

5-2014

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From Competition to Facilitation: Mechanisms of Species Interactions in a Novel World

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A DEPARTMENT HONORS THESIS SUBMITTED TO THE
DEPARTMENT OF BIOLOGY AT TRINITY UNIVERSITY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR GRADUATION WITH DEPARTMENTAL HONORS

17 April 2014

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Introduction

Invasive species outcompete and displace native species through competition and are an enormous threat to biodiversity (Sakai *et al.* 2001). Although competition theory has developed over the last ninety years, understanding why invasive species are so competitively superior remains elusive since they do not conform to traditional assumptions made in competition models. In order to improve understanding of the competitive exclusion of native species by exotic invasive species, I review in Chapter 1 the development of competition theory and models of competition through the last six decades and its application to recent theory on invasive species competitive dynamics. Then in Chapter 2, I elucidate studies I conducted to further development of competitive modeling through modification of the Carroll *et al.* (2011) mechanistic competition model. Chapter 3 is dedicated to a study designed to apply and test the modified model to a real world scenario of grassland competition. In this study, I aimed to understand mechanisms underlying the success of the non-indigenous, invasive, C₄ perennial grass King Ranch bluestem (*Bothriochloa ischaemum*) in competition with native, C₄ grass species sideoats grams (*Bouteloua curtipendula*) and little bluestem (*Schizachyrium scoparium*) in a growth chamber competition study. The work is ultimately designed to further theoretical understanding the competition dynamics of exotic, invasive species competition and provide insight into how to manage natives to enable their use in restoration and biocontrol.

Chapter 1

In this chapter, I provide a review of the theory and models of competition with the aim of identifying models suited for invasive species competition. Organisms compete over limited resources, leading to either coexistence or competitive exclusion. In order to predict outcomes of competition, mathematical models have been developed. Nonetheless, invasive species do not conform to traditional understanding of competition and thus present a novel problem.

Competition and Coexistence

Competition is an important biotic interaction that can affect the niche of a species (Gause 1934; Hutchinson 1965) and ultimately the presence, distribution and abundance of species in ecosystems. Competition for limited resources (*e.g.* space, water, sunlight, essential nutrients) occurs among individuals of a species (intraspecific competition) and between individuals of different species (interspecific competition (Clark and Evans 1954; Connell 1961). Resource utilization among competitors results in either exploitative or interference competition (MacIsaac and Gilbert 1991). Exploitative competition occurs when resource use by an organism leaves less of the resource available for other organisms (Tilman 1982). Resources that are frequently competed for in exploitative competition are nutrients. For example, desert rodents (*Rodentia*) and many ants (*Formicidae*) are granivores, or seed predators, that compete with one another over the limited supply of seeds (Brown *et al.* 1979). When a granivore collects and consumes a seed, the total number of seeds available to all granivores decreases. Therefore, exploitative interspecific competition occurs between desert rodents and ants for seeds. Interference competition occurs when access to a resource is prevented through hoarding (Schoener 1983). A

resource that is frequently competed over in interference competition is space. For example, red foxes (*Vulpes vulpes*) and arctic foxes (*Alopex lagopus*) compete over space for nesting dens. When one fox species inhabits a nesting site, that particular nesting site becomes unavailable for the other species. Therefore, interference competition occurs between these fox species for nesting dens (Tannerfeld *et al.* 2002). Regardless of the type of competition, competitive interactions among two species have two possible outcomes.

The two possible outcomes of competitive interactions are exclusion or coexistence. G.F. Gause (1934) describes these phenomena in his experiments of competing *Paramecium* species. *P. aurelia*, *P. caudatum*, and *P. bursaria* all experienced positive population trends when grown alone in culture tubes. However, *P. caudatum* experienced competitive exclusion and subsequent extinction when grown in culture with *P. aurelia*. In contrast, *P. caudatum* and *P. bursaria* coexisted and maintained viable populations when grown together in culture. This experiment gave rise to Gause's principle of competitive exclusion, which states that two species competing for the same resource cannot coexist if other ecological factors are constant (Gause 1934). The outcome of competition is determined by two qualities: niche differences and fitness differences.

Niche Differences

Niche difference is one factor that determines if competitive exclusion or coexistence will occur. Niche difference refers to the degree to which organisms differ in resource needs and/or utilization. When niches do not overlap, organisms do not share resource needs or utilization and will therefore coexist. When niches do overlap, species are utilizing resources in a similar manner and coexistence may or may not occur. The smaller the niche difference, the smaller the probability of coexistence and the greater the

probability of competitive exclusion. When niches entirely overlap, organisms entirely share the same resource needs and utilization. Species with complete niche overlap will experience either coexistence or competitive exclusion, depending on their fitness differences. When any amount of niche overlap occurs, fitness differences will contribute to determining the outcome of competition. The ability of species to be able to avoid competition through partitioning resources is considered a stabilizing mechanism since it promotes coexistence among species that might otherwise be driven to extinction (Chesson 1991; Chesson 2000).

Theoretically, only better competitors or species living with no biotic interactions can occupy the complete breadth of niche space for which they are suited, also known as a species fundamental niche. A species' fundamental niche is defined as a single axis or as an n dimensional hypervolume that encompasses a complete range of conditions under which an organism can maintain a viable population. In other words, a species fundamental niche describes the conditions under which a species *could* live in the absence of interactions with other species. Species, however, do not exist in vacuums. In competition, a species is limited from occupying its entire fundamental niche and is relegated to inhabiting the niche in which it can persist. This new niche manifestation is referred to as the realized niche of the species and is the environmental parameters that a species occupies in the presence of competition, predation, and other biotic interactions (Hutchinson 1965). An organism increases its niche difference with another organism by occupying the realized niche, which is more restricted than its fundamental niche or the one it could occupy. Thus, occupying a realized niche promotes coexistence through partitioning of resources, time, and space.

Niche partitioning has been described in three ways: classical, temporal, and spatial; all of which promote coexistence among organisms and species. Classical niche partitioning describes organisms differing in resource needs and/or utilization (MacArthur and Levins 1967; Tilman 1982). For example, Bellardi bog sedge (*Kobresia myosuroides*) and prairie bluebells (*Mertensia lanceolata*) have the same nitrogen uptake pattern (nitrate > ammonium > glycine). For prairie bluebells this pattern remains the same regardless of the absence or presence of competition. However, the nitrogen uptake pattern of Bellardi bog sedge changes in the presence of competition by increasing ammonium uptake over nitrate uptake. As a result, Bellardi bog sedge and prairie bluebells coexist because they partition nitrogen chemical forms (Ashton *et al.* 2010). Temporal niche partitioning describes organisms that may be limited to utilizing the same resource but differ in terms of when they exploit the resource (Armstrong and McGehee 1976; Chesson 1985). For example, American mink (*Neovison vison*) feed nocturnally in the absence of competitors and feed diurnally in the presence of the competitors, specifically otters (*Lutra lutra*) and polecats (*Mustela putorius*; Harrington *et al.* 2009). Spatial niche partitioning describes how organisms differ in where they utilize limiting resources (May and Hay 1981; Chesson 2000). For example, three genera of epibiotic barnacles partition attachment sites on green sea turtles (*Chelonia mydas*) in order to coexist. *Chelonibia testudinaria* is found on the surface of the carapace and plastron, *Platylepas* attaches to the soft areas, and *Stomatolepus transversa* bore into interdermal bone segments of the carapace and legs (Hayashi and Tsuji 2008). Partitioning reduces niche overlap to promote coexistence. Therefore, organisms can niche partition resources, time, and space in order to promote coexistence in an ecosystem.

Fitness Differences

Fitness difference also acts as a determinant of the probability of competitive exclusion or coexistence will occur. Fitness difference is the degree to which organisms differ in competitive ability. While niche partitioning is a stabilizing mechanism, fitness difference is an equalizing mechanism. When niches do not overlap to any degree, fitness difference does not contribute to either coexistence or competitive exclusion because organisms do not interact. In other words, equalizing mechanisms promote coexistence when stabilizing mechanisms are either absent or weak (Chesson 2000). However, when any amount of niche overlap occurs, fitness difference contributes to determining the outcome of competition. The smaller the niche difference, the greater the influence of fitness difference in determining the outcome of competition. In other words, fitness difference becomes more influential in competitive interactions as niche overlap increases. Where niches overlap, a small fitness difference promotes coexistence whereas a large fitness difference will result in competitive exclusion of the less fit species. The species with higher fitness (the competitive dominant) will persist at the expense of the less fit (competitive subordinate) species (Chesson 2008).

Just as niche overlap can be minimized through partitioning, fitness differences can be minimized through life history trade-offs. Fitness differences are minimized when trade-offs between competitive ability and mortality exist (Chesson and Huntly 1997). In traditional niche theory, superior competitors are thought to be limited by low fecundity, low recruitment ability, and short dispersal ranges. As a result, superior competitors lack the ability to exploit resource-rich conditions characteristic of early successional habitats. On the other hand, inferior competitors have high fecundity, high recruitment ability, long

dispersal ranges. As a result, inferior competitors can exploit resource-rich conditions characteristic of early successional habitats and can disperse offspring into these habitats before superior competitors. Since their fecundity, recruitment, and dispersal are limited, superior competitors cannot occupy and exploit all available niches, leaving gaps in the landscape that inferior competitors exploit (Levins and Culver 1971; Hastings 1980; Tilman *et al.* 1994; Bolker and Pacala 1999). Therefore, life history differences between superior competitors and inferior competitors promote coexistence both by reducing fitness differences and by creating niche differences.

Mitigation of fitness differences through the trade-off between competitive ability and mortality is illustrated by Grime's C-S-R triangle theory (Grime 1979). This trade-off causes the existence of three primary adaptive strategies among plants: competitive, stress-tolerant, and ruderal. Competitors are plant species adapted to thrive in areas of low intensity stress and low intensity disturbance, and as indicated by their name, they are strong competitors. Characteristics such as high fecundity, high growth rate, and high degree of phenotypic plasticity allow competitors to be flexible in morphology and adjust the allocation of resources. Stress tolerant species are plants that live in areas of high intensity stress and low intensity disturbance (i.e. deep shade, nutrient deficient soils, and high soil pH levels). In contrast to competitors, stress tolerant species have characteristics such as low growth rate, long life spans, high rate of nutrient retention, and low phenotypic plasticity in order to respond to environmental stress through physiological variability. Ruderal species are plants that thrive in areas of high intensity disturbance and low intensity stress. Characteristics such high growth rate and short life cycles allow ruderal species to promote a large number of seeds to colonize recently disturbed areas. However

ruderal plants also typically die when environmental stress events occur. The trade-off between competitive ability and mortality prevent a species from reaping the advantages of more than one of these strategies (Grime 1979). These life history differences between superior competitors and inferior competitors promote coexistence both by reducing fitness differences and by creating niche differences. Thus, understanding both stabilizing mechanisms (niche difference) and equalizing mechanisms (fitness difference) are important to determine if coexistence or competitive exclusion will occur when organisms interact.

Mathematical Models of Competition

In order to predict the outcomes of competition based on these stabilizing and equalizing mechanisms, mathematical models have been developed. The most important competition models, in chronological order, include Lotka-Volterra equations (Volterra 1928), MacArthur's Consumer-Resource Model (MacArthur 1970), Tilman's R^* (Tilman 1980), Chesson and Warner's storage effect (Chesson and Warner 1981), Loreau and Hector's additive partitioning of biodiversity effects model (Loreau and Hector 2001), and Carroll *et al.*'s mechanistic competition model (Carroll *et al.* 2011). The first two models, Lotka-Volterra and MacArthur's Consumer-Resource Model, both have a bias towards animals. For example, predator-prey relationships modeled by Lotka-Volterra are primarily applicable to animal systems, since plant competitive interactions cannot be characterized as predator-prey relationships. Through time, models expanded in scope to include plants and in particular, Tilman's R^* marks this shift in modeling to incorporate plants. Along with other developments in competition modeling, this progress took place only by building upon the work of previous theory and modeling, beginning with Lotka-

Volterra.

Forming the historical foundation of competition theory, Lotka-Volterra (L-V) equations are two first-order, non-linear, differential equations that describe the dynamics between a predator and its prey:

$$\begin{aligned} \text{a.} \quad & \frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1}\right) \\ \text{b.} \quad & \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - \frac{\alpha_{21} N_1}{K_2}\right) \end{aligned}$$

Equation a. describes predator population change through time, while equation b. describes prey population change through time. Both equations are expressed in population size (N), carrying capacity (K), growth rate (r), and competition coefficient (α). L-V equations present a fluctuating inverse relationship between predator and prey population sizes (Volterra 1928). Although a mathematical model will never fully mirror nature, the L-V equations are particularly limited because of its many unrealistic assumptions. For example, the equations assume no age structure, no genetic structure, no migration, no density-dependent factors, and no spatial structure (individual of one species interact with the entire population of the other species) occur in the predator or prey population. The model is also deterministic, excluding environmental complexity and randomness (Begon *et al.* 1996; Gotelli 1998). Experimental data from predator-prey systems more closely fits other mathematical models that incorporate carrying capacity, realistic functional responses, and environmental complexity, such as MacArthur's Consumer Resource Model (Huffakers 1958).

MacArthur's Consumer-Resource Model (MC-RM) is composed of two differential

equations describing interactions between a biotic resource and a consumer:

$$\begin{aligned} \text{c.} \quad & \frac{dR_i}{dt} = R_i r_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^n c_{ji} R_i X_j \quad \text{for } i = 1 \dots q \\ \text{d.} \quad & \frac{dX_i}{dt} = X_i b_i \left(\sum_{j=1}^q c_{ij} w_j R_j - m_i \right) \quad \text{for } i = 1 \dots n. \end{aligned}$$

Equation c. represents the dynamics of biotic resources and equation d. represents the dynamics of consumers. This stochastic model predicts that the i th biotic resource (R_i), or resource species, grows logistically at an initial rate (r_i) to carrying capacity (K_i) in the absence of a consumer. When present, the i th consumer exhibits a linear functional response, reducing resources as a constant per capita rate (c_{ij}) while assimilating biomass at factor w_j . Some consumer assimilated biomass is lost by factor m_i from mortality and metabolism and what remains is converted to new consumer biomass by factor b_i (MacArthur 1970). Assumptions of MC-RM include even distribution of resources and even distribution of consumers. MC-RM is both historically and presently extremely influential on competition theory (Abrams 1975; Schoener 1976; Carroll *et al.* 2011) and Tilman expands on this theoretical framework with his R^* model.

Building on MC-RM and also expanding in scope to focus on plants, Tilman's R^* model describes the dynamic relationship between competitors through their use of and effect on shared resources:

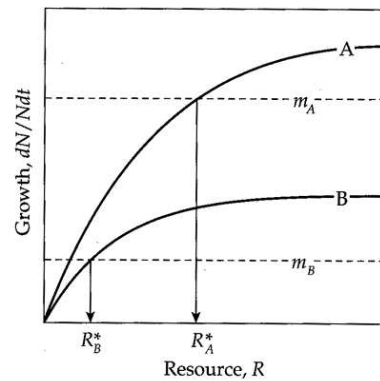


Figure 1

As shown in Figure 1, the growth rate of a species is a function of resource supply rate in the environment and species consumption. Resource availability is a function of resource supply rate in the environment and species consumption. Individual populations can increase in size, consuming more and more resource, until resources become limiting and constrain the population size to a level that can be supported by the resource supply rate. Species can then decrease resource levels to low values. Those species able to survive at this lower resource levels should outcompete other species when that resource is limiting. When two or more resources are limiting, moving toward a more realistic scenario, then trade-offs in the ability to use different resources may allow coexistence between competing species (Tilman 1980). While MacArthur and Tilman both focus on the relationship between consumers competing for resources, Chesson and Warner (1981) focus on how spatial and temporal variability promote coexistence through the storage effect.

Chesson and Warner's storage effect describes a mechanism of species coexistence through spatial and temporal variability. In a changing environment, a species cannot be the best performer under all conditions. Instead, each species responds differently to the

varying conditions. Each species' population stores gain under conditions when it performs best in order to survive losses under conditions when it does not perform best. Storage can occur through space and time. Spatial storage effect occurs when species benefit from environmental variation in patches across a landscape, and temporal storage effect occurs when species benefit from variation in environmental patterns in time. The storage effect (I) is expressed as the following:

$$e. \quad \Delta I = \gamma_i \text{Cov}(E_i, C_i) - \sum_{i \neq r} q_{ir} \gamma_r \text{Cov}(E_r, C_r)$$

The first term of equation e. is covariance between the environment (E_i) and competition (C_i), scaled by a factor of buffered population growth (γ), and the difference between the first and second terms is the difference in species responses to the environment (E_r) between competitors (C_r). The factor q_{ir} is a measure of how much the competition experienced by species r influenced the competition experienced by species i . Covariance between environment (either space or time) and competition and species-specific response to environment combine to dissociate impacts from the strongest intraspecific and interspecific competition experienced by a species population. Following this dissociating, subadditive (buffered) population growth limits the impact of interspecific competition when a species is not favored by the environment. As a consequence, the impact of intraspecific competition on the species favored by the environment is greater than the interspecific competition on species less favored by the environment. Coexistence is thus promoted by the storage effect when there is environmental variability in space and time (Chesson and Warner 1981; Chesson 1985; Chesson and Huntly 1989; Hatfield and Chesson 1996; Snyder and Chesson 2003).

While Chesson and Warner focus on how spatial and temporal variability impact outcomes of competition, Loreau and Hector are instead interested in how outcomes of competition impact biodiversity and productivity in a given ecosystem. Loreau and Hector present a model of additive partitioning to separate out the selection and complementarity effect. The selection effect is dominance by species with particular traits affecting ecosystem processes, or in other words, the selection effect is selective process that promotes dominance by species with extreme trait values. The complementarity effect is resource partitioning or positive interactions that lead to increased total resource use, or in other words, the complementarity effect is a permanent association between species that enhances collective performance. The two are separated through equation f. for net biodiversity effect (ΔY):

$$f. \quad \Delta Y = N \text{Cov}_{uw}(\Delta RY, M) + N E_{uw}(\Delta RY) E_{uw}(M)$$

where $\Delta RY_i = RY_{Oi} - RY_{Ei}$ is the difference between the observed yield of a mixture (RY_{Oi}) and its expected yield (RY_{Ei}) under the null hypothesis that there is no selection effect or complementarity effect. The expected value is the weighted average of the monoculture yields. Y_{Oi} and Y_{Ei} represent the observed and expected yield of species i . N is species richness and M_i is the monoculture yield of species i . RY_{Oi} is the observed relative yield of species i in mixture, and RY_{Ei} is expected relative yield of species i in mixture. Positive selection occurs if species with higher than average monoculture yields dominate the mixtures. Expressed in the first term of ΔY , the selection effect is measured by the covariance between the monoculture yield of species and their change in relative yield in mixture. Finally, a positive complementarity effect occurs if species yields in a mixture are

on average higher than expected on the basis of the weighted average monoculture yield of the species. Based on predictions from this model, the selection effect is zero on average and ranges from negative to positive in different locations depending on if communities are dominated by species with lower than average biomass or higher than average biomass. The model also predicts that the complementarity effect is overall positive, supporting Loreau and Hector's hypothesis that plant diversity influences primary production in grasslands through niche partitioning or facilitation (Loreau and Hector 2001). This theoretical approach of parsing out mechanisms and understanding their connection to ecosystem biodiversity and productivity is expanded by Carroll *et al.* (2011).

Carroll *et al.*'s mechanistic competition model links the causes and consequences of biodiversity through niche difference, which promotes coexistence, and fitness difference, which promotes competitive exclusion:

g.
$$S_i \equiv \frac{g_i(\mathbf{O}) - g_i(\mathbf{I}_{-i})}{g_i(\mathbf{O})}.$$

h.
$$\text{ND} \equiv 1 - \prod_{i=1}^n S_i^{1/n}$$

i.
$$\text{RFD} \equiv \exp \left[\left(\overline{(\ln S)^2} - \ln S^2 \right)^{1/2} \right]$$

j.
$$\text{RYT} = \frac{2 - (1 - \text{ND})(\text{RFD} + \text{RFD}^{-1})}{\text{ND}(2 - \text{ND})}.$$

Sensitivity (S) to competition is expressed in terms of growth rate in monoculture ($g_i(0)$)

and mixture ($g_i(I_i)$). Niche difference (ND) is defined by an average effect of interspecific competition (expressed in terms of sensitivity values in the model) and relative fitness difference (RFD) is defined by the variability in these effects. These two differences between individuals that influence coexistence also control the effect of biodiversity on biomass yield. Relative yield total (RYT) quantifies the influence of consumer diversity on consumer biomass at equilibrium, and it is expressed in terms of niche difference and relative fitness difference. RYT increases when mechanisms of coexistence increase, specifically when niche difference increases or when fitness differences decrease (Carroll *et al.* 2011).

Carroll *et al.* (2011) compare their model to Loreau and Hector's model of additive partitioning. Based on their own analysis, Carroll *et al.* claim that the complementarity effect gives a largely skewed estimate of resource partitioning and that the selection effect does not seem to isolate biomass changes attributable to species composition rather than species richness. This criticism has sparked debate between the modelers, and it is presently unclear if one model is more biologically accurate than the other (Carroll *et al.* 2012; Loreau *et al.* 2012). Regardless of any limitations or disagreements, Lotka-Volterra equations, MacArthur's Consumer-Resource Model, Tilman's R^* , Loreau and Hector's additive partitioning of biodiversity effects model, and Carroll *et al.*'s mechanistic competition model together form the core of competition theory. These theoretical models can be used to understand and solve problems, such as how invasive species competitively exclude native species.

Competition Theory in a Novel World – Invasive Species

Invasive species spread rapidly through ecosystems and reduce and eliminate

populations of native species through competitive exclusion (Usher *et al.* 1986; Melgoza *et al.* 1990; Wootton 1994; Petren and Case 1996; Ricciardi *et al.* 1998; Holway *et al.* 2002). The exact relationship between invasive species success and their competitive ability has rarely been confirmed experimentally, so theoretical models provide the best means to understand the competitive dynamics underlying invasions (Davis 2003; Levine *et al.* 2003). Based on the relative abundances of invasive to resident species, I expect invasive species to have small niche differences and large fitness differences with native species, resulting in competitive exclusion of native species.

Large fitness differences presumably result from the high fitness of invasive species since, compared to non-invasive species, invasive species experience fewer life history trade-offs. Dominant non-invasive species are limited by low fecundity, low recruitment ability, and short dispersal ranges. These life history trade-offs minimize fitness differences, allowing both dominant and subordinate non-invasive species to coexist (Levins and Culver 1971; Hastings 1980; Tilman *et al.* 1994; Chesson and Huntly 1997; Bolker and Pacala 1999). However, it is possible that invasive species experience fewer trade-offs because they have been released from the pressure of their natural pests and predators and have reallocated resources used for defense into reproduction and growth (Keddy *et al.* 1994; Blossey and Notzold 1995; Sakai *et al.* 2001). Confirmation of these theories should be tested experimentally and further development of models.

Literature Cited

- Abrams, P.A. 1975. Limiting similarity and the form of the competitive coefficient. *Theoretical Population Biology* **8**: 356-375.
- Armstrong, R.A. and R. McGhee. 1976. Coexistence of species competing for shared resources. *Theoretical Population Biology* **9**: 317-328.
- Ashton, I.W., A.E. Miller, W.D. Bowman, and K.N. Suding. 2010. Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* **91**: 3252-3260.
- Begon, M.L., J.L. Harper, C.R. Townsend. 1996. *Ecology: Individuals, Populations, and Communities*. 3rd edition. Blackwell Science Ltd. Cambridge, MA.
- Berg, W.A. 1993. Old World bluestem response to fire and nitrogen fertilizers. *Journal of Range Management* **46**: 421-425.
- Bever, J.D. 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist* **157**: 465-473.
- Blossey, B. and R. Notzold. 1995. Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *J. Ecol.* **83**: 887-889.
- Bolker, B.M. and S.W. Pacala. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.* **153**: 575-602.
- Brown, J.H., D.W. Davidson, and O.J. Reichman. 1979. An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist* **19**: 1129-1143.
- Bryan, G.G. and McMurphy, W.E. 1968. Competition and fertilization as influences on grass seedlings. *Journal of Range Management* **21**: 98-101.

- Carroll, I.T., B.J. Cardinale, and R.M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* **92**: 1157-1165.
- Carroll, I.T., B.J. Cardinale, and R.M. Nisbet. 2012. Niche and fitness differences relate the maintenance of diversity to ecosystem function: reply. *Ecology* **93**: 1487-1491.
- Chesson, P. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology* **28**: 263-287.
- Chesson, P. 1991. A need for niches? *Trends in Ecology and Evolution* **6**: 26-28.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**: 343-366.
- Chesson, P. 2008 Quantifying and testing species coexistence mechanisms. Pages 119-164. F. Valladares, A. Camacho, A. Elosegui, C. Gracia, M. Estrada, J.C. Senar, and J.M. Gili, editors. *Unity in Diversity: Reflection on Ecology after the Legacy of Romon Margelef*. Fundacion BBVA, Bilbao.
- Chesson, P. and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology and Evolution* **4**: 293-298.
- Chesson, P. and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* **150**: 519-553.
- Chesson, P. and R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* **117**: 923-943.
- Clark, P.J. and F.C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* **35**: 445-453.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the

- distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**: 710-723.
- Dabo, S.M., C.M. Taliaferro, S.W. Coleman, F.P. Horn, and P.L. Claypool. 1987. Yield and digestibility of Old World bluestem grasses as affected by cultivar, plant part, and maturity. *Journal of Range Management*. **40**: 10-15.
- Dabo, S.M., C.M. Taliaferro, S.W. Coleman, F.P. Horn, and P.L. Claypool. 1988. Chemical composition of Old World bluestem grasses as affected by cultivar and maturity. *Journal of Range Management* **41**: 40-48.
- Davis, M.A. 2003. Biotic globalization: does competition from introduced species threaten biodiversity. *BioScience* **53**: 481-489.
- Duke, J.A. and E.E. Terrell. 1974. Drop diversification matrix: introduction. *Taxon* **23**: 759-799.
- Gabbard, B.L. and N.L. Fowler. 2007. Wide ecological amplitude of a diversity reducing invasive grass. *Biological Invasions* **9**: 149-160.
- Gause, G.F. 1934. *The struggle for existence*. Hafner Publishing Company. New York, USA.
- Gotelli, N.J. 1998. *A Primer of Ecology*. 2nd edition. Sinauer Associates Inc. Sunderland, MA.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. Chichester, UK: John and Wiley & Sons Ltd.
- Hanselka, C. W. and F.S. Guthery. 1991. Bobwhite quail management in South Texas. *South Texas Rangelands*. Texas Agricultural Extension Service.
- Harrington, L.A., A.L. Harrington, N. Yamaguchi, M.D. Thom, P. Ferreras, T.R. Windham, and D.W. MacDonald. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? *Ecology* **90**: 1207-1216.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical*

- Population Biology **18**: 363-373.
- Hatfield, J. and P. Chesson. 1996. Multispecies lottery competition: a diffusion analysis. Pages 615-622 of *Structured Population Models in Marine, Freshwater, and Terrestrial Systems*. S. Tuljapurkar and H. Caswell. Chapman and Hall, New York, USA.
- Hayashi, R. and K. Tsuji. 2008. Spatial distribution of turtle barnacles on the green sea turtle, *Chelonia mydas*. *Ecol Res* **23**: 121-125.
- Hickman, K.R., G.H. Farley, R. Channell, and J.E. Steier. 2006. Effects of Old World bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. *The Southwestern Naturalist* **51**: 524-530.
- Holway, D.A., L. Lach, A.V. Suarez, N.D. Tsutsui, and T.J. Case. 2002. The causes and consequences of ant invasions. *Ann. Rev. Ecol. Syst.* **33**: 181-233.
- Huffakers, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**: 343-383.
- Hutchinson, G.E. 1965. The ecological theater and the evolutionary play. Page 139. Yale University Press, New Haven, Connecticut.
- Hutson, J.E., B.S. Rector, L.B. Merrill, and B.S. Engdahl. 1981. Nutritional Value of Range Plants in the Edwards Plateau Region of Texas. San Angelo, TX: Texas Agricultural Experiment Station. B-1357: 5-16.
- Keddy, P.A., L. Twolan-Strutt, and I.C. Wisheu. 1994. Competitive effect and response in 20 wetland plants: Are they consistent across three environments? *J. Ecol.* **82**: 635-643.
- Lee, B.A.V., R.S. Lutz, L.A. Hansen, N.E. Mathews. 1999. Effects of supplemental prey, vegetation, and time on success of artificial nests. *The Journal of Wildlife*

- Management **63**: 1299-1305.
- Levine, J.M., M. Vila, C.M. D'Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London B* **270**: 775-781.
- Levins, R. and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proc. Natl. Acad. Sci. USA*. **68**: 1246-1248.
- Loreau, M. and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**: 72-76.
- Loreau, M., J. Sapijanskas, F. Isbell, and A. Hector. 2012. Niche and fitness differences relate the maintenance of diversity to ecosystem function: comment. *Ecology* **93**: 1482-1487.
- MacArthur, R.H. 1970. Species packing and competitive equilibrium for many species. *Theoretical Population Biology* **1**: 1-11.
- MacArthur, R.H. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**: 377-387.
- MacIsaac, H.J. and J.J. Gilbert. 1991. Discrimination between exploitive and interference competition between Cladocera and *Keratella cochlearis*. *Ecology* **72**: 924-937.
- May, R.M. and M.P. Hay. 1981. The dynamics of multi-parasitoid host interactions. *Am. Nat.* **117**: 234-261.
- Mayer, P.M., S.J. Tunnell, D.M. Engle, E.E. Jorgensen, and P. Nunn. 2005. Invasive grass alters litter decomposition by influencing macrodetritivores. *Ecosystems* **8**: 200-209.
- McCoy, S.D., J.C. Mosley, and D.M. Engle. 1992. Old World bluestem seedlings in Western Oklahoma. *Rangelands* **14**: 41-44.

- McFarland, M.L., D.N. Ueckert, and S. Hartmann. 1987. Revegetation of oil well reserve pits in West Texas. *Journal of Range Management* **40**: 122-127.
- Melgoza, G., R.S. Nowak, R.J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* **83**: 7-13.
- Pase, C.P. 1971. Effect of a February burn on Lehman Lovegrass. *Journal of Range Management* **24**: 454-456.
- Petren, K. and T.J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* **77**: 118-132.
- Ricciardi, A., R.J. Neves, and J.B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *J. Anim. Ecol.* **67**: 613-619.
- Ruckman, E.M., S. Schwinning, and K.G. Lyons. 2012. Effects of phenology at burn time on post-fire recovery in an invasive C₄ grass. *Restoration Ecology* **20**: 756-763.
- Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. 2001. The population biology of invasive species. *Ann. Rev. Ecol. Syst.* **32**: 305-332.
- Schmidt, C.D., K.R. Hickman, R. Channell, K. Harmony, and W. Stark. 2008. Competitive abilities of native grasses and non-native (*Bothriochloa* spp.) grasses. *Plant Ecology* **197**: 69-80.
- Schoener, T.W. 1976. Alternatives to Lotka-Volterra competition: models of intermediate complexity. *Theoretical Population Biology* **10**: 309-333.
- Schoener, T.W. 1983. Field experiences on interspecific competition. *American Naturalist*.

122: 240-285.

Snyder, R. and P. Chesson. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecology Letters* **6**: 301-309.

Tannerfeldt, M., B. Elmhagen, and A. Angerbjorn. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132**: 213-220.

Tilman, D. 1980. A graphical-mechanistic approach to competition and predation. *American Naturalist* **116**: 362-393.

Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ USA.

Tilman, D., R.M. May, C.L. Lehman, and M.A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* **371**: 65-66.

Usher, M.B., H. Kornberg, J.W. Hornwood, R. Southwood, and P.D. Moore. 1986. Invasibility and wildlife conservation: invasive species on nature reserves [and discussion]. *Phil. Trans. R. Soc. Land B* **314**: 695-710.

Volterra, V. 1928. Variations and fluctuations in the number of individuals in animal species living together. *Ices Journal of Marine Sciences* **3**: 3-51.

Wilcox, B.P. 2010. Transformative ecosystem change and ecohydrology: ushering in a new era for watershed management. *Ecohydrology* **3**: 126-130.

Wiley, B.J. and H.W. Polley. 2006. Aboveground productivity and root-shoot allocation differ between native and introduced grass species. *Oecologia* **150**: 300-309.

Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological

communities. *Ann. Rev. Ecol. Syst.* **25**: 443-446.

Chapter 2

Introduction

With the aim of developing a mechanistic model to partition the elements of species competitive dynamics into niche and relative fitness differences, Carroll *et al.* (2011) published a novel approach based on MacArthur's Consumer-Resource Model (MacArthur 1970). Their contribution advanced the field through development of a biologically relevant model that allowed species interactions to be partitioned into niche and relative fitness differences through relatively straight-forward metrics that removed the requirements which make it difficult to measure resource fluctuations. It can be used to assess the mechanisms underlying novel interactions, specifically invasive species.

To investigate the mechanisms underlying competitive exclusion of native species by non-native invasive species, I applied data collected through competition study to the Carroll *et al.* model published in 2011 in *Ecology*. The model was derived directly from MacArthur's Consumer Resource Model (MC-RM) (MacArthur 1970) and aimed to partition the mechanisms of competition into niche and relative fitness differences and relative yield total based on each species' sensitivity to being grown alone and in competition. The model is suggested to work for n competing species (p. 1159-1160). I tested the applicability of the model in a two species grassland ecosystem in which I grew a focal native species sideoats grama (SOG) in intraspecific competition and in interspecific competition with a focal non-indigenous, invasive grass species King Ranch (KR) bluestem. Each monoculture pot contained 16 individuals, and each mixture pot contained 8 individuals of each species for a total density of 16 individuals. Four weeks after initial seeding, harvests were conducted in one week intervals. Three replicates were planted for

each harvest. Samples were dried for two days in a Fisher Scientific Isotemp oven at 70°C before aboveground biomass (AGB) and belowground biomass (BGB) of individuals were weighed. Total biomass (AGB + BGB) measurements were then used in the Carroll *et al.* model to calculate the species relative sensitivities to growth in intra- and interspecific environments (Table 1, Eq. 1); however, I discovered insurmountable limitations of the model, one of which was reported by Loreau *et al.* 2012, also in *Ecology*. The Carroll *et al.* model engaged us to think more deeply about the mechanisms driving competitive dynamics and the potential to model these processes. Here, I expand on the previous critique of the Carroll *et al.* model and offer suggestions for improving the model to better approximate real-world scenarios.

Carroll et al. Model

The Carroll *et al.* provide an exciting and novel approach to modeling competitive dynamics between species. The work advanced the field in a number of ways. First, the model aimed to characterize the mechanisms underlying competitive dynamics. While most models deal only with the outcomes of competition, Carroll *et al.*'s model aimed to partition competition into species niche differences (ND) and relative fitness differences (RFD) (Table 1, Eq. 2 and 4 respectively) (Grime 1979, Diggle 1976, Grace 1995, Weiner and Conte 1981). Secondly, incorporation of RFD is novel, since most models of competitive dynamics focuses solely on ND (Leibold 1995, Meentemeyer *et al.* 2008, Albrecht and Gotelli 2001, Kearney 2006). Distinction of this factor made the model particularly appealing for a study of invasive species that presumably have large RFD as compared to resident species and may partition resources in a less than predictable manner. These two

parameters are calculated based on each species' sensitivity to competition (Eq.1, Table 1)

Sensitivity is a function of growth rate in monoculture ($g_i(\mathbf{O})$) and mixture ($g_i(\mathbf{I}_{-i})$):

$$l. \quad S_i \equiv \frac{g_i(\mathbf{O}) - g_i(\mathbf{I}_{-i})}{g_i(\mathbf{O})}.$$

$$m. \quad ND \equiv 1 - \prod_{i=1}^n S_i^{1/n}$$

$$n. \quad RFD \equiv \exp \left[\left(\overline{(\ln S)^2} - \ln S^2 \right)^{1/2} \right]$$

If two species have a small ND, then examining RFD becomes important to determine the degree of competitive exclusion of the less fit species.

Thirdly, once S, ND, and RFD have been calculated, the model provides a link between the competitive outcomes and the productivity of a system through the relative yield total (RYT) (Eq. 7, Table 1):

$$k. \quad RYT = \frac{2 - (1 - ND)(RFD + RFD^{-1})}{ND(2 - ND)}.$$

This equation provides a means to understand the causes and consequences of biodiversity (i.e., complementarity) in a system and is therefore an important tool in understanding biodiversity-productivity relationships in systems (Carroll *et al.* Appendix B p. 2). Finally unlike many other competition models, the Carroll *et al.* model does not contain a resource variable and many of the other difficult ascertain variables that MC-RM contains. While the absence of these variables may be an oversimplification, the reduction in the variables that

need to be measured or approximated allows the model to be more easily applied to real systems, particularly systems where resource availability and acquisition can be difficult to track (*e.g.* soils). Growth rates in monoculture and mixture are the only variables that need to be measured to use this model. Thus, the ease with which the model can be applied to real systems facilitates a bridging of the gap between theoretical and applied research.

Nonetheless, my process of applying the Carroll *et al.* model to a competition experiment revealed three limitations. The first is that, despite claims made in the paper (p. 1160), the model mathematically excludes situations in which sensitivity values are negative. In other words, the model does not account for positive species interactions such as facilitation. In my system, *B. curtipendula* (the native species) follows the general expectation of species grown in competition with a higher growth rate in monoculture than in mixture. *B. ischaemum* (the non-indigenous, invasive species), however, has a higher growth rate when in mixture than when in monoculture (Figure 1). This result is supported by a previous study finding that *B. ischaemum* growth enhanced when grown in mixture with *Schizachyrium scoparium*, another native grass (Schmidt *et al.* 2008). The model does not account for facilitative effects. When the growth rate is greater for inter- than intraspecific competition, S (Eq.1, Table 1) becomes negative (Table 2). Since the ND equation uses a geometric mean, a negative S value cannot be applied to the ND equation. If an arithmetic mean is used instead of a geometric mean, negative sensitivity value(s) can result in a ND value of greater than 1. ND in this model scales between 0 and 1. Based on the Carroll *et al.* equation of ND, a ND value >1 is not scaled and could therefore be any value >1 . Since ND values >1 lack definition and also cannot be compared (*e.g.* how does a value of 0.3 compare to a value of 2?), negative sensitivity values resulting in ND values >1

violate the boundaries of the Carroll *et al.* model (Eq. 2, Table 1). Therefore, since negative sensitivity values are incompatible with the Carroll *et al.* model, the model mathematically excludes positive species interactions.

A second limitation in the Carroll *et al.* model, again, despite claims made by the authors, is that it applies only to two species systems. In their appendix, Carroll *et al.* present the derivation for ND, but do so for only two competing species. This expression for two species was then generalized for n number of species. I followed the same derivation and found that when ND for two species is derived from MC-RM, the equation is the same as the equation Carroll *et al.* proposes. However, I realized that the same argument cannot be expanded for three or more species. Therefore, I found that mathematically the expression cannot be expanded to more than a two species system (Eq. 2, Table 1; Table 3). The same conclusion was found previously using mathematical analytics with a four species system (Loreau *et al.* 2012).

The final issues I identified was confusing mathematical notation in the RFD equation. The RFD is the geometric standard deviation of the S values and the mathematical notation presented by Carroll *et al.* is confusing in its placement of the bars (Eq. 4, Table 1).

o.
$$RFD = \exp \sqrt{(\ln S)^2 - \ln(S^2)}$$

I present the notation of the RFD equation according to how I understand the equation and in notation that is clearer (Eq. 5, Table 1).

p.
$$RFD = \exp \sqrt{(\ln S)^2 - (\ln \bar{S})^2}$$

Proposal for a New Model

Since the strengths of the Carroll *et al.* model outweigh the limitations, I sought to overcome these limitations and propose a new direction for the model. The equation for S is unchanged from the Carroll *et al.* model since I found no limitations in this equation and was successfully able to derive it from MC-RM; however, changes were made to the remaining three equations.

The equation for ND underwent two modifications. The scope of the equation remains limited to two species since ND can only apply to two-species systems based on the mathematical derivation and simulations (Loreau *et al.* 2012). For situations in which species 1 and species 2 both have positive values of S, I made no further changes to the equation (Eq. 3a, Table 1). I propose a new equation for situations in which species 1 or species 2 are facilitated by the presence of the species. In other words, one of the species has a negative value of S (Eq. 3b, Table 1).

$$\text{r. } ND = \begin{cases} 1 - \sqrt{S_1 S_2} & \text{if } S_1 \text{ and } S_2 \text{ is positive} \\ 1 - \sqrt{\frac{S_1^2 + S_2^2}{2}} & \text{if } S_1 \text{ or } S_2 \text{ is negative} \end{cases}$$

This new equation accommodates both positive and negative values of S. Further, both of the equations for positive and negative S values produce ND values between 0 and 1.

The newly derived equation has two limitations; first, the equation is not derived from MC-RM. Second, it is an underestimation of the equation for positive S values (Figure 2). I find these limitations as acceptable tradeoffs in order to broaden the range of represented species interactions. Though in order to mitigate these limitations, I

incorporate both the ND equation based on the Carroll *et al.* model for positive S values and the ND equation I created for negative S values in order to maintain a connection to MC-RM (Eq. 3a, 3b, Table 1). In both the Carroll *et al.* model and the new model, RFD is a measure of the standard deviation of S. I changed the equation to an arithmetic standard deviation instead of a geometric standard deviation in order to accommodate situations in which an S value is negative (Eq. 6, Table 1).

s.
$$RFD = \sqrt{(S_1 - \bar{S})^2 + (S_2 - \bar{S})^2}$$

The equation for RYT is a summation of the two relative yields derived from MC-RM. Again, Carroll *et al.* uses a geometric approach while I use an arithmetic approach in order to accommodate for negative S values (Eq. 7 and 8 respectively, Table 1).

t.
$$RYT = \frac{2(1 - \bar{S})}{1 - S_1 S_2}$$

The Carroll *et al.* RYT equation and my RYT equation look wildly different because Carroll *et al.* chose to substitute S for the equivalent ND and RFD terms. I chose to leave the equation in its simplest form that expressed RYT in terms of S.

Conclusion and Future Work

My proposed model successfully overcomes the limitations of the Carroll *et al.* model and expands the range of competitive species interactions that can be considered. While I do not resolve every problem mentioned in previous critiques and my own equations have limitations, my proposed model is a step forward towards developing a mechanistic model of multiple species interactions. Currently there is no mechanistic

model that accounts for the complexity and diversity of species interactions in ecosystems and can also uncover who, how, and why ecosystems look and behave in the ways that they do. While no model will be able to do it all, this is a goal that is worth striving for.

Literature Cited

- Albrecht, M. and N.J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. *Oecologia* **126**: 134-141.
- Carroll, I.T., B.C. Cardinale, and R.M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* **92**: 1157-1165.
- Diggle, P.J. 1976. A spatial stochastic model of inter-plant competition. *Journal of Applied Probability* **13**: 662-671.
- Dukes, J.S. 2001. Productivity and complementarity in grassland microcosms of varying diversity. *Oikos* **94**: 468-480.
- Grace, J.B. 1995. On the measurement of plant competition intensity. *Ecology* **76**: 305-308.
- Grime, J. 1979. Plant strategies and vegetation processes. John Wiley and Sons, London, England, United Kingdom.
- Kearny, M. 2006. Habitat, environment, and niche: what are we modeling? *Oikos* **115**: 186-191.
- Leibold, M.A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology* **76**: 1371-1382.
- Loreau, M., J., Sapijanskas, F. Isbell, and A. Hector. 2012. Niche and fitness differences relate the maintenance of diversity to ecosystem function: a comment. *Ecology* **93**: 1482-1487.

MacArthur, R. 1970. Species packing and competitive equilibrium for manyspecies.

Theoretical Population Biology **1**: 1-11.

Meentemeyer, R.K., B.L. Anacker, W. Mark, and D.M. Rizzo. 2008. Early detection of
emerging forest disease using dispersal estimation and ecological niche modeling.

Ecological Applications **18**: 377-390.

Schmidt, C.D., K.R. Hickman, R. Channell, K. Harmony, and W. Stark. 2008. Competitive
abilities of native grasses and non-native (*Bothriochloa* spp.) grasses. Plant Ecology
197: 69-80.

Weiner, J. and P.T. Conte. 1981. Dispersal and neighborhood effects in an annual plant
competition model. Ecological modeling **13**: 131-147.

Tables and Figures

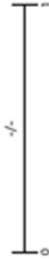

	Carroll et al. model	New model	Definition of variables
Sensitivity (\bar{S})		$S_i = \frac{g_i(O) - g_i(I-i)}{g_i(O)}$ <p>(1)</p>	$g_i(O)$ = growth rate when grown in monoculture $g_i(I-i)$ = growth rate when grown in mixture
Niche difference (ND)	$ND = 1 - \prod_{i=1}^n S_i^{1/n}$ <p>(2)</p> 	$ND = \begin{cases} 1 - \sqrt{S_1 S_2} & \text{if } S_1 \text{ and } S_2 \text{ is positive (3a)} \\ 1 - \sqrt{\frac{S_1^2 + S_2^2}{2}} & \text{if } S_1 \text{ or } S_2 \text{ is negative (3b)} \end{cases}$ 	S_i = sensitivity value of species i n = total number of species S_1 = sensitivity value of species 1 S_2 = sensitivity value of species 2
Relative fitness difference (RFD)	<p>Equation in Carroll et al. article:</p> $RFD = \exp \sqrt{(\ln \bar{S})^2 - \ln(S^2)}$ <p>(4)</p> <p>RFD equation based on Carroll et al. approach with my changes to the notation:</p> $RFD = \exp \sqrt{(\ln \bar{S})^2 - (\ln \bar{S})^2}$ <p>(5)</p>	$(6) \quad RFD = \sqrt{(S_1 - \bar{S})^2 + (S_2 - \bar{S})^2}$	S_1 = sensitivity value of species 1 S_2 = sensitivity value of species 2 \bar{S} = average of sensitivity values
Relative yield total (RYT)	$RYT = \frac{2 - (1 - ND)(RFD + RFD^{-1})}{ND(2 - ND)}$ <p>(7)</p>	$RYT = \frac{2(1 - \bar{S})}{1 - S_1 S_2}$ <p>(8)</p>	S_1 = sensitivity value of species 1 S_2 = sensitivity value of species 2 \bar{S} = average of sensitivity values ND = niche difference RFD = relative fitness difference

Table 1: Comparison of Carroll *et al.* model and the proposed new model's equations for sensitivity to competition (S), niche difference (ND), relative fitness difference (RFD), and relative yield total (RYT). Numbers to the left of each equation provide a reference number for each equation.

$$S_i = \frac{g_i(O) - g_i(L_i)}{g_i(O)}$$

In the case of King Ranch bluestem competing with sideoats grama:

$$g_i(O) = \text{growth rate in monoculture} = 0.0454\text{g/harvest}$$

$$g_i(L_i) = \text{growth rate in mixture} = 0.0505\text{g/harvest}$$

$$S_i = \frac{0.0454 - 0.0505}{0.0454} = -0.1123$$

$$n = \text{number of species} = 2$$

$$ND = 1 - \prod_{i=1}^2 S_i^{1/2}$$

Table 2: Example of exclusion of facilitative species interactions in the Carroll *et al.* model. Compared to when grown in mixture with sideoats grama (*Bouteloua curtipendula*), King Ranch bluestem has a lower growth rate (*Bothriochloa ischaemum var songaricus*) when grown in monoculture (0.0505 g/harvest and 0.0454 g/harvest respectively). Therefore, the sensitivity value (S) of King Ranch bluestem is negative. Niche difference (ND) cannot be calculated since the square root of a negative value is imaginary. Therefore since ND cannot be calculated using this ND equation from the Carroll *et al.* model, this model excludes facilitative interactions.

$$\frac{dR_i}{dt} = R_i r_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^n c_{ji} R_i X_j, \quad \text{for } i = 1, \dots, q$$

$$\frac{dX_i}{dt} = X_i b_i \left(\sum_{j=1}^q c_{ij} w_j R_j - m_i \right), \quad \text{for } i = 1, \dots, n$$

Equilibrium:

$$\frac{dR_i}{dt} = 0 = R_i r_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^n c_{ji} R_i X_j$$

$$\frac{dX_i}{dt} = 0 = X_i b_i \left(\sum_{j=1}^q c_{ij} w_j R_j - m_i \right)$$

$$0 = R_i r_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^n c_{ji} R_i X_j$$

$$R_i = \max \left(0, K_i - \frac{K_i}{r_i} \sum_{j=1}^n c_{ji} X_j \right)$$

assume $R_i > 0$ for all $i = 1, \dots, q$

$$R_i^* = K_i - \frac{K_i}{r_i} \sum_{j=1}^n c_{ji} X_j$$

$$0 = X_i b_i \left(\sum_{j=1}^q c_{ij} w_j R_j - m_i \right)$$

$$m_i = \sum_{j=1}^q c_{ij} R_i w_j$$

Definitions:

$$k_i = \sum_{h=1}^q c_{ih} w_h k_h - m_j \quad (1)$$

$$a_{ij} = \sum_{h=1}^q c_{ih} c_{jh} \frac{w_h k_h}{r_h} \quad (2)$$

$$R_i^* = K_i - \frac{K_i}{r_i} \sum_{j=1}^n c_{ji} x_j^* \quad (3)$$

In order to standardize, we combine Equation (3) with Equations (1) and (2)

$$\sum_{j=1}^n a_{ij} x_j^* = 1 \quad (4)$$

We introduce for simplification purposes a last standardisation term

$$x_j^* = \frac{x_j^*}{k_j a_{ij}^{-1}} \quad (5)$$

and using (5), we obtain the equation

$$\sum_{j=1}^n a_{ij} \frac{k_j}{k_i} a_{ij}^{-1} x_j^* = 1 \quad (6)$$

For 2 species, that is, $n = 2$ (i = index of species), Equation (6) becomes:

$$\frac{a_{i1} k_1}{a_{11} k_i} x_1^* + \frac{a_{i2} k_2}{a_{22} k_i} x_2^* = 1 \quad (7)$$

Noting that $S_1 = \frac{a_{12} k_2}{a_{22} k_1}$, $S_2 = \frac{a_{21} k_1}{a_{11} k_2}$.

Thus (7) becomes

$$\begin{cases} x_1^* + S_1 x_2^* = 1 \\ x_2^* + S_2 x_1^* = 1 \end{cases} \quad (8)$$

$$x_1^* = \frac{1 - S_1}{1 - S_1 S_2}, \quad x_2^* = \frac{1 - S_2}{1 - S_1 S_2}$$

x_2^* is defined provided that $1 - S_1 S_2 \neq 0$, that is, $1 - \sqrt{S_1 S_2}$.
Hence the equation of the Niche Difference for two species.

$$ND = 1 - \sqrt{S_1 S_2}.$$

Carroll et al. expanded to $n(n \geq 2)$ species:

$$ND = 1 - \sqrt[n]{S_1 S_2 \cdots S_n}.$$

However using (7) we show that this equation cannot be expanded to systems of more than two species.

Table 3: Derivation of the Carroll *et al.* model equation for niche difference from MacArthur's Consumer-Resource model and proof of the limitation of the Carroll et al equation for niche difference to systems of two species systems.

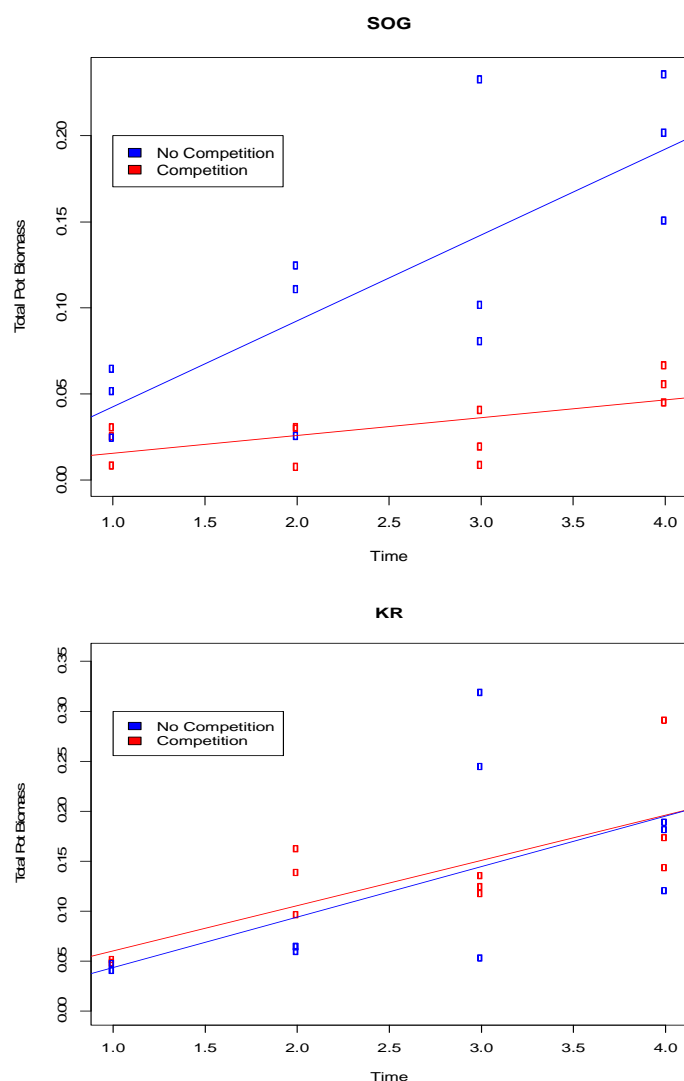


Figure 1: Time (harvests) versus total pot biomass (grams) for *Bouteloua curtipendula* (left) and (b) *Bothriochloa ischaemum var songaricus* (right) when grown in intraspecific and interspecific competition. *B. curtipendula* has a higher biomass when grown in monoculture than in mixture (0.0499 g/harvest and 0.0103 g/harvest respectively). In contrast, *B. ischaemum var songaricus* has a higher biomass when grown in mixture than in monoculture (0.0454 g/harvest and 0.0505 g/harvest respectively). Red colored points

represent total pot biomass measurements in mixture and blue colored points represent total pot biomass measurements in monoculture.

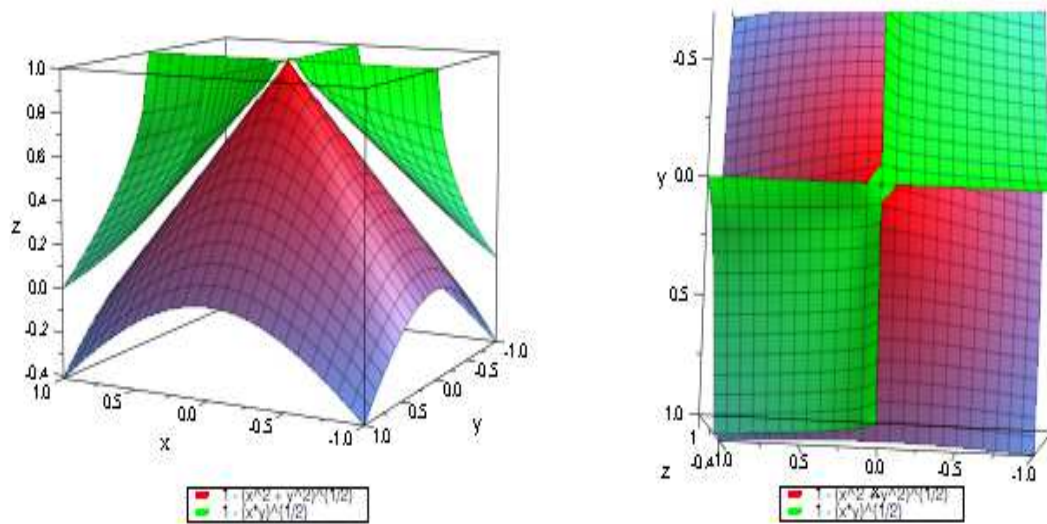


Figure 2: Side and aerial view of a three dimensional representations of sensitivity value of species 1 (S1), sensitivity value of species 2 (S2), and niche difference. Since sensitivity values (S) and niche difference (ND) values range between 0 and 1, all possible value combinations are graphically represented. The double diamond shaped, green figure represents the Carroll *et al.* model equations of S and ND (Eq. 1 and Eq.2, 3a respectively, Table 1). The tent shaped, purple figure represents my revision to the Carroll *et al.* model equation for ND (Eq. 3b, Table 1). Although my equation for ND (Eq. 3b, Table 1) is an underestimation of the Carroll *et al.* equation for ND (Eq. 2, 3a, Table 1), my ND equation does encompass all species interactions while the Carroll *et al.* ND equation excludes facilitative interactions as can be visualized by the presence of gaps in the Carroll *et al.* graphical representation.

Chapter 3

Introduction

King Ranch bluestem is an invasive, non-indigenous C4 grass and is responsible for homogenizing grasslands in the United States, primarily in Texas and Oklahoma (Gabbard and Fowler; Ruckman *et al.* 2012). Native to Eurasia, KR bluestem was originally brought to the United States to prevent erosion and improve pastures (Bryan and McMurphy 1968; Dabo *et al.* 1987). It has been used for 60 years or more, but the release of new, well-adapted cultivars has resulted in a dramatic increase in its use in the last 15 years (Dabo *et al.* 1988; McCoy *et al.* 1992). In addition to being used to prevent erosion and improve pastures as well as for re-vegetation of oil well reserve pits, restoration of wildlife habitat, and replacement of narcotic crops (Duke and Terrell 1974; McFarland *et al.* 1987; Lee *et al.* 1999). The spread of KR bluestem threatens conservation of savannas and subtropical grasslands since it reduces native biodiversity and transforms fundamental ecosystem processes (Mayer *et al.* 2005; Hickman *et al.* 2006; Wiley and Polley 2006; Schmidt *et al.* 2008; Wilcox 2010). KR bluestem is estimated to currently dominate 1 million hectares and this number is increasing (Ruckman *et al.* 2012). KR bluestem control methods have largely failed thus far. Therefore, a mechanistic understanding into how KR bluestem outcompetes native species may help in the search for more effective control measures. (Pase 1971; Berg 1993; Gabbard and Fowler 2007).

In the study described here, I focus on sideoats grama (*Bouteloua curtipendula*) and little bluestem (*Schizachyrium scoparium*), two native perennial C4 bunchgrasses currently being displaced by KR bluestem in Texas grasslands (Gabbard and Fowler 2006; Schmidt *et al.* 2007). They are considered to have high forage value, and exist in higher diversity

grassland ecosystems that provide cover and food resources for wildlife. Therefore, reductions in the prevalence of these two native species result in reductions in forage for wildlife and livestock and shelter for endangered species such as the Bobwhite quail (*Colinus virginianus*) (Hutson *et al.* 1981; Hanselka and Guthery 1991). Thus, the devastating decline of sideoats grama (SOG) and little bluestem (LB), among other species like them, makes understanding the mechanisms underlying the success of KR bluestem important.

Since KR bluestem excludes native species through competition, I hypothesize that KR bluestem and native species have small niche differences and large fitness differences. As C4 perennial bunchgrasses, KR bluestem, SOG, and LB are functionally similar, and therefore I hypothesize that they have a high degree of niche overlap. For example, these three species presumably overlap in functions such as germination time since they respond to environmental factors with similar responses, leading to intense competition. KR bluestem is expected to overlap more in niche with SOG than LB based on field observations. LB is relegated to shade found under tree crowns in mostly monocultures, and KR exists in high light in monocultures and mixtures with shade intolerant natives, including SOG (Fowler 2005). Invasive species experience fewer life trade-offs than native species because they have been released from the pressure of their natural pests and predators and have reallocated resources used for defense into reproduction and growth (Keddy *et al.* 1994; Blossey and Notzold 1995; Sakai 2001). Therefore, I hypothesize that KR bluestem has a large relative fitness difference with native species. I test this hypothesis by conducting a seedling competition study and by then applying this data to my modified version of Carroll *et al.*'s mechanistic competition model. This approach will

uncover the mechanisms that allow KR bluestem to be a successful invasive species. This information has the potential to be used to explore management practices to tip the scales to prevent, and even reverse (through native biocontrols), the establishment and spread of KR bluestem seedlings.

Plant establishment and growth are largely impacted by the mechanisms of seedling competition since outcomes of competition at the seedling stage will impact competitive dynamics during later life stages (Watt 1955; Keddy 2001; Howard and Goldberg 2001; Lamb and Cahill 2006). Seedling competition mechanisms can be described using a mechanistic competition model by Carroll *et al.* (2011).

$$u \quad S_i = \frac{g_i(O) - g_i(I_{-i})}{g_i(O)}$$

$$v. \quad ND = \begin{cases} 1 - \sqrt{S_1 S_2} & \text{if } S_1 \text{ and } S_2 \text{ is positive} \\ 1 - \sqrt{\frac{S_1^2 + S_2^2}{2}} & \text{if } S_1 \text{ or } S_2 \text{ is negative} \end{cases}$$

$$x. \quad RFD = \sqrt{\frac{(S_1 - \bar{S})^2 + (S_2 - \bar{S})^2}{2}}$$

$$y. \quad RYT = \frac{2(1 - \bar{S})}{1 - S_1 S_2}$$

This model links the causes and consequences of biodiversity through niche difference, which promotes coexistence, and fitness difference, which promotes competitive exclusion. Niche difference is defined by an average effect of interspecific competition (expressed in terms of sensitivity values in the model), and relative fitness difference is defined by the variability in these effects. These two differences between organisms that influence

coexistence also control the effect of biodiversity on biomass yield. Relative yield total quantifies the influence of consumer diversity on consumer biomass at equilibrium and is expressed in terms of niche difference and relative fitness difference. Relative yield total increases as mechanisms of coexistence are promoted, specifically when niche difference increases and when relative fitness difference decreases (Carroll *et al.* 2011). Therefore, this model quantifies competitive dynamics in order to predict if coexistence or competitive exclusion will occur and how competitive outcomes impact productivity of a system. In Chapter 2, I discussed the limitations of the Carroll *et al.* (2011) model and offered modifications that overcome these limitations. I will use my modified version of the model to investigate the mechanisms underlying the competitive success of invasive species, specifically KR bluestem, at the seedling stage against native species.

Materials and Methods

In order to assess the niche and relative fitness differences between KR bluestem and sideoats grama and between KR bluestem and little bluestem the species were grown in monoculture and each native species was grown with KR bluestem in a substitutive design (Harper 1977). The plants were grown in 8 cm x 8 cm wide and x 7 cm tall pots with monoculture and mixture densities held at a total of two individuals. The plants were grown in a Conviron PGR14 growth chamber. To promote germination, seedlings were grown for the first two weeks in 90% relative humidity, 22°C, and 100 μ mol of light, and for the remaining weeks the plants were grown in 40% relative humidity, 25°C, and 600 μ mol of light to increase stress and promote competition.

Plants were allowed to grow for two weeks before the first harvest. The remaining three harvests occurred in one week intervals. For each harvest, six replicates of each treatment were grown. Date of germination was recorded for individuals in all pots and germination dates of treatments were analyzed using an ANOVA. At the time of harvest, shoot height and root length were recorded. Samples were dried for two days in a Fisher Scientific Isotemp oven at 70°C. Above ground biomass (AGB) and below ground biomass (BGB) values from monoculture pots were divided by two in order to make densities comparable by species in mixture pots. Shoot height, root length, AGB, and BGB for treatments were each compared over time using MANOVA. Growth rates calculated across harvest data were applied to the Carroll *et al.* (2011) model equations with my modifications to quantify sensitivity to competition (S), niche difference (ND), relative fitness difference (RFD), and relative yield total (RYT) for competition between KR and SOG and between KR and LB.

Results

Germination times

Sideoats grama germinated in the least amount of time, and time to germinate between SOG in monoculture and mixture with KR did not differ from one another. All individuals of SOG in monoculture and in mixture with KR germinated in 5 days (Figure. 1; Table 1). Time to germinate of SOG monoculture and mixture with KR were significantly shorter than time to germinate of KR monoculture and KR mixture with LB. KR germination times in monoculture and in mixture with LB did not differ from one another (6.4 ± 0.7 days and 6.1 ± 0.7 days, respectively). LB in monoculture germinated in 6.8 ± 0.8 days, similar to

KR monoculture and KR mixture with LB. Though, LB in mixture with KR germinated in 6.9 ± 0.9 days, which was significantly longer than germination times for KR in monoculture and KR in mixture with LB, but not significantly longer than the germination time of LB in monoculture. Finally, KR in mixture with SOG germinated in 7.4 ± 0.5 days, which was not significantly longer than germination time of LB in mixture with KR, but was significantly longer than all other germination times (Figure 1; Table 1).

Harvest data

Shoot height: KR in monoculture, KR in mixture with SOG, KR in mixture with LB, and LB in monoculture had the shortest shoot heights (Figure 2; Table 2). While they were not significantly different from one another, these four species combinations were significantly shorter than LB in mixture with KR which had an average shoot height. SOG in monoculture and mixture had significantly taller shoot heights than all other species combinations. SOG in monoculture and mixture were not significantly different from one another (Figure 2; Table 2).

Root length: KR in monoculture, KR in mixture with SOG, KR in mixture with LB, SOG in mixture with KR, and LB in mixture with KR had root lengths that were not significantly different from one another (Figure 3; Table 3). LB in monoculture had significantly longer roots than KR in mixture with SOG and in mixture with LB, but LB in monoculture otherwise was not significantly different than the other species combinations in terms of root length. SOG in monoculture had significantly longer roots than all other species combinations except LB in monoculture and in mixture with KR. SOG in monoculture did not have a significantly different root length than LB in monoculture or in mixture with KR (Figure 3; Table 3).

Above ground biomass (AGB): KR in monoculture, in mixture with SOG, and in mixture with LB were not significantly different from one another (Figure 4; Table 4). LB in monoculture was only significantly different in its AGB from KR in mixture with SOG. LB in mixture with KR, SOG in monoculture, and SOG in mixture with KR were significantly larger in AGB than KR in monoculture, in mixture with SOG, and in mixture with LB (Figure 4; Table 4).

Below ground biomass (BGB): KR in monoculture, KR in mixture with SOG, KR in mixture with LB, SOG in mixture with KR, LB in monoculture, and LB in mixture with KR were not significantly different from one another. SOG in monoculture was significantly larger in terms of BGB compared to all other species combinations except for LB in monoculture (Figure 5; Table 5).

Applying data to modified Carroll et al. model

Growth rates for KR in monoculture, mixture with SOG, and mixture with LB were 0.0036 g/harvest, 0.0002 g/harvest, and -6.3×10^{-5} g/harvest respectively. Growth rates for SOG in monoculture and mixture were 0.0114 g/harvest and 0.0012 g/harvest respectively, while growth rates for LB in monoculture and mixture were 0.0064 g/harvest and 0.0049 g/harvest. When KR and SOG were grown together in mixture, KR had a S of 0.964 and SOG had a S of 0.8941. In this treatment, ND was 0.080, RFD was 0.037, and RYT was 1.037. When KR and LB were grown together in mixture, KR has a S of 1.018 and SOG had a S of 0.228. In this treatment, ND was 0.518, RFD was 0.558, and RYT is 0.982.

Discussion

Even though competition dynamics may change through time and life cycles, outcomes of seedling competition are especially important since they determine if a species

will establish and persist in an ecosystem (Grubb 1977; Keddy 2001; Howard and Goldberg 2001; Lamb and Cahill 2006). For example, even if a species is a strong competitor in its adult stage, its population size and distribution may be significantly limited if it is a weak competitor in its seedling stage and therefore unable to establish and persist (Chesson 2000; Howard and Goldberg 2001). Germination times provide first insight into competition outcomes since individuals can experience a significant advantage if germinating earlier than its competitors and can experience a significant disadvantage if germinating later than its competitors (Ellner 1986; Bush and Van Auken 1991).

In this study, SOG germinated in significantly less time than KR and LB. Germinating before other seedlings may give SOG a competitive advantage that enables it to be a dominant native species and to coexist with KR in the field. Also, KR took significantly more time to germinate when grown in mixture with SOG than when growing in monoculture, further increasing SOG's initial competitive advantage in establishing at the expense of KR. On the other hand, LB does not generally coexist with KR in the field when KR is present and LB is relegated to habitat under tree crowns. KR and most native species are not shade tolerant, so LB encounters minimal competition in shady habitats. When growing in or near areas where KR is present, its distributions do not extend too far beyond the tree crown where it would encounter KR (Fowler 2005). Overlap in germination time of LB with KR may further hinder establishment and spread of LB into high light areas from shaded areas.

The light intensity of 600 μmol used in the growth chamber is characteristic of low light conditions under tree crowns in field. Intensity of light in open, high light areas in the field is approximately ranges between 1600 to 1800 μmol (Chazdon and Fetcher 1984; Dai

et al. 2009). Competition dynamics have been found to change as a function of light intensity in subterranean clover (*Trifolium subterraneum*) and in marine phytoplankton (Black 1958; Sommer 1994), so competition dynamics of KR, SOG, and LB may also change as a function of light intensity. Thus, conclusions from the results from this study are limited to competition in field shade conditions.

Comparing growth of SOG and LB in monoculture and in mixture with KR in low light provides further insight into their competitive dynamics. Growth of SOG and LB in monoculture and in mixture with KR reveals a potential strategy to outcompete shade intolerant competitors at the seedling stage. When grown in mixture with KR compared to when grown in monoculture, LB had significantly taller shoots, SOG and LB grew shorter roots, LB had a greater AGB, and SOG had a smaller BGB. These shifts in growth patterns may be indicative of SOG and LB shifting resources from below ground to above ground to create structures to shade out shade intolerant competitors, including KR. SOG increases allocation of resources aboveground to presumably create shade in the presence of KR individuals. Since SOG is also intolerant to shade, SOG does not increase resource allocation aboveground to presumably create shade when grown in monoculture, in order to prevent shading out conspecifics (Fowler 2005). Even though it is shade tolerant, LB follows the same pattern presumably to avoid investment in more photosynthetic pigments and machinery that are necessary in lower light levels (Belsky 1994).

KR is more sensitive when growing in mixture with LB than SOG. KR and LB had a large ND, supporting the field observation that KR grows in open areas while LB is relegated to shady areas when KR is present. A large RFD between KR and LB suggests KR is less fit in shade conditions than LB because of shade intolerance. When grown together,

KR and LB resulted in a lower RYT, or lower biomass productivity, compared to when KR and SOG were grown together. KR had a negative growth rate when grown with LB, creating lower biomass in a system as KR became smaller and eventually absent in shady areas with LB. Therefore, large ND and RFD between KR and LB may be responsible for their rare coexistence in the field. In contrast, small ND and small RFD between KR and SOG are consistent with KR and SOG coexistence in the field.

Since native species do not germinate earlier than invasive competitors, they experience a disadvantage and may have trouble establishing and persisting at the seedling stage (Ellner 1986; Bush and Van Auken 1991; Chesson 2000; Howard and Goldberg 2001). Plug planting may therefore be a more successful alternative to seeding when restoring and managing for native grasslands (Walker *et al.* 2004; Getter and Rowe 2007; Wallin *et al.* 2009). SOG and LB are good candidates for this approach, as well as other grasses that create shade including blue grama (*Bouteloua gracilis*), green sprangletop (*Leptochloa dubia*), and Indian grass (*Sorghastrum nutans*) (Davidson and Davidson 2008). These species may also be effective at shading out other shade intolerant invasive grass species, including Kleberg bluestem (*Dichanthium annulatum*) (Van Devender *et al.* 2009).

These results demonstrate employment of experimental data in a theoretical model to explain mechanisms and trends found in nature. Our results provide insight into how LB and SOG can utilize shade to persist in Texas grasslands being rapidly homogenized by KR bluestem. Moving forward, mechanisms underlying competitive dynamics should be investigated in more native grasses, invasive grasses, life stages, light intensities, and environmental factors to fully grasp how competitive mechanisms function and change under different conditions and as an entire ecosystem.

Acknowledgments

I want to thank Trinity University Integrated Research in Biomathematics Program participants, Lyons' research group, my thesis committee (Dr. Lyons, Dr. Ribble, and Dr. Kwessi), and Michael San Inocencio for their support, guidance, and inspiration. I also want to thank the USDA-NIFA NRI Competitive Grant Program #2008-35320-18865, NSF Grant UBM-0926702, and Trinity University Mach Research Fellowship for providing the funding for this project.

Literature Cited

- Belsky, J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* **75**: 922-932.
- Berg, W.A. 1993. Old World bluestem response to fire and nitrogen fertilizers. *Journal of Range Management* **46**: 421-425.
- Black, J.N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterranean* L.) with particular reference to leaf area and the light microclimate. *Crop and Pasture Science* **9**: 299-318.
- Blossey, B. and R. Notzold. 1995. Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *J. Ecol.* **83**: 887-889.
- Bryan, G.G. and McMurphy, W.E. 1968. Competition and fertilization as influences on grass seedlings. *Journal of Range Management* **21**: 98-101.
- Bush, J.K. and O.W. Van Auken. 1991. Importance of time of germination and soil depth on growth of *Prosopis glandulosa* (Leguminosae) seedlings in the presence of a C4

- grass. American Journal of Botany **78**: 1732-1739.
- Carroll, I.T., B.J. Cardinale, and R.M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. Ecology **92**: 1157-1165.
- Chazdon, R.L. and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology **72**: 553-564.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. **31**: 343-366.
- Dabo, S.M., C.M. Taliaferro, S.W. Coleman, F.P. Horn, and P.L. Claypool. 1987. Yield and digestibility of Old World bluestem grasses as affected by cultivar, plant part, and maturity. Journal of Range Management. **40**: 10-15.
- Dabo, S.M., C.M. Taliaferro, S.W. Coleman, F.P. Horn, and P.L. Claypool. 1988. Chemical composition of Old World bluestem grasses as affected by cultivar and maturity. Journal of Range Management **41**: 40-48.
- Dai, Y., Z. Shen, Y. Liu, L. Wang, D. Hannaway, and H. Lu. 2009. Effects of shade treatments on photosynthetic capacity, chlorophyll fluorescence, and chlorophyll content in *Tetrastigma hemsleyanum* Diels et Gilg. Environmental and Experimental Botany **65**: 177-182.
- Davidson, D. and P. Davidson. 2008. Ten years of ecological restoration on a Texas Hill Country site. Ecological Restoration **264**: 331-339.
- Ellner, S. 1986. Germination dimorphisms and parent-offspring conflict in seed germination. Journal of Theoretical Biology **123**: 173-185.
- Fowler, N.L. 2005. An introduction to the vegetation and ecology of the Eastern Edwards Plateau (Hill Country) of Texas.

<<http://www.sbs.utexas.edu/fowler/docs/FowlereasternEP.pdf>>

- Gabbard, B.L. and N.L. Fowler. 2007. Wide ecological amplitude of a diversity reducing invasive grass. *Biological Invasions* **9**: 149-160.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of regeneration niche. *Biol. Rev.* **52**: 107-145.
- Harper, J.L. 1977. Population biology of plants. Academic Press. Science.
- Hickman, K.R., G.H. Farley, R. Channell, and J.E. Steier. 2006. Effects of Old World bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. *The Southwestern Naturalist* **51**: 524-530.
- Howard, T.G. and D.E. Goldberg. 2001. Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology* **82**: 979-990.
- Keddy, P.A., L. Twolan-Strutt, and I.C. Wisheu. 1994. Competitive effect and response in 20 wetland plants: Are they consistent across three environments? *J. Ecol.* **82**: 635-643.
- Keddy, P.A. 2001. Competition. – Kluwer.
- Lamb, E.G. and J.F. Cahill. 2006. Consequences of differing competitive abilities between juvenile and adult plants. *Oikos* **112**: 501-512.
- Mayer, P.M., S.J. Tunnell, D.M. Engle, E.E. Jorgensen, and P. Nunn. 2005. Invasive grass alters litter decomposition by influencing macrodetritivores. *Ecosystems* **8**: 200-209.
- McCoy, S.D., J.C. Mosley, and D.M. Engle. 1992. Old World bluestem seedlings in Western Oklahoma. *Rangelands* **14**: 41-44.
- Pase, C.P. 1971. Effect of a February burn on Lehman Lovegrass. *Journal of Range Management* **24**: 454-456.
- Ruckman, E.M., S. Schwinning, and K.G. Lyons. 2012. Effects of phenology at burn time on

- post-fire recovery in an invasive C₄ grass. *Restoration Ecology* **20**: 756-763.
- Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. 2001. The population biology of invasive species. *Ann. Rev. Ecol. Syst.* **32**: 305-332.
- Schmidt, C.D., K.R. Hickman, R. Channell, K. Harmoney, and W. Stark. 2008. Competitive abilities of native grasses and non-native (*Bothriochloa* spp.) grasses. *Plant Ecology* **197**: 69-80.
- Sommer, U. 1994. The impact of light intensity and daylength on silicate and nitrate competition among marine phytoplankton. *Limnol. Oceanogr* **39**: 1680-1688.
- Van Devender, T.R., F.J. Espinosa-Garcia, B.L. Harper-Lore, and T. Hubbard. 2009. Invasive plants on the move: controlling them in North America. Arizona-Sonora Desert Museum Press, Tuscan, Arizona, USA.
- Walker, K.J., P.A. Stevens, D.P. Stevens, J.O. Mountford, S.J. Manchester, and R.F. Pywell. 2004. The restoration and re-creation of species-rich lowland grassland on land formally managed for intensive agriculture in the UK. *Biological Conservation* **119**: 1-18.
- Wallin, L., B.M. Svensson, and M. Lonn. 2009. Artificial dispersal as a restoration tools in meadows: sowing or planting? *Restoration Ecology* **17**: 270-279.
- Watt, A.S. 1955. Bracken versus heather, a study in plant sociology. *J. Ecol.* **43**: 490-506.
- Wilcox, B.P. 2010. Transformative ecosystem change and ecohydrology: ushering in a new era for watershed management. *Ecohydrology* **3**: 126-130.
- Wiley, B.J. and H.W. Polley. 2006. Aboveground productivity and root-shoot allocation

differ between native and introduced grass species. *Oecologia* **150**: 300-309.

Tables and figures

	KR	KR-SOG	KR-LB	SOG	SOG-KR	LB	LB-KR
KR		<0.001**	0.649	<0.001**	<0.001**	0.134	0.04**
KR-SOG			<0.001**	<0.001**	<0.001**	0.04**	0.134
KR-LB				<0.001**	<0.001**	0.001**	<0.001**
SOG					1	<0.001**	<0.001**
SOG-KR						<0.001**	<0.001**
LB							0.999
LB-KR							

Table 1: P-values from comparisons with ANOVA of germination times of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)] (KR-LB), SOG in monoculture (SOG), SOG with KR (SOG-KR), LB in monoculture (LB), and LB with KR (LB-KR). Significance ($p \leq 0.05$) is denoted by ** symbol.

	KR	KR-SOG	KR-LB	SOG	SOG-KR	LB	LB-KR
KR		0.988	0.979	<0.001**	<0.001**	0.235	<0.001**
KR-SOG			1	<0.001**	<0.001**	0.119	<0.001**
KR-LB				<0.001**	<0.001**	0.098	<0.001**
SOG					0.716	<0.001**	<0.001**
SOG-KR						<0.001**	<0.001**
LB							0.094
LB-KR							

Table 2: P-values from comparisons with MANOVA of shoot height of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)] (KR-LB), SOG in monoculture (SOG), SOG with KR (SOG-KR), LB in monoculture (LB), and LB with KR (LB-KR). Significance ($p \leq 0.05$) is denoted by ** symbol.

	KR	KR-SOG	KR-LB	SOG	SOG-KR	LB	LB-KR
KR		0.774	0.701	0.001**	1	0.484	0.642
KR-SOG			1	<0.001**	0.974	0.05**	0.11
KR-LB				<0.001**	0.955	0.035**	0.085
SOG					0.006**	0.282	0.635
SOG-KR						0.483	0.58
LB							1
LB-KR							

Table 3: P-values from comparisons with MANOVA of root length of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)] (KR-LB), SOG in monoculture (SOG), SOG with KR (SOG-KR), LB in monoculture (LB), and LB with KR (LB-KR). Significance ($p \leq 0.05$) is denoted by ** symbol.

	KR	KR-SOG	KR-LB	SOG	SOG-KR	LB	LB-KR
KR		0.999	0.988	<0.001**	<0.001**	0.121	<0.001**
KR-SOG			0.888	<0.001**	<0.001**	0.039**	<0.001**

KR-LB	0.007**	<0.001**	0.515	<0.001**
SOG		0.975	0.533	0.888
SOG-KR			0.102	1
LB				1
LB-KR				

Table 4: P-values from comparisons with MANOVA of above ground biomass (AGB) of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)](KR-LB), SOG in monoculture (SOG), SOG with KR (SOG-KR), LB in monoculture (LB), and LB with KR (LB-KR). Significance ($p \leq 0.05$) is denotes by ** symbol.

	KR	KR-SOG	KR-LB	SOG	SOG-KR	LB	LB-KR
KR		0.949	0.941	0.019**	0.979	0.995	1
KR-SOG			1	0.001**	1	0.645	0.955
KR-LB				0.001**	1	0.625	0.955
SOG					0.001**	0.108	0.020**
SOG-KR						0.751	0.982
LB							0.995
LB-KR							

Table 5: P-values from comparisons with MANOVA of below ground biomass (BGB) of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)](KR-LB), SOG in monoculture (SOG), SOG with KR (SOG-KR), LB in monoculture (LB), and LB with KR (LB-KR). Significance ($p \leq 0.05$) is denotes by

** symbol.

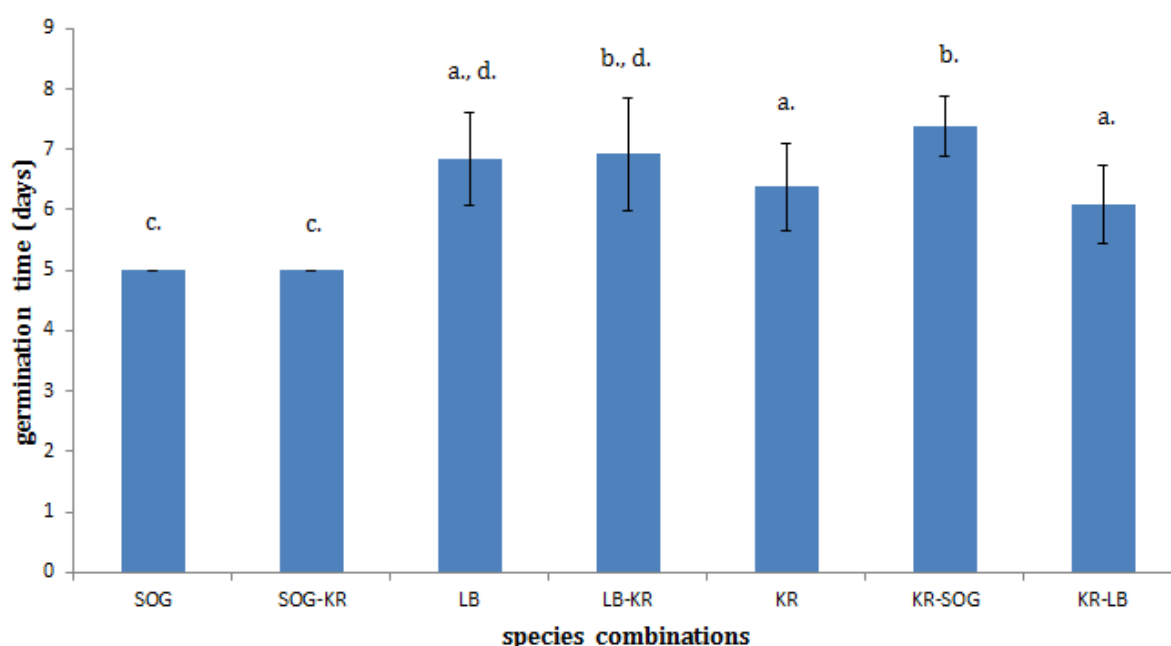


Figure 1: Germination times of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)] (KR-LB), SOG in monoculture (SOG), SOG with KR (SOG-KR), LB in monoculture (LB), and LB with KR (LB-KR). Error bars represent one standard deviation. Presence of corresponding letters above bars indicates that those species combinations are not significantly different. Absence of corresponding letters above bars indicates that those species combinations are significantly different.

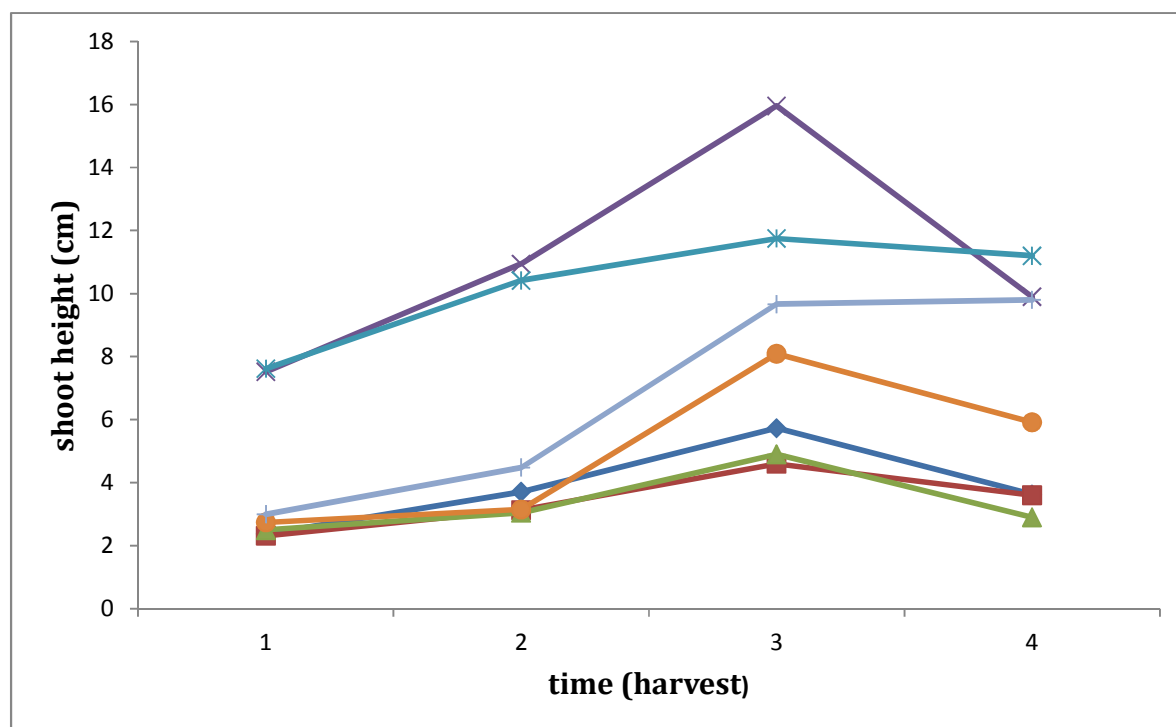


Figure 2: Shoot height of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR)(navy blue line), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG)(red line), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)](KR-LB)(green line), SOG in monoculture (SOG)(purple line), SOG with KR (SOG-KR)(aqua blue line), LB in monoculture (LB)(orange line), and LB with KR (LB-KR)(lavender line) over time.

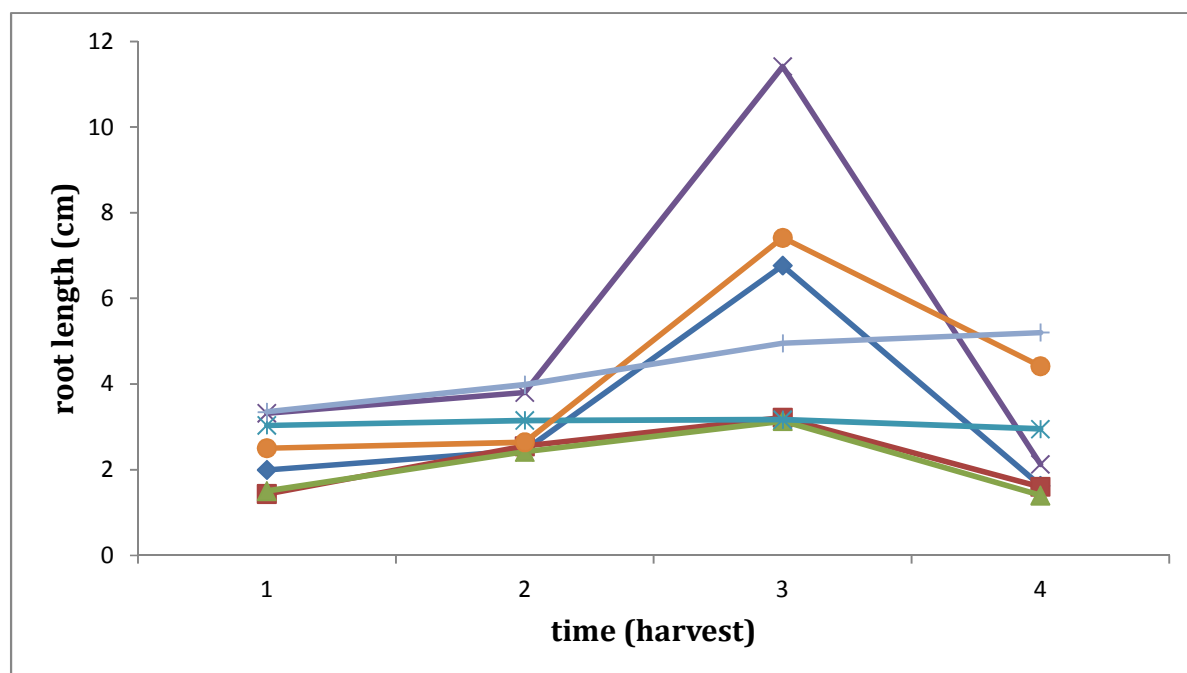


Figure 3: Root length of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR)(navy blue line), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG)(red line), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)](KR-LB)(green line), SOG in monoculture (SOG)(purple line), SOG with KR (SOG-KR)(aqua blue line), LB in monoculture (LB)(orange line), and LB with KR (LB-KR)(lavender line) over time.

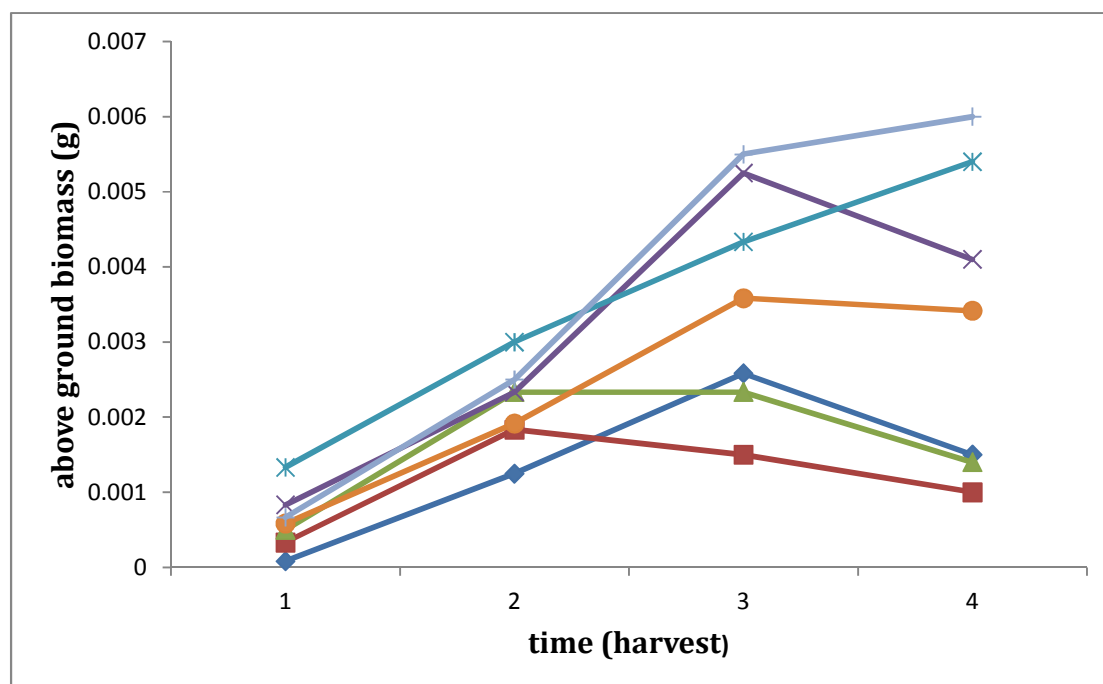


Figure 4: Above ground biomass of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR)(navy blue line), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG)(red line), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)](KR-LB)(green line), SOG in monoculture (SOG)(purple line), SOG with KR (SOG-KR)(aqua blue line), LB in monoculture (LB)(orange line), and LB with KR (LB-KR)(lavender line) over time.

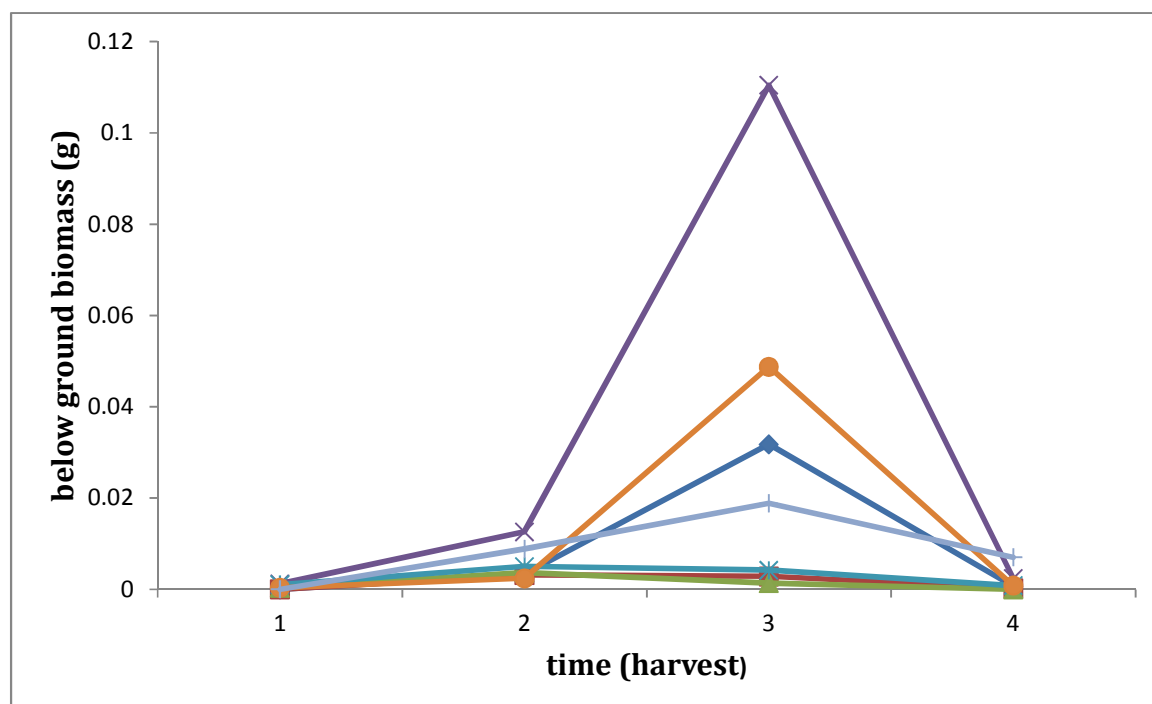


Figure 5: Below ground biomass of King Ranch (KR) bluestem (*Bothriochloa ischaemum*) in monoculture (KR)(navy blue line), KR bluestem with sideoats grama [*Bouteloua curtipendula* (SOG)] (KR-SOG)(red line), KR bluestem with little bluestem [*Schizachyrium scoparium* (LB)](KR-LB)(green line), SOG in monoculture (SOG)(purple line), SOG with KR (SOG-KR)(aqua blue line), LB in monoculture (LB)(orange line), and LB with KR (LB-KR)(lavender line) over time.