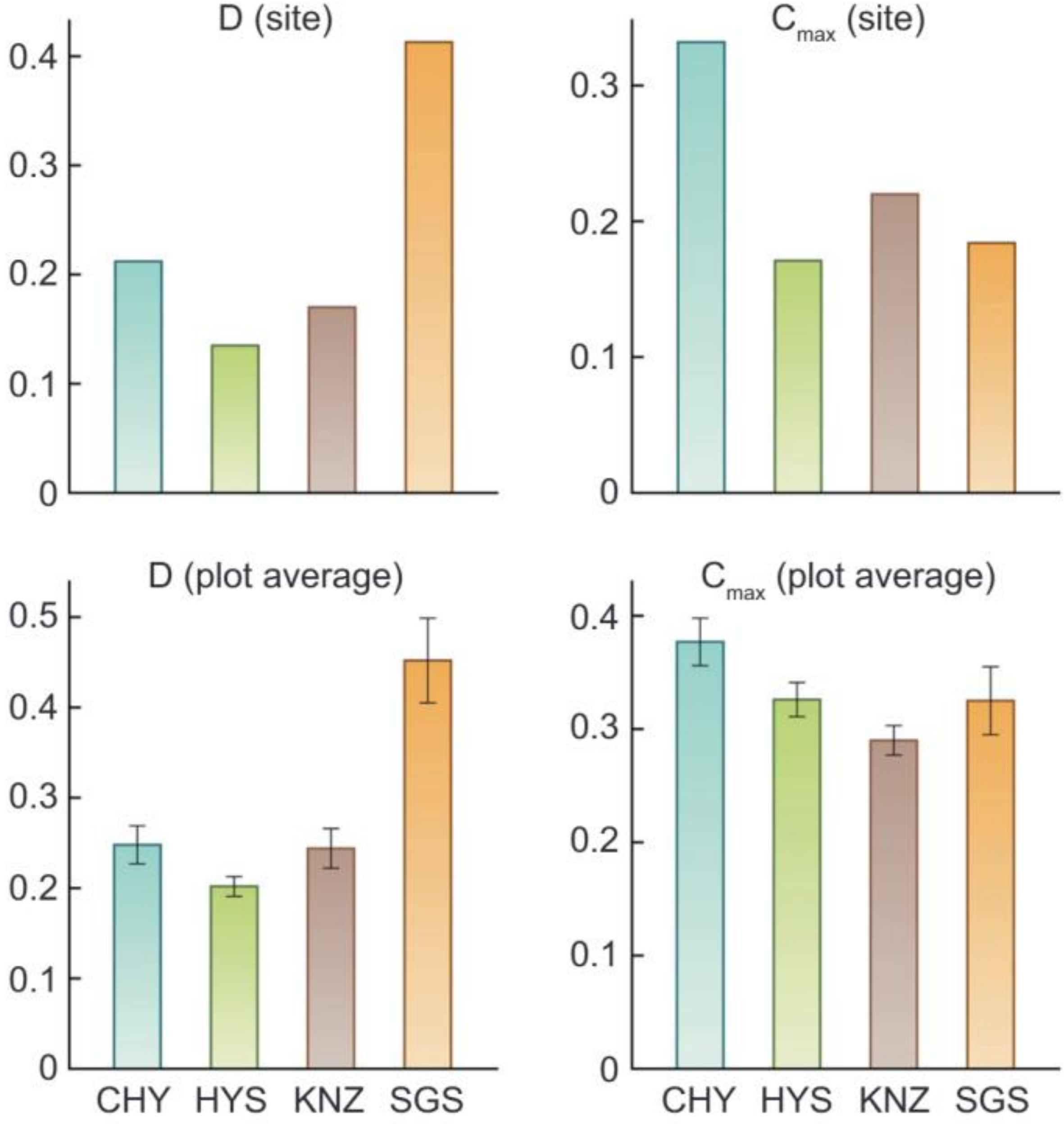


Figure 2.3: Measures of average plot-level codominance (C_{max}), Simpson’s dominance (D), and plot-level $C_{max}$and D (± confidence intervals at a = 0.05) at four Great Plains grasslands sites: a cool mixed-grass prairie near Cheyenne, Wyoming (CHY), a warm mixed-grass prairie near Hays, Kansas (HYS), a tallgrass prairie at Konza Prairie Biological Station near Manhattan Kansas (KNZ), and a shortgrass steppe near Fort Collins, Colorado (SGS). No replication was possible at the site scale, as indicated by the lack of error bars in the upper plots.

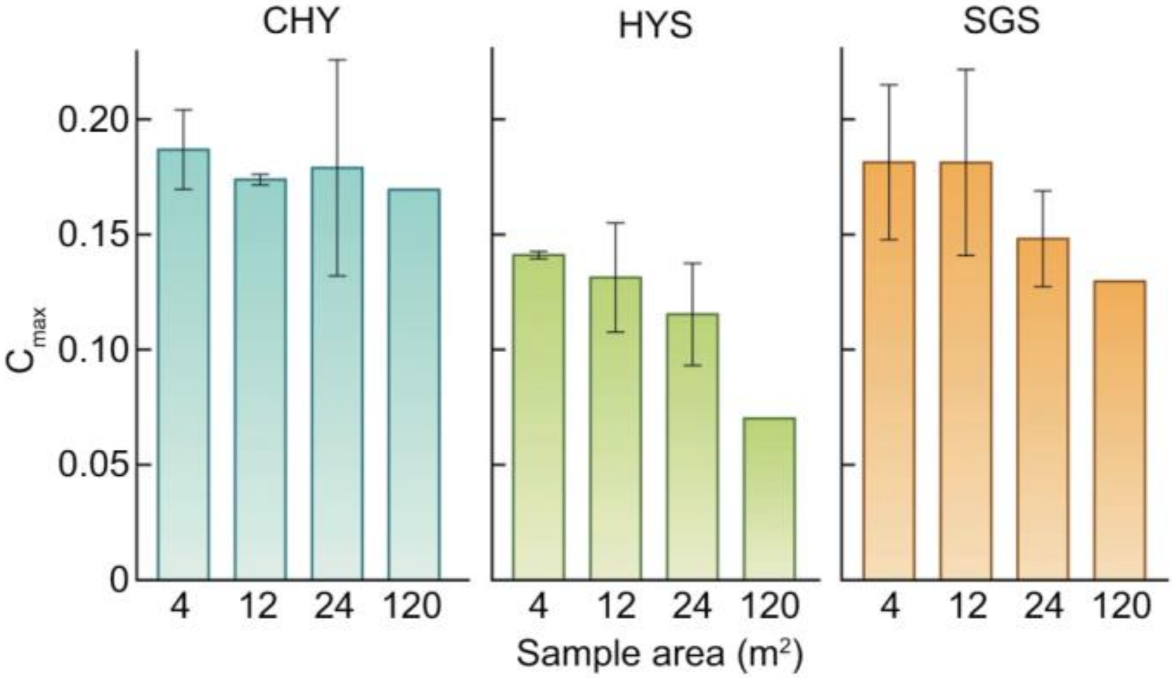


Figure 2.4: Average codominance (C_{max}) measured at increasing scales from plot-level (4 m^2) to block (12 m^2, cover averaged across three nearby plots before C_{max} calculation), to paired-blocks (24 m^2, averaged across six nearby plots), and site (120 m^2). Error bars indicate 5% confidence intervals. No replication was possible at the site scale, indicated by the missing error bars. Data obtained were from a drought experiment at three Great Plains grassland sites (CHY: cool mixed-grass prairie near Cheyenne, Wyoming; HYS: warm mixed-grass prairie near Hays, Kansas; SGS: shortgrass steppe near Fort Collins, Colorado) before treatment. While C_{max} is fairly invariant with increasing scale, it does tend to decline. The rate of decline is characteristic of the site observed, reflecting the rate of turnover of the species that are codominant within those sites. For example, the plots and blocks at HYS were spread further apart than at CHY and were separated by a drainage, and the turnover of codominant species here was greatest. In contrast, the turnover of codominant species across CHY, a relatively homogenous site, was minimal.

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CHAPTER 3: A SHIFT FROM COMPETITION TO FACILITATION WITH ABIOTIC STRESS IS LIMITED FOR TWO CODOMINANT GRASS SPECIES

3.1 OVERVIEW

It remains unclear how competitive exclusion is avoided between two ecologically, economically, and culturally important codominant grass species in the tallgrass prairie of the Great Plains, *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (70ndiangrass). These functionally similar C_4 grasses appear to coexist despite their considerable niche overlap and asymmetric competition and drought tolerance in favor of A. gerardii. Following the stress gradient hypothesis, it may be that the sum of the interactions between these species, which is typically negative (competitive) in aggregate due to similar resource requirements, shifts to positive (facilitative) as abiotic stress increases**.** For instance, if the canopy cover of the stronger competitor reduces the loss of subcanopy humidity or shallow soil moisture, recruitment of new *S. nutans* tillers may be extended further into the drought event than would occur in the absence of *A. gerardii*. As later months of the growing season are drier on average where these species are codominant, such a mechanism may enable *S. nutans* to recover from early season asymmetric competition and stabilize the codominant relationship. We tested this hypothesis in a greenhouse experiment in which we manipulated the availability of water in the latter half of a growing season when water is most limiting in the field. We found no evidence that a shift from a negative to positive interaction occurs, with each species performing similarly whether in mixed communities or monocultures. The similarities of the two species in their functional traits and responses to water limitations may limit such a shift in interaction net effects and suggest that other mechanisms are determining the coexistence of these co-occurring C4 grasses.

3.2 INTRODUCTION

In the mesic tallgrass prairies of the Great Plains, US, two C_4 grass species, *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash often coexist with such mutually high abundances (canopy cover percentages)J, population densities, and/or occurrence frequencies that they are considered codominant species (*sensu* (Gray, Komatsu, et al., 2021)(L. Brown, 1985; Duralia & Reader, 1993; Freeman, 1998; Hartnett et al., 1996; Smith & Knapp, 2003). In most years, these abundances result in high aboveground net primary productivity (ANPP) (Grime, 1998a; la Pierre et al., 2011; Smith & Knapp, 2003), making these species important contributors to ecosystem functioning and services, such as forage for grazing (Vinton et al., 1993), carbon sequestration and storage (Grime, 1998a; Kemp et al., 1994; Mahaney et al., 2008; Omonode & Vyn, 2006), nutrient cycling (Grime, 1998a; Mahaney et al., 2008), invasion resistance(Smith et al., 2004a), and aesthetic and cultural value. Though the population densities of these two grass species can fluctuate from year to year (A. Silletti & Knapp, 2002; Towne & Kemp, 2003), their codominant relationship has remained stable in the long term. For example, nearly a century ago, Weaver and Fitzpatrick reported abundances similar to those found today in eastern Kansas (Jones et al., 2016; Weaver & Fitzpatrick, 1932). However, despite their frequent description as codominant species in this region (L. Brown, 1985; Duralia & Reader, 1993; Freeman, 1998; Hartnett et al., 1996; Smith & Knapp, 2003), *A. gerardii* has been reported to be both more competitive for resources (A. M. Silletti et al., 2004a; Tilman & Wedin, 1991) and more drought-tolerant (Hoffman et al., 2018a; Hoffman & Smith, 2018a; A. Silletti & Knapp, 2002; Swemmer et al., 2006c).

Given the annually fluctuating population densities of the two species, and the competitive advantages in both wet and dry years attributed to *A. gerardii*, it is not clear how *S. nutans* maintains its role in the codominant relationship over the long term. This uncertainty is further shrouded by the many morphological and physiological similarities borne between *A. gerardii* and *S. nutans*. These species have multiple life-history traits in common, including long-lived genets (Gustafson et al., 2005; Keeler, 2004; Lauenroth & Adler, 2008b; USDA, 2021a, 2021b), C_4 photosynthetic pathways, reproduction mainly through rhizomatous cloning (i.e., ramets/tillers (Benson & Hartnett, 2006; Lauenroth & Adler, 2008b; McKone et al., 1998; USDA, 2021a, 2021b)), and bear similarities in their functional traits (e.g., leaf dimensions, leaf gas exchange rates, ANPP) (Forrestel et al., 2014, 2015) and responses to fire and grazing disturbances (Weaver, 1931; Weaver and Fitzpatrick, 1932; Hadley and Kieckhefer, 1963; Polley et al., 1992; Towne and Kemp, 2003; Bowles et al., 2011; Forrestel, Donoghue and Smith, 2014, 2015). Both are considered strong competitors under nitrogen limiting conditions (Berg, 1995; Silletti and Knapp, 2001; Lett and Knapp, 2003; Mulkey, Owens and Lee, 2008), and are tall-statured when flowering under mesic conditions (Weaver, 1931; Knapp and Hulbert, 1986), but are intolerant of shading (Weaver and Rowland, 1952; Lett and Knapp, 2003) and persistent grazing (Damhoureyeh & Hartnett, 2002; Hartnett et al., 1996; Vinton et al., 1993).

Despite all the similarities between the two grass species, they differ in a key way – in growth determinacy of tillers (McKendrick..) – which may contribute to the maintenance of the codominance relationship in space and time (Gray & Smith, in review). *A. gerardii* exhibits determinant growth, in which it recruits belowground buds into tillers almost exclusively in the early spring, and these tillers are annual in their lifespan (i.e., senesce in early fall). In contrast, *S. nutans* exhibits indeterminant growth whereby it can recruit belowground buds into tillers throughout the growing season, and later-recruiting tillers can overwinter as belowground buds and be recruited again the following growing season. This difference in growth determinacy results in contrasting intra-seasonal tiller dynamics, in which *A. gerardii* tiller numbers consistently decline during the growing season whereas *S. nutans* tiller numbers often increase or remain stable. These contrasting population dynamics could have important implications for the stability of codominance of the two species, (Gray & Smith, in review), and the stress gradient hypothesis is one possible mechanism that may explain how differing growth determinacy may promote stable codominance, particularly within the context of variation in stressful conditions during the growing season.

The stress gradient hypothesis posits that as the intensity of environmental stress increases, the functional sum of the effects of the multiple, simultaneously occurring interactions between competing species becomes less negative as some negative effects are mitigated, and/or the effects of some positive interactions are enhanced, making the presence of certain interspecific and otherwise deleterious neighbors beneficial for survival, growth, and/or reproduction relative to their absence (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Callaway & Walker, 1997; Olofsson et al., 1999; Ploughe et al., 2018). Alternatively, the two-phase resource dynamics hypothesis (Goldberg & Novoplansky, 1997) proposes that possibly similar outcomes can occur because resources are typically available in pulses, and interactions between plants and their abiotic environment become more important relative to resource competition as resources become less frequent (i.e., become more resource stressed). Such shifts in environmental conditions are common in mesic tallgrass prairie where *A. gerardii* and *S. nutans* codominate. Here, there is a high probability of drought (or dry conditions) occurring during each growing season, despite on average relatively high annual rainfall (Craine et al., 2012; Hayden, 1998; Knight et al., 1994). Drought-associated shifts in net interactions between neighboring species may occur if, for example, a competing species translocates water from deeper to shallower soils through tap roots (i.e., hydraulic lift (Dohn et al., 2013; Rambal & Joffre, n.d.; Weltzin & Coughenour, 1990)), if a species has physical defense mechanisms that extend protection to neighbors against the exacerbating effects of herbivores (Callaway, 1992; García et al., 2003; McAuliffe, 1986; Vinton et al., 1993), if heavy canopy cover of a species that reduces subcanopy light availability also reduces soil evaporation rates (Escudero et al., 2005; Kikvidze et al., 2006; Pugnaire et al., 2004) or increases humidity within the canopy(Aguirre et al., 2021; Cowles et al., 2016; A. Wright et al., 2014; A. J. Wright et al., 2021), or even if drought-induced mortality in one species increases the availability of resources for the surviving species that may otherwise have been depleted through intra-specific competition (de Dios et al., 2014; Lloret et al., 2004; Ploughe et al., 2018).

Evidence for intra-annual shifts between net negative vs. positive interactions has been observed in codominant species under stressful conditions induced by water limitation later in the growing season. For example, two codominant plant species in a subalpine environment were reported to shift between overall competitive to facilitative relationships as water availability regularly declined during the latter weeks of growing seasons of each year (Kikvidze et al., 2006). In their report, the authors attributed negative interactions in the early season to competition for light. This negative effect was reduced as precipitation declined and leaf cover decreased, and it was speculated that soil moisture may also have been conserved in the mixed communities compared to monocultures. Similarly, such a shift in the sum of interaction effects between *A. gerardii* and *S. nutans* may be a mechanism responsible for the stability of their codominant relationship. That is, if *S. nutans*, purportedly the less competitive and drought tolerant of the two species (Hoffman et al., 2018a; Hoffman & Smith, 2018a; A. Silletti & Knapp, 2002; A. M. Silletti et al., 2004a; Swemmer et al., 2006c), benefits from the presence neighboring *A. gerardii* individuals (relative to intra-specific ones) in the drier months of the growing season, the presence of *A. gerardii* individuals may increase the fitness of *S. nutans* during that time and reduce the probability of its competitive exclusion. Moreover, because *S. nutans* can recruit new tillers throughout the growing season while A. gerardii is not (McKendrick et al., 1975), drought-driven senescence of *A. gerardii* may facilitate the emergence and growth of young *S. Nutans* tillers by opening gaps in the canopy for light to reach the understory, allowing *S. nutans* populations to increase in density and recover from the asymmetry of competition suffered during the early season.

To test whether stressful conditions induced by late-season drought can shift the overall relationship between *A. gerardii* and *S. nutans* to one that is more facilitative, we performed a controlled greenhouse experiment using artificial communities. We compared the performance of these species in communities with interspecific mixes to those with only intraspecific neighbors. Using a simple response surface design, we tested the following hypotheses: 1) Water limitation (stress) would diminish the per capita performance of both species at both low and high community densities; 2) Increased community density would reduce the *per capita* performance of each species in monoculture at both high and low water availability levels; 3) Following the stress-gradient hypothesis, interspecific neighbors would alleviate a portion of the negative effects of water limitation relative to monocultures at a given total community genet density.

3.3 METHODS

We established artificial communities of varying densities from wild-collected seeds of *A. gerardii* and *S. nutans* (Star Seed Inc, Osborne KS). Community treatments included low (15 genets) and high (30 genets) density monocultures of each species, and a high total density mixture (15 genets of each species, 30 total genets) in 1-gallon pots and 3L of Pro-Mix High Porosity Biofungicide + Mycorrhizae potting soil, with ten replicates of each of the eight community combination treatments. The selected genet densities were within a range previously observed in a physically undisturbed, but annually burned lowland area where the species are codominant (unpublished data). To ensure sufficient germination, an excess of seeds of each species were spread randomly across soil surfaces and buried under 10 mm of potting soil. Once the successful germinants were identifiable to species, their surpluses were removed by hand, primarily from the perimeters of the pots to ensure that the remaining seedlings matched the target density and that no individuals were isolated from the community. Once most of the seedlings had produced their third leaves, 15mL of Osmocote Plus extended-release fertilizer was added to each of the pots. The communities were closely monitored throughout the experiment for any new germinants, and these individuals were removed upon detection.

Each of the community combination replicates was placed randomly within the greenhouse space and provided a minimum of 12 hours of sunlight daily. All the pots were rotated once every four days to reduce any biasing effects of variable light availability or microclimate conditions (Fig. S3.1)

For the first 78 days after seeding, all community combination replicates received 0.5L of water once every other day to simulate well-watered conditions. This volume fully saturated the soil, and excess water was able to drain. At the end of these 78 days, all the clonal offspring (i.e., ramets) of the original seedlings (i.e., genets) were counted. Following this two-day survey, half of the replicates were randomly selected to receive a watering frequency unaltered from the early season (control treatment), while the frequency of watering for the remaining replicates was reduced by half (drought treatment). The goal of the drought treatment was to simulate the late-season dry conditions that often occur under natural field conditions (Hayden, 1998). In a pilot study, both species were observed to have reduced ANPP and population growth rates at the lower watering rates (Gray, data not shown). Average soil moisture measurements (volumetric water content, VWC) were taken before and following each watering event using a hand-held soil moisture probe (Campbell Scientific, Logan UT). Immediately after watering, the soils in both treatments had similar VWC (38%, averaged across watering events and treatments), but had dissimilar VWC before watering (average of 20.8% VWC for the control and 7.4% for the drought treatments). By the middle of the late season, drought-treated *S. nutans* monoculture pots were observed to hold less water (average 18% post-event), but also to dry less quickly (average 10% pre-event). After 18 days, the drought-treated pots were observed to have less canopy cover (Fig. S3.1A), and so were grouped to avoid excessive shading from the control treatment pots. The pot rotation schedule was resumed after this rearrangement. (Fig. S3.1B)

A second ramet density survey was conducted at the end of the experiment (day 151) with living and senesced individuals counted separately. Daily watering was applied to all communities over the five days of the survey and two days before to facilitate the correct distinction between living and dead ramets. All aboveground biomass was clipped from each pot at the soil surface after it had been surveyed for ramet density. The biomass was sorted by species, dried in a heating oven at 60°C for 48 hours, and weighed to determine ANPP.

Statistical analysis

We compared performances of the different community combination and watering treatments in terms of three metrics considered relevant for long-term population dynamics and facilitation (e.g., Bronstein, 2009; J. H. Brown et al., 2004; Silvertown et al., 1993): 1) survivability, measured as the fraction of ramets recruited since the beginning of the experiment that maintained living leaf tissue until the date of the second (final) survey; 2) reproductive rate, measured as the total number of ramets produced per genet throughout the experiment; and 3) ANPP, measured as the average amount of aboveground biomass produced per genet, including the aggregate biomass of their ramets.

To test the hypothesis that the late-season drought treatment would reduce each species' *per capita* performance at both low and high monoculture densities, we compared the performance metrics of monocultures receiving the late-season drought to monocultures of equal genet densities receiving the control watering treatment. We used Wilcoxon rank-sum tests (H_0: Drought treatment has positive or no effect on *per capita* performance) to make these comparisons. The tests were run separately for each species and each monoculture density and corrected for multiple comparisons using Bonferroni adjustments and four degrees of freedom (12 comparisons in total (2 species * 3 metrics * 2 densities), alpha adjusted to 0.0042).

To test the hypothesis that increased monoculture density would reduce the *per capita* performance of genets, we compared each of the performance metrics between monocultures consisting of 15 genets to those with 30 genets using Wilcoxon rank-sum tests (H_0: positive or no effect of increased density on performance). This was done separately for each species and the drought and control treatments and corrected for multiple comparisons (12 total: 2 species * 3 metrics * 2 watering frequencies) using Bonferroni adjustments and four degrees of freedom (alpha adjusted to 0.0042).

To test the hypothesis that interspecific neighbors would mitigate a portion of the negative effects of environmental stress, we compared performance metrics of drought-treated monoculture communities with 30 genets to drought-treated mixed communities consisting of 15 genets of each species. We used Wilcoxon rank-sum tests (H_0: Negative effect of interspecific neighbors or no difference in performance between communities) to make these comparisons. Bonferroni adjustments were made to correct for multiple comparisons and four degrees of freedom (Six comparisons in total, alpha adjusted to 0.0083).

In the interest of highlighting factor effect differences, we calculated the effect sizes of each of the factors described above (drought, density, and interspecific neighbors in drought at high density) in terms of Hedge's q. This was done for both species and each of the performance metrics. Confidence intervals were corrected to account for the multiple comparisons related to each hypothesis using Bonferroni adjustments.

While mixed communities may not always mitigate the negative effects of late-season drought to the degree that the sum of their interactions becomes positive, the sum may become *less negative* under stressed abiotic conditions in comparison to highly competitive environments. To determine whether the mixed community treatment caused interactions between community members to be less negative under the drought treatment than in the control treatment, we calculated the relative neighbor effect (RNE) for the 30-genet mixed communities and 30-genet monocultures as described in Kikvidze et al. (2006):

$$\text{RNE} = (C - T) \,/\, max(C, T)$$

where C refers to the *per capita* performance metric (i.e., survivability, reproductive output, or ANPP, averaged across replicates) of the focal species in a mixed community, and T refers to the respective metric for the focal species in monoculture. When RNE is positive, it indicates that the performance of the focal species was facilitated by the presence of the interspecific neighbor, but a negative RNE indicates that the interspecific neighbor was more detrimental to the performance of the focal species than intraspecific neighbors at the same density. We then compared the RNE between the control and the drought-treated communities for each species to determine if the stress of the imposed drought caused RNE to become relatively less negative.

3.4 RESULTS

The drought treatment resulted in significant reductions in ANPP per genet of *A. gerardii* (41.0% mean reduction) and survival rates of *A. gerardii* ramets (42.3% mean reduction) within 30-genet, but not 15-genet monocultures (Fig. 3.1a-c). Likewise, the effect size (Hedge's q) of the drought treatment on ramet survival rate was significantly less than zero for the 30-genet monoculture, though the confidence interval for the effect of drought on ANPP included zero. The reproduction rate of *A. gerardii* ramets was not affected by drought at either the low or high genet densities.

Drought significantly reduced per genet ANPP of *S. nutans* in both 15-genet (32.3% mean reduction) and 30-genet monocultures (27.5% mean reduction, Fig. 3.1d). Trends toward reductions in ramet production rates in 15-genet monocultures and ramet survival rates in both genet densities were also observed, but these differences were not significant after adjusting for multiple comparisons, nor were the effect sizes significantly less than zero (Fig. 3.1e-f). No effect of drought was observed for the rate of *S. nutans* ramet production at the 30-genet density (Fig. 3.1e).

The comparison between droughted 30-genet monocultures and 30-genet mixed communities did not uncover any significant differences in any of the performance metrics of either species (Fig. 3.2), nor did any of the effect sizes differ significantly from zero. There was a trend towards reduced ANPP of *A. gerardii* and increased ANPP of *S. nutans* in the mixed community compared to their monocultures, but these differences were not significant after adjusting for multiple comparisons.

In most cases, our calculations of relative neighbor effect (RNE) found no significant difference between mixed and monoculture communities (Fig. 3.3), suggesting that neither *S.* nutans nor *A. gerardii* were typically facilitated by interspecific neighbor whether in the control or drought treatment. Further, the rate of *S. nutans* clonal reproduction was significantly lower in mixed communities under drought than in the monoculture, and the ANPP of *A. gerardii* was significantly lower in communities with *S. nutans* than in monocultures. This result was not universal, however, as *S. nutans per capita* ANPP was greater in the mixed communities, though the respective 95% confidence intervals narrowly overlapped with zero, indicating no significant difference between mixed communities and monocultures. Moreover, there were no significant differences between RNE values in the control and drought treatments for any performance metric in either species (Table S1).

3.5 DISCUSSION

We found that for the codominant grass species, *A. gerardii* and *S. nutans*, at least one aspect of performance (ANPP per genet, survival rate of ramets, or clonal reproduction rate per genet) declined either as a result of increasing intraspecific genet density, late-season drought, or both (Fig. 3.1), in agreement with our first and second hypotheses. While our expectation – that increasing the density of identical competitors would result in more negative net interactions – was confirmed by this study (Fig. 3.1), the effects of the density and drought treatments differed for each of the performance metrics. The drought treatment primarily affected ANPP in both species (Fig. 3.1), confirming our expectation that late-season water limitation can indeed be a stress factor for both species that results in diminished performance. However, the lesser effects on ramet reproduction rates and survivability suggest that the drought treatment did not simulate extreme conditions (Smith, 2011) and that the degree of water limitation imposed on these species was not outside the range of conditions they are capable of surviving. Ramet survivability was only significantly affected in the higher genet density *A. gerardii* populations (Fig. 3.1c). In contrast, the ANPP of both species was negatively affected by both increasing genet densities in monocultures and by drought (Figs 3.1a, d). As might be expected from long-lived species, this suggests that survivability is the more valued trait for maintaining the long-term demographic stability of both these perennial species, with sacrifices in ANPP being preferable to premature senescence (Obeso, 2002a). While ramet death does not necessarily result in genet death, early senescence diminishes genet resource control and hinders meristem development, resulting in lost opportunities for the ramet production that ultimately sustains genet (and population) longevity (Hartnett

& Bazzaz, 1985; Hutchings & Wijesinghe, 1997; Jeník, 1994; Matsuo et al., 2018). Population growth per genet of *S. nutans*, but not of *A. gerardii* was also significantly reduced by increasing monoculture density under both watering treatments, suggesting that ramet survivability is prioritized for *S. nutans* over asexual reproduction as intraspecific competition increases. Because *A. gerardii* exhibits determinate growth and typically early-season-only generation of annual ramets (McKendrick et al., 1975), intraspecific density effects may have less of an impact on that species' asexual reproduction and long-term population dynamics than on *S. nutans*, which is biennial (produces over-wintering ramets in the late season) and reproduces indeterminately (McKendrick et al., 1975). However, it is not yet clear how late-season droughts or intraspecific densities affect overwintering belowground bud banks and the initiation of next-season tillering of either species.

In contrast to the stress gradient hypothesis, we did not find evidence that *S. nutans* populations experiencing late-season soil water deficits are facilitated by *A. gerardii* neighbors. Instead, we observed that reductions of both *A. gerardii* and *S. nutans* performance associated with drought conditions did not differ significantly when comparing monocultures to equal-density species mixtures (Fig. 3.2, 3.3). These findings are in remarkably close agreement with those of Duralia and Reader (1993), who found in seeding and removal experiments that while competitor density reduces the field performance of *A. gerardii*, *S. nutans,* and a third perennial grass species, *Dicanthelium oligosanthes*, the identity of the competitor, whether intra- or interspecific, was of little consequence. The present study extends these findings by showing that these overall competitive relationships can persist despite water stress. However, there may have been a trend of increasing *S. nutans* ANPP in mixed communities compared to monocultures (accompanied by a decrease in *A. gerardii* ANPP, Fig. 3.2), which would support the stress gradient hypothesis as it pertains to this performance metric for this species. Additional replicates may be necessary to thoroughly rule out this possibility.

Our evaluation of the relative neighbor effect (RNE) found that the values for *S. nutans* most often overlapped with zero, with the exception that *per capita* ramet recruitment under drought conditions was significantly reduced when communities included *A. gerardii* genets (Fig. 3.3). That ramet survival rates and ANPP were not similarly affected by *A. gerardii* under drought conditions is suggestive of a reallocation of resources away from reproduction and towards survival and competitive resource capture when in mixed communities. Such plastic reallocations of investments between vegetative growth and reproductive structures are commonly examined, but with mixed findings (Gardner & Mangel, 1999; Gioria & Osborne, 2014; J. Guo et al., 2020; Kumari et al., 2020; Liu et al., 2021; Obeso, 2002b; Tonnabel et al., 2017). Since *S. nutans* ramets are biennial or longer-lived, reproductive opportunities may remain open if ramet survival is ensured. While average *S. nutans* RNE values for ANPP were positive, an observation suggesting facilitation, they could not, by a narrow margin, be statistically distinguished from zero. Additional replicates would likely clarify this relationship. Nevertheless, there was no difference in RNE between the control and drought treatments for *S. nutans* ANPP, so while facilitation may occur, we did not find support for the hypothesis that environmental stress alters net interactions associated with ANPP of these species. Instead, it may be that *S. nutans* is favoring aboveground allocation of resources at the expense of roots when in proximity with *A. gerardii*, perhaps to better compete for light, another plastic response to competition and resource limitation that has previously been reported (Franzese & Ghermandi, 2014; Martina & von Ende, 2012; D. A. Maurer & Zedler, 2002; Robakowski et al., 2018). However, since we did not measure belowground productivity, we cannot confirm whether this happened or not.

The RNE values for *A. Gerardii* were always significantly negative (ramet survival rates in control conditions, ANPP in control and drought) or overlapping with zero (Fig. 3.3), indicating that the effects of *S. nutans* neighbors were either detrimental relative to those of *A. gerardii* neighbors, or they could not be distinguished from intra-specific effects. Moreover, as with *S. nutans*, there was no difference in RNE between control and drought conditions for any of the performance metrics of *A. gerardii*. While the drought conditions we imposed may have been too extreme (or not extreme enough) to allow interactions between the species to shift (in aggregate), which would reflect the patterns observed at low or high rates of stress in already stressful environments (e.g., arid ecosystems (Maestre et al., 2005)), the similarity of RNE values between control and drought treatments in both species and the general failure of the drought to cause severe reductions in either the rates of ramet survival or ramet reproduction in either species (Fig. 3.1) does not support this notion. Nor does the fact that the drought treatment reduced ANPP, which suggests water limitation was substantial enough to limit growth.

The two subalpine species presented by Kikvidze et al. (2006) that annually experience shifts in cumulative interactions from net competitive to net facilitative during the drier late seasons included a perennial C_3 bunchgrass (*Hordeum violaceum*) and a perennial leguminous forb (*Trifolium abiguum*). The species presented in our study, both rhizomatous C_4 grasses, are at least superficially more similar to one another in comparison. Given the morphological and physiological similarities of *A. gerardii* and *S. nutans* and the functional similarity of their responses to water stress in particular, our observations suggest that shifts towards net positive interspecific interactions under increasing environmental stress may be limited by the functional similarity of those species. Indeed, when taken to an extreme, if two species share an identical response to some form of stress, then no advantage can be expected by having interspecific rather than intraspecific neighbors as the severity of that stress increases (Eränen & Kozlov, 2009; Fajardo & McIntire, 2011). Thus, shifts from net negative to net positive may be hindered not only by a breakdown of certain positive interactions as environmental stress approaches extremes, but the similarities in the ways that species respond to stress may also place limits on the range of net interactions between species and their associated capacities for stabilizing their coexistence in fluctuating environments (Chesson, 2000; Maestre et al., 2009). Thus, considerations of functional traits and their relationships with species responses to stress should enhance understanding of species interactions across stress gradients (Fig. 3.4 (Butterfield & Callaway, 2013)).

Our finding that the typically negative (competitive) species interactions between *A. gerardii* and *S. nutans* appear to remain so (or perhaps become more negative) under more stressful (dry) conditions suggests that the frequently observed codominance between these species are facilitated by mechanisms other than periodic stress-driven shifts in net interaction signs. In contrast to the findings of others, rather than receiving temporary relief from competition brought about by stressful environmental conditions, we suspect that competitive exclusion can be as likely or more so under stress, depending on the severity of the stress and the similarity of the species responses to it. As such, we caution against overconfidence in interactive stress mitigation as a mechanism for maintaining biodiversity in variable environments when the species involved bear substantial functional similarities in their responses to that variability, though our methodology may have been less powerful than *in situ* removal experiments for detecting shifts in interaction types (He et al., 2013). More remains to be investigated, including the potential for mitigation of other forms of stress (e.g., heat, flooding, herbivory), the effects of stress during different periods of the growing season (i.e., early season, mid-season), and the effects of stress occurring across different time scales (i.e., interannual). However, given climate-change-associated projections of increasing intra- and interannual frequency of drought conditions in regions where *A. gerardii* and *S. nutans* are currently codominant (Cook et al., n.d.), the long-term stability of their populations should be fully considered. Further study using consistent methodologies into the variability of net interactions between plant species across a gradient of similarities in traits and responses to stress is also strongly recommended.

3.6 FIGURES

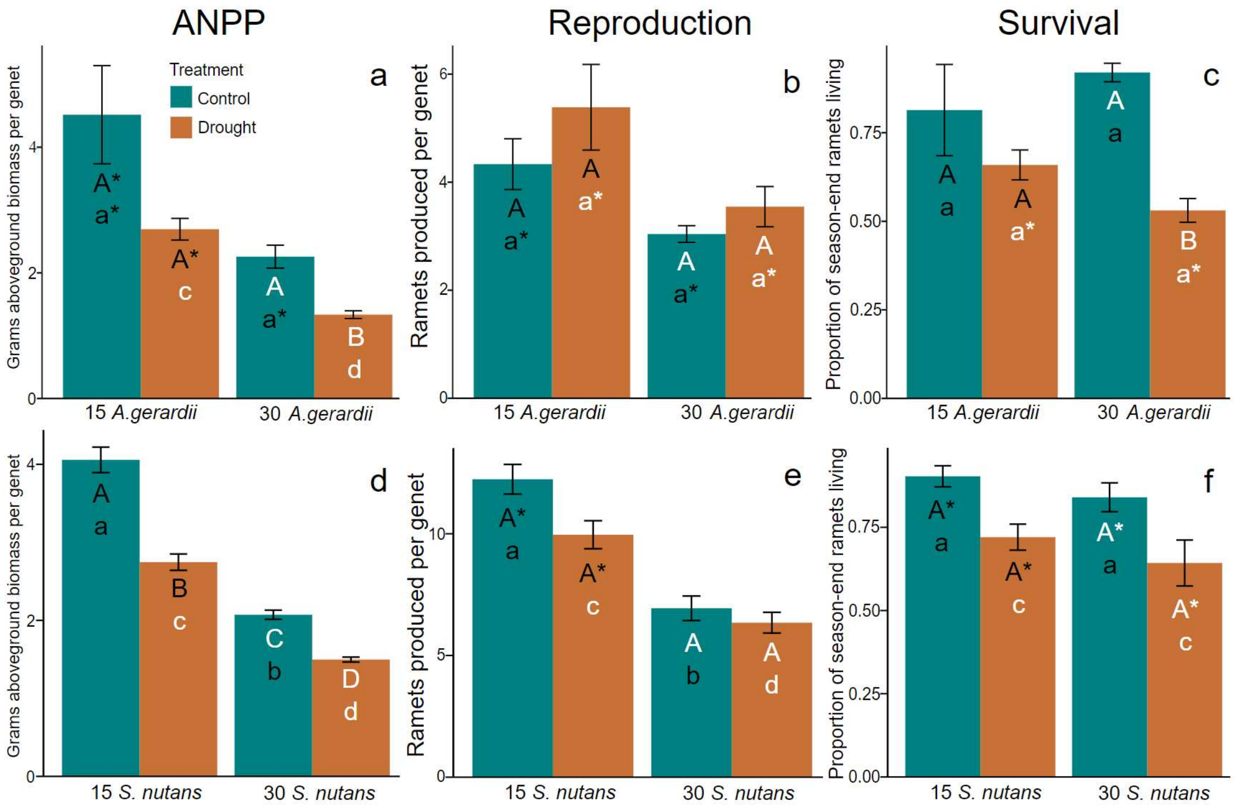

Fig. 3.1 Performance of (a-c) *A. gerardii* and (d-f) *S. nutans* monocultures under late-season un-stressed (control) and stressed (drought) conditions at both low (15 genets) and high (30 genets) densities of identical competitor genets. Differing *capital letters* indicate significant differences resulting from the water treatment (at constant densities). Differing *lower case letters* indicate significant differences resulting from the density treatment within each water treatment. Asterisks indicate significant differences only before Bonferroni adjustment. Error bars indicate estimates of standard error.

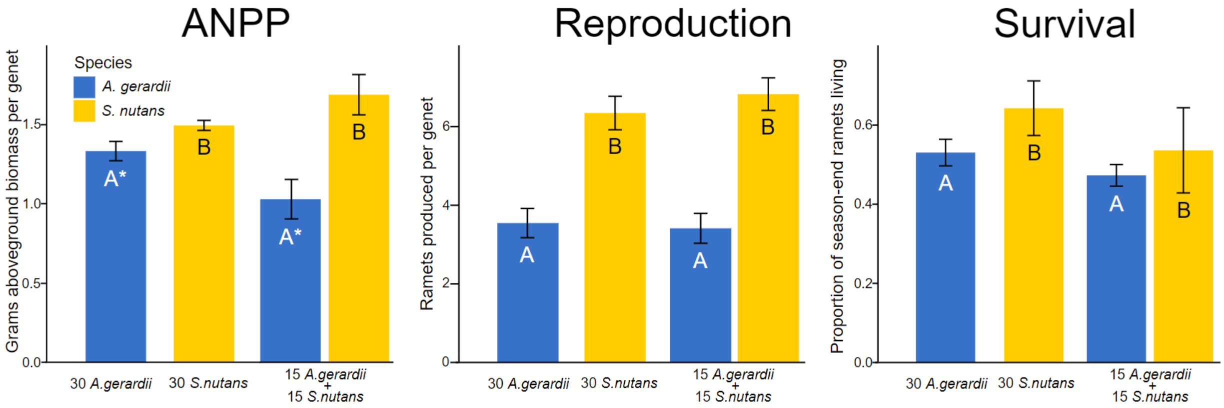

Fig. 3.2 Performance of *A. gerardii* and *S. nutans* under the effect of interspecific competitors (right two columns). All communities depicted contained 30 total genets and were subjected to the late-season drought treatment. Asterisk indicates significance only before adjustment (0.008<a<0.05). Letters indicate significantly different values for each species, but no performance metrics of either species were significantly affected by neighbor species identity. Error bars indicate estimates of standard error.

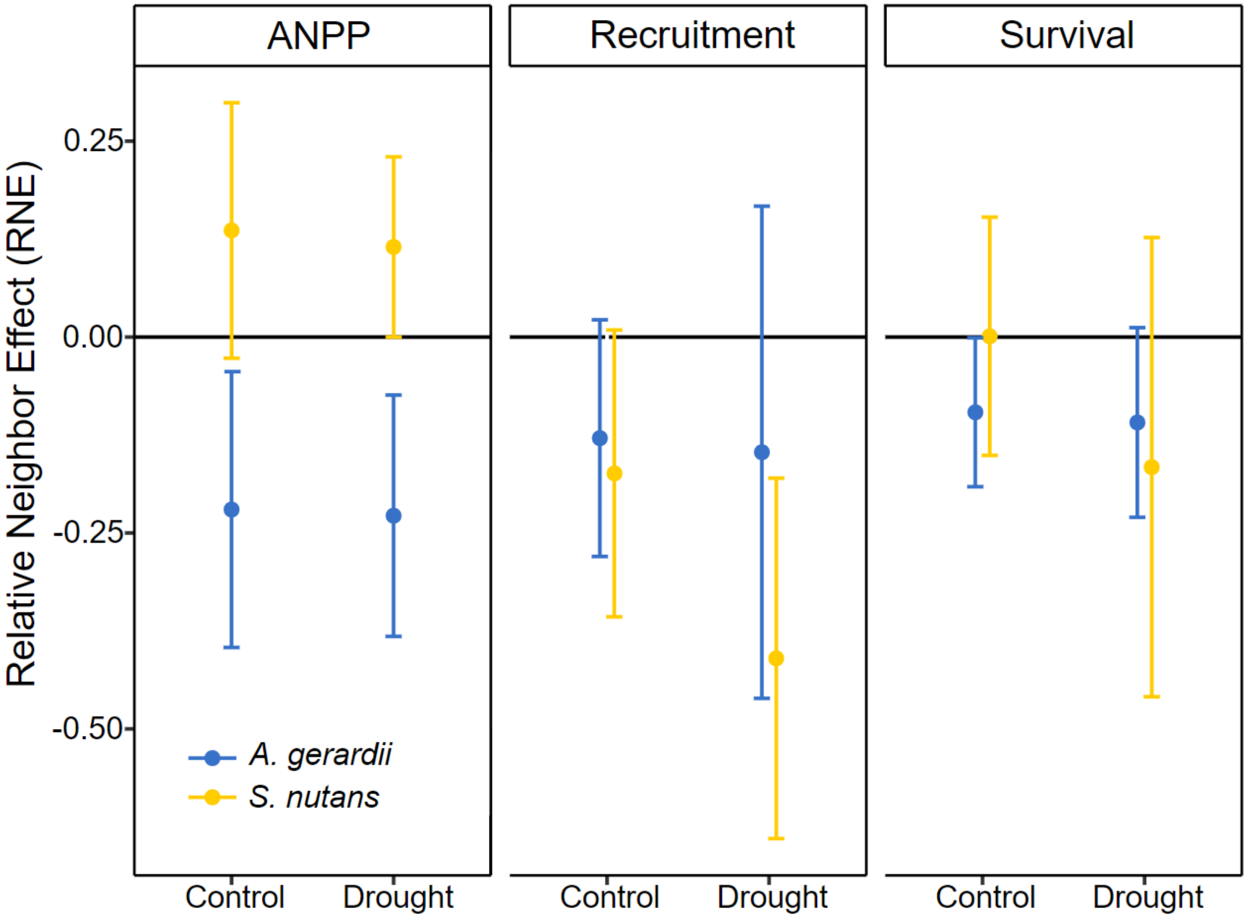

Fig. 3.3 Relative neighbor effects of competing species *A. gerardii* and *S. nutans*. Values are averages for the five replicates within each watering and community treatment and error bars indicate 5% confidence intervals. Indicates the performance of the focal species in communities mixed with its competing species relative to its performance in monoculture at the same total community genet density. Performance metrics include, from left to right: ANPP (aboveground net primary production per genet), recruitment (ramets produced per genet), and survival (proportion of ramets produced that remained alive at experiment completion). Positive values indicate the focal species is facilitated by interspecific neighbors, negative indicates an antagonistic relationship, and a value of zero indicates that the performance of the focal species is unaffected by the species identity of its neighbor.

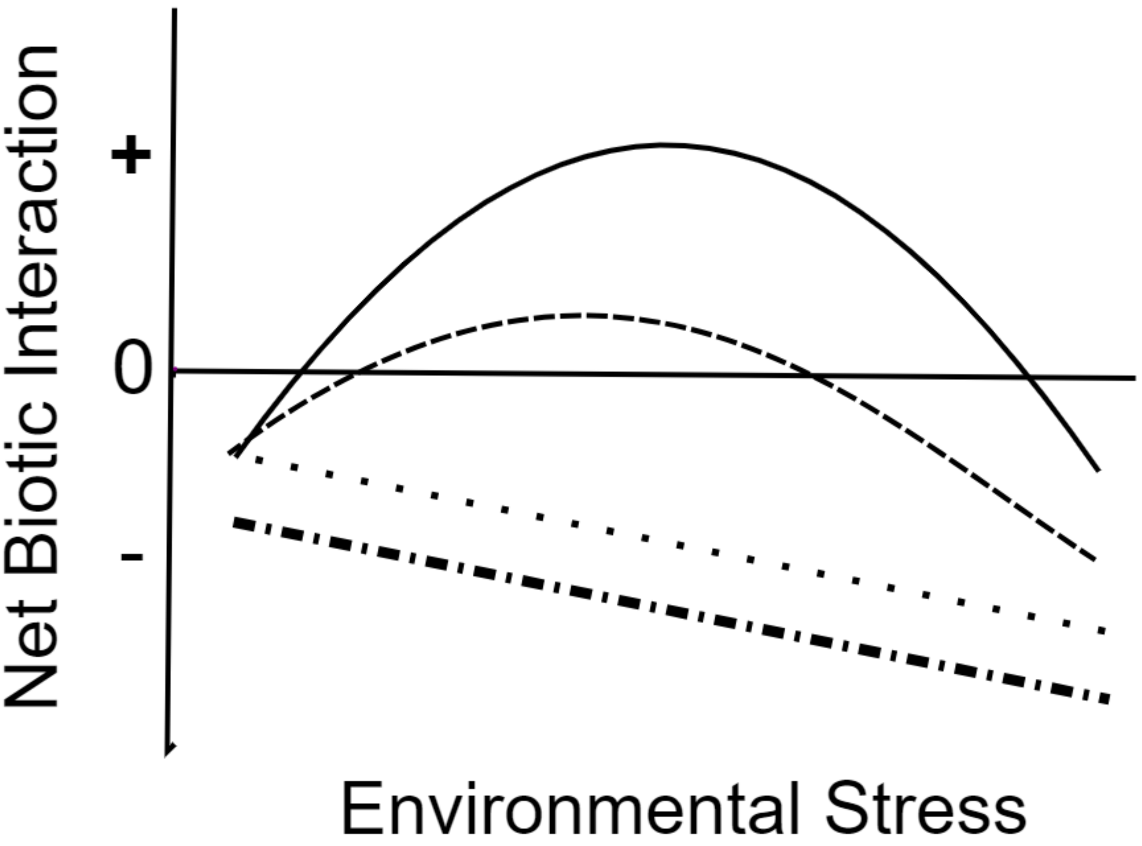

Fig. 3.4 Proposed modifications to the framework for exploring the relationship between interspecific plant net biotic interactions and environmental stress. The existing framework is illustrated by the solid line, with the proposed modifications in the dashed and dotted lines. Interacting species resembling one another in the ways that they obtain resources and respond to stress and/or limitations in the availability of those resources may have fewer opportunities to shift net biotic interactions to positive when those stresses and resource limitations are encountered (dashed line). Species that perfectly resemble one another (dotted line) should see no benefit, nor detriment, from having interspecific rather than intraspecific neighbors under stressful conditions. Increasing the total density of identical competitors is expected to exacerbate negative interactions among them (dash-dot line) under the full range of environmental stress (ignoring density effects at very low densities, e.g., Allee effects).

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CHAPTER 4: CONTRASTING INTRA-SEASONAL POPULATION DYNAMICS OF TWO CODOMINANT SPECIES ARE CONSISTENT ACROSS SPATIAL AND TEMPORAL SCALES

4.1 OVERVIEW

Despite asymmetric competition and a wide array of functional similarities, two ecologically important C_4 perennial grass species, *Andropogon gerardii* and *Sorghastrum nutans*, frequently codominate areas of the mesic tallgrass prairie of the US Great Plains. While both are rhizomatous, primarily asexually reproducing grasses, a subtle difference in their vegetative reproduction strategies may play a role in preventing the exclusion of *S. nutans,* the presumed weaker competitor in this region. The determinate growth of *A. gerardii*, in which tillers are recruited from belowground buds and senesce within a single growing season, limits intra-seasonal tiller recruitment regardless of the quality of conditions affecting photosynthetic rates. In contrast, *S. nutans* exhibits indeterminate growth, in which tillers are recruited throughout the growing season with later-recruiting tillers reemerging the next season. This contrasting growth behavior of *S. nutans* may enable this species to recover from asymmetric competition in years when late-season growing conditions are sufficiently favorable, reaffirming its codominant relationship with *A. gerardii*. However, until now the differential growth determinacy and its implications for population dynamics have only been informally observed. We examined the consistency of growing season population dynamics (measured as seasonal change in tiller densities) of each grass species in native tallgrass prairie in Kansas across a landscape varying in topography and fire management regimes and over 8 years, as well as in sites at the core (Kansas) and western periphery (Colorado) of the species' distributions, which also represent mesic vs. xeric conditions. We found that the tiller densities of *A. gerardii* decline within seasons with striking consistency regardless of topographic position, fire regime, or spatio-temporal scale. In contrast, we found the seasonal dynamics of *S. nutans* tiller densities, while more variable and dependent on abiotic conditions and disturbance regime, tend to remain stable or increase. These observations lay the groundwork for establishing differences in growth determinacy as a potentially important yet underappreciated mechanism promoting coexistence and codominance among perennial plant species.

4.2 INTRODUCTION

The determinacy of growth and reproduction among plants, while historically important in the context of agricultural applications (Hauggaard-Nielsen & Jensen, 2001; Huyghe, 1998), has with few exceptions (Hinman & Fridley, 2018; McKendrick et al., 1975; Seiwa, 2000) received relatively little attention in the ecology of native plant communities. Determinate behavior is exhibited when processes such as plant growth, flowering, or vegetative reproduction begin and end on a genetically predetermined schedule, e.g., 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 some 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; J. W. White et al., 1992).

Though growth determinacy trait data is not often collected in native plant communities, determinately growing species can 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 at any time whenever 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 similar and competitive species. Because environmental conditions suitable for growth may persist after processes in determinate species conclude, indeterminately growing species may be able to gain late-season advantages or recover from asymmetric competition 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.

In contrast to the relationships between winter and summer annuals (Q. Guo & Brown, 1997), or between cool- and warm-season grasses (Monson et al., 1983), for example, dissimilarities in growth determinacies could enable individuals of strongly competing species to have broadly or entirely overlapping periods of activity. If so, 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.

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). The more competitive of the two in this region, *A. gerardii* (A. M. Silletti et al., 2004a), is a determinately growing perennial warm-season (C_4) grass that vegetatively produces annual tillers within a limited period from mid- to late April (Benson & Hartnett, 2006; McKendrick et al., 1975). Its codominant, *S. nutans,* indeterminately produces biennial or potentially longer-lived tillers, a process that begins in the same weeks as *A. gerardii* but can continue throughout the growing season until water becomes too limited or temperatures become too cold (Benson & Hartnett, 2006; McKendrick et al., 1975). Despite differences in determinacy, these two species are very similar in their morphology, 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., 2018a; Lett & Knapp, 2003; Mulkey et al., 2008; A. Silletti & Knapp, 2002; A. M. Silletti & Knapp, 2001a; Swemmer et al., 2006a; Weaver & Rowland, 1952). Given their broadly overlapping niche requirements, the determinate growth form of *A. gerardii* may play an important role in enabling the less competitive species, *S. nutans*, to maintain its codominant status.

To lay the groundwork for establishing determinacy of tiller growth as a niche axis contributing to coexistence and/or codominance, we studied the seasonal population (tiller) dynamics of the codominant grasses, *A. gerardii* and *S. nutans,* in the field. We observed the intra-seasonal tiller density dynamics of *A. gerardii* and *S. nutans* and how they vary over the long-term and spatially across the distribution of the two species from mesic to xeric sites. We also observed how the intra-seasonal density dynamics of the two species vary with topographical position, which is associated with water availability (Oviatt, 1998, Nippert & Knapp, 2007), and frequency of fire, a key disturbance in the tallgrass prairie (Blair, 1997; Briggs et al., 2002; Briggs & Knapp, 1995; Ojima et al., 1994; Wan et al., 2001). If growth determinacy via vegetative recruitment is important for codominance, the expectation is where plant species are persistently codominant, differences in the patterns of intra-seasonal population dynamics due to contrasting growth determinacy can provide a more responsive, but less competitive species periodic opportunities to recover from early-season competitive disadvantages. Accordingly, we hypothesized *A. gerardii* tiller densities should 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 though 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 soil type 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, soil type, and fire frequency, as well as regionally in mesic vs. xeric sites, varying not only in magnitude but in direction as well. While this study was not controlled and cannot show that codominance results causally from variability in determinacy, we found that these prerequisites are typically met.

4.3 METHODS

To address our research hypotheses, we conducted population density censuses at a mesic tallgrass prairie site in Kansas and xeric grassland sites along the Front Range in Colorado. Two types of censuses were conducted in Kansas, one distributed over four watersheds varying in fire frequency and across upland and lowland topographies (spatial census), and the other at a single location that was measured repeatedly over 8 years (temporal census). The spatial census in Colorado was conducted at sites along the Front Range (S. fig. 4.1). Population density censuses were conducted for *A. gerardii, S. nutans*, and for all other individuals (either as functional groups or species) co-occurring within each of two 20 x 50 cm subplots located in each 2 x 2 m plot. These measurements were made twice each growing season, the first in late Spring (Kansas: May 26 to June 5, 2017, and May 18 to May 23, 2018; Colorado: June 11 to June 27, 2017, and June 6 to June 16, 2018), and the second in late Summer (Kansas: August 5 to August 2017 and August 9 to August 16, 2018; Colorado: August 27 to September 5, 2017, and August 30 to September 3, 2018).

Both the spatial and temporal censuses in Kansas were conducted within the Konza Prairie Biological Station (KPBS; 39.107, -96.609, S. Fig 4.1), 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), with mean annual precipitation of 835mm (Craine et al., 2012; Hayden, 1998), ~70% of which falls during the growing season(Hayden, 1998). The Kansas spatial census included twenty 2 x 2 m plots located within each of four watersheds, ten of which were placed in upland areas with shallow soils and ten in poorly drained lowland areas with deep soils, totaling 80 plots. Two sampling frames, measuring 20 x 50cm, were positioned in opposite corners of each plot. Both focal species are common throughout much of the Konza Prairie (Freeman, 1998), so the plots for the spatial census were placed in random locations within each of the selected watersheds. 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 four years, also in the spring (watersheds 4A and 4F). Neither of these latter watersheds was burned in 2017, but 4A was burned in Spring 2018. Both *A. gerardii* and *S. nutans* are, with some spatial and temporal variability, more common in the annually burned watersheds, particularly in the lowland topographic positions (Hartnett et al., 1996; A. Silletti & Knapp, 2002; Towne & Kemp, 2008). All species within each plot were censused in 2018, but, apart from the two study species, identification was limited to functional groups in 2017.

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, 2011b), located in an annually burned and ungrazed lowland site at KPBS. In each 6 x 6 m RaMP (n = 6 control plots), growing season rainfall was intercepted during each precipitation event and then all the collected water was immediately added to the control plots through an overhead sprinkler system after each rainfall event. Annual censuses were measured in two permanent 20 x 50 cm subplots located within a 2 x 2 m plot within each RaMP structure. Due to unforeseen circumstances, we were unable to collect temporal census data in 2008 and 2011.

The spatial censuses conducted in Colorado took place in 2017 and 2018 from different pairs of subplots in 19 plots established along the Front Range (S. Fig 4.1), the eastern edge of the Rocky Mountains, and the western range limits of both species (Bock & Bock, 1998a; Keeler, 2004; USDA, 2021b, 2021a; Weaver, 1931; Weaver & Fitzpatrick, 1932). The 19 plots were distributed in xeric tallgrass prairie sites in southern Boulder and isolated populations of *A. gerardii* in northern Fort Collins (S. Fig 4.1, Table 4.1). The plots varied in soil moisture availability, community composition, and grazing regimes. This region is considered semi-arid, with highly variable annual precipitation averaging between

406 mm near Fort Collins and 486 mm near Boulder (Hansen et al., 1978). Neither of the focal study species is as common in this region as in Kansas (Bock & Bock, 1998b; Keeler, 2004), so plots were placed at the centers of populations of either *A. gerardii* or *S. nutans* (10 plots for each species), in contrast to the Kansas plots, almost all of which contained individuals of both species. The emergence of tillers of these species occurs later than in Kansas, so each measurement was taken following each Kansas census. Due to unforeseen, independent factors that prevented their resampling, four of the plots were re-established locally in 2018 (details in supplementary table 1).

Statistical Analysis

We analyzed the Kansas spatial censuses, Kansas temporal censuses, and the Colorado temporal censuses independently, using each to address our first two hypotheses: 1) the population densities of the two species change intra-seasonally, and 2) intra-seasonal dynamics differ depending on species. 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 and were excluded, we analyzed the Colorado spatial censuses at the subplot level, rather than averaging beforehand. To examine the effect of seasonality on population densities, we analyzed both absolute densities (simple count of individuals of each species in a sampling unit) and relative densities (proportion of a community that a species composes). To examine the effect of species identity on intra-seasonal population density dynamics, we analyzed absolute changes in density (difference between late and early absolute densities of a species) and relative changes in density (ratio of absolute change in density to early-season absolute density).

We found that a large proportion of our data groupings for the spatial censuses were not normally distributed and, to maintain consistency, elected to use non-parametric analyses for all comparisons. To determine whether the absolute densities of the two species changed during the growing seasons of the spatial censuses, we used Wilcoxon signed ranked tests with early and late season densities paired according to their sampling unit (average of subplots for Kansas, subplots for Colorado), and then calculated the means of the early and late densities and their estimated standard errors. These calculations were made independently for *A. gerardii* and *S. nutans*, the region where they were observed (Kansas or Colorado), and the year measurements were taken (2017 or 2018). This process was repeated for relative densities. Bonferroni corrections were used to determine significance. For these tests, adjustments for four comparisons were used (two years, absolute and relative dynamics: adjusted alpha = 0.0125)

For the temporal census, we used the Shapiro-Wilks tests of non-normality and visually confirmed using QQ-plots and histograms that our comparison groups were reasonably normally distributed. However, one of the control plots demonstrated absolute densities and population dynamics of *A. gerardii* that were in strong contrast to the remaining five plots, and we elected not to include it in analyses of absolute densities as it was consistently found to be a highly influential extreme outlier (S. Fig. 4.2). This plot was not found to be an outlier for *A. gerardii* relative densities or dynamics, however, and thus was included in this measurement. To determine whether absolute densities tend to change consistently from year to year, we used repeated measure mixed linear models with census date (early or late) as a fixed effect and year nested within plots as random effects. This process was performed independently for each species and was repeated for relative densities.

We performed a second set of analyses to address our second hypothesis that the identity of the species (*A. gerardii* or *S. nutans*) is a factor in determining intra-season population dynamics. Both the spatial and temporal censuses were analyzed for these effects. For the Colorado spatial census, we used unpaired Wilcoxon rank-sum tests for differences in either the absolute or 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 (two years, absolute and relative dynamics adjusted alpha = 0.0125)

For the Kansas spatial census, we examined the effects of topography and fire frequency on absolute and relative population dynamics separately, using Wilcoxon rank-sum tests to determine whether each species population dynamics differed either by its location in upland or lowland positions (irrespective of fire frequency) or by the frequency of fire application: annual or once every four years (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 dynamics, two years, adjusted alpha = 0.0125). Because one watershed (4A) but not the other (4F) was burned in 2018 before that year's censuses, we also used Kruskal-Wallis tests to determine if there were differences between these watersheds in the absolute and relative dynamics of the two study species and whether those differences depended on topographical position. Further, because these watersheds are independent of one another, we also performed other comparisons to determine baseline differences. These included direct comparisons between the two watersheds in 2017 to establish whether differences existed in the absence of a fire application, between 4A in 2017 and 4A in 2018 to determine whether any differences could be seen within a watershed after the application of fire, and between 4F in 2017 and 4F in 2018 to determine if any differences seen in 4A between years could be explained by factors other than the fire application (e.g., differences in climate conditions between years). Bonferroni adjustments were made to correct for eight comparisons (two years, within/between watersheds, absolute and relative dynamics, adjusted alpha = 0.00625).

4.4 RESULTS

Seasonal density dynamics of A. gerardii and S. nutans

We found that the absolute density of *A. gerardii* declined significantly from early to late growing seasons for both the Kansas and Colorado spatial censuses in 2017 and 2018 (Tables S2, S3, and that there was a consistent density decline in the temporal census (Fig. 4.1a, Table 4.4). The relative densities of *A. gerardii* populations also declined in both the spatial and temporal Kansas censuses (Fig. 4.1b, Tables S2-S4). However, they remained comparatively unchanged in the Colorado populations despite the significant decline in average absolute densities (Fig. 4.1, Table S2).

The seasonal dynamics of absolute densities of *S. nutans* were less consistent than for *A. gerardii*. In the Colorado censuses, *S. nutans* absolute density did not change significantly from early to late growing seasons in either 2017 or 2018 (Fig. 4.1a, Table S2-S3), though the relative densities increased over the growing season in 2017 (Fig. 4.1b). The results in the Kansas censuses depended on the year. In 2017, both *S. nutans* absolute and relative densities increased from early to late growing seasons in Kansas (Fig. 4.1b, Table S3), but only the relative density increased in 2018. Despite this interannual inconsistency observed in the Kansas and Colorado spatial censuses, we found in the temporal Kansas census that the absolute and relative densities of *S. nutans* significantly increased on average over the growing season (Fig. 4.1, Table S4).

While the seasonal dynamics of *S. nutans* populations depended somewhat on region and year, we found that the seasonal dynamics of the two species always differed (Fig. 4.2). Both the absolute and relative dynamics (positive vs. negative seasonal change) of *A. gerardii* and *S. nutans* were significantly different from each other (with *A. gerardii* being more negative) in both years of the Colorado (Table S2) and Kansas spatial censuses (Table S3), and they were different on average in the temporal census (Table S4).

Topography and fire frequency effects on seasonal dynamics

Overall, the effects of fire frequency (Table S5) and topographic position (Table S6) on the seasonal density dynamics of the two grasses were inconsistent. Neither the absolute nor the relative seasonal dynamics of *A. gerardii* differed significantly between areas with different fire application frequencies in 2017), but the absolute dynamics were significantly more negative in annually burned areas in 2018 (Fig. 4.3). The absolute dynamics of *S. nutans* were similarly positive between annually and infrequently burned watersheds in 2017 (Fig. 4.3). However, there was a decline in *S. nutans* tiller density in the annually burned watersheds but an increase in density in the infrequently burned watersheds in 2018 (Fig. 4.3). The relative dynamics were only significantly different in 2018, being more positive in the infrequently burned watersheds. The absolute and relative dynamics of *A. gerardii* differed by topographic position in 2017 (Fig. 4.3), with greater tiller density declines in the lowland areas. However, these effects were not observed in 2018. For *S. nutans*, absolute and relative density dynamics showed no significant difference between upland and lowland sites in 2017 (Fig. 4.3). However, more positive relative dynamics were observed in lowlands in 2018 along with a correspondingly higher average increase in absolute density, though this increase was non-significant.

Direct fire effects on seasonal dynamics

One of the two infrequently burned watersheds received a fire application in 2018 (4A but no 4F), and thus we could examine the direct effects of fire on seasonal dynamics. There was a significant difference between the dynamics of *S. nutans* in the burned watershed (4A) when compared to the unburned watershed (4F), which was not burned. However, this difference was only in terms of absolute dynamics (more positive in 4A), not relative (Fig. 4.3, Table S7), and a significant difference was also observed in 2017 in the absence of a fire application in both watersheds. There was also a difference in the dynamics of *S. nutans* within the 4A watershed between the 2017 and 2018 growing seasons (Fig 4.3, Table S7), with 2018 having a greater absolute increase in *S. nutans* population density. Though this change was not reflected in the relative dynamics, the difference does stand in contrast to the 4F watershed, in which there was no significant difference between the two years in either absolute or relative density dynamics of *S. nutans* (Table S7). No differences in the absolute or relative dynamics of *A. gerardii* were observed for any of the comparisons between 4A and 4F or between years within each watershed (Fig. 4.3, Table S7).

4.5 DISCUSSION

We investigated whether the population densities of the determinately growing perennial grass, *A. gerardii*, consistently declined across broad spatial scales and from year to year and whether those declines were affected by fire frequency and topographic position. We concurrently investigated whether a commonly codominant species, *S. nutans*, which is an indeterminately growing but otherwise functionally similar species to *A. gerardii*, demonstrated intra-seasonal stability or increases in population densities, and whether these dynamics are also consistent across spatial and temporal scales and affected fire frequency and topographic position. We consider these to be prerequisites to provide support for differences in determinacy to be a factor in promoting coexistence and the codominant relationship observed between these two species in portions of their geographic distributions.

We found that *A. gerardii* population densities consistently declined from early to late growing seasons. The absolute number of individuals declined in all the populations sampled, showing consistent intra-seasonal reductions across local landscapes, regions of the US that represent the core vs. edge locations of their longitudinal distributions (northeastern Kansas vs. the northern Front Range of CO), and on average over 8 years. We also found that these dynamics did not differ according to the long-term difference in fire frequency regimes, nor were they significantly affected by the direct effects of fire (e.g., leaf tissue and meristem removal, soil dehydration, nitrogen vaporization) applied shortly before early-season sampling. Though topographical position in Kansas, and thus water availability, did affect the degree of absolute and relative dynamics of *A. gerardii* in 2017 (but not 2018), both upland and lowland populations experienced a decline in densities, with the larger declines occurring in lowland areas. The relative densities of *A. gerardii* also declined in the Kansas spatial census and on average in the Kansas temporal census, though this did not occur in the Colorado spatial census in 2017 or 2018. This disparity between the dynamics of the Colorado absolute and relative densities can be explained by concurrent declines in the densities of other species within the censused subplots causing the share of total community abundance held by *A. gerardii* to remain somewhat constant despite tiller loss.

As expected, the population density dynamics of *S. nutans* were less consistent than those of *A. gerardii* but tended to show intra-seasonal increases. Over the eight years of the temporal census, *S. nutans* absolute and relative densities increased on average each season, though absolute declines did occur in 2005 and 2013 (S. Fig. 4.3). Relative densities increased in both Colorado and Kansas in both years, but absolute density only increased in Kansas and only in 2017. These increases in relative density in the absence of absolute density changes can be explained by declines in the population densities of other species within the censused subplots. The effects of fire, fire frequency, and topographic position were also less consistent. Fire frequency was important in 2017 when absolute densities increased more in annually burned watersheds than in infrequently burned watersheds, but this observation reversed in 2018 when densities declined in annually burned watersheds. Similarly, topographic positioning did not result in differences in *S. nutans* density dynamics in 2017, but densities increased in lowlands in 2018, while they decreased in uplands. Furthermore, the application of fire in 2018 did not appear to strongly affect these dynamics but may have had a significant effect on the populations before the early-season observations. These inconsistencies suggest that the dynamics of *S. nutans* may be more responsive to factors that vary on shorter-than-seasonal time scales, such as changes in humidity, temperature, precipitation events, and resource availability.

Despite the variation in the seasonal dynamics of *S. nutans* in comparison to consistent declines of *A. gerardii* over the growing season, we found that the intra-seasonal dynamics of the two species are reliably different from one another, both in terms of absolute density changes and changes relative to their respective early season densities. This can be accounted for by the unfaltering regularity of annual *A. gerardii* population thinning coupled with the tendency of *S. nutans* densities to either increase, remain constant, or, in rare cases, thin but to a lesser extent than its codominant partner. This suggests that in the case of these species the theoretical prerequisite for our proposed codominance mechanism is consistently met: the influence of a more competitive species regularly declines each growing season, presenting the opportunity for other species to gain temporary advantages and recover from the earlier periods of asymmetric competition, provided that environmental conditions are favorable to growth. Further, the rate of thinning of the more competitive species appears to be negatively density-dependent, as evidenced by the larger proportional declines in the Kansas lowlands. This is consistent with one of the requirements of the storage effect – that intra-specific competition is strongest when environmental conditions are most favorable to growth (Chesson, 2000) – which may further stabilize the relationship between *A. gerardii* and *S. nutans* in these areas with higher water availability. However, we recognize that other factors must certainly be playing a role in the high abundances of *A. gerardii* and *S. nutans* observed in eastern Kansas, regardless of whether the mechanism discussed here is important. For instance, 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 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 of environmental conditions found there. These trends continue with increasing relative abundances of both species with increasing average water availability (Weaver & Fitzpatrick, 1932), and particularly of *S. nutans* in the southeastern United States (D. A. Brown, 1993; Epstein et al., 1998b).

Though seldom investigated or reported, and not featured within species trait databases (e.g., TRY, Fraser, 2020; Kattge et al., 2020😉), growth and reproductive determinacy traits potentially represent additional niche axes along which species may be differentiated. In association with other trait axes (Blonder, 2018; Hutchinson, 1957), growth determinacy may also contribute to coexistence stability at the community scale. Moreover, differences in determinacy do not necessarily prohibit the active periods of photosynthesis of competing species from overlapping to any degree other than at the population scale. In contrast to the limitations imposed by temporal niche partitioning (Kindscher & Wells, 1995; Silvertown et al., 2015; Sweet & Holt, 2015; Wilsey et al., 2011) these traits may be an important factor in plant species codominance since individuals of both species can be fully active throughout the growing season. 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. However, because this study was not a controlled experiment, we cannot make strong inferences regarding a causal relationship between growth determinacy and codominance. Greenhouse or field experiments with artificial communities constructed of plant species with varying growth determinacies and varying environmental conditions that are important for growth (and their temporal patterns) may shed additional insight on this question.

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. Revegetating with perennial plant species that have a diversity of growth determinacies may lead to more species-rich community establishment and longer-term stability in restoration projects. However, the dependence of this mechanism on suitable growth conditions following the programmed decline of the more competitive species may represent a vulnerability to conservation under climate change. Because the general pattern we observed in the Kansas temporal census was for *S. Nutans* population densities to increase through the growing season then begin the next season at a lower population density, consecutive years with late-season dryness may be especially problematic for species. For example, the population densities of *S. nutans* remained stable in both growing seasons of the Colorado spatial censuses, but the 2018 early season population density was less than the early season density of the year prior. It may be noted as well that our method of surveying tiller densities with a census of tillers 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, particularly in the case of *S. nutans.* This may suggest that *S. nutans* requires more favorable conditions (e.g., larger precipitation totals) than were present in Colorado during these years for the rate of late-season tiller recruitment to exceed the rates of tiller senescence and mortality. That is, intra-seasonal population density stability may not be sufficient for inter-seasonal stability for this species. 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. With only two years of such observations in Colorado and Kansas, however, this evidence is limited and longer-term research into the stability of this species under future drought scenarios will be necessary.

In conclusion, the consistency of the seasonal dynamics of populations 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 and in space. 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, within our study, we observed several other perennial plant species within the community that declined during the growing season (e.g., *Panicum virgatum*, *Carex 110eliophile*, *Carex meadii*, *Poa pratensis*, *Sporobolus asper*, forb species in aggregate) or either increased in density or remained stable (e.g., *Bouteloua curtipendula*, *Schizachyrium scoparium*). This suggests that the mechanism we have described for stabilizing populations of competing perennial plant species may be widespread and diffuse. Secondly, the 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 provide a consistent advantage to one species or the other. 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. The role of determinism proposed here will require more rigorous study through controlled experiments to assess how widespread variation in determinism may be in natural communities and the role it may play in the coexistence and codominance of perennial plant species.

4.6 TABLES

Table 4.1. Site names and locations of the 19 Colorado plot sites.

Site	Plot	Focal Species	Latitude	Longitude	Notes
Reservoir Ridge NA A	1	*A.gerardii*	40.6037	-105.1686	
Reservoir Ridge NA A	2	*A.gerardii*	40.6038	-105.1684	
Reservoir Ridge B	1	*A.gerardii*	40.6089	-105.1662	
Reservoir Ridge B	2	*A.gerardii*	40.6091	-105.1662	
Maxwell NA	1	*A.gerardii*	40.5583	-105.1437	
Maxwell NA	2	*A.gerardii*	40.5591	-105.1439	
Coyote Ridge NA	1	*A.gerardii*	40.4821	-105.133	
Coyote Ridge NA	2	*A.gerardii*	40.4825	-105.1333	
South Boulder Creek A	1	*S.nutans*	39.9593	-105.2375	
South Boulder Creek A	2	*S.nutans*	39.9592	-105.2377	
South Boulder Creek A	1	*A.gerardii*	39.9581	-105.2391	
South Boulder Creek A	2	*A.gerardii*	39.9579	-105.2392	
South Boulder Creek B	1	*S.nutans*	39.9522	-105.2437	
South Boulder Creek B	2	*S.nutans*	39.9521	-105.2435	
South Boulder Creek B	1	*A.gerardii*	39.9523	-105.2436	
South Boulder Creek B	2	*A.gerardii*	39.952	-105.2438	
South Boulder Creek C	1	*S.nutans*	39.95	-105.2512	
South Boulder Creek C	2	*S.nutans*	39.9501	-105.251	
South Boulder Creek C	1	*A.gerardii*	39.95	-105.2512	
South Boulder Creek C	2	*A.gerardii*	39.9499	-105.2513	
South Boulder Creek D	1	*S.nutans*	39.9489	-105.2595	unused after 2017
South Boulder Creek D	2	*S.nutans*	39.9489	-105.2597	unused after 2017
South Boulder Creek E	1	*S.nutans*	39.9478	-105.2599	unused after 2017
South Boulder Creek E	2	*S.nutans*	39.9476	-105.2599	unused after 2017
South Boulder Creek E	1	*S.nutans*	39.947	-105.2572	surveyed only after 2017
South Boulder Creek E	2	*S.nutans*	39.947	-105.2572	surveyed only after 2017
Jewel Mountain	1	*S.nutans*	39.8858	-105.2463	
Jewel Mountain	2	*S.nutans*	39.8857	-105.2465	
Van Vleet A	1	*S.nutans*	39.9697	-105.2178	
Van Vleet A	2	*S.nutans*	39.9698	-105.2177	
Cherryvale A	1	*S.nutans*	39.9765	-105.2023	
Cherryvale A	2	*S.nutans*	39.9765	-105.2025	
Cherryvale B	1	*S.nutans*	39.9722	-105.1988	
Cherryvale B	2	*S.nutans*	39.9724	-105.1989	
Cherryvale	1	*A.gerardii*	39.9757	-105.2012	
Cherryvale	2	*A.gerardii*	39.976	-105.2012	
Van Vleet B	1	*S.nutans*	39.969	-105.219	surveyed only after 2017
Van Vleet B	2	*S.nutans*	39.969	-105.219	surveyed only after 2017

Table 4.2: Comparison tests for the Front Range, Colorado spatial censuses in 2017 and 2018. Abbreviations: Year 17 and 18 refer to 2017 and 2018; DV (dependent variables) include AD (absolute density), RD (density relative to community total), ACD (absolute change in density), and RCD (change in density relative to early-season densities); IV (independent variables); DF (degrees of freedom); Ange (*Andropogon gerardii*); Sonu (*Sorghastrum nutans*).

Species	Test	DV	IV	Random Factor(s)	DF	Stat	p	means (confidence interval)
Ange	Wilcox (paired)	AD	Season	Subplot	19	158	0.002	Early: 73.32 (23.25); Late: 59.68 (19.23)
Ange	Wilcox (paired)	RD	Season	Subplot	19	89	0.829	Early: 0.39 (.1); Late: 0.4 (.1)
Sonu	Wilcox (paired)	AD	Season	Subplot	18	53.5	0.469	Early: 49.61 (12.54); Late: 50.72 (14.77)
Sonu	Wilcox (paired)	RD	Season	Subplot	18	59	0.016	Early: 0.25 (.07); Late: 0.29 (.08)
Both	Wilcox	ACD	Species	N/A	18	81.5	0.011	Ange: -13.5 (8.42); Sonu: 1.11 (9.57)
Both	Wilcox	RCD	Species	N/A	18	139	0.0071	Ange: -0.19 (.08); Sonu: 0.05 (.17)
Ange	Wilcox (paired)	AD	Season	Subplot	20	176	0.0012	Early: 80.2 (27.2); Sonu: 54.8 (15.8)
Ange	Wilcox (paired)	RD	Season	Subplot	20	77	0.312	Early: 0.327 (.082); Late: 0.362 (.087)
Sonu	Wilcox (paired)	AD	Season	Subplot	18	70	0.776	Early: 41.7 (13.1); Late: 43.4 (13.1)
Sonu	Wilcox (paired)	RD	Season	Subplot	18	53	0.167	Early: 0.191 (.074); Late: 0.219 (.062)
Both	Wilcox	ACD	Species	N/A	18	71.5	0.002	Ange: -25.83 (15.48); Sonu: 1.72 (8.51)
Both	Wilcox	RCD	Species	N/A	18	78	0.004	Ange: -0.25 (.15); Sonu: 0.133 (.217)

Table 4.3: Comparison tests for Konza Prairie, Kansas Spatial Censuses in 2017 and 2018. Abbreviations: Year 17 and 18 refer to 2017 and 2018; DV (dependent variables) include AD (absolute density), RD (density relative to community total), ACD (absolute change in density), and RCD (change in density relative to early-season densities); IV (independent variables); DF (degrees of freedom); Ange (*Andropogon gerardii*); Sonu (*Sorghastrum nutans*).

Year	Species	Test	DV	IV	Random Factor	DF	Statistic	p	means (confidence interval)
17	Ange	Wilcox (paired)	AD	Season	Plot	80	2695	<.0001	Early: 55.06 (10.2); Late: 43.32 (7.3)
17	Ange	Wilcox (paired)	RD	Season	Plot	80	2953	<.0001	Early: 0.36 (.04); Late: 0.302 (.04)
17	Sonu	Wilcox (paired)	AD	Season	Plot	80	814	0.0002	Early: 27.36 (4.7); Late: 31.17 (4.7)
17	Sonu	Wilcox (paired)	RD	Season	Plot	80	736	<.0001	Early: 0.182 (.02); Late: 0.214 (.02)
17	Both	Wilcox (paired)	ACD	Species	Plot	80	198	<.0001	Ange: -11.75 (3.9); Sonu: 3.8 (2.62)
17	Both	Wilcox (paired)	RCD	Species	Plot	80	397	<.0001	Ange: -0.115 (.11); Sonu: .369 (.2)
18	Ange	Wilcox (paired)	AD	Season	Plot	79	3064	<.0001	Early: 59.25(8.4); Late: 47.75 (7.0)
18	Ange	Wilcox (paired)	RD	Season	Plot	79	2281	0.0006	Early: 0.304(.04); Late: 0.286 (.04)
18	Sonu	Wilcox (paired)	AD	Season	Plot	79	1388	0.847	Early: 34.24 (4.9); Late: 34.34 (4.6)
18	Sonu	Wilcox (paired)	RD	Season	Plot	79	534	<.0001	Early: 0.173 (.02); Late: 0.208 (.03)
18	Both	Wilcox (paired)	ACD	Species	Plot	79	408	<.0001	Ange: -11.5 (2.22); Sonu: 0.095 (2.75)
18	Both	Wilcox (paired)	RCD	Species	Plot	79	411	<.0001	Ange: -0.18 (.03); Sonu: 0.24 (.14)

Table 4.4: Comparison tests for RaMPs experiment (Konza, Kansas) temporal censuses from 2005-2013. Abbreviations: DV (dependent variables), IV (independent variables), RV (random variables), numDF (numerator degrees of freedom), denDF (denominator degrees of freedom). Year is nested within replicate plots. Plot 11 was excluded from analyses that included absolute density of *A. gerardii*, where this measure, and its absolute seasonal change, were extreme outliers. Rel tiller density refers to the proportion of the total community density that is composed of the focal species. Rel density change refers to the seasonal change in tiller density relative to early-season densities. The independent variable "season" refers to the early or late season. The independent variable "species" refers to *A. gerardii* or *S. nutans*. ANOVA tables were generated using the *lme*() function in the R package "nlme" after confirming the assumptions for ANOVA were met.

Formula	Species	DV	IV	RV	ANOVA Table	numDF	denDF	F-value	p-value
Density ~ Season, random = ~1|Plot/Year	*A. gerardii*	tiller density	season	year	(intercept)	1	34	130.742	<.0001
					Season	1	34	89.108	<.0001
	S. nutans	tiller density	season	year	(intercept)	1	41	45.031	<.0001
					Season	1	41	16.689	0.0002
Rel. Density ~ Season, random = ~1|Plot/Year	*A. gerardii*	rel. tiller density	season	year	(intercept)	1	41	33.71	<.0001
					Season	1	41	81.273	<.0001
	S. nutans	rel. tiller density	season	year	(intercept)	1	41	68.71	<.0001
					Season	1	41	132.149	<.0001
Density Change ~ Species, radom = ~1|Plot/Year	NA	density change	species	year	(intercept)	1	34	4.731	0.0367
					Species	1	34	92.812	<.0001
Rel. Density Change ~ Species, random = ~1|Year/Plot	NA	rel. density change	species	year	(intercept)	1	41	0.531	0.47
					Species	1	41	62.472	<.0001

Table 4.5: Comparison tests for effects of fire frequency (annual Spring fire or Spring fire once every 4 years) in 2017 and 2018. Abbreviations: Year 17 and 18 refer to 2017 and 2018; DV (dependent variables) include AD (absolute density), RD (density relative to community total), ACD (absolute change in density), and RCD (change in density relative to early-season densities); IV (independent variables); DF (degrees of freedom); Ange (*Andropogon gerardii*); Sonu (*Sorghastrum nutans*).

Year	Species	Test	DV	IV	Random	DF	Stat	p	means (confidence interval)
2017	Ange	Wilcox	ACD	Burn Frequency	Plot	39	552	0.026	Annual: -16.96 (7.24); Four Year: -6.66 (2.61)
2017	Ange	Wilcox	RCD	Burn Frequency	Plot	30	858	0.456	Annual: -0.157 (.066); Four Year: -0.074(.202)
2017	Sonu	Wilcox (paired)	ACD	Burn Frequency	Plot	39	856	0.456	Annual: 3.54 (4.25); Four Year: 4.08 (3.3)
2017	Sonu	Wilcox (paired)	RCD	Burn Frequency	Plot	80	763	0.872	Annual: 0.286 (0.187); Four Year: 0.449 (0.356)
2018	Ange	Wilcox	ACD	Burn Frequency	Plot	39	422	0.0004	Annual: -15.19 (2.98); Four Year: -7.9(2.99)
2018	Ange	Wilcox	RCD	Burn Frequency	Plot	39	662	0.329	Annual: -0.204 (.034); Four Year: -0.159(.077)
2018	Sonu	Wilcox	ACD	Burn Frequency	Plot	39	302	<.0001	Annual: -6.1 (3.67); Four Year: 6.14 (3.2)
2018	Sonu	Wilcox (paired)	RCD	Burn Frequency	Plot	39	294	<.0001	Annual: -0.083 (.076); Four Year: 0.565 (.305)

Table 4.6: Comparison tests for Konza, Kansas effects of topographical position (upland well-drained soils or lowland poorly-drained soils) in 2017 and 2018: Abbreviations: Year 17 and 18 refer to 2017 and 2018; DV (dependent variables) include AD (absolute density), RD (density relative to community total), ACD (absolute change in density) and RCD (change in density relative to early-season densities); IV (independent variables); DF (degrees of freedom); Ange (*Andropogon gerardii*); Sonu (*Sorghastrum nutans*).

Year	Species	Test	DV	IV	Random	DF	Statistic	p	means (confidence interval)
2017	Ange	Wilcox	ACD	Topography	Plot	39	505	0.0071	Lowland: -17.71 (7.19); Upland: -5.94(2.41)
2017	Ange	Wilcox	RCD	Topography	Plot	39	523	0.0113	Lowland: -0.127 (.201); Upland: -0.103 (.081)
2017	Sonu	Wilcox (paired)	ACD	Topography	Plot	39	726	0.6	Lowland: 3.56 (4.67); Upland: 4.05 (2.72)
2017	Sonu	Wilcox (paired)	RCD	Topography	Plot	39	764	0.88	Lowland: 0.427(.351); Upland: 0.312 (.21)
2018	Ange	Wilcox (paired)	ACD	Topography	Plot	39	686	0.359	Lowland: -13.03(3.5); Upland: -10.01(2.84)
2018	Ange	Wilcox (paired)	RCD	Topography	Plot	39	767	0.948	Lowland: -0.188 (.062); Upland: -0.176 (.057)
2018	Sonu	Wilcox (paired)	ACD	Topography	Plot	39	1015	0.0214	Lowland: 4.0 (3.78); Upland: -3.71 (3.77)
2018	Sonu	Wilcox (paired)	`	Topography	Plot	39	962	.0451	Lowland: 0.275 (.196); Upland: 0.208 (.288)

Table 4.7: Comparison tests for the direct effects of fire application (in 4A but not 4F), and covariates (year, topography, and watershed). Abbreviations: DV (dependent variables) include AD (absolute density), RD (density relative to community total), ACD (absolute change in density) and RCD (change in density relative to early-season densities); IV (independent variables); DF (degrees of freedom); Ange (*Andropogon gerardii*); Sonu (*Sorghastrum nutans*).

Year	Species	Test	DV	IV	DF	p	means (confidence interval)
2018	Ange	Kruskal	ACD	Watershed/ Fire Application/ Topography	40	0.93	4A Lowland: -16.4 (12.32); 4A Upland: -10.6 (12.3); 4F Lowland: -18.0 (12.3); 4F Upland -18.2 (12.3)
2018	Ange	Kruskal	RCD	Watershed/ Fire Application/ Topography	40	0.206	4A Lowland: -.189; 4A Upland: -0.111; 4F Lowland: -0.27; 4F Upland: -0.173
2018	Sonu	Kruskal	ACD	Watershed/Fire Application/ Topography	40	0.0017	4A Lowland: 29.4 (10.83); 4A Upland: 16.4 (10.830); 4F Lowland: 0.6 (10.8); 4F Upland: 2.7 (10.8)
2018	Sonu	Kruskal	RCD	Watershed/Fire Application/ Topography	40	0.4483	4A Lowland: 0.532; 4A Upland: 0.461; 4F Lowland: 0.109; 4F Upland: 0.669
2017	Ange	Kruskal	ACD	Watershed/ Topography	40	0.644	4A Lowland: -4.4 (12.0); 4A Upland: -6.7 (12.0); 4F Lowland: -12.7 (12.0); 4F Upland -15.8 (12.0)
2017	Ange	Kruskal	RCD	Watershed/ Topography	40	0.102	4A Lowland: -0.062; 4A Upland: -0.0907; 4F Lowland: -0.317; 4F Upland: -0.1671
2017	Sonu	Kruskal	ACD	Watershed/ Topography	40	0.0063	4A Lowland: 18.3 (9.84); 4A Upland 5.9 (9.84); 4F Lowland: 8.2 (9.84); 4F Upland: -4.2 (9.84)
2017	Sonu	Kruskal	RCD	Watershed/ Topography	40	0.0068	4A: 0.633 (.399); 4F: 0.072 (.227)
Both	Ange	Kruskal	ACD	Fire Application/ Year/Topography	40	0.653	Lowland 2017: -4.4; Lowland 2018: -16.4; Upland 2017: -6.7; Upland 2018: -10.6
Both	Ange	Kruskal	RCD	Fire Application/ Year/Topography	40	0.772	Lowland 2017: -0.062; Lowland 2018: -0.164; Upland 2017: -0.091; Upland 2018: -0.111
Both	Sonu	Kruskal	ACD	Fire Application/ Year/Topography	40	0.049	Lowland 2017: 18.3; Lowland 2018: 29.4; Upland 2017: 5.9; Upland 2018: 16.4
Both	Sonu	Kruskal	RCD	Fire Application/ Year/Topography	40	0.558	Lowland 2017: .958; Lowland 2018: .532; Upland 2017: .308; Upland 2018: .461
Both	Ange	Kruskal	ACD	Year/Topography	40	0.921	Lowland 2017: -12.7; Lowland 2018: -18.0; Upland 2017: -15.8; Upland 2018: -18.2
Both	Ange	Kruskal	RCD	Year/Topography	40	0.18	Lowland 2017: -0.317; Lowland 2018: -0.270; Upland 2017: -0.167; Upland 2018: -0.173
Both	Sonu	Kruskal	ACD	Year/Topography	40	0.391	Lowland 2017: 8.2; Lowland 2018: 0.6; Upland 2017: -4.2; Upland 2018: 2.7
Both	Sonu	Kruskal	RCD	Year/Topography	40	0.515	Lowland 2017: 0.166; Lowland 2018: 0.109; Upland 2017: -0.022; Upland 2018: .669

4.7 FIGURES

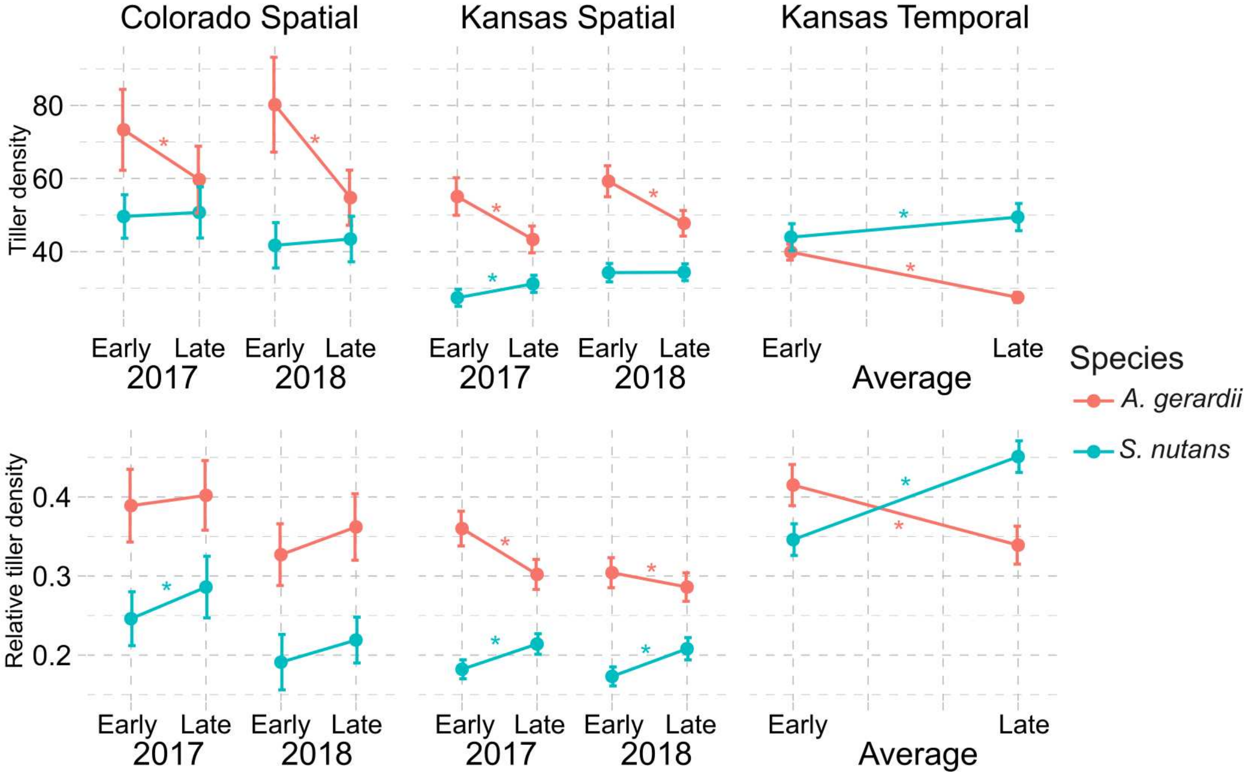

Figure 4.1: Top Row: Absolute densities (average number of tillers per $0.1m^2$ subplot) of *A. gerardii* and *S. nutans* in the Colorado spatial censuses, Kansas spatial censuses, and the Kansas temporal census (averaged across 2005-2013). Bottom row: Relative densities (proportion of total community number of tillers) measured from the same plots. Asterisks indicate significant differences between early and late season absolute densities or relative densities. Error bars indicate standard error estimates.

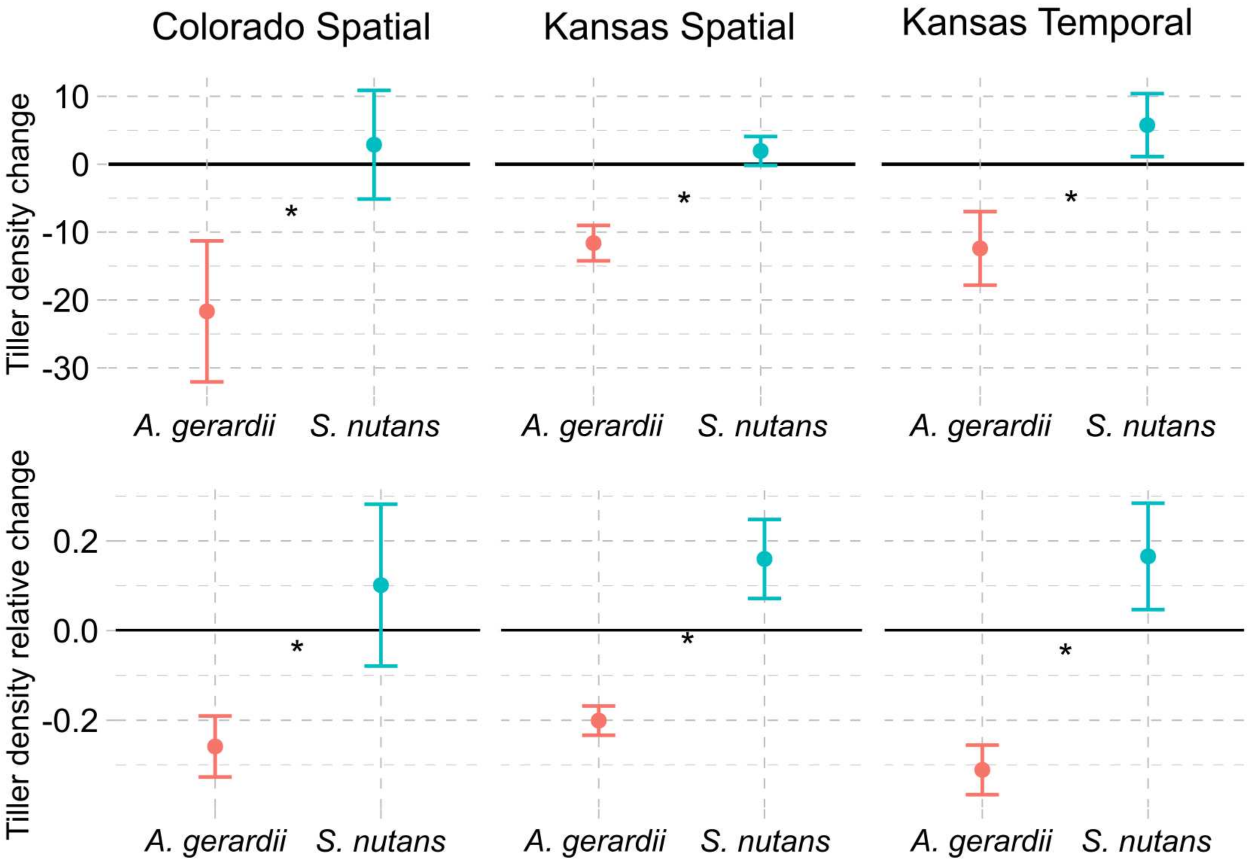

Figure 4.2. Average absolute (top row) and relative (bottom row) changes in tiller densities in the three surveys: Colorado Spatial (averaged across 2017 and 2018), Kansas Spatial (averaged across 2017 and 2018), and Kansas Temporal (averaged across 2005-2013). Error bars indicate estimates of standard error. Asterisks indicate significant differences between the two species. Values greater than 0 (highlighted by the darker horizontal grid lines) indicate that the species' tiller density increased seasonally on average. Absolute change formulated as late-season density – early-season density. Relative change is formulated as absolute change divided by early-season density.

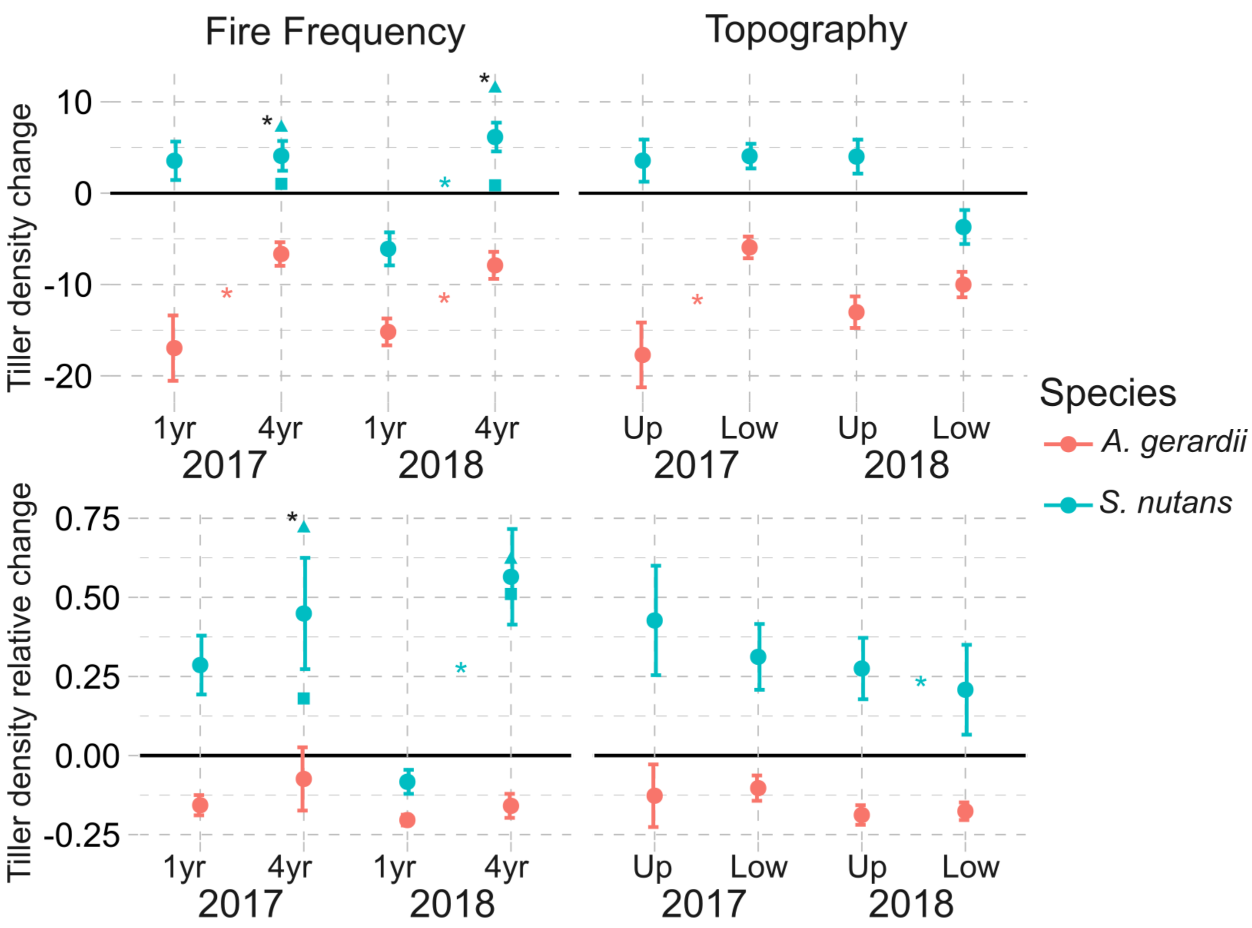

Figure 4.3: Effects of fire frequency (1-year or 4-year fire return, left column) and topographic position (drier upland or wetter lowland, right column) on absolute seasonal changes in tiller density (tillers 0.1 m^{-2}), calculated as early-season density minus late-season density, for *A. gerardii* and *S. nutans* (top row). The bottom row shows seasonal changes in tiller abundance within populations of *A. gerardii* and *S. nutans*, relative to their respective early-season tiller abundances (calculated as absolute seasonal changes divided by early-season densities). Blue and red asterisks indicate significant differences between the seasonal dynamics of a species under the different fire regimes or topographies. Triangles indicate *S. nutans* population 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.

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CHAPTER 5: DIFFERENTIAL, POPULATION-LEVEL RESPONSES TO INTRA- AND INTER-SEASONAL VARIABILITY IN WATERING DRIVE CODOMINANCE STABILIZATION

5.1 OVERVIEW

Codominance among plants may be stabilized by differences in their growth determinacies. If a stronger competitor can increase in abundance only within periodic and limited periods (determinate growth form) co-occurs with an indeterminately growing species – one that is capable of growth whenever growing conditions are suitable, the weaker competitor may be able to recover from asymmetric competition during the periods when the determinate species is in seasonal stasis. To test how differences in growth determinacy may stabilize coexistence between two codominant plant species, we conducted a greenhouse experiment in which grew two naturally-occurring codominant C4 grasses, *Andropogon gerardii* and *Sorghastrum nutans*, and manipulated the timing and quantity of water availability across two growing seasons. We found that the determinately growing grass species, *A. gerardii*, was insensitive to variations in late-season watering frequency. Instead, this grass species showed growth responses only at the beginning of each growing season. In contrast, *S. nutans*, the indeterminately growing species, matched its tillering activity to changes to late-season watering frequencies. Importantly, we found that population densities of the two species were more similar in treatments in which watering frequency differed between seasons, compared to treatments in which the frequencies remained constant between seasons or varied only within seasons. The combination of variability in water availability both within and between seasons further stabilized density balances between the two grass species. This stabilization was characterized by increases in *S. nutans* density under high watering frequency, dramatic declines in *S. nutans* in late seasons with low watering frequencies, and *A. gerardii* densities that declined or remained stable regardless of late-season watering frequencies. Together, these results suggest that the stability of codominance between these species is affected by temporal variability in growing conditions (particularly between seasons) and differential demographic responses to those variabilities between the species.

5.2: INTRODUCTION

Like dominant species (*sensu* Avolio et al. 2019), codominant plant species (*sensu* Gray et al. 2021) are key drivers of many of the functions of the ecosystems (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Gaston, 2011a; Gray, Smith, et al., 2021; Grime, 1998a; Smith et al., 2004a). As the species that aggregately comprise more than half the abundance of a community (Gray, Smith, et al., 2021), codominant species contribute more than subordinate species to community productivity (Chen et al., 2012; Cramer et al., 2001; Fay et al., 2003; Frank et al., 2015; Grime, 1998a; Olesen & Bindi, 2002; Piao et al., 2013; Smith et al., 2020; Smith & Knapp, 2003; Susan Moran et al., 2014), carbon capture (Chen et al., 2012; Frank et al., 2015; Novick et al., 2016; Piao et al., 2013; Sitch et al., 2008; Slette et al., 2021; R. Zhang et al., 2020), erosion control (Allen & Breshears, 1998; Lee & Gill, 2015; Slette et al., 2021; X. Zhang & Wang, 2015), and other functions and services including the facilitation of the subordinate species (Gaston, 2010a; Grime, 1998a; Smith et al., 2004a; Smith & Knapp, 2003). Unlike dominant species, however, codominant species can also contribute to community stability through redundancy by responding asynchronously to factors such as drought, pathogens, and herbivory, thereby buffering ecosystem functions against their potential impacts (Pérez-Ramos et al., 2017; Tilman & Downing, 1994; Wilcox, Tredennick, et al., 2017; Yachi & Loreau, 1999). Moreover, given their similarly high relative abundance, codominant species may be well-positioned to play a critical role, through compensatory population growth, in the timely functional recovery of some ecosystems following a major disturbance-related loss of another codominant (Adler & Bradford, 2002b; Lyons et al., 2005; Naeem & Li, 1997; Walker et al., 1999; Yachi & Loreau, 1999).

Given the importance of codominant species, it is necessary that the mechanisms that maintain such relationships, and the vulnerabilities of those mechanisms, are well understood (Gray et al. 2021).

Multiple mechanisms that have been reported to result in codominant relationships include tradeoffs between the abilities of species to compete or colonize unoccupied habitat (Duan et al., 2015; Zedler & West, 2008), tradeoffs between competitive ability or tolerance of harsh conditions (Hartvigsen, 2000; Ribichich & Protomastro, 1998), allelopathic or consumer control that affects only the more competitive species (Augustine et al., 2017; Goheen et al., 2007; Meier et al., 2009), facilitation of only the less competitive species (Petanidou et al., 1995), spatial niche partitioning (Breshears et al., 1997; Cohn et al., 2011; Dias & Melo, 2010a; Ward et al., 2013), and differences in life-stage mortality rates (Mori & Komiyama, 2008; Witwicki et al., 2016). Each of these mechanisms shares the common trait that the codominant species involved respond differently, through differences in their morphologies and/or physiologies, to changing environmental conditions over time and/or space, a prerequisite of stabilizing mechanisms (Chesson, 2000). However, some species pairs maintain codominant relationships despite remarkably similar sets of morphological and physiological traits. Among these include *Andropogon gerardii* Vitman (big bluestem) and *Sorghastrum nutans* (L.) Nash (indiangrass) which are codominant in many areas of the mesic tallgrass prairies of the Great Plains, US (L. Brown, 1985; Duralia & Reader, 1993; Freeman, 1998; Hartnett et al., 1996; Smith & Knapp, 2003).

While there are some notable differences between *A. gerardii* and *S. nutans,* these co-occurring grasses were historically considered ecological equivalents (Duralia & Reader, 1993; Freeman, 1998; Hartnett et al., 1996), both for their roles in ecosystem function and their responses to several key environmental factors. For example, both species are tall, warm-season C_4 grasses that reproduce primarily by cloning *via* rhizomatous runners (Benson & Hartnett, 2006; Lauenroth & Adler, 2008a; McKone et al., 1998; USDA, 2021a, 2021b), spread very slowly by seed (Benson & Hartnett, 2006), tolerate low nitrogen environments (Berg, 1995; Lett & Knapp, 2003; Mulkey et al., 2008; A. M. Silletti & Knapp, 2001a), tend to have higher densities in frequently burned, ungrazed areas (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 tolerate drought but not shade (Hoffman & Smith, 2018a; Lett & Knapp, 2003; A. Silletti & Knapp, 2002; Swemmer et al., 2006b; Weaver & Rowland, 1952). While *A. gerardii* has been reported to be the more drought tolerant and competitive of the two in mesic regions (Hoffman et al., 2018a; A. Silletti & Knapp, 2002; A. M. Silletti et al., 2004a; Swemmer et al., 2006b), these differences are relatively small, even when compared to other C_4 grasses (Forrestel et al., 2014, 2015). Moreover, while a mutualistic relationship could enable codominance between species without requiring differential responses to environmental variability (Kikvidze et al., 2006; Pueyo et al., 2016), and *A. gerardii* has been shown to facilitate certain subordinate species (Smith et al., 2004a), we did not find evidence in previous work that *A. gerardii* and *S. nutans* facilitate one another either under favorable or harsh growing conditions (Gray & Smith, in review (a)).

Despite these similarities, the densities of populations of *A. gerardii* have been observed to consistently decline during most growing seasons, while those of *S. nutans* tend to concurrently increase (McKendrick et al., 1975). This distinction arises from a somewhat cryptic difference in vegetative reproduction strategies. Populations of *S. nutans* begin each season at relatively low densities, consisting of the surviving biennial tillers produced the previous year (McKendrick et al., 1975). These populations then indeterminately produce new biennial tillers throughout the remainder of the growing season until either cold temperatures or insufficient water become prohibitively limiting. As a result, when late-season growing conditions provide sufficient precipitation, *S. nutans* populations end at greater densities than they began the season with (Gray & Smith, in review (b)). However, this late-season rainfall does not have the same effect on *A. gerardii.* Recruitment from *A. gerardii* genets occurs determinately, with nearly all new tillers emerging by late spring (Benson & Hartnett, 2006; McKendrick et al., 1975; Ott & Hartnett, 2011). These populations then remain stable or exhibit self-thinning for the remainder of the growing season, regardless of the temporal pattern or volume of rainfall (Gray & Smith, in review (b)).

While these differences may be subtle, given the morphological and physiological similarities between these species, they could be sufficient for *S. nutans* to overcome its competitive disadvantage to maintain its codominant status with *A. gerardii*. In years when late growing seasons provide sufficient water, light, and nutrient resource availabilities, *S. nutans* populations may be able to recover from earlier competitive disadvantages and recruit enough new tillers to maintain or restore population densities to match those of *A. gerardii*. Such a mechanism would require the stronger competitor to be relatively unreactive (i.e., differential responses to environmental variability, Chesson 2000), but not necessarily at the individual level. Instead, individuals could maintain *per capita* resource acquisition rates while the population at large experiences demographic stasis or decline as recruitment programmatically pauses and/or a limited portion of the population undergoes senescence.

Although regular patterns of intra-seasonal demographic declines of *A. gerardii* are observed to occur concurrently with (less) regular intra-seasonal increases in *S. nutans* population densities (Gray & Smith, in review (b)), these studies were observational and could not as such causally demonstrate that differences in recruitment determinacies assists these species in becoming codominant. We sought to address this by directly manipulating intra- and inter-seasonal precipitation patterns in a greenhouse setting, testing the outcomes of competition in artificially constructed communities containing both species, and confirming the described observations of field population density dynamics. We further designed our experiment to determine whether the interaction between intra- and inter-seasonal variability is required to stabilize the relationship between *A. gerardii* and *S. nutans*, or whether variability in either time scale is sufficient to do so. Lastly, we examined measures of aboveground productivity to establish whether any effects on population densities are also reflected in traits that are important in the functioning of ecosystems.

5.3 METHODS

Our experiment consisted of a total of eight pairs of treatments that varied the frequency of watering events over two growing seasons (Fig. 5.1). The first pair of treatments varied the frequency of watering *within seasons* only: Treatment 1 – Wet early season 1, dry late season 1, wet early season 2, dry late season 2 (WD/WD); Treatment 2 – Dry early season 1, wet late season 1, dry early season 2, wet late season 2 (DW/DW). We expected WD/WD to strongly favor *A. gerardii* with the majority of water applications occurring consistently during the early season when this species is actively recruiting and reaching peak densities (Benson & Hartnett, 2006; McKendrick et al., 1975). We expected DW/DW to be the most favorable treatment for *S. nutans* with early-season dry conditions being consistently unfavorable for *A. gerardii* recruitment (McKendrick et al., 1975). The second pair of treatments varied the frequency of watering *between seasons, but not within seasons* (WW/DD and DD/WW). We expected a shift within these patterns in the degree of dominance from one season to the next, presenting as similar average abundances across seasons, but high variabilities in the ratios of species' densities and *A. gerardii* becoming more dominant in dry seasons. The third pair of treatments varied the frequency of watering *both within and between seasons* (WD/DW and DW/WD), and we again expected similar average species' densities, but density ratios to be less variable compared to patterns with interannual variability alone. The final pair of treatments represent baselines for comparisons, with no variability in the frequency of watering either within or between seasons (WW/WW and DD/DD). With its greater competitive ability and drought tolerance (A. M. Silletti et al., 2004b; A. M. Silletti & Knapp, 2001a), we expected *A. gerardii* to be favored under both of these patterns.

We established ten replicate potted plant communities for each of the treatments from field-collected seed (Star Seed Inc, Osborn KS), each consisting of an equal number of genets (seedlings) of *A. gerardii* and *S. nutans*. We overseeded 80 one-gallon pots containing a consistent volume of Pro-Mix High Porosity Biofungicide + Mycorrhizae potting soil with approximately fifty seeds of each species, then covered the seeds with 2 cm of the potting soil. During the germination period, each pot was randomly placed on a single greenhouse bench and supplied with enough water to fully saturate the soil, then covered with clear plastic to maintain a humid microclimate. Water was applied every other day and any excess was allowed to drain. After most of the seeds had germinated and generated at least two secondary leaf blades (day 18, Fig. 5.2) the communities were manually thinned to population densities of 15 seedlings per species. During the thinning, individuals were selected for removal such that the remaining seedlings were similarly well-developed, that individuals of the two species were intermixed, and that no individuals were isolated from the community. We continued the same watering frequency for an additional seven days to ensure vigorous establishment, after which the plastic bags were removed, and the early season drought treatments were begun in the DD and DW treatments. The drought treatments consisted of watering the soil in the treated pots to full saturation once every four days, as opposed to the two-day interval that was maintained in the wet treatment (WW and WD).

Each of the two seasons was split into two halves: early season and late season. The two seasons were separated by clipping at the soil surface and a 30-day induced dormancy at -4°C, with a saturating water supplement provided to each pot at the midpoint of dormancy. Following the dormancy period, all pots were supplied with water daily for 14 days to ensure they reached their recovery potentials. Both early seasons were maintained for 78 days, beginning the day after seeding in season one, and the day after cold storage removal in season two. At the end of each early season, tiller density censuses were conducted by hand, with the number of individuals of each species and the number of living and dead tillers counted separately. These censuses were conducted over periods of two days with daily watering applied throughout and continuing for two days afterward to help compensate for any unintentional disturbance caused by the manual counting. In the treatments featuring intra-annual watering frequency variability (WD and DW), watering frequency reversals were begun at the ends of the early season tiller density surveys, again with wet treatment watering applied every other day, and drought treatment watering applied every 4th day. This change in patterns marked the initiation of the late season. The late season lasted 73 days in season one but was extended to 90 days in season two due to scheduling conflicts. Tiller density censuses were repeated at the ends of the late seasons, again with daily watering to facilitate differentiation between living and dead tillers. At the end of the second late-season census, aboveground biomass was collected at the soil surface. This material was separated by species, dried at 60°C for 48 hours, and weighed.

Statistical analysis

We hypothesized that *A. gerardii* would be incapable of intra-seasonal increases in density after an initial tillering period and that this behavior would be unaffected by late-season water availability treatments. To test this, we calculated proportional changes in tiller density for this species within each replicate by measuring absolute gains or losses of tillers and relativized these changes to their respective early-season densities:

$$relative\ density\ change = \frac{late\ density - early\ density}{early\ density}$$

These relative changes were then tested for significance using single-sample Wilcoxon signed-rank tests with the null hypothesis that they were less than or equal to zero. Given our previously observed dynamics, we expected that we would not reject the null hypotheses for this species under any of the tested watering treatment patterns. The relative changes occurring within each season and watering treatment were tested independently. For the first season tests, replicates were grouped by the season 1 patterns: WW/, WD/, DW/, and DD/. For the second season, replicates were grouped by their full two-season patterns.

We used the same tests to independently examine the intra-seasonal relative dynamics of *S. nutans*, but we expected that our null hypothesis – that tiller densities would decline or remain static – would be rejected when water availability patterns featured a wet late season. In the treatments that featured drought in the first late-season (WD/ and DD/), *S. nutans* experienced severe to complete mortality in all replicates during the induced dormancy period. This surprising and unfortunate event limited our analyses of the dynamics of *S. nutans* and their communities in these treatments to the first season only.

We used multiple approaches to address the question of whether intra- and inter-annual variability in growing conditions can stabilize a codominant relationship between our test species.

Following the qualitative definition of codominance introduced in Gray e*t al.* (2021) that species pairs must not be present in ratios of abundance exceeding 3:1 relative to one another (above which would be considered a monodominant-subordinate type relationship), we tested whether either the densities of *A. gerardii* tillers were significantly more than three times those of *S. nutans* within the same replicates. We first calculated the ratios within each replicate, then averaged those ratios across replicates within each treatment. This was repeated for the inverse: the average ratio of *S. nutans* tillers to those of *A. gerardii*. Calculations were made independently for each treatment pattern and for each of three timescales: for each census date, the average of the two censuses within each season, and the average of all census dates. In each case, ratios were tested to determine whether they were significantly greater than 3:1 using single-sample Wilcoxon signed-rank tests and the null hypothesis that they were less than or equal to 3. We were particularly interested in whether the variance in tiller density ratios across each of the surveys was significantly greater in the inter-annual variability treatment (WW/DD) than in the inter- and intra-annual variability treatment (DW/WD), as both were expected to shift the advantage from one season to the next, but the latter was expected to have less-extreme shifts in dominance. We tested whether the degree of asymmetry of the densities of *S. nutans* to *A. gerardii* tillers over time depended on the treatment using a two-sample Wilcoxon signed-rank test. Because the present study included only the two focal species, we could not account for the second aspect of the qualitative codominance definition set out in Gray *et al.* (2021), as that criterium involves distinguishing the abundance of a set of purportedly codominant species and the next most abundant (subordinate) species.

In our second approach to establishing whether the treatments differed in their effects on community structure, we used Kruskal-Wallis analysis of variance of the differences between the numbers of tillers of the two species within replicates (i.e., $A.gerardii\ \ tillers\ -\ \#\,S.nutans\ tillers$), again considering each of the three timescales independently. These differences were then examined in Tukey-adjusted *post-hoc* comparisons to determine whether any patterns had a significantly greater bias towards either species or greater balance between them.

In our last approach, we calculated shared abundance as the harmonic mean of the densities (relative to total community density) within each replicate and then averaged across all survey dates. Shared abundance (*A*) is described in Gray et al. (2021) as a codominance metric that increases both with higher relative abundances of the included species and with a greater similarity between the abundances of those species. The harmonic mean thus differentiates between codominant sets composed of species with similar, intermediate abundances from those sets that have the same arithmetic mean, but a greater variance in the abundances of the component species. In special cases, such as this experiment, in which each community consists of only two species, *A* only increases in response to greater similarity in the abundances of those species since their relative abundances always sum to 1. Kruskal-Wallis analysis of variance was again used to determine whether the treatment patterns affected shared abundance averaged over time.

5.4 RESULTS

In the first season of the experiment, there were no significant increases in *A. gerardii* densities after the initial germination event and manual thinning (Fig. 5.3, S. Fig. 5.1,). The densities in the WD/ treatment declined by 56% on average between the early and late season censuses, while those in the WW/, DD/, and DW/ treatments remained on average nearly unchanged from earlier densities. The inability of *A. gerardii* to generate new tillers in the later parts of the growing season was evidenced again in the second season, with tiller densities declining in all treatment patterns except WD/DW, where they were relatively static (Fig. 5.2, 5.3B).

The density dynamics of *S. nutans* were more dependent on the watering pattern treatment (Fig. 5.3, S. Fig. 5.1). In the first season, all patterns except WD/ were accompanied by a significant intra-seasonal increase in *S. nutans* tiller densities, and the largest of these increases occurred the DW/ treatment (Fig. 5.3). This change was significantly greater than the proportional increase in the WW/ treatment, but not the DD/ treatment. The absolute increase in tillers was also significantly greater in the

DW/ treatment (+45.8 tillers ± 8.77) than in the DD/ (+15.6 ± 9.48) and WW/ (+17.6 ±13.1) treatments. In the second season, significant density increases occurred under the WW/WW (+32.1 ± 29.7) and DW/DW (+44.3 ± 34.8) patterns, while those populations under the DW/WD pattern (-76.5 ± 47.1) significantly declined (Fig. 5.3). Some of the replicates under the WW/DD pattern (+21.6 ± 28.8) showed increased *S. nutans* tiller densities, but this was not a significant change on average.

By the first census (end of first early season), on average, neither species had generated tillers in excess of the 3:1 ratio in abundance over the other to be considered monodominant (i.e., not codominant) in either the control or drought treatment (S. Fig. 5.2). However, by the end of the first late season, *S. nutans* populations had significantly surpassed this threshold in one treatment pattern, DW/, and approached the 3:1 ratio in two others: WW/ and DD/ (Fig. 5.4). This degree of density imbalance did not occur again until the fifth survey (end of second late season, Fig. 5.4, S. Fig. 5.2) when *S. nutans* became significantly monodominant in the DW/DW treatment. Most replicates in the WW/WW and WW/DD treatments also became heavily weighted towards *S. nutans*. Neither species achieved monodominance when averaged across surveys within each season (S. Fig. 5.2), but *S.* nutans was significantly monodominant in the DW/DW treatment when averaged across all four surveys (Fig. 5.4). The average variance over all surveys in the ratio of *S. nutans* to *A. gerardii* was considerably greater in the WW/DD treatment than in the DW/WD (S. Fig. 5.2).

While population density balances were consistently biased towards greater *S. nutans* representation across treatments (except in season two in the treatments in which *S. nutans* populations did not re-emerge after dormancy), there were significant differences between the precipitation pattern treatments in the degree of their effects on the first season, second season, and two-season average species density balances (Fig. 5.5). In season one, the bias towards *S. nutans* was greatest in the WW/ and DW/ treatments, which were not significantly different from each other (Fig. 5.5). Likewise, the balances in the DD/ and WD/ treatments were similar. In the second season, the DW/WD (intra- and inter-annual watering variability) was significantly less biased towards *S. nutans* than either the WW/WW (no variability) or DW-DW (intra-annual variability) treatments (Fig. 5.5). Despite relatively low bias on average, variance among the replicates in the WW/DD (inter-annual variability) treatment was high, resulting in no significant differences between this treatment and any of the others. The higher-amplitude dynamics of the second season tended to overwhelm those of the first season in our analyses, and as such, each of these observations was mirrored in the two-season average (Fig. 5.5).

The two-season average shared abundance significantly differed between DW/DW, which had the lowest mean shared abundance, DW/WD, which had the highest, and WW/WW, which was intermediate (Fig. 5.6A). The shared abundance in the WW/DD treatment did not differ significantly from any of the other treatments. The greater shared abundance in DW/WD resulted from the greater similarity between the densities of the species, rather than from higher total community densities (Fig. 5.6B). Total community abundance was highest in the WW/WW treatment and intermediate in the DW/DW treatment, but these were heavily biased towards *S. nutans* (Fig. 5.5). In contrast, the average total community density in the DW/WD treatment was the lowest among the treatments, but with similar contributions coming from each species.

The production of aboveground biomass in the second season also varied across the watering treatments (Fig. 5.7). As with tiller recruitment, the balance of biomass contribution consistently leaned toward *S. nutans*, but this bias was significant only in the WW/WW and DW/DW treatments (Fig. 5.7A). Shared abundance of biomass was similar across most treatments but was significantly lower in the DW/DW treatment than in the DW/WD and WW/DD treatments (Fig. 5.7B) despite having significantly greater total biomass than in the WW/DD treatment (Fig. 5.7C). Total biomass production was greatest in the WW/WW treatment, though not significantly greater than In the DW/DW and DW/WD treatments (Fig 5.7C).

5.5 DISCUSSION

We found evidence that inter-annual variability in water availability is associated with more stable codominance between competitive species pairs with contrasting determinate and indeterminate growth behaviors, relative to those treated with water availability patterns that either do not vary or only vary intra-seasonally. Moreover, we found that the interaction between both intra- and interannual variability in water availability may enhance this stabilizing effect, as best illustrated by the consistently low ratio of *S. nutans* to *A. gerardii* tillers across samplings in the DW/WD treatment compared to the WW/DD treatment. Further, while these two patterns resulted in statistically similar balances in tiller and biomass production in the second season, the balance in DW/WD was significantly different from those of WW/WW and DW/DW, while the balance of WW/DD was not.

Interestingly, the tiller density balances observed at the census dates were consistently biased in favor of *S. nutans*, the purportedly less drought-resistant and less competitive species of the two. The greater drought tolerance of *A. gerardii* was evident despite intra-seasonal declines that were sensitive to late-season watering frequency. For instance, peak seasonal *A. gerardii* tiller densities were greater in the second season than in the first across all treatment patterns, though this increase was modest in those populations to which the WD/ treatment was applied. This was in striking contrast to the *S. nutans* populations that received the drought treatment in the first late season, virtually all of which failed to re-emerge in the second season. The question of species' relative competitive abilities is less clear. Previous observations in removal experiments have shown a positive effect of *A. gerardii* removal on *S. nutans* growth rates, but not the reverse (A. M. Silletti et al., 2004a), indicating asymmetric competition in favor of *A. gerardii,* but this relationship may be context-dependent. While *A. gerardii* is relatively more abundant in mesic grasslands such as at the Konza Prairie in northeastern Kansas, *S. nutans* tends to be the more abundant of the two in the wetter regions to the south and east (D. A. Brown, 1993; Epstein et al., 1998a; USDA, 2021b). The frequency of our saturating water additions during the wet phases of the treatment patterns may have been enough to simulate environments where *S. nutans* is the stronger competitor. However, we also conducted a census at the beginning of the second season, shortly after the induced dormancy was terminated. The balances in this census shifted considerably towards *A. gerardii* and became temporarily biased towards this species in the WW/ treatment. We suspect that the greater competitive ability of *A. gerardii* is not reflected within seasons but requires observations over several seasons to become clear.

The factors underlying the proposed mechanism of codominance stabilization were in large part observed to be operating in our experiment. This mechanism is characterized by the inability of a purportedly more competitive species, *A. gerardii* in this instance, to respond to the late-season conditions that a less competitive species can rapidly capitalize upon. While the higher-frequency late season watering resulted in higher tiller recruitment rates in *A. gerardii* at the beginning of the following season, this delay in response occurred during the time that *S. nutans* was generating new biennial tillers. In the first season, these factors resulted in static *A. gerardii* population densities in the DD/, DW/, and WW/ treatments and a density decline in the WD/ treatment. Declines were more consistent in the second season, with the only static population dynamics occurring in the WD/DW treatment. In contrast, *S. nutans* populations responded more immediately to high (and low) frequency late-season water additions, increasing their population densities in the DW/ and WW/ treatments in the first season and the WW/WW and DW/DW treatments in the second. Moreover, those populations that began with a dry early season followed by wet late seasons (DW/, DW/DW) ended with densities that were not significantly different from those that received frequent watering throughout the season (WW/, DD/WW, WW/WW). This is indicative of a high potential for population growth when conditions permit that is also tempered by negative density dependence. Late-season tiller recruitment typically required sufficient water availability and densities declined rapidly in response to late-season drought in the WD/ (season 1) and DW/WD (season 2) treatments.

Surprisingly, populations of *S. nutans* that were kept dry for entire seasons did not experience the same rate of decline as those that experienced dry late seasons that were preceded by wet early seasons, and instead remained stable in season 2 (WW/DD) and increased in season 1 (DD/), which was reflected both in their relative and absolute dynamics (Fig. 5.3, S. Fig 5.1B). This suggests that *S. nutans* is particularly vulnerable to late-season drought if the tillers had been recruited and matured under less harsh conditions and that early season conditions can have an acclimatizing effect. This reflects the findings of Swemmer et al. (2006) that while *A. gerardii* does not produce new tillers in the late season, it can respond to late-season drought by increasing the leaf turnover of existing tillers and generating potentially more dry-tolerant leaves. In contrast, *S. nutans* must confront declining watering frequencies with relatively older, larger leaves that require more resources to maintain and from which more water can be lost. This may present a unique challenge for this species in regions where intra-annual rainfall variability is expected to increase as a result of global warming.

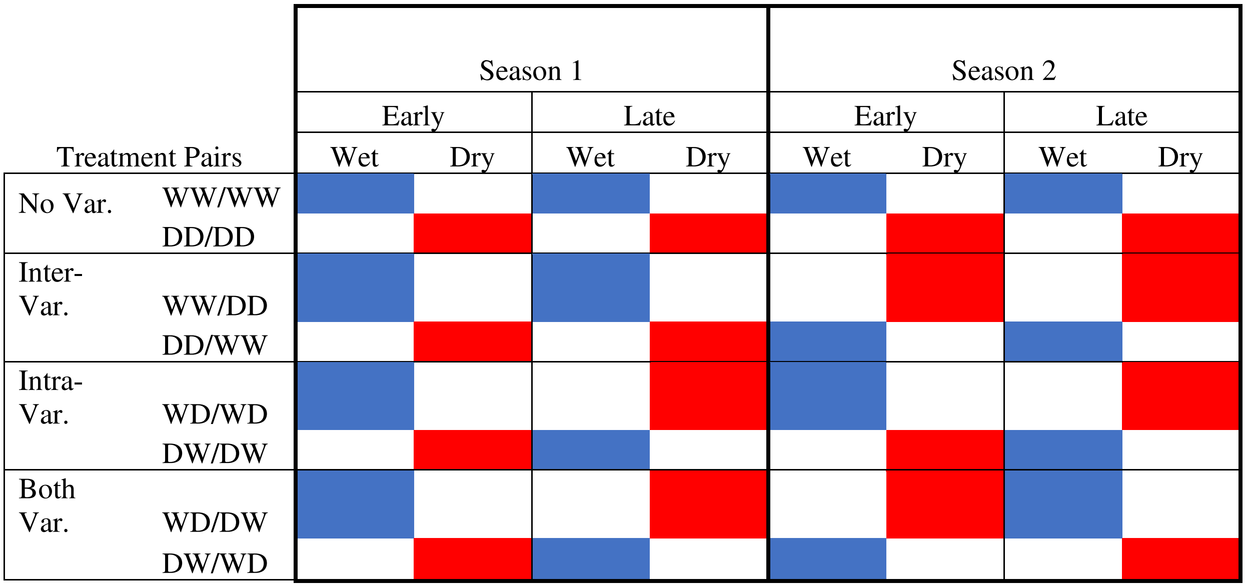
While there were increases in *S. nutans* tiller densities in the first season's DD/ treatment, these populations still experienced severe mortality during the 30-day dormancy period between seasons. It may be that this was a limitation of our experimental design, which began with community assembly from seed. These genets would have had no legacy of the previous year's production of viable buds with which to recover from a seasonal drought during which few tillers were recruited. Similarly, populations from the WD/ treatment failed to re-emerge in the second season. This limitation unfortunately prohibited most analyses of second-season *S. nutans* and community dynamics in the DD/DD, DD/WW, WD/WD, and WD/DW treatments. Though it may be challenging to generate communities with equal representations of both species due to the connectivity of genets and dissimilarity of tillering behaviors among species, future experiments of this kind may have greater success after an initial drought-free season that ensures robust population establishment and the formation of healthy bud banks.

Considering these species-specific behaviors together, since the tillering responses of the two species to late-season moisture availability are asynchronous (*S. nutans* recruiting upon water availability, *A.*

gerardii recruitment being delayed until the following season), *S. nutans*, the generally assumed inferior competitor, appears to benefit disproportionately from favorable late-season growing conditions (i.e., sufficient water availability). During these periods, this species gains tillers in what may constitute a relaxed competitive environment relative to what may otherwise exist if *A. gerardii* tiller densities were increasing simultaneously. This in turn could provide the key occasional opportunities for *S. nutans* to recover from the typically asymmetric competition and restore codominance in regions where rainfall varies both intra- and (more importantly) inter-annually, such as the tallgrass prairie region of the Central US. However, while this mechanism may be necessary, it is not sufficient for codominance between these species. For example, we have previously observed the same intra-seasonal population dynamics from these species in a more xeric region along the Front Range of the Rocky Mountains in Colorado, US (Gray and Smith, in review (b)), but these populations are relatively small, isolated, and subordinate to more dry-adapted grass species such as *Pascopyrum smithii* and *Bouteloua gracilis.* Other contributions to the success of these species elsewhere may include adaptations better suited to regionally endemic collections of factors such as frequent burning, exclusion of domesticated grazers, poor nutrient availabilities, and mesic climates (with occasional droughts) compared to their subordinate species. While these factors can be seen as providing fuel for the high abundance (dominance) of either *A. gerardii* or *S. nutans*, the mechanism we have described here may be a key component of their niche differentiation and prevention of competitive exclusion (codominance).

Artificial selections based on differences in the determinacy of growth have long been utilized in agriculture to facilitate either more efficient, single-event harvests (determinate selection) or more frequent, lower-yield harvests (indeterminate selection) (Hauggaard-Nielsen & Jensen, 2001; Huyghe, 1998). These developments have relied on the selection of desired traits from the varieties found in nature, and it is likely that natural plant communities also contain this diversity both within and between species. This warrants substantial consideration for conservation, restoration, and general ecological understanding. Common species are the key contributors to ecosystem functions (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Grime, 1998a; Smith et al., 2004a), but their losses have occurred and may become more frequent in coming years as a result of rapidly shifting climatic conditions, land-use changes, and accelerated introductions of plant species and their pathogens (Anagnostakis, 1987; Ash et al., 1997; Bale et al., 2002b; Bokhorst et al., 2008; Cantarel et al., 2013; Condon et al., 2011; Dillemuth et al., 2009; Fernandez-Winzer et al., 2020; Gaston & Fuller, 2008; Isbell et al., 2013; Kelly & Goulden, 2008; Llorens et al., 2004; Mal et al., 1997; Nuzzo, 1999; Sasaki & Lauenroth, 2011a; Smith et al., 2020; Smith & Knapp, 2003; Theoharides & Dukes, 2007; Vinton et al., 1993; Visser et al., 2002b; M. A. White, 2012). It will become increasingly important to fully understand the characteristics of common (dominant) species, including the determinacy of their growth, to better predict the consequences of, and prevent, their losses (Avolio, Forrestel, Chang, la Pierre, et al., 2019; Gaston, 2010a, 2011a; Gaston & Fuller, 2008). This knowledge can also provide a tool to restorationists when selecting species for seed mixes (Laughlin et al., 2018). In combination with other considerations, assuring that diversity of growth determinism is included in re-established communities could prevent monodominance while providing enhanced stability during unforeseen perturbations. In the short term, determinacy diversity provides a steadier rate of community productivity throughout the growing season, as the indeterminately growing species increase in abundance and biomass at the same time that determinately growing species are declining (Loreau et al., 2003; Shanafelt et al., 2015; Valencia et al., 2020; Wilcox, Tredennick, et al., 2017). On a longer timescale, if the included species share redundant functional contributions but differ in their determinacy, one could buffer the community function against otherwise greater loss, or even provide compensatory population growth to restore total function (Adler & Bradford, 2002b; Mori et al., 2013; Wilcox, Tredennick, et al., 2017). Finally, growth determinacy, having been largely overlooked in coexistence theory, represents an exciting avenue for further exploration. We have provided causal evidence that varying water availabilities can interact with differential growth determinacy to enhance codominance stability in a controlled greenhouse setting, but the importance of this mechanism in natural communities will need to be assessed. Moreover, variabilities of other resources and disturbances may also interact with this form of niche differentiation. Headways made in these directions should provide insights for conservation goals and more successful, resilient restoration work.

5.6 FIGURES



Treatment Pairs		Season 1				Season 2			
		Early		Late		Early		Late	
		Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
No Var.	WW/WW	🟦		🟦		🟦		🟦	
	DD/DD		🟥		🟥		🟥		🟥
Inter-Var.	WW/DD	🟦		🟦			🟥		🟥
	DD/WW		🟥		🟥	🟦		🟦	
Intra-Var.	WD/WD	🟦			🟥	🟦			🟥
	DW/DW		🟥	🟦			🟥	🟦	
Both Var.	WD/DW	🟦			🟥		🟥	🟦	
	DW/WD		🟥	🟦		🟦			🟥

Figure 5.1 List of treatment patterns. Blue indicates watering every other day during that period. Red indicates watering every fourth day. Treatment pairs include “No Var.”, meaning that the frequency of watering was never varied throughout the experiment (either watered every other day throughout, (WW/WW,) or watered every fourth day throughout (DD/DD)). The second treatment pair, “Inter- Var.” featured variability between seasons, but not within seasons. The “Intra- Var.” treatment pair featured watering frequency variability with seasons, but the same pattern was repeated in the same season, and therefore did not have inter-annual variability. The “Both Var.” treatment pair featured both variations in watering frequency within each season and differences in those patterns between seasons.

Figure 5.2 Timeline of events during the experiment. Events occurring during the first season appear in grey boxes, and those in the second season are in black boxes.

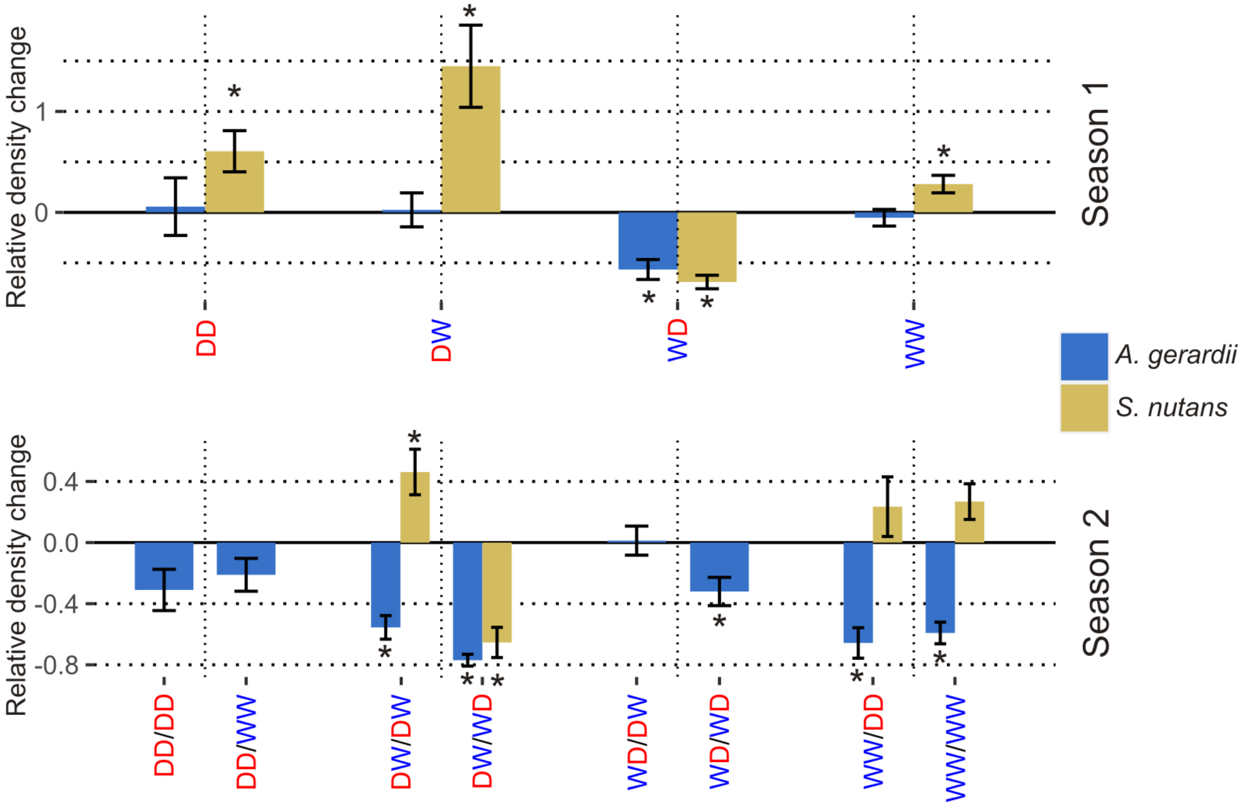


Figure 5.3 Average relative density changes for *A. gerardii* and *S. nutans* occurring between early and late season 1 (top row) and early and late season 2 (bottom row). Changes are relative to respective early season densities. Error bars indicate estimates of standard error. Asterisks indicate density changes differing significantly from zero.

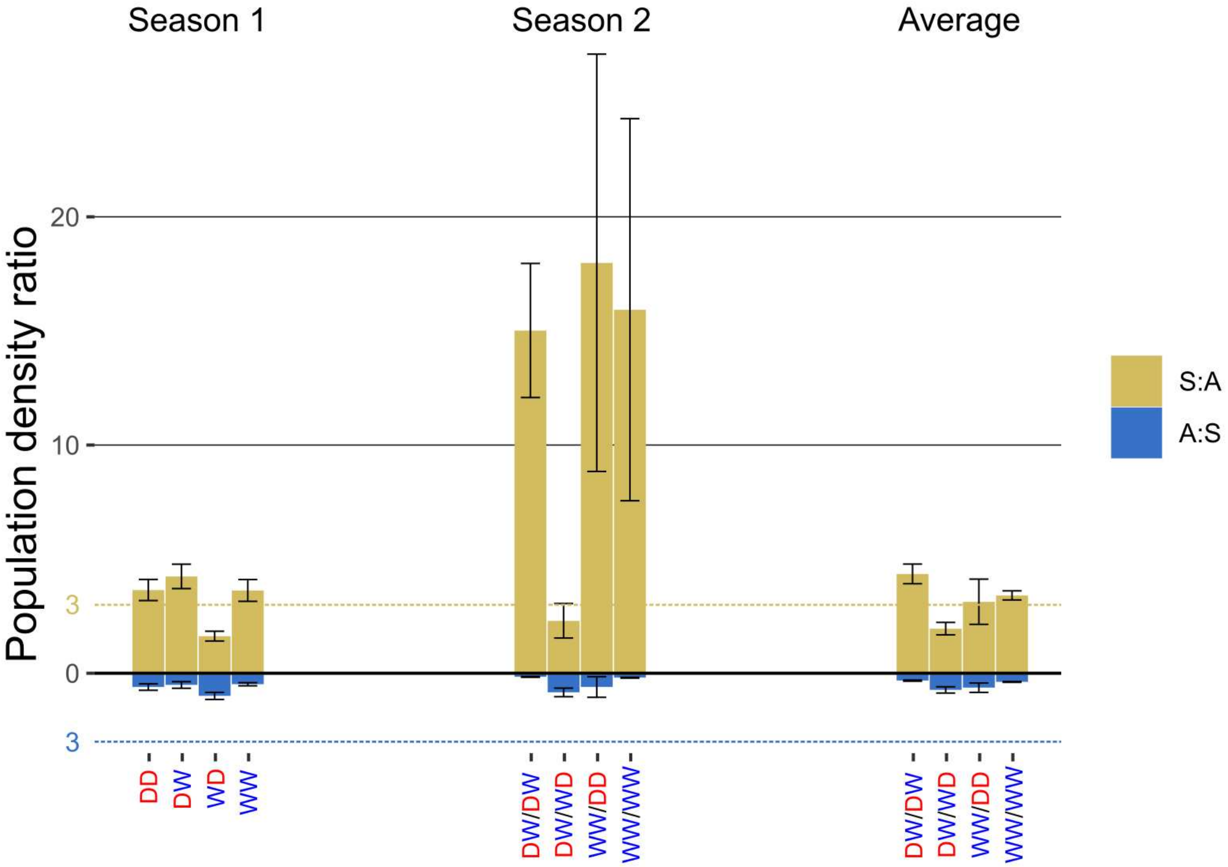


Figure 5.4 Population density ratios at end of season 1, at the end of season 2, and on average across all density surveys (early and late, both seasons). The S:A ratio is the average ratio of *S. nutans* ramets to *A. gerardii* ramets within each treatment. The A:S ratio is the average ratio of *A. gerardii* ramets to *S. nutans* ramets within each treatment. Error bars indicate estimates of standard error. Dashed lines indicate the 3:1 ratio threshold for mono-dominance of the species indicated by the matching color.

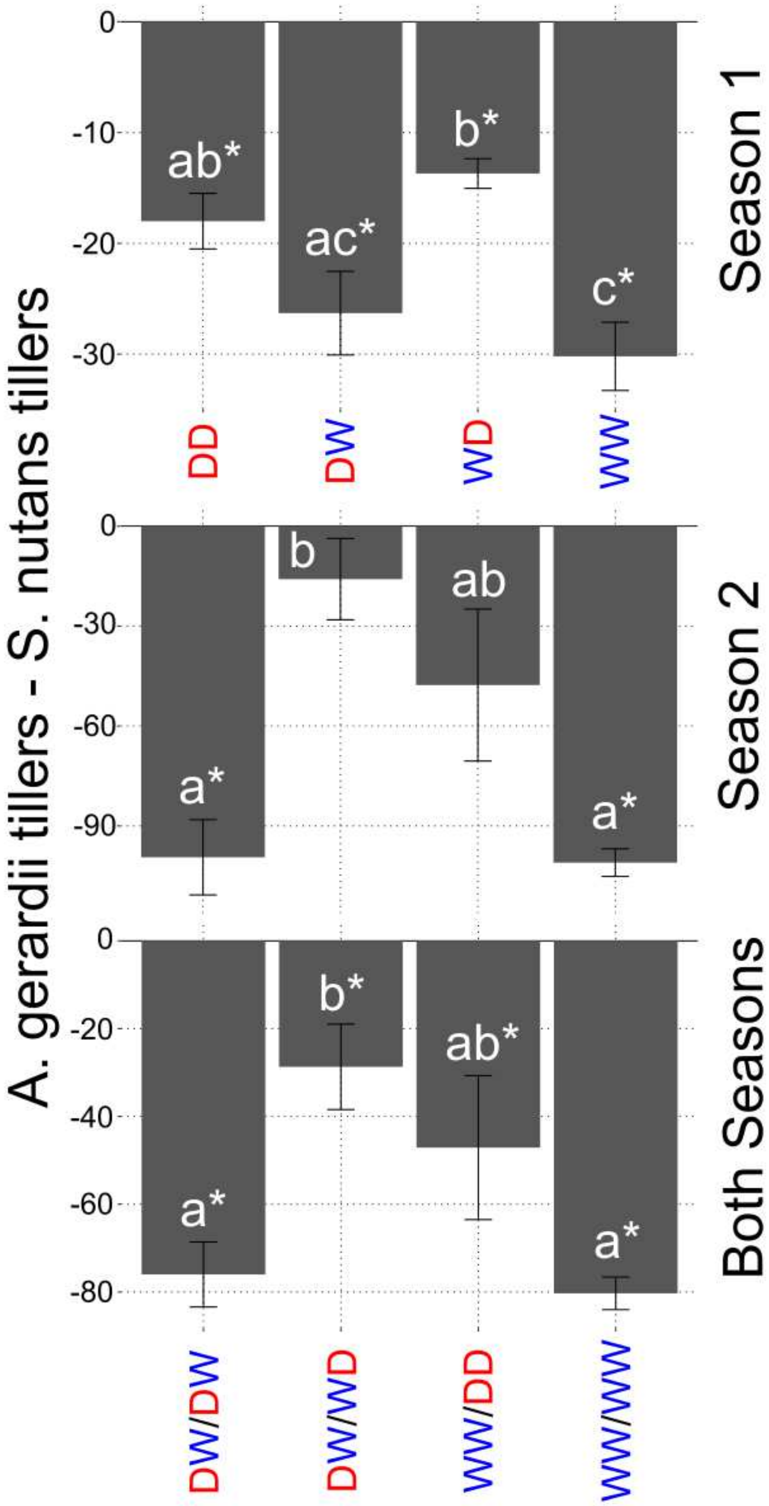


Figure 5.5 Season 1 average (top), season 2 average (middle), and overall average (bottom) tiller balances, as calculated by the number of tillers of *S. nutans* subtracted from the number of tillers of *A. gerardii* within each replicate and averaged within treatment patterns. Error bars indicate standard error estimates. White letters indicate significantly different groupings Asterisks indicate balance significantly in favor of *S. nutans*.

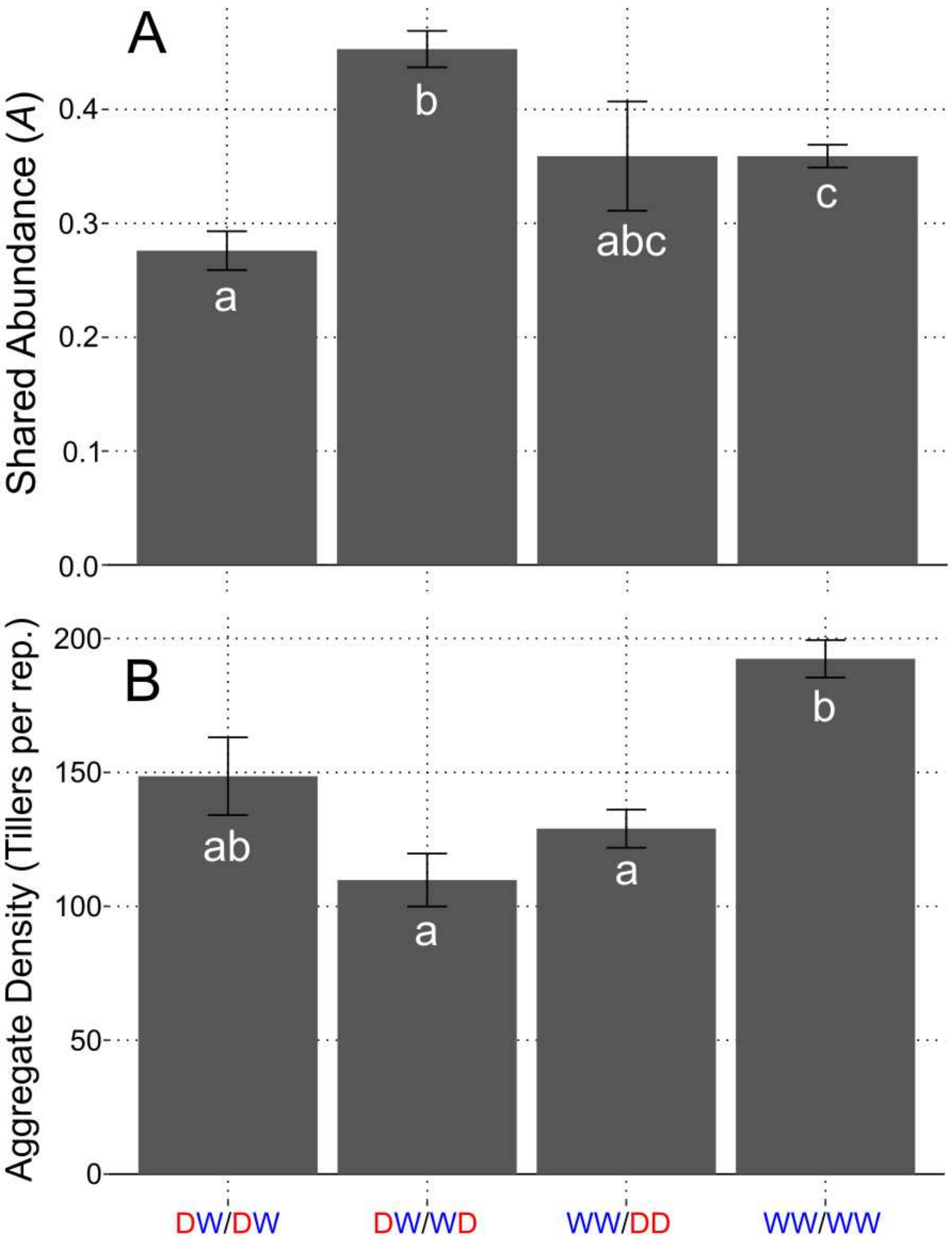


Figure 5.6 A) Shared abundance (harmonic means of species' relative abundance within each replicate) between *A. gerardii* and *S. nutans*, averaged across all surveys. Higher shared abundance indicates a greater similarity of densities between the two species. **B)** Total community densities, averaged across all surveys. Error bars indicate standard error estimates. White letters indicate significantly different groupings.

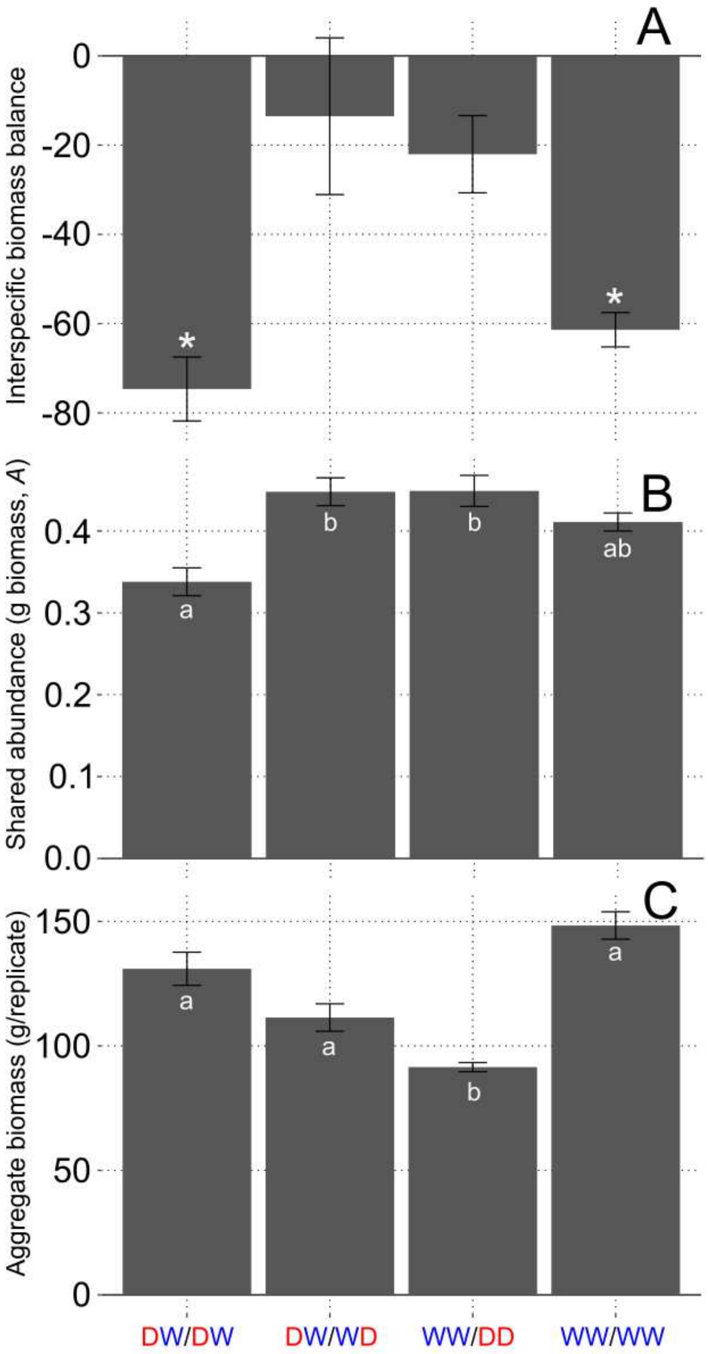


Figure 5.7 Second season biomass in different treatments. The interspecific biomass balance (grams biomass of *S. nutans* subtracted from grams biomass of *A. gerardii*) is shown in A. Negative values indicate biomass produced by *S. nutans* was greater than that produced by *A gerardii* within the same replicate, on average. Asterisks indicate values significantly less than zero. Shared abundance (*A*) in terms of aboveground biomass produced is shown in B. Larger values indicate more similar biomass productivity among the two species. White letters indicate significantly different groupings. The aggregate, total community aboveground biomass is shown in C. These are the sum of the grams of biomass produced by the two species. White letters indicate significantly different groupings.

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CHAPTER 6: CONCLUSIONS

The development of this dissertation has yielded three novel, potentially important inroads to improved understanding of plant species interactions, coexistence, codominance, community-dependent ecosystem functions, and vulnerabilities of those functions. The first of these is that while the term codominance has long been in part of the common vernacular of the ecological science community, there has been no formal agreement on its meaning. Both the definitions of codominance and the meanings implied by abundance data associated with so-called codominant species have thus far been inconsistent. To begin the process of building a deeper understanding, we require a common vocabulary to recognize similarities and differences among our observations. The second chapter of this dissertation provides such a definition, synthesized from the more consistent explanations and implications previously given, and generalized to reflect relative abundance. This definition also draws intuitive thresholds, which if adopted, could assure readers that various communities with species sets labeled as codominant will have structural similarities. Having recognized this commonality between them, the causes and effects of differences between such communities can be explored within new contexts that highlight how and if species and their codominance *per se* drive ecosystem function. This chapter also provides quantitative approaches to drawing comparisons between communities: the shared abundance (A) and optimized codominance (C_{max}) metrics. These measures are based on the harmonic mean, giving them the ability to distinguish between codominant species sets in which aggregate abundance is evenly split from those that have the same, but less equally distributed aggregate abundance. Requiring only relative abundance data, adoption of these metrics is simple and would facilitate more meaningful comparisons between communities residing in different ecosystems, under different experimental treatments, or existing at different times, allowing correlations to be drawn between the degree of codominance and measures of ecosystem function, such as productivity, invasibility, and stability. Insights gained from these comparisons could provide valuable direction for conservation, providing new goals that focus on maintaining not just conspicuously dominant species, or rare species in danger of extinction, but sets of codominant species that, if lost, would endanger the stability and adaptability of ecosystems in a changing world. Likewise, restoration ecology could benefit from such studies, and inform the design of seed mixes that are more successful in establishing, and more resilient to environmental variability.

The second key advance presented in this dissertation relates to the stress gradient hypothesis (SGH). While the SGH has ample evidence to support it (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Callaway & Walker, 1997; He et al., 2013; Olofsson et al., 1999; Ploughe et al., 2018), others have demonstrated that there are limitations in the capacity of competitors to become facilitative as abiotic stress increases (Butterfield et al., 2016; Holmgren & Scheffer, 2010; Michalet et al., 2006, 2014; Ploughe et al., 2018). In some cases, ecosystems are pushed to extremes and stress becomes so severe that the mechanisms involved in the interaction shifts break down (Butterfield et al., 2016; Michalet et al., 2014; Ploughe et al., 2018). For example, if accessible moisture becomes entirely depleted, canopy cover provided by an interspecific species can no longer provide any meaningful reductions in soil evaporation (Butterfield et al., 2016). A second, related limitation to the effect relates to our failure to recognize that average environmental conditions are in many cases, such as in arid ecosystems, already severely stressful (Michalet et al., 2006; Ploughe et al., 2018). In such cases, facilitation may already be occurring (in agreement with the SGH) but increases in abiotic stress would show increasingly negative interactions, rather than positive, as the mechanisms of facilitation are driven towards collapse. Indeed, reductions in stress would in these cases often result in the observation of increased facilitation, rather than more increasingly negative interactions, deceivingly in contradiction of the SGH. Lastly, another limitation of the stress gradient hypothesis results not from a breakdown of facilitation, but an increase in the intensity of competition for increasingly limited resources (Michalet et al., 2014). For example, if a threshold intensity of drought is reached and one species responds to the water limitation by increasing root growth, its competitor may lose access to this resource even as it becomes less abundant. While the mechanisms of facilitation may still be operating in such a case, they become overridden by the enhanced competitive effects. These limitations are observed when comparing communities at different levels of environmental stress because their effects are variable. However, this dissertation introduces the possibility of a more cryptic form of limitation on the SGH: similarities between the interacting species in their physiological and morphological characteristics, and more specifically, similarities of their functional responses to the stressor (Chapter 3). An extreme example illustrates this: if two species are identical in their response to an abiotic stressor, then neither can gain any benefit from having interspecific neighbors as opposed to intraspecific ones. This is not to say that they cannot facilitate one another, but the effects are indistinguishable from Allee effects. Evidence for this limitation was shown in chapter 3, with *Andropogon gerardii* and *Sorghastrum nutans* responding to late-season drought the same way, whether they encountered the water limitation in single-species communities, or as mixes. Much more work remains to be done to firmly establish the importance of this limitation, including the imposition of stress on a variety of species mixes that include a gradient of similarities among them, as well as experiments in the field using a variety of stressors, timing of stress, and combinations of stressors. The results of this work could be critical for the success of both restoration and conservation efforts because, if consistent, it would demonstrate that it is a mistake to rely on positive shifts in species interactions to mitigate the effects of increasing abiotic stress until a better understanding of the individual species' responses to that stress is reached.

The third advance offered in this dissertation is a reexamination of growth and recruitment determinacy. While some species grow or reproduce only within a pre-programmed, limited window of time regardless of the favorability of conditions for further growth or recruitment (determinate), others can contemporaneously respond to variability in those conditions and continuously grow and reproduce until abiotic conditions become limiting (indeterminate) (McKendrick et al., 1975). The former is a front-loading strategy, where resources are genetically “hardwired” to be invested only when they are most likely to be beneficial, thus sacrificing some capacity to profit from unexpected boons. The latter strategy, while more flexible, is also more vulnerable to any negative shifts in abiotic conditions that follow recent resource investments that have yet to yield returns. Despite its long history as an important topic in agricultural science (Hauggaard-Nielsen & Jensen, 2001; Huyghe, 1998), growth determinacy has been almost entirely overlooked in plant community ecology (but see Hinman & Fridley, 2018; McKendrick et al., 1975; Seiwa, 2000)and could be an essential niche axis (sensu Hutchinson, 1957) facilitating coexistence among some species. By affecting the population-scale ability of species to respond to environmental variability without requiring functional, *per capita* differences, variations in growth and/or recruitment determinacy could enable species that have broad niche overlap, similar forms, and little difference in fitness to avoid competitive exclusion and stably coexist. If those species are both highly adapted to their environment, this mechanism could extend to facilitating not just coexistence, but codominance. During my study of the intra-annual population dynamics of *A. gerardii* and *S. nutans*, I also monitored the dynamics of their neighboring species. A cursory look at these dynamics quickly revealed differences in recruitment determinacy among these species, suggesting that variability along this niche axis may not only be important for the codominant species but common and diffusely operating to promote community-scale coexistence. It is therefore important to note that this mechanism is reliant upon temporal heterogeneity in the favorability of growing conditions. If either the average favorability of such conditions declines or the variability of such is altered, the mechanism may be apt to break down, resulting in important consequences for plant species composition. These factors must also be kept in mind in conservation planning. If such a systemic collapse were to occur, the contributions of the species involved, particularly those that are codominant, to ecosystem function and stability could be quickly lost to competitive exclusion (Gaston & Fuller, 2008; Sasaki & Lauenroth, 2011b; Smith et al., 2020; Smith & Knapp, 2003). However, restoration planning could benefit substantially if knowledge is gained of species growth and recruitment determinacies and is applied in developing seed mixes that result in less synchronous community resource investments.

Assuming that the interpretation of the evidence for this mechanism has been correct, any attempt to determine how *S. nutans* has remained abundant alongside *A. gerardii* - the more competitive (A. M. Silletti et al., 2004a) and drought-tolerant (Hoffman et al., 2018a; Hoffman & Smith, 2018a; A. Silletti &

Knapp, 2002; Swemmer et al., 2006c) of the species in a region that is characterized by alternating wet (productive) and dry (unproductive/unfavorable) conditions (Craine et al., 2012; Hayden, 1998) – would not have been possible without viewing these species as a pair. By considering not just the traits of one species, but the interactions of traits across both species, the story begins to unfold. The inability of *A. gerardii* population densities to respond concurrently to late-season precipitation appears to be the species' one weakness in the region, perhaps hindering its ability to become even more dominant. At the same time, the remarkably regular seasonal pattern of *A. gerardii* density decline may further enable *S. nutans* to respond to late-season precipitation by making light and other resources more available to young new tillers. If *A. gerardii* was instead an indeterminately tillering species, *S. nutans* would either not be codominant, or the dynamics of the two species would be more synchronous. In either case, ecosystem function would be less stable (Ma et al., 2021; Valencia et al., 2020; Yachi & Loreau, 1999).

This is not to say that this mechanism is acting in isolation to stabilize codominance between *A. gerardii* and *S. nutans*, or between any other species that benefit from varying in their growth or recruitment determinacies. Indeed, many of the mechanisms outlined in Chapter 1 of this dissertation are doubtlessly operating in concert to generate codominated species assemblies. For *A. gerardii* and *S. nutans*, there are several partner mechanisms that most likely play key roles. First, both species certainly have a similar degree of adaptation to range of environmental conditions found in the mesic prairie, as is undoubtedly true for any set of codominant species. Second, it remains possible that *A. gerardii* directly facilitate *S. nutans* in ways there weren't examined here (Chapter 3), such as at different times of the season, or through mitigation of other stress factors or severities of stress. It may also be that their interactions in the field differ from those in the greenhouse. Third, in addition to differences in determinacy, other life-history tradeoffs could also play a role. There is some evidence that *S. nutans* is more opportunistic than *A. gerardii*, with longer, but less robust runners and roots, a higher density bud bank, smaller buds (unpublished data), and more rapid reproduction under wet conditions (Chapter 5). Along with the greater drought tolerance of *A. gerardii*, these distinctions suggest a colonization-tolerance tradeoff can occur under the right circumstances. Of the remaining mechanisms discussed in the first chapter, there are several that have elements that, though unlikely to affect the relationship between *A. gerardii* and *S. nutans*, could be affecting both of their relationships with the remainder of their communities. First, both species are obligate mutualists with mycorrhizal fungi. These associations are of considerable importance in the nutrient-poor grasslands where they are codominant and may give them an advantage over less-abundant species that do not have the benefit of enhanced absorptive ability granted by microscopic partners. Second, either spatially attenuated dominance or spatial niche partitioning is certainly important for these species on a continental scale (D. A. Brown, 1993; Epstein et al., 1998a; Keeler, 1990; USDA, 2021b, 2021a)but may also be occurring more subtly across resource gradients at the local scale, as suggested by the decline in abundance of *S. nutans* when going from infrequently burned uplands to lowland areas of the Konza Prairie, while *A. gerardii* shows the opposite trend. However, both species show increased abundances in lowland areas in the annually burned watersheds where they are more codominant. Third, consumer control may be affecting other species disproportionately, and there is evidence that C_4 grasses are not as favored by some grazers than are C_3 species. Fourth, *S. nutans* root exudates do show some allelopathic effects, though they do not appear to affect *A. gerardii* (Parker, 2000). If other species are affected by these chemicals, then both *A. gerardii* and *S. nutans* may show increased relative abundance. Many, if not all these factors may be working in concert with the niche difference in recruitment determinacy to promote and stabilize codominance between these species. Determining the relative importance of each mechanism, whether there are inter-dependencies among them, and what the consequences of their losses might be are all appropriate next steps for developing a more complete understanding of codominance.

While codominance has been recognized for many decades, it has not always been interpreted as more than just multiple, independently abundant species, despite the knowledge that has been gained regarding the links between biodiversity and ecosystem function. In marrying the concepts of dominance and biodiversity and how they each affect ecosystems, this modest shift in perspective begins to address the limitations we impose on ourselves by strictly picking sides. Far more work needs to be done, but the prospects for a greater understanding of fundamental ecological topics like species abundance, stable coexistence, and how ecosystems respond to environmental variability are exciting. Field experiments that manipulate the intra-seasonal and interannual patterns of precipitation received by codominated *A. gerardii-S. nutans* communities will help determine the importance of the growth determinacy niche axis in stabilizing their coexistence and how its loss could affect ecosystem functioning. Similar tests involving mixtures of other species known to vary along this axis will help determine the generality of the mechanism, and whether it, in concert with other mechanisms, can help stabilize whole communities. Tests using seed mixes with species varying in growth and recruitment determinacy under a variety of growing condition patterns will determine whether restoration efforts might be stifled by cryptically synchronous dynamics among the species used for revegetation. Beyond the role of determinacy, more needs to be known about codominance in general – how common is it, how common are the various mechanisms that drive it, what are their vulnerabilities, and what are the consequences of their collapse? For instance, when is codominance truly an interaction between the traits of the participant species, and when it is just mutually independent abundance, and are there differences in how these scenarios drive ecosystem function? Species removal studies that compare different types of codominant species sets could help to clarify this (e.g., Kikvidze et al., 2006). In conclusion, I believe there is much that can be learned about the plant communities around us, how their species interact, and how those interactions affect their surroundings. Much has been learned about these subjects, either through the focused study of either the most dominant species or of the emergent properties of biodiversity, but I believe much more is hiding in plain sight where these two properties meet.

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APPENDICES

CHAPTER 2 APPENDIX:

BOX 2.1. CODOMINANCE INDEX, C_{max}, USAGE ILLUSTRATION:

We created 12 simple communities that specifically differed in relative abundances of seven species, and thus the degree of dominance or evenness (Box 2.1 Table, A). We find that lower C_{max} values occur both in highly *mono*-dominated communities (such as 1, 3, 4, and 5), where abundance is not well-shared among species in the codominant subset, and in communities, such as 2, where abundance is overly shared with the whole community (i.e., highly even). As such, C_{max} appears capable of distinguishing these types of communities from those that are highly codominated (e.g., 11, 12).

However, at intermediate values of C_{max}, ambiguities can arise. For example, while the C_{max} values of communities 9 and 10 are identical, the communities are quite dissimilar (Box 2.1 Table, A). Abundance is more equitably shared in the codominant subset of community 10, while the codominant subset of community 9 contains a larger portion of the total abundance of its community. This comparison illustrates the balance that C_{max} strikes in representing both the disparity between the codominant subset and the most abundant subordinate species (A_n vs S_j, respectively) and the sharing of abundance within the codominant subset, but it also exposes its limitations in distinguishing between highly mono-dominated and highly even communities. Nevertheless, other well-known metrics such as Simpson's D can distinguish between these communities, with community 9 ($D = 0.45$) having a higher dominance value than 10 ($D = 0.33$). As such, we envision C_{max} as a complement to other diversity metrics.

While any number of species (n) can be included in a community's codominant subset, C_{max} is only derived from a codominant subset consisting of the optimal number of species for that community's particular species composition. For example, community 8a is identical to community 8, but a different number of species was used in its calculation of C_n (Box 2.1 Table, B). In this case, the subtraction of the relatively high abundance of the primary subordinate species j $(= 4)$ from shared abundance A_3 gives a suboptimal C_n less than C_{max}. By comparing all the possible calculations of C_n for community 8, we can determine the most appropriate number of species to be included in its codominant subset, and therefore the number of species that may be more important in the functioning of their ecosystems. In this case, because the calculation using $n = 4$ has the highest value of C_n (i.e., C_{max}), we would conclude that communities with this set of abundances would optimally be considered to have four codominant species.

The inverse issue arises between communities 10 and 10a, which are also identical in composition (Box 2.1 Table, B). In calculating C_n for community 10a ($n = 3$), a low-abundance species is included in the codominant subset, and a relatively low index value is the result. The C_{max} value is instead found for the C_n formulation of community 10 ($n = 2$), and we, therefore, conclude that these communities would optimally be considered to have only two codominant species.

While the selection of the most appropriate number of species to include in the codominant subset can sometimes be obvious, as, in the above examples, it can also be far less so. A comparison of the calculations of C_n for communities 6, 6a, and 6b illustrates a situation where the appropriate number of codominant species is far less clear (Box 2.1 Table, B). Here species 4 is distinctively more abundant than species 5, but also distinctively less abundant than species 3. Calculation of C_{max} is a helpful tool in such scenarios, providing a quantitatively-defensible number of species to consider codominant.

Box 2.1 Table. A) The communities are arranged by increasing C_{max}. RA1 – RA7 = Relative abundances of the seven most abundant species within each community. Species included in the codominant subset are in bold. B). Examples of how C_{max} values vary depending on which species are included in the codominant subset. Bold indicates which species were included in the codominant subset. D = Simpson's dominance.

A)

Community	RA 1	RA 2	RA 3	RA 4	RA 5	RA 6	RA 7	C_{max}	D
1	**0.9**	**0.05**	0.05	0	0	0	0	0.04	0.81
2	**0.15**	**0.15**	**0.15**	**0.15**	**0.15**	**0.15**	0.1	0.05	0.14
3	**0.8**	**0.1**	0.1	0	0	0	0	0.08	0.66
4	**0.6**	**0.2**	0.2	0	0	0	0	0.10	0.43
5	**0.9**	**0.09**	0.01	0	0	0	0	0.15	0.82
6	**0.4**	**0.3**	**0.2**	0.09	0.01	0	0	0.19	0.29
7	**0.3**	**0.3**	**0.3**	0.1	0	0	0	0.20	0.27
8	**0.25**	**0.25**	**0.24**	**0.24**	0.02	0	0	0.22	0.23
9	**0.6**	**0.3**	0.1	0	0	0	0	0.30	0.45
10	**0.4**	**0.4**	0.1	0.1	0	0	0	0.30	0.33
11	**0.45**	**0.45**	0.1	0	0	0	0	0.35	0.41
12	**0.45**	**0.45**	0.02	0.02	0.02	0.02	0.02	0.43	0.40

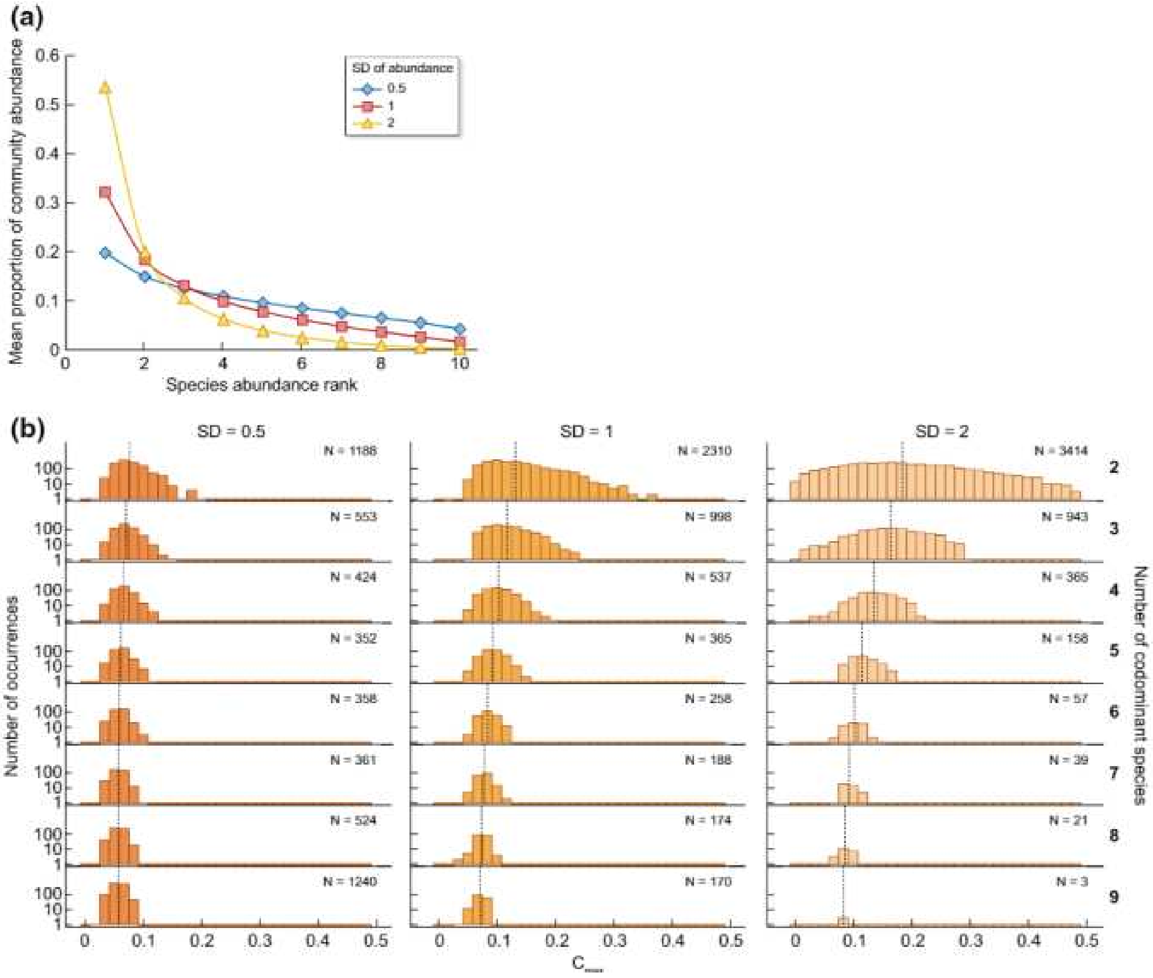
B)

Community	RA 1	RA 2	RA 3	RA 4	RA 5	RA 6	RA 7	C_{max}	D
6	**0.4**	**0.3**	**0.2**	0.09	0.01	0	0	0.19	0.29
6a	**0.4**	**0.3**	0.2	0.09	0.01	0	0	0.14	0.29
6b	**0.4**	**0.3**	**0.2**	**0.09**	0.01	0	0	0.17	0.29
8	**0.25**	**0.25**	**0.24**	**0.24**	0.02	0	0	0.22	0.23
8a	**0.25**	**0.25**	**0.24**	0.24	0.02	0	0	0.01	0.23
11	**0.45**	**0.45**	0.1	0	0	0	0	0.35	0.41
11a	**0.4**	**0.4**	**0.1**	0.1	0	0	0	0.10	0.33

BOX 2.2: EVALUATION OF THE CO-DOMINANCE INDEX, C_{max}, WITH SIMULATED DATA.

The distributions of C_{max} values depended on the community type (determined by the standard deviations used to generate component species abundances, Box 2.2 Figure, A) and the number of species in the optimal codominant subset (Box 2.2 Figure, B). While most of the distributions were approximately normal, they were increasingly broad and skewed towards lower values of C_{max} as the number of codominant species decreased, suggesting that although having fewer species in the optimal codominant subset confers the potential for higher C_{max}, this scenario also can result in some of the lowest C_{max} values. Nevertheless, the mean C_{max} was greatest for communities with only two codominant species (Box 2.2 Table). This the codominance index will often yield the highest values (i.e., C_{max}) when considering only two species to be codominant. Thus, we recommend that multiple co-dominant subsets be examined but that the subset with the largest C_{max} value be reported. This approach allows C_{max} to serve as a guide in determining how many species should be considered codominant.

Across all codominant subset sizes, C_{max} was more closely associated with A_l than with S_s, where l and s refer to the values of n and j, respectively, that result in the highest value of C_n ($m = 0.80, r^2 = 0.91$, and $m = 0.14, r^2 = 0.06$, respectively, both $p < 0.001$). However, the relative importance of A_l and S_s in determining C_{max} depended on the number of species in the C_{max}-associated codominant subset. Correlations between C_{max} and A_l were stronger and more positive for smaller codominant subsets and became weaker and more negatively correlated when nine species were included in the subset, ranging from $r^2 = 0.834$ ($m = 0.92,\ p < 0.001$) with two species to $r^2 \cong 0$ ($m = -0.12,\ p = 0.31$) with eight species. The opposite behavior was observed for the associations between S_s and C_{max}, being weakest in communities with the fewest codominant species ($r^2 = 0.05, m = -0.54,\ p < 0.001$) and strongest in the most even communities ($r^2 = 0.90, m = -0.80,\ p < 0.001$). Overall, these results suggest that large A_l values will typically control C_{max} values in highly codominated communities, rather than small S_s values, especially given that highly codominated communities are likely to have fewer codominant species.



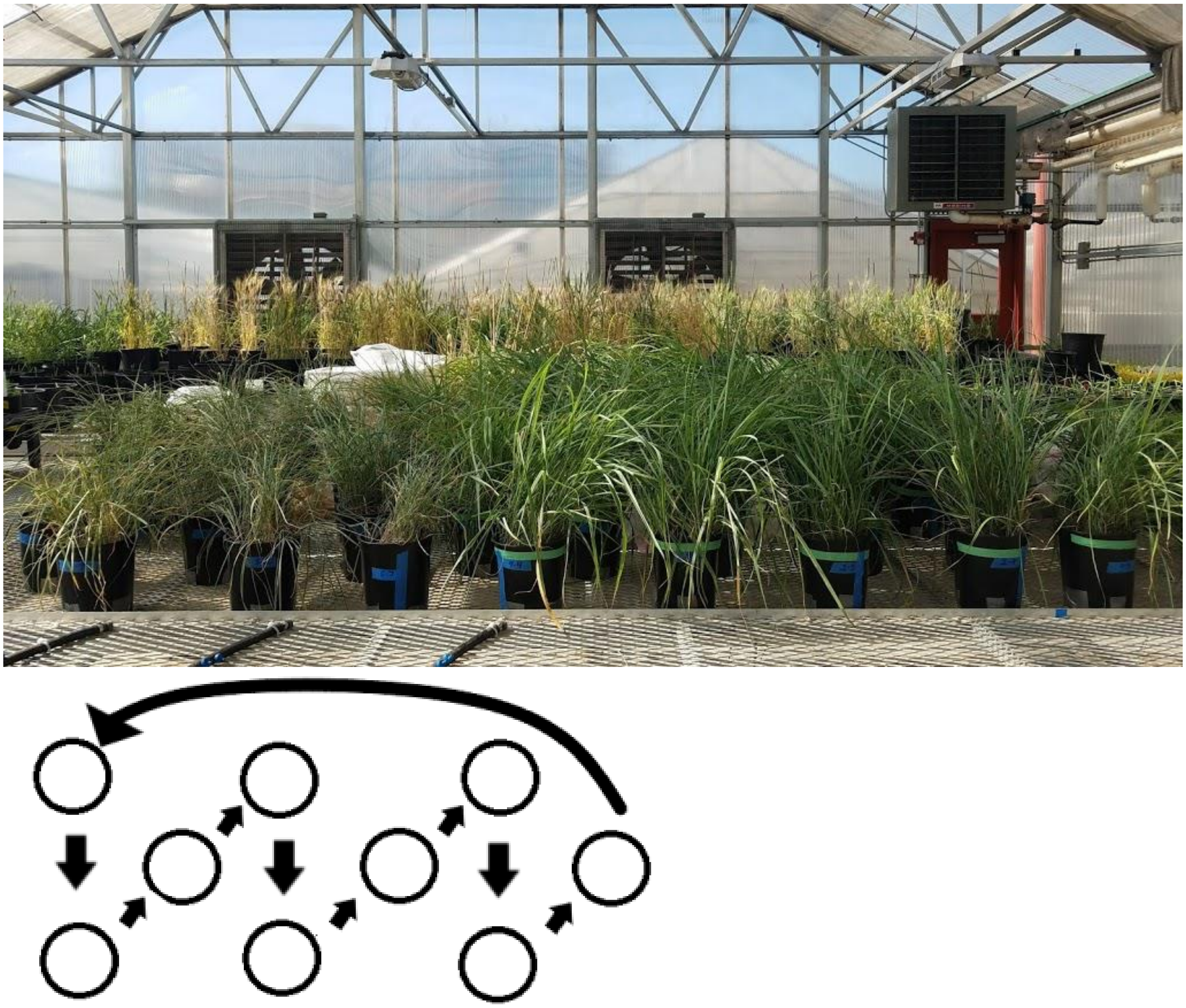
Box 2.2 Figure: (Top) Rank abundance curves, averaged across all simulated communities and grouped by the standard deviations used in generating species abundances. (Bottom) Distributions of C_{max}values grouped by the standard deviations of species abundances used in generating the simulated communities (sd = 0.5, 1, or 2), and the number of species in the codominant subset that resulted in the largest codominance (C_{max}). Mean $C_{max}$for each group is given by dashed lines. The number of communities having the indicated number of codominant species for each community type is given by N.

Box 2.2 Table: ANOVA table and least-square means for C_{max} values grouped by the number of species included in the codominant subset that resulted in that C_{max} value (i). C_{max} values varied substantially within each codominant subset size, resulting in a low $adj. R^2 = 0.242$, but were on average greater when fewer species codominated. Confidence intervals of least-square means were adjusted using the Bonferroni method.

	Estimate	Std. Error	t value	Pr(>|t|)
intercept ($i = 2$)	0.148	0.00073	200.99	<2e-16
$i = 3$	-0.024	0.00143	-16.62	<2e-16
$i = 4$	-0.048	0.00183	-26.08	<2e-16
$i = 5$	-0.063	0.00219	-28.83	<2e-16
$i = 6$	-0.076	0.00247	-30.76	<2e-16
$i = 7$	-0.082	0.00262	-31.14	<2e-16
$i = 8$	-0.086	0.00239	-35.91	<2e-16
$i = 9$	-0.089	0.00178	-50.06	<2e-16
Residual standard error: 0.0611 on 14992 degrees of freedom. Multiple R-squared: 0.242, Adjusted R-squared: 0.242. F-statistic: 685.1 on 7 and 14992 DF, p-value: <2.2e-16.				

Codominant species (i)	LS Mean	Std. Error	DF	lower CL	upper CL
2	0.148	0.0007	14992	0.146	0.149
3	0.124	0.0012	14992	0.121	0.127
4	0.099	0.0017	14992	0.096	0.105
5	0.085	0.0021	14992	0.079	0.091
6	0.072	0.0024	14992	0.065	0.078
7	0.066	0.0025	14992	0.059	0.073
8	0.062	0.0023	14992	0.056	0.068
9	0.058	0.0016	14992	0.054	0.063

CHAPTER 3 APPENDIX:

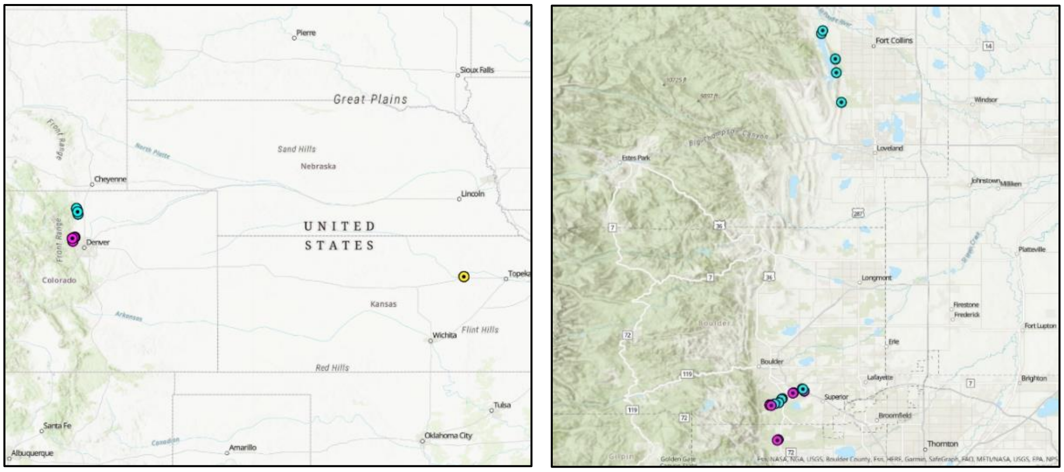


Supplementary Figure 3.1: (A) Illustrative photograph of treated communities. The pots on the left side show communities receiving the late-season drought treatment after 18 days, and the pots on the right show pots receiving the control treatment. These pots were mixed randomly before the 18th day following the initiation of the late-season drought treatment, but the relatively low canopy cover of the drought-treatment pots necessitated their grouping together to avoid shading from the control-treatment plants. After 18 days post-initiation of the late-season drought treatment, all pots were rotated according to (B) every 4 days.

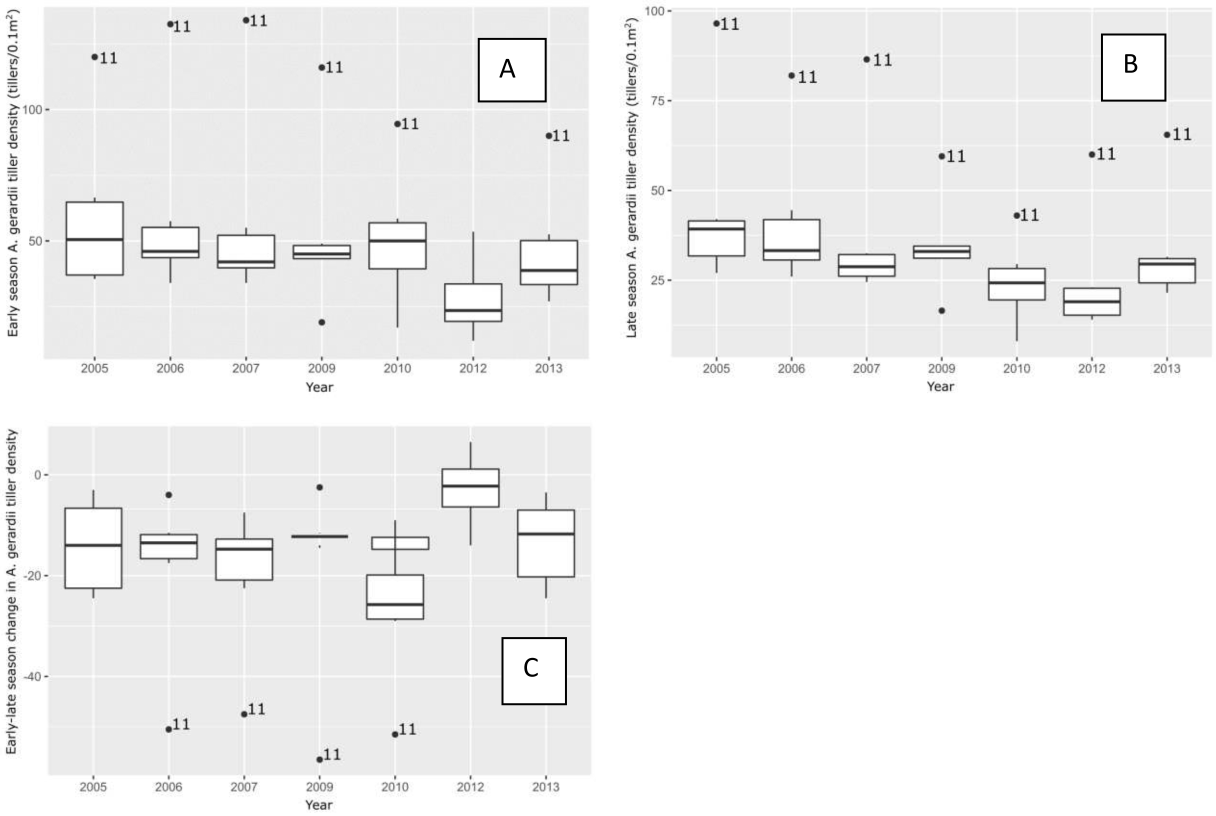
Supplementary Table 3.1: Wilcox tests for differences in RNE values between control and drought treatment. The two species and their three performance metrics were tested independently.

Species	Metric	Control RNE	Drought RNE	N	statistic	p-value
A.gerardii	ANPP	-0.22	-0.228	5	11	0.841
A.gerardii	Reproduction	-0.129	-0.147	5	17	0.421
A.gerardii	Survival	-0.096	-0.109	5	15	0.69
S.nutans	ANPP	0.136	0.115	5	14	0.841
S.nutans	Reproduction	-0.174	-0.41	5	19	0.222
S.nutans	Survival	-0.096	0.001	5	16	0.293

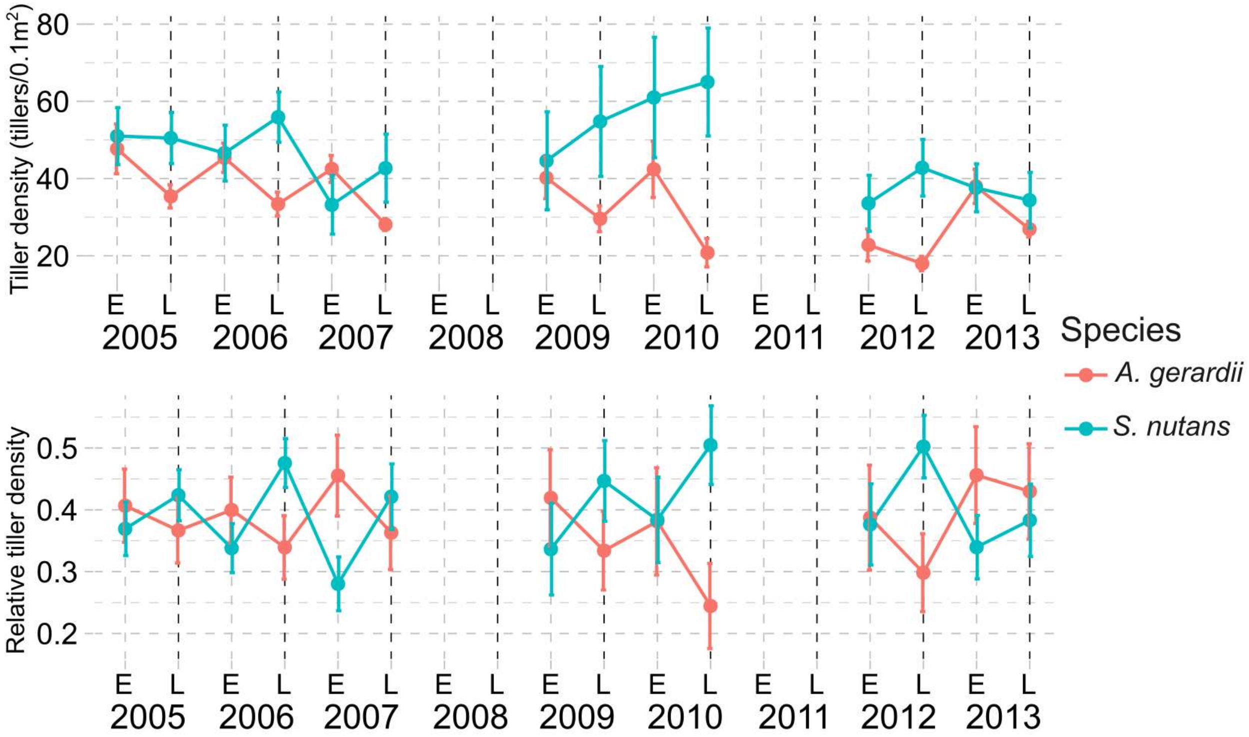
CHAPTER 4 APPENDIX:



Supplemental Figure 4.1: Overview maps of the Konza (yellow point) and Front Range Colorado census plot locations at the state scale (left) and a more local scale (right). Blue points indicate *A. gerardii* plots and pink points indicate *S. nutans* plots. The plots near Fort Collins were located within properties under the ownerships of the Fort Collins Natural Areas program and City of Boulder Open Space and Mountain Parks. See Table S1 for coordinates.

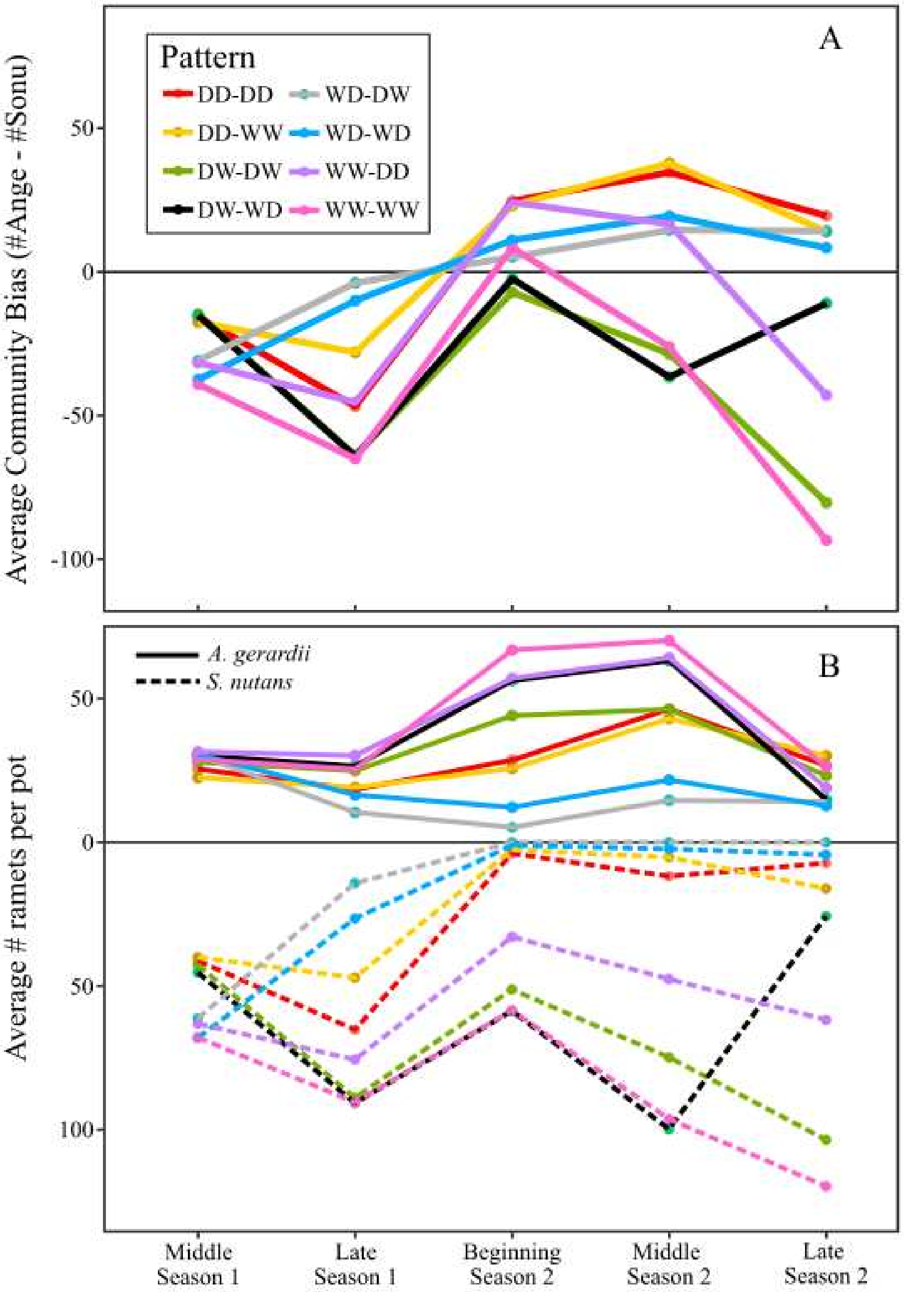


Supplemental Figure 4.2: Early-season (a) and late-season (b) absolute densities of *Andropogon gerardii* in the RaMPs experiment for years 2005 to 2013. Seasonal changes in the absolute density of *A. gerardii* are depicted in (c). All extreme outliers (those with values labeled) were observed in a single plot, and this plot was excluded from analyses involving either absolute densities or absolute density dynamics. However, the relative densities and dynamics of *A. gerardii* did not have extreme outliers, and no plots were excluded from analyses involving relative densities or relative density dynamics.

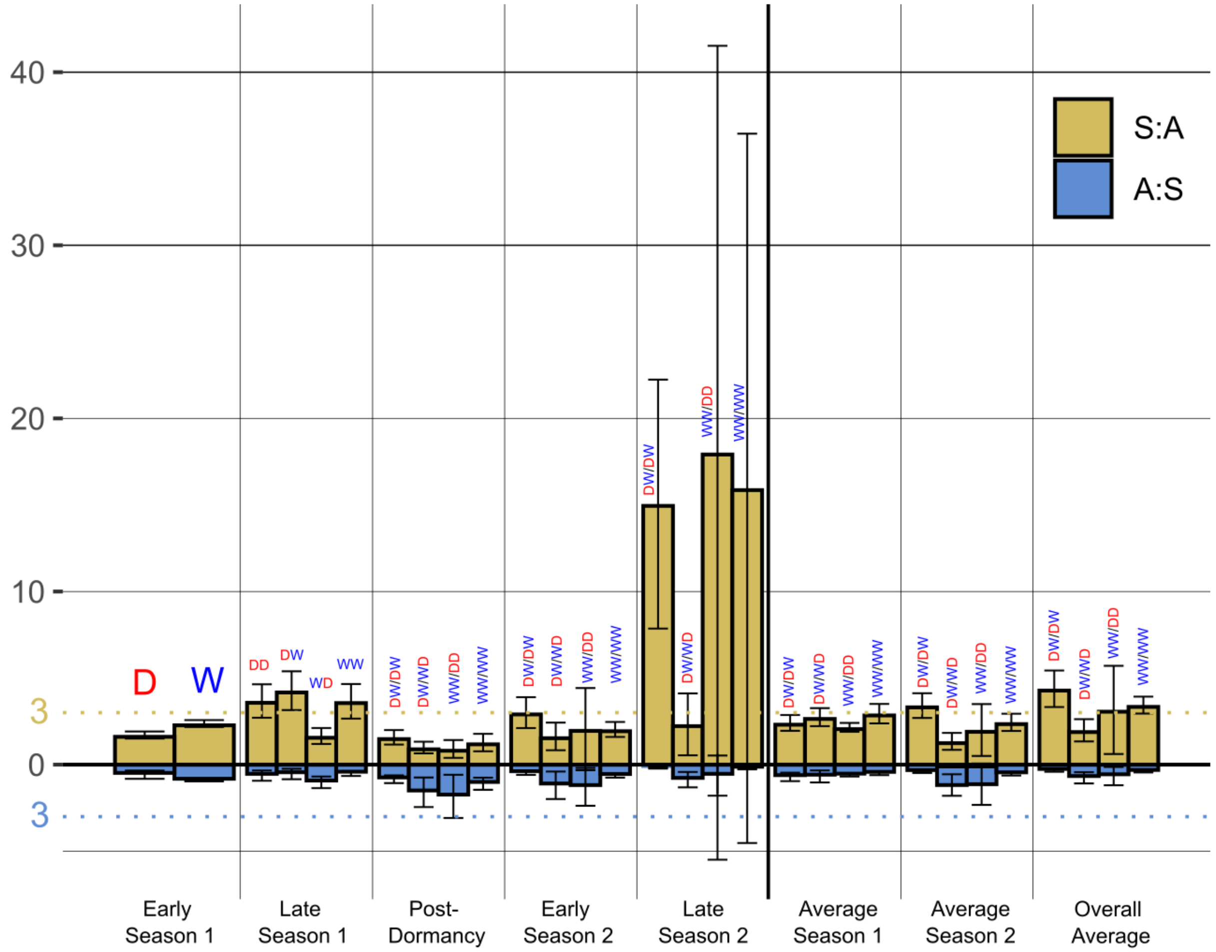


Supplemental Figure 4.3: Time series of *A. gerardii* and *S. nutans* absolute (top row) and relative densities (proportion of total community density represented by each focal species, bottom row) over time in the RaMPs experiment. E indicates early season (late May to Early June) and L indicates late season (August). Note that 2008 and 2011 densities were not measured and are not included. Points are averages across replicates and error bars indicate estimates of standard error.

CHAPTER 5 APPENDIX:



Supplemental Figure 5.1 Tiller dynamics of *A. gerardii* and *S. nutans* averaged across all replicates within each watering pattern treatment. Error bars have been removed for clarity, but significant overlap in confidence intervals was common (S. Table 1, 2). In the upper figure (A), the balance of species representation (# *A. gerardii* tillers - # *S. nutans* tillers) is represented. Positive numbers indicate a greater number of *A. gerardii* tillers than those of *S. nutans* at that survey date. Numbers closer to zero indicate a similar number of tillers of each species, though the total number of tillers varied between treatments. The average dynamics of the tiller densities of each species are depicted separately in the lower figure (B).



Supplemental Figure 5.2 From left to right: tiller density ratios for all surveys conducted, the averages of the surveys within each season, and the average across all surveys. The S:A ratio is the average ratio of *S. nutans* ramets to *A. gerardii* ramets within each treatment. The A:S ratio is the average ratio of *A. gerardii* ramets to *S. nutans* ramets within each treatment. Error bars indicate **5% confidence intervals**. Dashed lines indicate the 3:1 ratio threshold for mono-dominance of the species indicated by the matching color. Treatment patterns are indicated above each bar.

Supplemental Table 5.1 Average community bias values from S. Figure 1 (A), with their 5% confidence intervals. Biases calculated as the differences between density averages of the two species within each pattern, at each time step. Negative numbers indicate that *S. nutans* had a higher average ramet density.

Variability Scale	Pattern	Time Step	Bias	5% CI
No variability	DD/DD	Middle Season 1	-15.7	9.00
No variability	WW/WW	Middle Season 1	-39.1	8.28
Intra-seasonal	DW/DW	Middle Season 1	-14.7	12.40
Intra-seasonal	WD/WD	Middle Season 1	-37.5	7.19
Inter-seasonal	DD/WW	Middle Season 1	-17.5	8.72
Inter-seasonal	WW/DD	Middle Season 1	-31.6	12.71
Scale interaction	DW/WD	Middle Season 1	-15.1	11.70
Scale interaction	WD/DW	Middle Season 1	-30.9	4.87
No variability	DD/DD	Late Season 1	-46.8	13.21
No variability	WW/WW	Late Season 1	-65	18.68
Intra-seasonal	DW/DW	Late Season 1	-64	28.43
Intra-seasonal	WD/WD	Late Season 1	-10	11.38
Inter-seasonal	DD/WW	Late Season 1	-28	20.51
Inter-seasonal	WW/DD	Late Season 1	-45.4	25.20
Scale interaction	DW/WD	Late Season 1	-64.2	24.77
Scale interaction	WD/DW	Late Season 1	-3.8	7.39
No variability	DD/DD	Beginning Season 2	24.7	9.28
No variability	WW/WW	Beginning Season 2	8.4	24.29
Intra-seasonal	DW/DW	Beginning Season 2	-7.1	20.27
Intra-seasonal	WD/WD	Beginning Season 2	11.1	12.80
Inter-seasonal	DD/WW	Beginning Season 2	23.1	12.33
Inter-seasonal	WW/DD	Beginning Season 2	24.2	22.02
Scale interaction	DW/WD	Beginning Season 2	-2.4	29.98
Scale interaction	WD/DW	Beginning Season 2	5.2	5.50
No variability	DD/DD	Middle Season 2	34.6	16.96
No variability	WW/WW	Middle Season 2	-26.1	40.43
Intra-seasonal	DW/DW	Middle Season 2	-28.5	45.50
Intra-seasonal	WD/WD	Middle Season 2	19.4	19.63
Inter-seasonal	DD/WW	Middle Season 2	37.9	16.20
Inter-seasonal	WW/DD	Middle Season 2	16.6	43.44
Scale interaction	DW/WD	Middle Season 2	-36.6	53.91
Scale interaction	WD/DW	Middle Season 2	14.6	13.10
No variability	DD/DD	Late Season 2	19.5	10.23
No variability	WW/WW	Late Season 2	-93.4	58.61
Intra-seasonal	DW/DW	Late Season 2	-80.3	66.64
Intra-seasonal	WD/WD	Late Season 2	8.4	10.11
Inter-seasonal	DD/WW	Late Season 2	14	29.36
Inter-seasonal	WW/DD	Late Season 2	-42.9	50.09
Scale interaction	DW/WD	Late Season 2	-10.9	14.32
Scale interaction	WD/DW	Late Season 2	14.2	12.19

Supplemental. Table 5.2 Average number of ramets per plot from S. Fig 2 (B) with the 5% confidence intervals of each species in the columns to the immediate right of their respective species' average densities. Density averages calculated across replicates within each treatment pattern, at each time step.

Variability Scale	Pattern	Time Step	A. gerardii density	5% CI	S. nutans density	5% CI
No variability	DD/DD	Middle Season 1	25.5	7.0	41.2	12.5
No variability	WW/WW	Middle Season 1	28.8	5.0	67.9	5.6
Intra-seasonal	DW/DW	Middle Season 1	27.9	3.1	42.6	11.7
Intra-seasonal	WD/WD	Middle Season 1	30.6	4.7	68.1	5.6
Inter-seasonal	DD/WW	Middle Season 1	22.5	9.4	40	15.6
Inter-seasonal	WW/DD	Middle Season 1	31.5	7.9	63.1	7.5
Scale interaction	DW/WD	Middle Season 1	30.2	8.2	45.3	13.2
Scale interaction	WD/DW	Middle Season 1	30.4	3.1	61.3	5.9
No variability	DD/DD	Late Season 1	18.4	8.0	65.2	18.7
No variability	WW/WW	Late Season 1	25.5	7.3	90.5	14.4
Intra-seasonal	DW/DW	Late Season 1	24.9	7.9	88.9	22.1
Intra-seasonal	WD/WD	Late Season 1	16.5	11.1	26.5	15.7
Inter-seasonal	DD/WW	Late Season 1	19.1	10.1	47.1	24.4
Inter-seasonal	WW/DD	Late Season 1	30.2	8.1	75.6	24.2
Scale interaction	DW/WD	Late Season 1	26.5	5.7	90.7	23.7
Scale interaction	WD/DW	Late Season 1	10.4	7.2	14.2	12.2
No variability	DD/DD	Beginning Season 2	28.6	11.3	3.9	3.1
No variability	WW/WW	Beginning Season 2	66.9	18.9	58.5	25.3
Intra-seasonal	DW/DW	Beginning Season 2	44.1	9.1	51.2	24.9
Intra-seasonal	WD/WD	Beginning Season 2	12.2	13.4	1.1	2.5
Inter-seasonal	DD/WW	Beginning Season 2	25.7	11.4	2.6	3.9
Inter-seasonal	WW/DD	Beginning Season 2	57.1	21.0	32.9	23.2
Scale interaction	DW/WD	Beginning Season 2	56.3	20.1	58.7	29.0
Scale interaction	WD/DW	Beginning Season 2	5.2	5.5	0	0.0
No variability	DD/DD	Middle Season 2	46.4	18.0	11.8	10.5
No variability	WW/WW	Middle Season 2	70.2	13.5	96.3	41.8
Intra-seasonal	DW/DW	Middle Season 2	46.3	13.9	74.8	35.9
Intra-seasonal	WD/WD	Middle Season 2	21.7	20.6	2.3	5.2
Inter-seasonal	DD/WW	Middle Season 2	43.1	14.1	5.2	7.4
Inter-seasonal	WW/DD	Middle Season 2	64.2	22.2	47.6	31.9
Scale interaction	DW/WD	Middle Season 2	63.2	26.1	99.8	46.0
Scale interaction	WD/DW	Middle Season 2	14.6	13.1	0	0.0
No variability	DD/DD	Late Season 2	26.7	9.6	7.2	7.2
No variability	WW/WW	Late Season 2	26.3	10.3	119.7	53.2
Intra-seasonal	DW/DW	Late Season 2	23.2	14.2	103.5	56.1
Intra-seasonal	WD/WD	Late Season 2	12.7	11.1	4.3	8.5
Inter-seasonal	DD/WW	Late Season 2	30.1	11.1	16.1	23.3
Inter-seasonal	WW/DD	Late Season 2	18.9	10.1	61.8	42.3
Scale interaction	DW/WD	Late Season 2	14.8	9.7	25.7	12.0
Scale interaction	WD/DW	Late Season 2	14.2	12.2	0	0.0