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Ecophysiology and Ecosystem-level Impacts of an Invasive C_4 Perennial Grass, *Bothriochloa ischaemum*

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Ecophysiology and Ecosystem-level Impacts of an Invasive C_4 Perennial Grass, *Bothriochloa ischaemum*

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Amie ak Kuddi Bah, tuddi naa yeen suma leegay bii.

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Ecophysiology and Ecosystem-level Impacts of an Invasive C_4 Perennial Grass, *Bothriochloa ischaemum*

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The University of Texas at Austin, 2013

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Abstract: The anthropogenic introduction of species into new ecosystems is a global phenomenon, and identifying the mechanisms by which some introduced species become dominant in their introduced ranges (i.e., invasive) is crucial to predicting, preventing, and mitigating the impacts of biological invasions. Introduced perennial C_4 grasses are invading semi-arid grassland and savanna ecosystems throughout the south-central U.S. We hypothesized that in these semi-arid ecosystems, where variable precipitation patterns strongly influence vegetation dynamics, the success of an invasive plant species may be due in part to ecophysiological traits that enable high performance in response to unpredictable water availability. We also hypothesized that increased primary productivity and decreased plant input quality associated with these grass invasions have the potential to alter ecosystem carbon and nitrogen cycling and storage by altering the ratio of inputs (productivity) to outputs (decomposition/respiration). We tested the first hypothesis by quantifying ecophysiological performance differences between an invasive C_4 grass, *Bothriochloa ischaemum*, and co-occurring C_3 and C_4 native grasses under wet and dry conditions in the field and under two levels of simulated precipitation frequencies in a greenhouse experiment. We tested the second hypothesis by

examining whether increased primary productivity and decreased C_3:C_4 grass ratios in savanna grass-matrices associated with *B. ischaemum* invasion altered (1) plant input quality and thus nutrient cycling and/or (2) net ecosystem carbon uptake in invaded areas. *B. ischaemum's* success as an invader was not directly related to its ability to cope with precipitation variability and availability, but its ability to rapidly produce large amounts of biomass may allow it to directly out-compete native species. *B. ischaemum* invasion decreased plant input quality and soil nitrogen availability. *B. ischaemum* invasion shifted ecosystem C-uptake from being nearly year-round to occurring predominantly in the summer. Greater C-uptake during the summer and under drier conditions compensated for a shorter growing seasons in *B. ischaemum*-invaded areas and cumulative annual NEE was similar between invaded and native-dominated areas. We conclude that *B. ischaemum*'s impacts on soil nitrogen availability and plant-canopy microhabitat may allow it to exclude native species from invaded areas, but that its impacts on ecosystem C sequestration may be small.

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Introduction

The anthropogenic introduction of alien species into new ecosystems is a global phenomenon. Although very few introductions of alien species result in self-sustaining populations, and only a small fraction of these self-sustaining populations dominate their communities, many alien species that do become dominant have very large negative impacts on local and global species composition and other severe ecological and economic consequences (Mack et al. 2000, Pimentel et al. 2001). While the magnitude and direction of plant invasion impacts vary, plant invasions are generally associated with decreased native species diversity, enhanced aboveground primary productivity, and changes in ecosystem carbon and nitrogen cycling in invaded ecosystems (Liao et al. 2008, Vila et al. 2011). Identifying the mechanisms by which alien species invade ecosystems and affect ecosystem processes is integral to predicting, preventing, and mitigating the impacts of biological invasions.

While many invasive plant species possess characteristics that are novel to the ecosystems that they invade (Fargione et al. 2003, Callaway and Ridenour 2004), other invaders area functionally similar to the native species that they displace (Daehler 2003, Funk and Vitousek 2007). Substantial shifts in dominant plant life form (e.g., the invasion of annuals into perennial ecosystems or shrubs into grasslands) are expected to result in substantial changes in ecosystem function (Gill and Burke 1999, Drenovsky and Batten 2007, Hooker et al. 2008, Mahaney et al. 2008), but more subtle changes in plant community composition (e.g., the replacement of native perennial grasses by an invasive one) can have impacts of similar magnitudes (Christian and Wilson 1999, Huxman et al. 2004, Reed et al. 2005, Hamerlynck et al. 2010, 2012a). In the case of perennial grasses introduced into grasslands and savannas for forage improvement and soil erosion control,

species were specifically selected for their ease of establishment, forage quality, grazing and drought tolerance, and high productivity (Donahue 1999). These selected traits can contribute to the invasiveness of an introduced grass and thereby increase its potential as an ecosystem transformer. A number of these introduced grasses have become invasive, and increases in aboveground primary productivity associated with their invasion, as well as subtle differences in ecophysiology between themselves and the natives species they are displacing, have resulted in extensive changes in ecosystem function in invaded areas (Christian and Wilson 1999, Wiliams and Baruch 2000, Huxman et al. 2004, Reed et al. 2005, Hamerlynck et al. 2010, Scott et al. 2010, Hamerlynck et al. 2012a).

Bothriochloa ischaemum var. songarica, King Ranch Bluestem, is a C_4 perennial grass native to Eurasia where it is a climax species in arid and semi-arid environments (Akhani and Zeigler 2002, Wang 2003). In the 1930's, B. *ischaemum* was introduced in the United States for pasture improvement and soil stabilization (Gabbard and Fowler 2007) and has since invaded a diverse array of habitat types throughout Texas and Oklahoma (Diggs et al. 1999, Turner et al. 2003, Gabbard and Fowler 2007). When *B. ischaemum* invades central Texas ecosystems it replaces both native C_3 and C_4 grasses and converts C_3/C_4 mixed grasslands and savanna grass-matrices into dense, C_4-dominated *B. ischaemum* near monocultures. The changes in species composition associated with *B. ischaemum* invasion have implications for regional carbon sequestration, nitrogen and water cycling, and cattle production in these ecosystems (Berg and Sims 1984, Gunter et al. 1997, Nagy et al. 1998, Anderson et al. 2001, Maherali et al. 2002, 2003, Harmoney and Hickman 2004, Wilsey and Polley 2006). Although something is already known about *B. ischaemum*'s community-level impacts and invasion dynamics (Hickman et al. 2006, Gabbard and Fowler 2007, Alofs and Fowler 2010, 2013), the mechanisms by which it becomes dominant in south-central US

ecosystems and how its invasion affects ecosystem processes in invaded areas are still unclear.

In this work we examined whether differences in ecophysiological traits between an invasive species, *B. ischaemum*, and co-occurring natives have facilitated the success of the invasive species in semi-arid grasslands and savanna grass-matrices in central Texas. Additionally, we investigated the ecosystem-level impacts of shifts in dominant plant physiology that result from the invasion of mixed C_3/C_4 ecosystems by the introduced C_4 grass *B. ischaemum*.

Chapter 1: Do ecophysiological characteristics explain *B. ischaemum*'s successful invasion of central Texas ecosystems?

ABSTRACT

The anthropogenic introduction of alien species into new ecosystems is a global phenomenon, and identifying the mechanisms by which some introduced alien species become dominant in their introduced ranges (i.e., invasive) is crucial to predicting, preventing, and mitigating the impacts of biological invasions. We hypothesized that in arid and semi-arid ecosystems, where highly variable annual and seasonal precipitation patterns exert strong influence over vegetation dynamics, the success of an invasive plant species may be due in part to ecophysiological traits that enable high performance in response to unpredictable water availability. We tested this hypothesis by quantifying both short-term and long-term ecophysiological performance differences between an invasive C_4 perennial grass *Bothriochloa ischaemum*, and co-occurring C_3 and C_4 native grasses under wet and dry conditions in the field and under two levels of simulated precipitation frequencies in a greenhouse experiment. Our results indicate that superior performance for traits that promote survival in water-limited ecosystems is not the basis for *B. ischaemum's* successful invasion of these ecosystems. On the contrary, some native C_4 grasses are capable of out-performing *B. ischaemum* under dry conditions. Although its short-term photosynthetic performance was similar to or worse than native C_4 species under dry conditions, *B. ischaemum* was as capable as native species of utilizing pulses in soil moisture, and its performance under wet conditions was similar to or greater than those of the native species we monitored. *B. ischaemum* produced significantly more biomass than native species under both average and low soil moisture treatments in the greenhouse, indicating that it may be outperforming native species in the long-term even if it appears to lose under dry conditions in the short-term. We

conclude that *B. ischaemum*'s ability to rapidly produce large amounts of biomass may allow it to directly out-compete some native species. Regardless of how it becomes dominant, our field results indicate that *B. ischaemum* invasion is likely to result in decreased growing season length in invaded areas. Additionally, greater sensitivity to decreased water availability in the invasive has the potential to decrease ecosystem productivity in invaded areas as precipitation events become less frequent with climate change.

INTRODUCTION

The anthropogenic introduction of alien species into new ecosystems is a global phenomenon. Although very few introductions of alien species result in self-sustaining populations, and only a small fraction of these self-sustaining populations dominate their communities, many alien species that do become dominant have very large negative impacts on local and global species composition and other severe ecological and economic consequences (Mack et al. 2000, Pimentel et al. 2001). As a result, the mechanisms that facilitate invasions have been intensely researched (Elton 1958, Lonsdale 1999, Mitchell et al. 2006, Ren and Zhang 2009).

A fundamental understanding of the ecophysiological traits that facilitate invasion is crucial to predicting, preventing and mitigating the impacts of biological invasions. However identifying a trait or suite of traits that make species invasive or communities susceptible to invasion has proven difficult. Perhaps due to the diversity of conditions under which invasions take place, a wide variety of hypotheses about which biotic and abiotic factors facilitate invasion has been developed (Mitchell et al. 2006). Most of these hypotheses predict invader success will be more likely where alien species are functionally different from native species. There are many empirical examples in which

novel traits have apparently promoted invasions (Fargione et al. 2003, Callaway and Ridenour 2004) but there are also many examples in which invaders are functionally similar to the natives they displace (Christian and Wilson 1999, Daehler 2003, Smith and Knapp 2004, Funk and Vitousek 2007). Theoretically, invasive species are more likely to be similar to native species in ecosystems where strong abiotic filters exist (Mitchell et al. 2006, Broennimann et al. 2007). While there is evidence that abiotic resource limitation has resulted in functionally similar invaders (Funk and Vitousek 2007), functional differences have also contributed to invader success in ecosystems where abiotic factors play a large role in determining species composition (Frasier and Cox 1994, Kulmatiski et al. 2006).

Performance differences in plant ecophysiological traits, such as photosynthetic capacity and resource competition and utilization, have been credited with promoting the success of several plant invaders (Baruch et al. 1985, Frasier and Cox 1994, Nagy et al. 1998, Baruch and Goldstein 1999, Wiliams and Baruch 2000, Nagel and Griffin 2001, Mc Dowell 2002, Farnsworth and Meyerson 2003, Gulias et al. 2003, Nagel and Griffin 2004, Ward et al. 2006, Ren and Zhang 2009, Penuelas et al. 2010, Matzek 2011, 2012). In particular, successful invasive plant species that are functionally similar to native species typically gain higher returns (e.g., higher photosynthetic capacity and growth rates) with lower levels of resource investment (Baruch and Goldstein 1999, Nagel and Griffin 2001, Mc Dowell 2002, Nagel and Griffin 2004, Penuelas et al. 2010, Matzek 2011, 2012). Relative performance differences between species for these traits can shape community species composition by determining reproductive success.

Relative performance differences between native and invasive species in an ecosystem are not static, but shift with changes in environmental conditions (Alpert et al. 2000, Daehler 2003, Mata et al. 2013). This is particularly important in highly variable

environments such as arid and semi-arid regions where precipitation variability plays a large role in maintaining species diversity (Chesson et al. 2004, Adler et al. 2006). Precipitation in arid and semi-arid ecosystems is available in discrete events, and inter-annual and seasonal changes in the temporal distribution of rainfall have large impacts on soil moisture and plant productivity (Fay et al. 2002, 2003, Ogle and Reynolds 2004, Reynolds et al. 2004, Ignace et al. 2007). In these ecosystems, performance differences between native and invasive species' drought responses and opportunistic use of precipitation pulses can give invasive plants competitive advantages over natives (Baruch and Fernández 1993, Frasier and Cox 1994, Fernandez and Reynolds 2000, Kulmatiski et al. 2006), with resulting effects on ecosystem functions (Huxman et al. 2004, Potts et al. 2006a, Scott et al. 2010). Given that many arid and semi-arid ecosystems are predicted to experience increased variability in precipitation with less frequent, more intense precipitation events as a result of global climate change (Easterling et al. 2000, Diffenbaugh et al. 2005, Leung and Gustafson 2005), understanding what role climate variability plays in facilitating invasions is crucial (Dukes and Mooney 1999).

In this study we ask whether differences in ecophysiological traits between an invasive species and co-occurring natives have facilitated the success of the invasive species in semi-arid grasslands in central Texas. The invasive species is a C_4 perennial grass, *Bothriochloa ischaemum var. songarica,* King Ranch Bluestem. It is native to Eurasia, where it is a climax species in shallow and rocky soils in arid and semi-arid environments (Akhani and Zeigler 2002, Wang 2003). It was released as a pasture and rangeland improvement species in the 1930s (Gabbard and Fowler 2007), and has since invaded a diverse array of habitat types throughout Texas and Oklahoma, replacing both C_3 and C_4 native grasses in central Texas (Diggs et al. 1999, Turner et al. 2003, Gabbard and Fowler 2007). Its presence is negatively correlated with plant, avian and rodent

species richness and diversity (Sammon and Wilkins 2005, Hickman et al. 2006, Gabbard and Fowler 2007) and it invades both disturbed and recently undisturbed areas (Eck and Sims 1984, Gabbard and Fowler 2007). The conversion of C_3/ C_4 mixed grasslands and savannas into C_4-dominated, *B. ischaemum* monocultures has implications for regional carbon sequestration, nitrogen and water cycling and cattle production in these systems (Berg and Sims 1984, Gunter et al. 1997, Nagy et al. 1998, Anderson et al. 2001, Maherali et al. 2002, 2003, Harmoney and Hickman 2004, Wilsey and Polley 2006). Although something is already known about *B. ischaemum*'s community-level impacts and invasion dynamics (Hickman et al. 2006, Gabbard and Fowler 2007, Alofs and Fowler 2010, 2013), the mechanisms by which it becomes dominant in south-central US ecosystems are still unclear.

We hypothesized that in semi-arid savanna ecosystems in central Texas, where highly variable annual and seasonal precipitation patterns exert strong influence over vegetation dynamics (Fuhlendorf et al. 2001), the invasion success of *B. ischaemum* is due in part to ecophysiological traits that enable high performance in response to unpredictable water availability. The traits we focused on were water-use efficiency, precipitation pulse utilization and drought dormancy, all of which are common drought strategies used by perennial grasses in semi-arid ecosystems (Knapp and Medina 1999). We hypothesized that (1) *B. ischaemum* would invest fewer resources in leaves and receive higher photosynthetic returns on leaf investments than native grasses even under low-water conditions, (2) a combination of higher water-use efficiency and lower sensitivity to drought would allow *B. ischaemum* to maintain higher photosynthetic activity at lower water levels and delay drought-induced senescence and dormancy than native species, and (3) *B. ischaemum* would be better able to take advantage of available moisture after a dry period (i.e., it would have higher soil moisture pulse utilization) than

native species. Any one of these differences, or all three, could account for *B. ischaemum* outcompeting native species.

We tested these hypotheses by quantifying both short-term and long-term ecophysiological performance differences between *B. ischaemum* and co-occurring C_3 and C_4 native grasses under wet and dry conditions in the field and under two levels of simulated precipitation frequencies in a greenhouse experiment. We use our results to discuss future interactions between native grasses and this invasive species under the influences of climate change.

METHODS

Experimental designs

Field study

We compared the ecophysiological traits described below between *B. ischaemum* and both C_3 and C_4 native grasses in the field in ungrazed, unmown plots within the 279 acre Landscape Restoration Research Area at the Lady Bird Johnson Wildflower Center (WFC), a research unit of the University of Texas at Austin, Austin, Texas (N 30 11'3",W 97 52'27", 800' elevation). This property was managed for cattle production prior to its acquisition by the WFC in 1999. WFC is located in central Texas *Quercus fusiformis - Juniperus ashei* savanna in the Texas Hill Country on the eastern edge of the Edwards Plateau. The grass matrix of the savanna at this site is characterized by C_4 grasses, including *Bothriochloa laguroides* subsp. *torreyana, Bothriochloa ischaemum* and *Hilaria belangeri,* C_3 grasses, including *Nassella leucotricha,* and over 200 species of forbs. The invading grass, *B. ischaemum,* is rapidly becoming the dominant species in the areas where we worked. The native species we measured in the field were four C_4 and one C_3 perennial grasses that are all common at this site and widely distributed

throughout central Texas grasslands and savannas. They were two taller (50 - 200 cm) C_4 bunch grasses, *B. laguroides* and *Schizachyrium scoparium*, one mid-height (55 -90 cm) C_4 bunch grass, *Eragrostis intermedia*, one short, stoloniferous C_4 grass, *H. belangeri*, and a mid-height C_3 bunch grass, *N. leucotricha*. The C_4 grasses in this study represent two C_4 sub-types: *B. ischaemum, B. laguroides* and *S. scoparium* are NADP-ME species, and *E. intermedia* and *H. belangeri* are NAD-ME species.

Soils at this site are limestone-derived thermic Lithic Argiustolls of the Speck Series, which are nearly level stony clay loams to gravelly clays, 30 - 50 cm in depth (Soil Survey Staff, NRCS, USDA 2009). Rainfall and temperatures in the Austin area are highly variable, with a mean annual precipitation of 840 (± 250 sd) mm. The growing season in this area is often bimodal with a decline in activity during the hottest part of the summer (for all plants) (July -September) and (primarily for C_4 species) during the winter (January - February). However, the seasonality of plant activity is highly variable and primarily dependent on water availability. Annual rainfall and temperatures differed greatly between the two years of our study (Figure 1.1). In 2006, cumulative annual rainfall was 860 mm, the majority of which (82%) fell before the end of June. Temperatures were high and highly variable in 2006. As a result, 2006 had distinct wet and dry seasons and a bimodal growing season in which the majority of plant activity occurred March to June and October to December. In 2007, cumulative rainfall was 1192 mm and fell at regular intervals throughout the spring and into the early fall with relatively little rainfall after October. Temperatures were also more moderate and less variable in 2007. As a result, 2007 had a continuous growing season that did not end until the fall brought colder weather.

In both years, we measured leaf-level gas exchange, light-response curves and light-saturated net photosynthesis (A_{net}), transpiration (E), and stomatal conductance (g_{sw})

(all described below), on randomly selected individual plants from within 0.75 ha plots; the same plants were repeatedly measured throughout the year. In 2006, we compared ecophysiological traits of *B. ischaemum* to two native species, *B. laguroides* and *N. leucotricha,* in 6 plots in early growing season (April 4 and 11, 2006), summer wet period (July 13 – 14, 2006), summer dry period (August 17 – 18, 2006) and late growing season (September 30, 2006 and October 5, 2006). In 2007, we compared *B. ischaemum* traits to 5 native grass species, *B. laguroides* and *N. leucotricha* and three additional native grass species, *E. intermedia, H. belangeri* and *S. scoparium* in 3 plots six times, approximately monthly from April through October (April 12 and 19, May 16 - 18, June 13 - 14, July 10 - 11, August 12 - 14 and October 10 and 14). In both years, measurements for each time point were conducted over the course of 2 - 3 days. A list of measured, estimated and calculated variables and the tables and figures in which they appear is provided in Tables 1.1.a – 1.1.c. Environmental conditions varied considerably among measurement time points, which allowed us to observe species at a variety of temperatures and moisture levels (Table 1.2).

We collected the leaves used for gas exchange and analyzed them for both carbon and nitrogen content to compare long-term investments in leaf material (as total nitrogen and carbon content per leaf area and leaf construction costs) and short-term photosynthetic returns on those investments (as nitrogen-use efficiency, photosynthetic-energy-use efficiency and mass-based photosynthesis) between *B. ischaemum* and native species. In 2006, we analyzed the leaves collected for gas exchange on three dates (April, July, and October) in four plots. In 2007, we did these analyses each time we made gas exchange measurements in all 3 plots.

Greenhouse experiment

We used a greenhouse experiment to compare the ecophysiological responses of *B. ischaemum* and 3 native species to simulated precipitation events. The native species used in this experiment were two C_4 bunch grasses, *B. laguroides* and S. *scoparium,* and a C_3 bunch grass, *N. leucotricha.*

Plants were germinated in March 2007 in the Welch Greenhouse on the main campus of the University of Texas at Austin, Austin, TX from seed in 9 cm pots containing native soil from the WFC. *B. laguroides* and *N. leucotricha* seeds were collected from the WFC in 2006. *B. ischaemum* (King Ranch Bluestem variety) were purchased from Turner Seed, Brackenridge, TX, and seeds of *S. scoparium* were purchased from Native American Seed, Junction, TX. After 10 months, we transplanted the seedlings into gallon (4404 cc) pots on January 16, 2008, using 16:1 native soil: coarse sand mixture to improve drainage within pots. Average bulk density for soils in gallon pots was 0.61 ± 0.04 g soil cc^{-1}, which is lower than field-measured bulk density (1.36 ± 0.04 g soil cc^{-1}), but soil water loss trials comparing pot bulk densities ranging from 1.5 - 0.5 g soil cc^{-1} indicated that a pot soil bulk density ~0.65 g soil cc^{-1} produced soil water loss rates closest to those observed in the field at temperature and humidity levels similar to those in the greenhouse.

During germination and seedling establishment, we watered plants as needed, approximately twice a week. We rotated pots twice weekly to decrease the chances of measured variables being influenced by plant position on greenhouse benches. Once plants were established in the gallon pots, we watered them once weekly until watering treatments began. Plants in gallon pots were grouped in bins to keep pots upright and to facilitate pot rotation on the greenhouse bench. Each water treatment (see below) was applied to two bins of plants. Each bin contained two individuals of each species for a

total of eight plants per bin. To reduce the effects of crowding within bins, we used empty pots as spacers (pot tops were 91.44 cm^2) between pots that contained plants. We rotated pots within bins, but not between bins; bins were rotated on greenhouse benches.

In mid-March 2008, when plants were approximately a year old, we randomly assigned four plants of each species to one of two watering treatments: (1) frequent precipitation pulse (high-water treatment) and (2) infrequent precipitation pulse (low-water treatment). We watered plants in the high-water treatment to field capacity once every 7 - 10 days, the approximate 20-yr average number of dry days between fall pulses (1987 - 2007 for Austin Bergstrom Airport, Austin, TX; average ± 1 sd = 9.07 ± 12.22 dry days). We watered plants in the low-water treatment to field capacity once every 20 days, approximately the fall average number of dry days between precipitation pulses + 1 standard deviation. We chose to simulate a fall precipitation regime because predicted decreases in the frequency of fall precipitation events (Leung and Gustafson 2005) have the potential to greatly impact the length of the growing season (Risch and Frank 2007) and overall species composition and productivity in these ecosystems (Fuhlendorf et al. 2001) All plants were cycled through 40 days of treatment before plants in both treatments were subjected to a 14-day dry-down, during which plants were not watered. After the 14-day dry-down, we watered all plants to field capacity and then returned them to their previously established watering cycles until May 28, 2008, when we harvested all of the plants. The purpose of the 14-day dry-down and subsequent simulated soil moisture pulse was to compare species' responses to precipitation pulses under average and drier conditions. Plants were harvested and biomass allocation and leaf investment data were collected as described below.

During the initial and second dry-down periods in the low-water treatment, soil moisture and temperature probes were installed in all sixteen pots in that treatment group,

four pots for each of the four species. During this period, soil moisture and temperature were monitored in the high-water treatment in one pot of each of the four species. This was done so that we could compare soil moisture draw-down rates among species in the low-water treatment during the initial and second dry-down periods. After the initial and second dry-down periods, we removed half of the probes in the low-water treatment pots and re-installed them in pots in the high-water treatment. We monitored soil moisture and temperature continuously throughout the remainder of the experiment in a total of 16 pots, two pots of each species in each treatment. Soil moisture and temperature in pots without sensors were assumed to be the average of the two monitored pots for that species in their respective treatments. Soil moisture (S-SMC-M005, ECH_2O probe, Decagon Devices, Inc., Pullman, WA, USA and Onset Computer Corp, Pocasset, MA, USA) and temperature probes (S-TMA-M006, Onset Computer Corp, Pocasset, MA, USA) were installed 2 – 7 cm within pots and interfaced with HOBO Micro Station data loggers (H21-002, Onset Computer Corp, Pocasset, MA, USA). Ambient irradiance, air temperature and relative humidity were monitored during the experiment using a Li190sb quantum sensor (LI-COR, Lincoln, Nebraska, USA and Campbell Scientific, Inc. Logan, UT, USA) and a HMP 45C relative humidity and temperature sensor (Campbell Scientific, Inc. Logan, UT, USA) interfaced with a CR23x data logger programmed using PC200W software (Campbell Scientific, Inc. Logan, UT, USA). Relative humidity (RH) and air temperature (T_{air}) were used to calculate air vapor pressure deficit (VPD_{air}) and probe measured soil moisture was used to calculate relative soil water content (RSWC) as a ratio of measured volumetric soil moisture content to soil moisture content at field capacity. Daily values for measured environmental variables and dates of leaf-level gas exchange measurements are reported in Figure 1.2.

We compared species responses to decreasing relative soil moisture content (RSWC) during sequential dry-down periods by making leaf-level gas exchange measurements (light-saturated A_{net}, E, and g_{sw} and light-response curves) on plants in the low-water treatment at the start of and during the initial (0 - 20 days of treatment) and second (21 - 40 days of treatment) 20-day soil dry-down periods. We made measurements three days during the initial dry-down (days 1, 5 and 17 of treatment) and four days during the second dry-down (days 20, 28, 34 and 37 of treatment).

Leaf-level gas exchange measurements were made on all plants in both treatments on days 54, dry soil conditions, prior to a soil moisture pulse application ("pre-pulse"), and 57, wet soil conditions, after a soil moisture pulse application ("post-pulse"), of treatment. We used these measurements to test whether species differed in how they responded to a pulse in soil moisture after 40 days of water treatments by comparing pulse responses between the invasive and native grasses within treatments. Pulse response was calculated as the difference in gas exchange measurements post-pulse, 2 days after a soil moisture pulse application, and pre-pulse, after 14 days of soil drying, divided by post-pulse values. We suspected that the relationship between species for photosynthetic characteristics might differ between the leaf and whole-plant level, so we also used gas exchange measurements from day 57 to compare leaf-level and plant-level values of A_{net} and E under wet conditions between species in both treatments. We estimated plant-level A_{net} and E by treating individual plants like big leaves and multiplied leaf-level values of variables by leaf area per plant (LAP, see below).

Measurements in both experiments

Gas exchange measurements

We compared leaf-level gas exchange characteristics among species in both the field and the greenhouse using a portable photosynthesis system (LI-6400, LI-COR, Lincoln, Nebraska, USA). During measurements, an LED Red/Blue light source (LI-COR 6400-02B, LI-COR, Lincoln, Nebraska, USA) was used to control light levels within the leaf chamber and a CO_2 injector system (LI-COR 6400-01, LI-COR, Lincoln, Nebraska, USA) was used to maintain 400 ppm CO_2 within the reference cell. In the field, we allowed relative humidity and temperature within the leaf chamber to approximate that of ambient conditions because we were interested in seasonal photosynthetic responses, and this minimized differences in chamber conditions during and between measurements within time points. In the greenhouse, we maintained block temperature at 20°C and leaf chamber relative humidity at ~50%. In both the field and greenhouse experiments, we measured light-saturated net photosynthesis (A_{net}, μmol CO_2 m^{-2} s^{-1}) and light-response curves (the response of A_{net} to different levels of photosynthetically active radiation, Q, μmol photons m^{-2} s^{-1}). Measured rates of transpiration (E, H_2O mmol m^{-2} s^{-1}) and stomatal conductance ($g_{sw,}$ H_2O mmol m^{-2} s^{-1}) at light saturation were used to calculate transpiration-based (A_{net}:E) and conductance-based (A_{net}:g_{sw}) instantaneous water-use efficiencies (mmol CO_2: mol H_2O).

Gas exchange measurements were made on the first fully expanded leaf of a single tiller on individuals of each species except the two narrow-leaved species, *N. leucotricha* and *H. belangeri*. For these species, we placed three leaves of the same individual within the leaf chamber to increase leaf surface area within the leaf chamber to a level similar to that of the other species.

After each field measurement, we harvested monitored leaves and enclosed them in plastic bags with moist paper towels and placed them in a cooler until they could be scanned for leaf surface area. We scanned field-collected leaves at 800 dpi using a desktop scanner (HP Deskjet F300 All-in-One Series, Hewlett Packard) and analyzed leaf images using ImageJ (Wayne Rasband, Research Services Branch, NIH, Bethesda, MD, USA). In the greenhouse, we did not harvest monitored leaves until the conclusion of the experiment. Leaf areas were obtained from digital images of measured leaves placed beside a ruler for scale taken at the time of each gas exchange measurement using a digital camera (Stylus 410 Digital, Olympus Imaging Inc., Center Valley, PA, USA) and ImageJ. Final leaf areas were determined on harvested leaves. We initially used species-specific regression models to predict camera-determined leaf area (LA_{cam}) from scanned leaf area (LA_{scan}). The relationship between leaf areas derived using the two methods did not differ significantly by species, so we used a single regression equation using data from all of the species to correct camera-measured leaf areas for leaf-level measurements that we made in the greenhouse before plants were harvested (eq. $LA_{corrected} = (LA_{cam} - 0.0521) / 0.9$; $R^2 = 0.90$; $F_{1,31} = 348.70$, $P < 0.0001$). LI-COR 6400 data files were reprocessed to correct calculations for leaf surface area using the LI6400sim 5.3 software *recompute* function (LI-COR, Lincoln, Nebraska, USA).

Light response curves

Leaves were placed in the leaf chamber at ambient Q and allowed to equilibrate for 5 minutes before exposing them to 8 different light set points (2000, 1500, 1000, 300, 80, 50, 20, 0 $\mu molm^{-2}s^{-1}$) to provide data for A_{net} /Q curves. At each set point, we allowed net photosynthetic rates to equilibrate until stability criteria (< 1% coefficient of variation and slope < 1 over a 15 sec period) for leaf chamber CO_2, H_2O and flow rate were met.

A_{net} /Q curves were fit using the *nlsList* function in the *nlme* library in R (R Development Core Team 2008). The function, *nlsList,* uses a Gauss-Newton algorithm to determine the nonlinear least squares estimates of the parameters in a nonlinear regression model and assumes that residuals are approximately normally distributed (Pinhero and Bates 2004). We used this function to fit individual curves to each set of 8 light-level responses using the formula:

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where the measured variables A_{net} (net photosynthesis) and Q (light level or irradiance) were used to estimate apparent quantum yield (Φ), maximum light-saturated photosynthesis (A_{max}), convexity (Θ) and dark respiration (R_d) (Lambers et al. 2000). Φ, the rate of increase in CO_2 assimilation as irradiance increases, describes the efficiency with which light is converted into fixed carbon at lower irradiance levels when photosynthetic rates are limited by light availability. Θ determines the photosynthetic efficiency at intermediate light levels as photosynthesis switches from being light-limited to being carboxylation-limited. Θ ranges in value from 0 – 1, with Θ = 1 being the most efficient transition from light-limited to carboxylation-limited photosynthesis.

Leaf investments and photosynthetic returns: carbon and nitrogen analyses

Field-collected leaves and leaves harvested from greenhouse-grown plants were dried to a constant weight at 65°C, weighed and ground for carbon and nitrogen analysis. We fine-ground leaf material using a Mini-Beadbeater-96 (BioSpec Products, Inc., Bartlesville, OK) by shaking samples for 10 minutes in sealed 2 mL stainless steel micro-vials with 8 - 10 2.3 mm chrome-steel beads. Ground samples were analyzed for carbon and nitrogen at the University of Georgia Analytical Chemistry Lab, Athens Georgia, using an NA1500 C/H/N Analyzer (Carlo Erba Strumentazione, Milan, Italy).

We used measured leaf masses and areas to calculate specific leaf areas (SLA; m^2 g^{-1} leaf) of samples. Combustion measured nitrogen content (TN, % leaf mass) was convert to nitrogen per unit area leaf (NLA, g N per m^2 leaf) using SLA. We calculated construction cost (CC, g glucose m^{-2} leaf) of leaf tissue, that is, grams of glucose required to synthesize one m^2 of leaf tissue, using leaf tissue C content (TC, % leaf mass) converted to an area basis using SLA (Vertregt and Penning de Vries 1987). For field-collected leaves we also calculated photosynthetic returns on C, N and biomass invested in leaves. We calculated instantaneous photosynthetic returns on leaf N investments, nitrogen use efficiency (PNUE), as A_{net} per gram of nitrogen invested in leaf material (μmol CO_2 g^{-1} N s^{-1}). CC was used to calculate photosynthetic energy use efficiency (PEUE) as A_{net} achieved per unit energy invested in leaf material (μmol CO_2 g^{-1} glucose s^{-1}). We calculated mass-based photosynthetic capacity (A_{mass}; μmol CO_2 g^{-1} leaf s^{-1}) by multiplying area-based A_{net} by SLA.

Biomass harvesting

At the conclusion of the greenhouse experiment, we harvested the biomass of greenhouse-grown plants. We separated biomass into roots, leaves, and stems, dried the samples for 3 days at 65°C and weighed them. Leaf sheathes were included in stem biomass because preliminary data indicated that sheath photosynthetic rates were more similar to stem photosynthetic rates than they were to those of leaf blades. We used plant total biomass, shoot:root biomass, root:total biomass, leaf:total biomass (i.e., leaf mass ratio, LMR), and stem: total biomass to compare allocation of resources under the two water treatments among species. Plant total leaf area (LAP; m^2) was calculated as the total leaf mass of an individual multiplied by that individual's SLA. From total plant leaf areas we calculated leaf area ratios (LAR, total plant leaf area m^2 per kg total biomass) of

plants. We used leaf C and N content, SLA and LAR to compare investment in photosynthetic surface area within and between water treatments among species.

Data analysis

To determine whether the invader invested fewer resources in leaves we compared long-term leaf investment (in the greenhouse and in the field) and biomass allocation-patterns (in the greenhouse) between the invasive and native species under dry and wet conditions in the greenhouse and in the field during a dry year and a wet year. We tested whether the invasive species outperformed native species photosynthetically or received higher photosynthetic returns on leaf investments under low-water conditions by comparing short-term photosynthetic rates and returns on leaf investments (carbon-, nitrogen- and mass-bases photosynthetic-use efficiencies) between the invasive and native species in the field during a dry year and a wet year. To determine whether a combination of higher water-use efficiency and lower sensitivity to drought would allow the invader to maintain higher photosynthetic activity at lower water levels, we compared short-term photosynthetic responses and water-use efficiency to soil moisture availability during two soil dry-downs in the greenhouse and during a dry year and a wet year in the field. We used our precipitation manipulation experiments in the greenhouse to examine (1) whether *B. ischaemum* differs from natives in its long-term (i.e., biomass allocation) and short-term (photosynthetic) responses to soil moisture availability and (2) whether *B. ischaemum* differs from native species in its short-term responses to a pulse in soil moisture availability after a 14-day dry period.

We compared long-term leaf investment and short-term photosynthetic response variables from field-collected data among species for the two years separately using ordinary least squares models (*proc glm* in SAS, SAS Institute Inc., Cary, NC, USA).

Each response variable (A_{net}, A_{max}, R_d, G_{sw}, E, Φ, Θ, mass- and area-based leaf investment characteristics, and photosynthesis-based use efficiencies) was analyzed separately. *Species* (3 species in the first year, 6 in the second; see above) was considered to be a fixed-effect categorical variable and *plot* was a random-effect categorical variable. *F*-values of differences among species were therefore calculated using the mean squares of the *species X plot* term in the same model as the denominator.

The date on which each measurement was made (*doy*, Julian day-of-year) was also included in the model as a fixed-effect categorical variable, because there was no expectation of a linear relationship between the dates on which measurements were made and any response variable. We also included the interaction of species and date (*species X doy*) in the initial models in order to examine differences among species in their responses to season.

We also included a set of environmental variables (either VPD_{air} and RSWC or T_{air}, RH, and RSWC) as covariates in the initial models for all variables except leaf investment characteristics and estimated light-use efficiency parameters for the year 2006 light-curve measurements (A_{max}, R_d, Φ, and Θ). We used relative humidity (RH) and air temperature (T_{air}) measured within the leaf chamber to calculate air vapor pressure deficit (VPD_{air}). We collected soil samples at the time of leaf-level measurements to determine gravimetric soil moisture content (g H_2O g^{-1} soil). Gravimetric soil moisture from field-collected soil samples was used to calculate relative soil water content (RSWC) as a ratio of measured gravimetric soil moisture content to soil moisture content at field capacity determined in the laboratory for soils at field-measured bulk densities. Because some of the environmental variables included in the models may have non-linear effects on the response variables, we also included the squares of these variables in each initial model. To test whether species differed in their

responses to these environmental variables, we first compared their linear and quadratic slopes among species (coded as "interaction" terms in SAS: *species X* VPD_{air}, *species X* VPD_{air}^2, *species X RSWC*, *species X* $RSWC^2$). The initial models included each covariate, each covariate squared and its linear and quadratic interaction terms. If a quadratic interaction term was non-significant, it was deleted from the model and the model re-run with only the corresponding linear interaction term; if the linear interaction term was not significant in this second model, it was also removed, and the model run with only the covariate and its square; finally, if the squared covariate was non-significant in the third model, it was also dropped.

We modeled long-term responses to soil moisture availability (water treatment) in our greenhouse work, final plant biomass, biomass allocation ratios (such as root:shoot and root:total) and leaf characteristics (such as SLA and leaf N and C content), using *treatment*, *species* and *treatment x species* as fixed effects and *bin* as a random effect in mixed models (*proc mixed*) in SAS (Littell et al. 1996). Transforming biomass ratios did not improve the models, so analyses are reported using untransformed data.

In our greenhouse studies, we tested whether short-term responses to soil moisture availability differed between *B. ischaemum* and three native species using three different analyses. First, we tested whether RSWC decreased at different rates in pots containing different species during the initial and second dry-downs separately by modeling RSWC as a linear and quadratic function of day of experiment, *doe* (as a continuous variable) and *species* and their two-way interaction terms (*species X doe, species X* doe^2) as fixed effects using mixed models (*proc mixed* in SAS; Little et al. 1996). *Bin* was included in the models as a random-effect categorical variable. Because pots were repeatedly measured, individual plants in pots as a function of *doe* was included in the model as a *repeated* statement. Second, we compared measured (A_{net}, E, and g_{sw}), fitted (Φ, A_{max}, Θ,

and R_d), and (water-use efficiencies) calculated variables among species in the low-water treatment during the initial and second dry-down periods separately. For each dry-down period, we used mixed effects models that included *RSWC* as a continuous variable fixed effect and *species* and day of the experiment (*doe*) as categorical fixed-effects. *Bin* was included in models as a random effect when it contributed significantly to the variance in the response variable. Both linear and quadratic relationships with RSWC were tested for each response variable. We were primarily interested in species-level differences in response variables as soil moisture decreased (*species x RSWC* and *species x RSWC* ^{2}) and included *doe* in the models to account for variability between time points that was due to sources other than soil moisture, such as temperature or ambient light. Because plants were repeatedly measured, individual plant as a function of *doe* was included in the model as a *repeated* statement. Third, we compared A_{net} and E for plants at the leaf-level and at the whole-plant level after the 14-day dry-down (pre-pulse) and two days after the plants were watered to field capacity (post-pulse) both water treatments. We modeled leaf-level and whole-plant level A_{net} and E using *species* and *bin* as fixed and random effects respectively using mixed effects models (*proc mixed*) in SAS® for pre-pulse and post-pulse measurements separately.

To determine whether the invader was better able to take advantage of available moisture after a dry period (i.e., had higher soil moisture pulse utilization) than native species, we compared species' ability to utilize a pulse in soil moisture after a 14-day dry-down in the greenhouse. We compared change in measured (A_{net}, E, and g_{sw}), fitted (Φ, A_{max}, Θ, and R_d), and calculated (water-use efficiency) variables among species within water treatments. Pulse response was calculated as the differences in post-pulse (wet) values and pre-pulse (dry) values divided by post-pulse values for proportion change in a variable in response to the soil moisture pulse. Comparisons of species

responses to a soil moisture pulse within treatments were modeled using *species* as a fixed effect and *bin* as a random effect in mixed effects models in SAS using *proc mixed*. Transforming pulse response data did not improve the models; therefore analyses are reported using untransformed data.

RESULTS

Leaf-level and whole-plant level investments

We hypothesized that one reason *B. ischaemum* is a successful invader is due to a lower long-term investment of resources in leaves compared to native species coupled with a higher photosynthetic return on those leaves. We did not find consistent evidence that the invasive grass, *B. ischaemum*, invested less in its leaves than most of the native C_4 grasses we used for comparison. Although we observed some inter-annual variability in the field, we found no consistent differences in leaf-level nitrogen (TN, % leaf mass; NLA, g N m^{-2} leaf) or carbon (TC, % leaf mass; CC, g glucose m^{-2} leaf) investments between the invasive grass and the native C_4 species we examined (Tables 1.3 - 1.7). The invasive did, however, invest less biomass per unit leaf area (i.e., higher specific leaf area; SLA; m^2 g^{-1}) than several of the native species, but not consistently less than *B. laguroides* and *S. scoparium* (Tables 1.3, 1.4, 1.6, 1.7). Mass- and area-based nitrogen investments (TN, % leaf mass; NLA, g N m^{-2} leaf) tended to be lower in the invasive and native C_4 species and than in the native C_3 species, but this was not always the case (Tables 1.3 - 1.6). Mass-based carbon leaf investments (TC, % leaf mass) were generally similar among the invasive and native species, except during the dry year in the field (2006) when *B. ischeamum* invested less carbon per gram of leaf than the two native species with which it was compared (Table 1.3, 1.5). In both the field and greenhouse experiment, all of the C_4 grasses, including *B. ischaemum,* had lower leaf construction

cost (CC, g glucose m^{-2} leaf) and leaf quality (higher C:N) than the native C_3 grass, *N. leucotricha* (Tables 1.3 – 1.7).

At the whole-plant level, *B. ischaemum* had significantly higher root, stem and total biomass than each native C_3 and C_4 species grown in the greenhouse (Tables 1.8, 1.9). *B. ischaemum* also had the lowest ratio of leaf biomass to whole plant biomass (leaf:total, Tables 1.8, 1.9). Leaf area per kg of total plant biomass (leaf area ratio, LAR; m^2 leaf kg^{-1} total plant biomass) was lower in the invasive and *B. laguroides* than in *N. leucotricha* and *S. scoparium* (Tables 1.6, 1.7). Although *B. ischaemum* invested less of its total biomass in leaves than the other species, it nevertheless had a higher leaf area per plant (LAP; m^2) than the native C_4 species in our experiment (Tables 1.6, 1.7).

Gas exchange and photosynthetic returns on leaf investments in the field

On a leaf-level basis, our results do not indicate that *B. ischaemum* has any advantage over its native counterparts through higher carbon gain or lower water loss. While leaf-level photosynthetic rates (A_{net}, µmol CO_2 m^{-2} s^{-1}) were similar between *B. ischaemum* and the majority of the native species with which it was compared in the field (Figure 1.3; Tables 1.10, 1.11), the invasive grass was outperformed at the leaf level photosynthetically by *B. laguroides* in the spring and fall of the dry year (2006) and in the late summer of the wet year (2007). Transpiration (E, mmol H_20 m^{-2} s^{-1}; Figure 1.4) and stomatal conductance (g_{sw}, mmol H_20 m^{-2} s^{-1}; Figure 1.5) rates were generally similar between the invasive and native C_4 species (Tables 1.10, 1.11). Both transpiration-based (A_{net}:E) and conductance-based (A_{net}:g_{sw}) water-use efficiencies (WUE) were also not significantly higher in the invasive species than in the majority of the native species. With the exceptions of the short C_4 grass *H. belangeri*, which had significantly lower WUE than the other C_4 grasses in the spring, and the native C_3 grass *N. leucotricha*,

WUE was similar between the invasive and the native species in the field (Figures 1.6, 1.7; Tables 1.10, 1.11). Estimated light curve parameters (A_{max}, θ, Φ, and R_d) did not indicate that *B. ischaemum* was more light-use efficient or capable of higher rates of light-saturated photosynthesis (A_{max}) than native species in the field. A_{max} were similar between the invasive and the native C_4 species and significantly lower in the native C_3 species, and respiration rates (R_d) did not differ among species (Table 1.12). There were some species-level differences in convexity, which was significantly higher in *N. leucotricha* and *B. laguroides* than in the other species measured, but otherwise, light curve parameters did not indicate large differences in species' light-use efficiency (Tables 1.12).

The invasive, *B. ischaemum* also did not consistently have higher short-term photosynthetic returns on leaf investments compared to most of its native counterparts in the field. Although, *B. ischaemum* did received significantly higher photosynthetic returns on leaf carbon (PEUE; Figure 1.8), nitrogen (PNUE; Figure 1.9), and biomass (A_{mass}; Figure 1.10) investments than *H. belangeri* and *N. leucotricha,* it received returns on leaf investments that were similar to or lower than those of the other native C_4 species (Table 1.12). All of the C_4 species, including *B. ischaemum* had higher A_{mass}, PNUE, and PEUE than the native C_3 grass, *N. leucotricha* (Table 1.12).

Sensitivity to drought

Long-term responses (i.e., leaf investment and biomass allocation) to decreased water availability were similar between the invasive and native species in the field and in the greenhouse. In the field during the dry year, the invasive and native species all decreased leaf investments in response to decreased water availability. However, decreases in leaf N content (TN) and leaf quality (increased C:N) were significantly

smaller in the invasive than they were in native species (significant species-date term in Table 1.4; Figure 1.11). Similarly, plants in the low-water treatment in the greenhouse all decreased investment of resources in photosynthetic surface areas and increased investment in roots. The exception was that leaf nitrogen investment was only significantly reduced for *B. laguroides* and *N. leucotricha* in the low-water treatment; *B. ischaemum* and *S. scoparium* did not significantly alter their leaf N investment in response to decreased water availability (TN; Tables 1.5, 1.6). The invasive and native species all increased root allocation, as measured by root:shoot and proportion of root biomass out of total plant biomass (root:total), and decreased leaf C investments and aboveground biomass allocation under lower water availability (Tables 1.7 – 1.9).

In addition, we did not see evidence that photosynthetic rates of the invasive were less sensitive to drought conditions than those of native species during our soil dry-down trials in the greenhouse. In fact, photosynthetic rates (A_{net}; Figure 1.12) and water-use efficiencies (A_{net}:g_{sw}; Figure 1.13) in *B. ischaemum* decreased more quickly than those of the native species as soil moisture declined during sequential dry-downs in the greenhouse (Tables 1.13, 1.14). Faster declines in photosynthetic rates in *B. ischaemum* leaves were associated with faster soil moisture draw-down rates in *B. ischaemum* pots (Figure 1.14; Table 1.15). Despite significantly lower stomatal conductance (g_{sw}; Tables 1.13, 1.14) and transpiration (E; Figure 1.15; Table 1.13, 1.14) in *B. ischaemum*, water-use efficiency (A_{net}:g_{sw}; Figure 1.13) in the invasive grass was similar to or lower than that measured in the native grasses as soil moisture declined in the greenhouse. While the invasive maintained water-use efficiencies comparable to those of the native C_4 species under wet soil conditions, it had significantly lower water-use efficiencies under dry soil conditions. As soils dried, the native C_3 grass, *N. leucotricha* reduced conductance at a cost to photosynthesis but still maintained water-use efficiency. All of the species

eventually decreased stomatal conductance in order to reduce water loss, but the invasive species did so at a larger cost to carbon fixation than did the two native C_4 species. Estimated photosynthetic light-use efficiency parameters did not indicate that the invasive was more light-use efficient or capable of higher rates of A_{max} than natives (Tables 1.13, 1.14).

Comparison of species soil moisture pulse response

Although *B. ischaemum* appeared to be more sensitive to declining water availability during soil moisture dry-downs in the greenhouse low-water treatment, the invasive was just as resilient as native species were once water was available again. After 14 days of soil drying, all of the species in both water treatments except *S. scoparium* had decreased photosynthetic rates in order to reduce water loss and maintain water-use efficiency. *S. scoparium* maintained higher water loss in order to maintain high levels of photosynthesis as soils dried. Two days after the soil moisture pulse, pulse responses for photosynthetic and transpiration rates were similarly positive in the invasive species and two of the native species, *B. laguroides* and *N. leucotricha* (Figure 1.16; Table 1.16). Pulse responses were negative for *S. scoparium*: photosynthesis and transpiration rates decreased slightly after the soil moisture pulse. Water-use efficiency did not significantly change in any of the species in response to the soil moisture pulse (Figure 1.16; Table 1.16).

Leaf-level versus whole-plant photosynthetic performance

While *B. ischaemum* did not outperform native species photosynthetically at the leaf-level, larger leaf area per plant in the invasive caused slightly more carbon to be fixed and water to be lost per individual for *B. ischaemum* when soil conditions were wet. At the leaf-level, A_{net} was similar between the invasive and native species under both dry

and wet conditions in the low-water treatment (Figure 1.17a; Table 1.17). At the plant level, however, A_{net} was slightly higher for *B. ischaemum* individuals than individuals of the native species under wet conditions in the low-water treatment (Figure 1.17b; Table 1.17). Transpiration rates (E) were slightly (though not significantly) lower in the invasive at the leaf level (Figure 1.18a), but E were slightly higher in the invasive than the native C_4 species at the whole-plant level (Figure 1.18b; Table 1.17).

DISCUSSION

Precipitation variability and availability constitute strong primary filters for species composition in these central Texas semi-arid savannas, but our results suggest that superior performance for traits that promote survival in water-limited ecosystems is not the basis for *B. ischaemum's* successful invasion of these ecosystems. On the contrary, the native C_4 grasses, *B. laguroides* and *S. scoparium*, are capable of out-performing *B. ischaemum* as soil moisture becomes limiting. Although its short-term photosynthetic performance was similar to or worse than native C_4 species under dry conditions, *B. ischaemum* was just as capable as the native species of utilizing pulses in soil moisture, and its performance under wet soil conditions was similar to or greater than those of the native species we monitored. However, *B. ischaemum* produced significantly more biomass and leaf area than native species under both average and low soil moisture frequency in the greenhouse, indicating that it may be outperforming native species in the long-term even if it appears to lose under dry conditions in the short-term. While greater biomass production can be a competitive advantage for plant species, it may not be the primary mechanism by which *B. ischaemum* out-competes native species (Isbell et al. 2009, Wilson et al. 2012). Our results suggest that its ecophysiology allows *B. ischaemum* to enter and survive in this system, but superior performance under dry

conditions is not the primary mechanism by which it becomes dominant. Instead, the exclusion of native species from invaded areas may be driven directly by competition in the form of biomass (crowding, shading, etc.) or indirectly by shifts in community-level factors (Isbell et al. 2009, Wilson et al. 2012) and changes in ecosystem functions resulting from its presence (Ruffner et al. 2012, Chapter 2).

Explaining *B. ischaemum*'s invasive success

Translating average photosynthetic performance into superior biomass production

The first question is how does *B. ischaemum* out-produce native species at the whole-plant biomass level when it does not out-perform native species at the leaf-level? In several cases, invasive plants are thought to out-compete native plant species in part by realizing higher returns on leaf investments to fuel higher growth rates that allow them to out-produce native species (Baruch et al. 1985, Baruch and Goldstein 1999, Nagel and Griffin 2001, Mc Dowell 2002, Nagel and Griffin 2004, Penuelas et al. 2010). In our greenhouse study, however, significantly higher biomass production was not paired with significantly higher carbon fixation rates and higher returns on leaf investments at the leaf level. How was *B. ischaemum* able to out-produce natives at the whole-plant level when it does not have any obvious advantage at the leaf level? We propose that while the invasive and native species fix roughly the same amount of carbon per plant, they may differ in how they allocate that fixed carbon (i.e., photosynthate). There are several ways in which *B. ischaemum* might differ from native species in how it allocates carbon: (1) *B. ischaemum* may be able to convert carbon into new biomass more efficiently than native species (i.e., it may respire less per unit new biomass made), (2) *B. ischaemum* may invest less carbon in stem and/or root materials than do native species, and/or (3) *B. ischaemum* may allocate less carbon belowground to mycorrhizal associates and root

exudates, (i.e., the release of carbon from living plant roots into the soil). Additionally, it is possible that higher photosynthetic returns on leaf investments over short periods of time, like those we saw in the field during June and July in the wet year (2007), may enable *B. ischaemum* to fuel intense bursts of growth that result in significantly higher end-of-season biomass. Whether any or all of these factors contribute to *B. ischaemum*'s ability to out-produce native species remains to be investigated.

The role of biomass quality and quantity in invasion

Introduced *Bothriochloa* spp. are known to have significantly higher growth rates and to produce significantly more biomass than many of the native species they encounter in the central North American ecosystems where they have been introduced (Coyne and Bradford 1985, Harmoney and Hickman 2004, Wilsey and Polley 2006, Schmidt et al. 2008). But is higher biomass production in *B. ischaemum* responsible for its invasive success? Higher productivity and lower quality plant inputs (Chapter 2) associated with *B. ischaemum* may facilitate its invasion of new ecosystems via direct competition (shading, nutrient acquisition, etc.) and/or indirectly by altering ecosystem composition (in the soil microbial and herbivore communities for example) and function (nutrient cycling and availability). Although the mechanisms of *B. ischaemum* invasion would be expected to depend in part on the stage of invasion (Theoharides and Dukes 2007) and environmental context (Alpert et al. 2000), they may also be specific to native species or groups of native species (Carey et al. 2004). In our study, it seems that there are two groups of native species: (1) those that are less functionally similar to *B. ischaemum* and are therefore more susceptible to its indirect impacts on nutrient cycling; and (2) those that are functionally similar or superior to *B. ischaemum* but may be susceptible to its indirect impacts on soil community composition (Wilson et al. 2012).

Direct competition and indirect impacts of invasion on ecosystem function may play a larger role in an invasive plant's success when native species are less functionally similar to the invasive plant. *B. ischaemum's* ability to rapidly produce larger amounts of biomass may allow it to out-perform slower growing species with higher investment in their leaves such as *N. leucotricha, H. belangeri* and *E. intermedia.* In such cases, *B. ischaemum* can preempt its native neighbors' access to light, soil moisture and other resources which can lead to the exclusion of those species. In addition, *B. ischaemum* invasion is associated with decreased soil inorganic nitrogen availability in invaded areas (Ruffner et al. 2012, Chapter 2), a possible mechanism for the exclusion of native plants with lower nitrogen-use efficiency, such as *N. leucotricha* and *H. belangeri*, from invaded areas.

While a variety of mechanisms may be responsible for *B. ischaemum*'s success as an invader, indirect impacts mediated by community-level factors may play a larger role in *B. ischaemum* invasion than direct competition when it dominates native species that are functionally similar or superior to it, such as *B. laguroides* and *S. scoparium*. When grown in the field in mixtures with native species, *B. ischaemum* and other alien species in Texas grasslands were found to drive declines in diversity by reducing species interaction mechanisms that maintain diversity, such as mutualisms and niche partitioning, not directly via asymmetric competition, i.e. species that produce larger amounts of biomass competitively exclude less productive species (Isbell et al. 2009). Another study that focused on plant-soil feedbacks and grew two dominant C_4 perennial native species (*Andropogon gerardii* and *S. scoparium*) in soil collected from areas invaded by *B. ischaemum* and *B. bladhii* concluded that the invasive grasses' negative impacts on arbuscular mycorrhizal fungal (AMF) associations with native plant roots and alterations to the soil community were responsible for the suppression of native plant

growth (Wilson et al. 2012). AMF play a vital role in ecosystem function and maintaining plant species diversity in ecosystems (van der Heijden et al. 2005) and plant species composition influences AMF community composition in grassland ecosystems (Eom et al. 2000). Additionally, invasive grasses have been shown to decrease the richness of AMF associations with native plant roots and to alter mycorrhizal community structure in other systems (Hawkes et al. 2006). The details and mechanisms of *B. ischaemum*'s impacts on plant-soil feedbacks have yet to be worked out.

The role of water availability in invasion: taking advantage of the wet years

Strategies for coping with water stress in water-limited systems vary greatly among species, but not consistently between native and invasive species (Funk and Zachary 2010). We found this to be the case in our greenhouse study where the species we observed all differed slightly from one another in their short-term strategies for coping with water stress. In the short-term, *B. ischaemum* and *N. leucotricha* were less efficient with water under dry conditions and more sensitive to soil moisture availability than *S. scoparium* and *B. laguroides* during soil dry-down experiments in the greenhouse. *S. scoparium,* which is capable of surviving high levels of dehydration (Hake et al. 1984), was able to maintain significantly higher rates of photosynthesis than the other species when soil moisture was low because it did not decrease stomatal conductance and thus internal CO_2 concentrations in order to reduce water loss. Some work shows that declining intercellular and bundlesheath CO_2 concentrations and not biochemical regeneration limit C_4 photosynthesis under water-stressed conditions (Lal and Edwards 1996). This may explain how *S. scoparium* benefits from accepting water loss to maintain stomatal conductance and hence CO_2 uptake. *B. laguroides* maintained high levels of net photosynthesis at low levels of conductance in both wet and dry soil conditions which

may be the result of higher biochemical efficiency and/or differences in bundle-sheath structure (Ghannoum 2009). As soils dried, *N. leucotricha* reduced conductance at a cost to photosynthesis but still maintained water-use efficiency. As soil moisture declined during our greenhouse experiments, *B. ischaemum* experienced faster declines in photosynthetic rates and down-regulated transpiration at a higher cost to photosynthesis than *B. laguroides* and *S. scoparium*. Larger root biomass likely allowed *B. ischaemum* to exploit available soil moisture in pots at a faster rate than native species, a possible disadvantage to native neighbors in the field if *B. ischaemum* is able to preempt available soil water. From this, it appears that *B. ischaemum* is opportunistic: *B. ischaemum* made the most of soil water while it was available and then shut down photosynthetically under drier conditions.

Whatever disadvantages *B. ischaemum* may suffer under dry conditions, it was able to produce significantly more biomass than native species under both water treatments in our greenhouse work. Whether or not this phenomenon transfers from the greenhouse to the field is debatable. Other work that monitored aboveground net primary productivity (ANPP) in *B. ischaemum*-dominated and native savanna grass-matrix plots at our field site over the course of four growing seasons found that ANPP was similar between invaded and native plots in two dry years and in one wet year with highly variable precipitation (Basham and Poteet *unpublished data*). The only year in which *B. ischaemum* plots out-produced native plots was during a wet year in which precipitation was regular throughout the growing season and temperatures were low and not variable. This indicates that precipitation variability and timing may play a role in *B. ischaemum* invasion. Once established in a community, *B. ischaemum* may not become dominant within that community until a series of high rainfall years allows it to out-produce neighbors or accumulate enough standing dead biomass to negatively impact neighbors.

If so, increased precipitation variability due to climate change may slow *B. ischaemum* invasion. The role of precipitation variability in *B. ischaemum*'s community- and ecosystem–level impacts will need to be more closely examined in the field before the relationship between water availability and *B. ischaemum* invasion can be fully understood.

Predicting ecosystem-level impacts of invasion and the role of climate change

Our results indicate that changes in species composition that result from *B. ischaemum* invasion have the potential to alter ecosystem response to soil moisture availability and possibly decrease ecosystem carbon storage. We found that *B. ischaemum* was more sensitive to declining soil moisture than native C_4 species, which could result in lower productivity in invaded ecosystems as precipitation frequency decreases with climate change. Additionally, *N. leucotricha* and other C_3 species are active year-round in this ecosystem, while *B. ischaemum* is dormant from December until March. Shifts in C_3:C_4 biomass associated with *B. ischaemum* invasion may therefore decrease ecosystem growing season length and ecosystem carbon uptake.

The mechanisms by which particular grass species dominate grassland and savanna systems are unclear, but temperature and water availability are hypothesized to determine the ratio of C_3:C_4 species in these systems (Edwards et al. 2010). While C_3 species in savannas and grasslands are expected to benefit from increasing atmospheric [CO_2] (Reich et al. 2001), increasing temperatures and decreasing precipitation frequency associated with climate change may counter advantages of increased CO_2 availability for C_3 species (Winslow et al. 2003). This might lead us to predict that climate change will only exacerbate the decline of C_3 species associated with *B. ischaemum* invasion in these ecosystems. However, the C_3 grass *N. leucotricha* and others like it may be uniquely

positioned to thrive under these anticipated changes. *N. leucotricha* possesses heat and water-deficit tolerance similar to some C_4 species in this system (Hicks et al. 1990). These traits may allow it to take advantage of increasing atmospheric CO_2 despite higher temperatures and less frequent rainfall. *B. ischaemum* also responds positively to increases in atmospheric CO_2 levels (Anderson et al. 2001), benefiting primarily from increased water-use efficiency and decreased water deficits under drought conditions (Polley et al. 2002). Thus increasing atmospheric [CO_2] could help this invader to cope with drier climatic conditions. Many of the C_4 species in this system have the capacity to respond positively to increasing atmospheric [CO_2] (LeCain and Morgan 1998); however, different C_4 species may saturate at different levels of atmospheric [CO_2]. For example, *S. scoparium* may experience smaller benefits from elevated [CO_2] than the invader (Polley et al. 1996, Reich et al. 2001, Polley et al. 2002). At least one other invasive C_4 perennial grass is expected to benefit more from elevated atmospheric [CO_2] than its primary native competitor (Baruch and Jackson 2005). How increasing N, CO_2 and temperatures and decreasing precipitation frequency impact *B. ischaemum* invasion and ecosystem productivity in these systems will depend on how limiting CO_2 is relative to other resources and whether species differ greatly in their requirements for resources that become limiting once CO_2 is no longer limiting. Interactions between elevated CO_2, N deposition and changing climatic conditions can have very different impacts on ecosystem composition and function than any one of these factors acting alone (Zavaleta et al. 2003)

CONCLUSIONS

Although *B ischaemum's* success as an invader is not directly related to its ability to cope with precipitation variability and availability, its ability to rapidly produce large

amounts of biomass may allow it to directly out-compete native species with which it is less functionally similar. Additionally, its impacts on ecosystem function, e.g., decreased nitrogen availability, may allow it to exclude these species from invaded areas. In cases where native species are functionally similar to *B. ischaemum*, its indirect impacts on ecosystem composition and community-level factors are more likely explanations for its success. Regardless of how it becomes dominant, *B. ischaemum* invasion is likely to result in decreased growing season length in invaded areas. Additionally, greater sensitivity to decreased soil moisture availability in the invasive has the potential to decrease ecosystem productivity in invaded areas as precipitation events become less frequent with climate change.

Table 1.1.a. List of variables measured, calculated, and estimated in the field at the Wildflower Center (WFC) and in the greenhouse (GH) in Chapter 1.

Type of Variable	Variable	Description	Units	Tables			Figures	
				WFC 2006	WFC 2007	GH	WFC	GH
Long-term Leaf Investments	SLA	specific leaf area	m^2 leaf area g^{-1} leaf mass	1.3, 1.4	1.3, 1.4	1.6, 1.7		
	TN	total nitrogen content	%	1.3, 1.4	1.3, 1.4	1.5, 1.6	1.11b	
	TC	total carbon content	%	1.3, 1.4	1.3, 1.4	1.5, 1.6		
	NLA	area-based nitrogen content	g N m^{-2} leaf	1.3, 1.4	1.3, 1.4	1.5, 1.6		
	CC	grams of glucose used to construct m^{-2} leaf	g glucose m^{-2} leaf	1.3, 1.4	1.3, 1.4	1.5, 1.6		
	C:N	carbon to nitrogen ratio of tissues		1.3, 1.4	1.3, 1.4	1.6, 1.7	1.11a	
	LAR	leaf area per unit total plant biomass	m^2 kg^{-1}			1.6, 1.7		
	LAP	leaf area per individual plant	m^2			1.6, 1.7		
Long-term Biomass Allocation	total biomass		g			1.8, 1.9		
	root biomass		g			1.8, 1.9		
	leaf biomass		g			1.8, 1.9		
	stem biomass		g			1.8, 1.9		
	root : shoot	ratio of belowground to aboveground biomass				1.8, 1.9		
	root : total	ratio of root biomass to total biomass				1.8, 1.9		
	leaf : total	ratio of leaf biomass to total biomass				1.8, 1.9		
	stem : total	ratio of stem biomass to total biomass				1.8, 1.9		

Table 1.1.b. List of variables measured, calculated, and estimated in the field at the Wildflower Center (WFC) and in the greenhouse (GH) continued.

Type of Variable	Variable	Description	Units	Tables			Figures	
				WFC 2006	WFC 2007	GH	WFC	GH
Leaf-level Gas exchange	A_{net}	net photosynthesis (leaf-level)	µmol CO_2 m^{-2} s^{-1}	1.10	1.11	1.13, 1.14, 1.16	1.3	1.12, 1.17a
	A_{net}	net photosynthesis (plant-level)	µmol CO_2 s^{-2}	1.10	1.11	1.17		1.17b
	E	transpiration (leaf-level)	mmol H_2O m^{-2} s^{-1}	1.10	1.11	1.13, 1.14, 1.16		1.15, 1.18a
	E	transpiration (plant-level)	mmol H_2O s^{-2}	1.10	1.11	1.17	1.4	1.18b
	g_{sw}	stomatal conductance	mmol H_2O m^{-2} s^{-1}	1.10	1.11	1.13, 1.14, 1.16	1.5	
	A_{net} : E	transpiration-based water use efficiency	µmol CO^2 : mmol H_2O	1.10	1.11	1.13, 1.14, 1.16	1.6	
	A_{net} : g_{sw}	conductance-based water use efficiency	µmol CO^2 : mmol H_2O	1.10	1.11	1.13, 1.14, 1.16	1.7	1.13
Light Response Curves Parameters	A_{max}	maximum light saturated photosynthesis	µmol CO_2 m^{-2} s^{-1}	1.12	1.12	1.13, 1.14, 1.16		
	Φ	apparent quantum yield	rate of increase in CO_2 assimilation as irradiance increases	1.12	1.12	1.13, 1.14, 1.16		
	Θ	Convexity	effciency of the transition between light-limited to carboxylation-limited photosynthesis (values range from 0 - 1)	1.12	1.12	1.13, 1.14, 1.16		
	R_d	day-time dark respiration	µmol CO_2 m^{-2} s^{-1}	1.12	1.12	1.13, 1.14, 1.16		

Table 1.1.c. List of variables measured, calculated, and estimated in the field at the Wildflower Center (WFC) and in the greenhouse (GH) continued.

Type of Variable	Variables	Description	Units	Tables			Figures	
				WFC 2006	WFC 2007	GH	WFC	GH
Photosynthetic returns on leaf investments	PEUE	photosynthetic energy-use efficiency	µmol CO_2 g^{-1} glucose s^{-1}	1.12	1.12		1.8	
	PNUE	photosynthetic nitrogen-use efficiency	µmol CO_2 g^{-1} N s^{-1}	1.12	1.12		1.9	
	A_{mass}	mass-based phtotsynthesis	µmol CO_2 g^{-1} leaf s^{-1}	1.12	1.12		1.10	
Environmental Drivers	RSWC	relative soil water content		1.2	1.2	1.15		1.2, 1.14
	RH	relative humidity	%	1.2	1.2			
	T_{air}	air temperature	Celcius	1.2	1.2		1.1	
	VPD_{air}	air vapor pressure deficit		1.2	1.2			1.2
	PAR	photosynthetically active radiation	µmol photons m^{-2} s^{-1}					1.2

Table 1.2. Environmental conditions during leaf-level measurements made at the WFC.

Environmental conditions during leaf-level measurements made at the WFC during the 2006 and 2007 growing seasons. Environmental variables are air vapor pressure deficit (VPD_{air}), percent relative humidity (RH), air temperature (T_{air}), and relative soil water content (RSWC). Values are monthly means (± 1 SE).

Year	Month	VPD_{air}	RH (%)	T_{air}	RSWC
2006	April	2.4 (0.11)	42.43 (3.34)	27.26 (1.93)	0.44 (0.02)
	July	3.2 (0.2)	46.04 (2.3)	34.43 (0.83)	0.39 (0.01)
	August	2.74 (0.17)	43.69 (2.02)	33.87 (0.67)	0.25 (0.02)
	October	2.87 (0.14)	40.4 (2.34)	30.38 (1.04)	0.51 (0.02)
2007	April	1.42 (0.08)	56.4 (1.81)	25.11 (0.48)	0.82 (0.01)
	May	1.61 (0.04)	52.47 (0.98)	26.06 (0.35)	0.7 (0.02)
	June	2.09 (0.13)	57.46 (1.85)	32.33 (0.47)	0.55 (0.01)
	July	1.67 (0.1)	65.08 (1.82)	31.97 (0.42)	0.75 (0.02)
	Aug	1.96 (0.14)	60.84 (1.9)	32.59 (0.6)	0.55 (0.02)
	Oct	1.73 (0.1)	61.08 (1.7)	30.66 (0.64)	0.68 (0.03)

Table 1.3. Long-term leaf investment indicators measured for field-collected leaves.

Long-term leaf investment indicators, specific leaf area (SLA; m^2 g^{-1} leaf), leaf total nitrogen content (TN; % leaf mass), leaf nitrogen content per unit leaf area (NLA; g N m^{-2} leaf), leaf total carbon content (TC; % leaf mass), leaf construction cost (CC; g glucose m^{-2} leaf), and leaf C:N, for leaves collected from the invasive species, *B. ischaemum* and native species in the field at the WFC during the 2006 and 2007 growing seasons. Values are annual means (± 1 SE) of 4 individuals of each species in 2006 and three individuals of each species in 2007. Significant differences between species are indicated by different lower case letters. Where there were no significant differences among species no letters are used (pair-wise *F*-test of linear contrasts of means, $P < 0.05$).

Year	2006			2007					
Species	*B. ischaemum*	*B. laguroides*	*N. leucotricha*	*B. ischaemum*	*B. laguroides*	*E. intermedia*	*H. belangeri*	*N. leucotricha*	*S. scoparium*
SLA	0.191 (0.01) a	0.233 (0.016) b	0.155 (0.016) c	0.184 (0.011) a	0.207 (0.011) b	0.146 (0.007) c	0.152 (0.007) c	0.122 (0.006) d	0.184 (0.009) a
TN	1.65 (0.06) a	2.14 (0.156) b	2.28 (0.19) b	1.59 (0.05) a	1.9 (0.05) b	1.57 (0.04) a	1.5 (0.04) a	1.69 (0.1) a	1.53 (0.05) a
NLA	0.881 (0.03) a	0.92 (0.024) a	1.53 (0.075) b	0.91 (0.05) a	0.95 (0.06) b	1.1 (0.04) b	1.00 (0.03) a	1.39 (0.06) c	0.87 (0.05) a
TC	40.85 (0.28) a	42.06 (0.323) b	42.02 (0.38) b	40.28 (0.33)	42.04 (0.29)	41.83 (0.24)	40.04 (0.45)	41.84 (1.87)	42.51 (0.61)
CC	55.25 (3.56) a	48.9 (3.9) a	81.11 (10.82) b	56.8 (3.43) a	53.79 (2.91) a	74.13 (2.52) b	64.44 (1.63) a	87.48 (5.91)b	63.34 (4.52) a
CN	25.2 (1.03) a	20.96 (1.69) b	20.28 (2.09) b	25.67 (0.79) a	22.42 (0.59) b	26.92 (0.68) ac	26.95 (0.6) ac	25.13 (0.67)a	28.28 (1.04) c

Table 1.4. Ordinary least squares (OLS) model results for long-term leaf investment indicators measured for leaves collected in the field at the WFC during the 2006 and 2007 growing seasons.

Fixed effects in the models are *species*, *day-of-year* (DOY) and their interaction term (*species X doy). Plot* was considered a random effect in the model, thus F-values of differences among species were calculated using the mean squares of the *species X plot* term from the same model as the denominator. *F*-values (degrees of freedom) are reported. Bold type indicates values are significant at the $P < 0.05$ level. Measured variables are specific leaf area (SLA; $m^2 g^{-1}$ leaf), leaf total nitrogen content (TN; %), leaf nitrogen content per unit leaf area (NLA; g N m^{-2} leaf), leaf total carbon content (TC; %), leaf construction cost (CC; g glucose m^{-2} leaf), and leaf quality (C:N). Data from each year was analyzed separately.

Year	2006					2007				
Variable	SPP	PLOT	SPP X PLOT	DOY	SPP X DOY	SPP	PLOT	SPP X PLOT	DOY	SPP X DOY
SLA	**23.92 (2, 6)**	0.86 (3, 18)	1.54 (6, 18)	**53.91 (2, 18)**	**4.91 (4, 18)**	**30.41 (5,10)**	**5.10 (2, 60)**	1.02 (10, 60)	**17.31 (5, 60)**	**2.77 (25, 60)**
TN	**32.11 (2, 6)**	0.17 (3, 18)	0.91 (6, 18)	**66.88 (2, 18)**	**6.97 (4, 18)**	**6.01 (5, 10)**	0.56 (2, 60)	1.25 (10, 60)	**3.11 (5, 60)**	1.13 (25, 60)
NLA	**37.43 (2, 6)**	0.02 (3, 18)	1.72 (6, 18)	0.54 (2, 18)	1.81 (4, 18)	**13.86 (5, 10)**	0.75 (2, 60)	1.58 (10, 60)	**4.86 (5, 60)**	**1.85 (25, 60)**
TC	**6.84 (2, 6)**	2.05 (3, 18)	1.71 (6, 18)	**6.55 (2, 18)**	**10.38 (4, 18)**	1.01 (5, 10)	0.55 (2, 60)	1.23 (10, 60)	0.80 (5, 60)	0.46 (25, 60)
CC	**19.46 (2, 6)**	0.22 (3, 18)	1.75 (6, 18)	**55.63 (2, 18)**	**11.75 (4, 18)**	**9.00 (5, 10)**	0.36 (2, 60)	1.48 (10, 60)	**3.80 (5, 60)**	1.21 (25, 60)
CN	**6.84 (2, 6)**	0.46 (3, 18)	0.69 (6, 18)	**154.68 (2, 18)**	**9.13 (4, 18)**	**9.97 (5, 10)**	0.53 (2, 60)	1.04 (10, 60)	**5.42 (5, 60)**	**1.73 (25, 60)**

Table 1.5. Long-term leaf investment indicators for the invasive, *B. ischaemum*, and three native grasses grown under two water treatment levels, high water (watered every 7-10 days) and low water (watered every 20 days), in a greenhouse.

Values are means (± 1 SE) for total leaf nitrogen content (TN), per gram of leaf and per unit leaf area (NLA), and total carbon content per gram of leaf (TC) and leaf construction cost (CC). Asterisks indicate significant differences between water treatments within species (e.g. a variable differed between *B. ischaemum* in the low-water and high-water treatments; **P* < 0.05; ** *P* < 0.01; * *P* < 0.001). Significant differences between species are indicated by different lower case letters beside the low-water values. Where there were no significant differences among species no letters are used (pair-wise *F*-test of linear contrasts of means, *P* < 0.05).**

Species	Treatment	TN (% of leaf mass)	NLA (g N m^{-2})	TC (% of leaf mass)	CC (g glucose m^{-2})
B. ischaemum	High Water	1.72 (0.04)	0.82 (0.07)	42.84 (0.43)	54.09 (4.41)
	Low Water	1.62 (0.08) a	0.78 (0.09) ac	43.96 (0.20)	56.30 (6.06) a
B. laguroides	High Water	1.67 (0.03)	0.87 (0.05)	43.71 (0.27)	63.39 (4.21)
	Low Water	1.32 (0.07) b*	0.54 (0.03) a	41.68 (3.03)	42.54 (5.99) a
N. leucotricha	High Water	2.13 (0.09)	1.51 (0.08)	42.21 (0.14)	73.77 (7.49)
	Low Water	2.22 (0.05) c**	1.38 (0.07) b	43.08 (0.37)	70.47 (2.51) b
S. scoparium	High Water	1.88 (0.12)	1.10 (0.08)	43.59 (0.54)	69.01 (7.64)
	Low Water	1.48 (0.14) a	0.81 (14) c	41.69 (0.48)	55.83 (5.86) a

Table 1.6. Mixed effects model results for leaf investment indicators for greenhouse-grown plants.

Long-term leaf investment indicators were compared between the invasive, *B. ischaemum* and three native grasses (SPP) grown under two water treatment levels (TRT), high water (watered every 7-10 days) and low water (watered every 20 days), in a greenhouse. Values shown are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effect *bin*. Bold type indicates values are significant at the $P < 0.05$ level. Italics indicate nearly significant values at the $0.5 < P < 0.10$ level. Long-term leaf investment indicators are total leaf nitrogen content (TN; % of leaf mass) and N content per unit leaf area (NLA), total carbon content (TC; % of leaf mass) and leaf construction cost (CC; g glucose m^{-2} leaf), leaf carbon to nitrogen ratio (C:N), specific leaf area (SLA; g leaf surface area leaf per g leaf), leaf area plant mass ratio (LAR; leaf surface area m^2 per kg of plant biomass) and leaf area per plant (LAP; leaf surface area m^2 per individual).

Leaf Investments	Fixed Effects			Random Effect
Variable	TRT	SPP	TRT X SPP	Bin σ^2
TN	**4.42 (1, 22)**	**21.08 (3, 22)**	**4.22 (3, 22)**	0.002
NLA	**12.01 (1, 24)**	**33.25 (3, 24)**	1.44 (3, 24)	0
TC	0.56 (1, 24)	0.37 (3, 24)	0.91 (3, 24)	0
CC	**5.49 (1, 22)**	**6.27 (3, 22)**	1.00 (3, 22)	1.49
C:N	**7.94 (1, 22)**	**16.91 (3, 22)**	*2.79 (3, 22)*	0.76
SLA	**5.61 (1, 24)**	**8.67 (3, 24)**	0.95 (3, 24)	0
LAR	*3.81 (1, 24)*	**6.63 (3, 24)**	2.03 (3, 24)	0
LAP	*3.92 (1, 24)*	**5.57 (3, 24)**	0.13 (3, 24)	0

Table 1.7. Long-term leaf investments measured for greenhouse-grown plants.

Leaf carbon to nitrogen ratio (C:N), specific leaf area (SLA; g leaf surface area leaf per g leaf), leaf area plant mass ratio (LAR; leaf surface area m^2 per kg of plant biomass) and leaf area per plant (LAP; leaf surface area m^2 per individual) for the invasive and three native grasses grown under two water treatment levels, high-water (watered every 7-10 days) and low-water (watered every 20 days), in a greenhouse. Values are means (± 1 SE). Lower case letters indicate significant differences among species (pair-wise *F*-test of linear contrasts of means, $P < 0.05$).

Species	Treatment	Leaf C:N	SLA ($m^2 g^{-1}$)	LAR ($m^2 kg^{-1}$)	LAP (m^2)
B. ischaemum	High Water	25.01 (0.55)	21.23 (1.82)	2.50 (0.13)	0.0098 (0.0008)
	Low Water	27.30 (1.37) a	21.64 (2.21) a	2.34 (0.17) a	0.0083 (0.0013) a
B. laguroides	High Water	26.16 (0.54)	19.16 (1.06)	2.60 (0.28)	0.0073 (0.0005)
	Low Water	31.50 (0.62) a	24.66 (1.22) a	2.93 (0.46) a	0.0063 (0.0011) b
N. leucotricha	High Water	20.01 (0.92)	13.84 (1.24)	5.14 (0.59)	0.0090 (0.0006)
	Low Water	19.47 (0.46) b	16.11 (0.64) b	3.76 (0.08) b	0.0073 (0.0011) a
S. scoparium	High Water	23.49 (1.52)	17.33 (1.67)	4.05 (0.67)	0.0060 (0.0008)
	Low Water	28.83 (2.57) a	19.47 (1.80) c	2.42 (0.35) b	0.0053 (0.0007) b

Table 1.8. Biomass allocation measured for greenhouse-grown plants.

Leaf, stem, root and total biomass, root: shoot ratio and biomass allocation to roots, stems and leaves as proportions of total measured biomass measured for the invasive and three native grass species for plants grown under greenhouse conditions under two water treatments, high-water (watered every 7-10 days) and low-water (watered every 20 days). Values are means (± 1 SE). Different lower case letters indicate significant differences between species (pair-wise *F*-test of linear contrasts of means, $P < 0.05$).

Species	Treat-ment	Total Biomass (g)	Root Biomass (g)	Leaf Biomass (g)	Stem Biomass (g)	Root: Shoot	Root : Total	Leaf : Total	Stem : Total
B. ischaemum	High Water	3.97 (0.22)	1.93 (0.11)	0.75 (0.06)	1.59 (0.10)	0.81 (0.03)	0.48 (0.01)	0.20 (0.01)	0.40 (0.01)
	Low Water	3.55 (0.25) a	1.95 (0.23) a	0.63 (0.05) a	1.22 (0.07) a	1.04 (0.09)	0.54 (0.02)	0.18 (0.02) a	0.35 (0.02) a
B. laguroides	High Water	2.92 (0.31)	1.32 (0.09)	0.90 (0.09)	1.21 (0.07)	0.61 (0.11)	0.44 (0.04)	0.32 (0.04)	0.43 (0.04)
	Low Water	2.21 (0.08) b	1.35 (0.31) b	0.55 (0.09) a	0.60 (0.13) b	1.17 (0.08)	0.61 (0.02)	0.25(0.02) b	0.27 (0.01) a
N. leucotricha	High Water	2.08 (0.30)	0.89 (0.22)	0.88 (0.02)	0.52 (0.07)	0.65 (0.05)	0.43 (0.01)	0.42 (0.01)	0.25 (0.02)
	Low Water	1.92 (0.08) c	1.11 (0.08) c	0.65 (0.03) a	0.36 (0.03) c	1.09 (0.08)	0.57 (0.02)	0.34 (0.01) c	0.20 (0.01) b
S. scoparium	High Water	1.69 (0.25)	0.80 (0.16)	0.43 (0.08)	0.54 (0.05)	0.79 (0.17)	0.44 (0.06)	0.27 (0.02)	0.34 (0.06)
	Low Water	2.05 (0.15) c	1.18 (0.06) c	0.44 (0.05) b	0.62 (0.12) c	1.18 (0.16)	0.58 (0.04)	0.21 (0.01) d	0.30 (0.04) a

Table 1.9. Mixed effects model results for individual plant biomass and biomass allocation ratios in greenhouse-grown plants.

Plant biomass and biomass allocation ratios were compared between the invasive, *B. ischaemum* and three native grasses (*SPP*) grown under two water treatment levels (*TRT*), high water (watered every 7-10 days) and low water (watered every 20 days), in a greenhouse. Values shown are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effect *bin*. Bold type indicates values are significant at the $P < 0.05$ level. Italics indicate nearly significant values at the $0.5 < P < 0.10$ level.

Biomass	Fixed Effects			Random Effect
Variable	TRT	SPP	TRT X SPP	Bin σ^2
Total Biomass	1.17 (1, 24)	**15.96 (3, 24)**	1.14 (3, 24)	0
Root Biomass	1.31 (1, 24)	**9.81 (3, 24)**	0.37 (3, 24)	0
Leaf Biomass	**11.12 (1, 24)**	**7.81 (3, 24)**	2.09 (3, 24)	0
Stem Biomass	**14.87 (1, 24)**	**39.31 (3, 24)**	**4.70 (3, 24)**	0
Root : Shoot	**28.86 (1, 24)**	0.47 (3, 24)	0.81 (3, 24)	0
Root : Total	**28.13 (1, 24)**	0.13 (3, 24)	0.98 (3, 24)	0
Leaf : Total	**34.79 (1, 24)**	**75.05 (3, 24)**	*2.49 (3, 24)*	0
Stem : Total	**11.89 (1, 24)**	**9.49 (3, 24)**	1.52 (3, 24)	0

Table 1.10. Ordinary least squares model results for leaf-level gas exchange measured at the WFC during the 2006 growing season.

A_{net}, E, g_{sw}, A_{net}:E and A_{net}:G_{sw} were compared between the invasive and two native species at the WFC. Fixed effects in the models are *species (SPP)*, *day-of-year* (DOY), and their interaction term (*species X doy).* Environmental covariates included in the models were air vapor pressure deficit (VPD_{air}), relative soil water content (RSWC), their squares (VPD_{air}^2, $RSWC^2$) and their two-way interaction terms with *species*. *Plot* was considered a random effect in the model, and therefore *F*-values of differences among species were calculated using the mean squares of the *species X plot* term from the same model as the denominator. *F*-values (degrees of freedom) are reported. Bold type indicates values are significant at the $P < 0.05$ level. Italics indicate values are nearly significant at the $0.05 < P < 0.1$ level.

Year	Variable	SPP	PLOT	SPP X PLOT	DOY	SPP X DOY	VPD_{air}	VPD_{air}^2	SPP X VPD_{air}	SPP X VPD_{air}^2	RSWC	$RSWC^2$
2006	A_{net}	**8.07 (2, 10)**	0.72 (5, 37)	**2.21 (10, 37)**	**91.37 (3, 37)**	**5.17 (6, 37)**	0.03 (1, 37)	0.61 (1, 37)	0.06 (5, 37)	**3.57 (2, 37)**	0.10 (1, 37)	**6.92 (1, 37)**
	E	0.42 (2, 10)	1.75 (5, 42)	1.68 (10, 42)	**44.97 (3, 42)**	2.12 (6, 42)	**7.43 (1, 42)**				**0.02 (1, 42)**	**5.66 (1, 42)**
	g_{sw}	2.90 (2, 10)	0.68 (5, 43)	1.09 (10, 43)	**48.97 (3, 43)**	**2.45 (6, 43)**					0.20 (1, 43)	**4.11 (1, 43)**
	A_{net} : E	**8.37 (2, 10)**	1.98 (5, 44)	**2.51 (10, 44)**	**14.69 (3, 44)**	1.84 (6, 44)	**6.45 (1, 44)**					
	A_{net} : G_{sw}	**11.06 (2, 20)**	1.04 (5, 41)	**2.64 (10, 41)**	**8.34 (3, 41)**	**2.73 (6, 41)**	0.33 (1, 41)	**7.41 (1, 41)**	*3.01 (2, 41)*			

Table 1.11. Ordinary least squares model results for leaf-level gas exchange measured at the WFC during the 2007 growing season.

Net photosynthetic (A_{net}), transpiration (E), stomatal conductance (g_{sw},) and water-use efficiency (A_{net}:E and A_{net}:G_{sw}) measured for the invasive and two native species at the WFC. Fixed effects in the models are species (SPP), day-of-year (DOY), their interaction term (SPP X DOY). *).* Environmental covariates included in the models were air vapor pressure deficit (VPD_{air}), relative soil water content (RSWC), their squares (VPD_{air}^2, $RSWC^2$) and their two-way interaction terms with *species*. Plot was considered a random effect in the model. *F*-values (degrees of freedom) are reported. Bold type indicates values are significant at the $P < 0.05$ level. Italics indicate values are nearly significant at the $0.1 < P < 0.05$ level.

Year	Variable	SPP	PLOT	SPP X PLOT	DOY	SPP X DOY	VPD_{air}	RSWC	$RSWC^2$	SPP X RSWC	SPP X $RSWC^2$
2007	A_{net}	**5.29 (5, 10)**	**3.24 (2, 48)**	**2.19 (10, 48)**	**16.79 (5, 48)**	**1.81 (25, 48)**					
	E	2.02 (5, 10)	**3.29 (2, 46)**	**3.18 (10, 46)**	**35.32 (5, 46)**	**1.81 (25, 46)**					
	g_{sw}	**5.04 (5, 10)**	0.17 (2, 30)	**2.81 (10, 30)**	**15.10 (5, 30)**	**3.59 (25, 30)**		3.27 (1, 30)	0.64 (1, 30)	1.42 (5, 30)	**4.97 (5, 30)**
	A_{net} : E	**5.00 (5, 10)**	0.40 (2, 59)	**3.44 (10, 59)**	**2.77 (5, 59)**	1.16 (25, 59)	**21.75 (1, 59)**				
	A_{net} : g_{sw}	**17.98 (5, 10)**	4.54 (2, 53)	1.81 (10, 53)	**5.36 (3, 53)**	**2.66 (25, 35)**		**6.70 (1, 53)**		2.06 (5, 53)	

Table 1.12. Ordinary least squares model results for estimated light curve parameters (A_{max}, θ, Φ and R_d) and photosynthetic returns on leaf investments (PNUE, PEUE and A_{mass}) for the invasive and native species at the WFC during 2006 and 2007.

Fixed effects in the models are *species (SPP)*, *day-of-year* (DOY), and their two-way interaction term (*species X doy). Plot* was considered a random effect in the model, thus *F*-values of differences among species were calculated using the mean squares of the *species X plot* term from the same model as the denominator. *F*-values (degrees of freedom) are reported. Bold type indicates values are significant at the $P < 0.05$ level. Italics indicate values are nearly significant at the $0.1 < P < 0.05$ level.

Year	Variable	SPP	PLOT	SPP X PLOT	DOY	SPP X DOY
2006	A_{max}	**18.92 (2, 4)**	1.03 (2, 18)	0.29 (4, 18)	**17.05 (3, 18)**	1.58 (6, 18)
	θ	0.36 (2, 4)	0.16 (2, 18)	1.74 (4, 18)	**97.89 (3, 18)**	1.89 (6, 18)
	Φ	**16.63 (2, 4)**	0.82 (2, 18)	0.63 (4, 18)	**9.18 (3, 18)**	**12.44 (6, 18)**
	R_d	1.15 (2, 4)	1.59 (2, 18)	1.76 (4, 18)	*2.80 (3, 18)*	0.85 (6, 18)
	PNUE	**91.33 (2, 6)**	0.36 (3, 18)	0.37 (6, 18)	**29.51 (2, 18)**	**4.41 (4, 18)**
	PEUE	**66.76 (2, 6)**	0.50 (3, 18)	1.01 (6, 18)	**80.62 (2, 18)**	**13.96 (4, 18)**
	A_{mass}	**58.43 (2, 6)**	0.9 (3, 18)	0.83 (6, 18)	**54.49 (2, 18)**	**8.96 (4, 18)**
2007	A_{max}	**5.48 (5, 10)**	2.38 (2, 47)	**2.40 (10, 47)**	**24.94 (5,47)**	**2.36 (25, 47)**
	θ	**5.30 (5, 10)**	**3.77 (2, 48)**	0.54 (10, 48)	**13.08 (5, 48)**	**3.10 (25, 48)**
	Φ	0.46 (5, 10)	0.15 (2, 54)	**3.74 (10, 54)**	**3.85 (5, 54)**	1.50 (25 , 54)
	R_d	5.56 (5, 10)	0.08 (2, 47)	0.70 (10, 47)	**3.18 (5, 47)**	1.37 (25, 47)
	PNUE	**9.34 (5, 10)**	2.04 (2, 42)	**2.60 (10, 42)**	**11.32 (5, 42)**	**3.05 (25, 42)**
	PEUE	**4.51 (5, 10)**	1.44 (2, 49)	1.48 (10, 49)	**5.72 (5, 49)**	1.59 (25, 48)
	A_{mass}	**16.48 (5, 10)**	**4.09 (2, 58)**	1.81 (10, 58)	**10.90 (5,58)**	**3.06 (25, 58)**

Table 1.13. Mixed effects model results for leaf-level gas exchange measurements and photosynthetic light-use efficiency parameters compared between species in the low-water treatment during the initial dry-down.

Variables are net photosynthesis (A_{net}), transpiration (E), and stomatal conductance rates (g_{sw}), transpiration-based (A_{net} : E) and conductance-based (A_{net} : g_{sw}) water-use efficiency, light saturated photosynthesis (A_{max}), convexity (Θ), apparent quantum yield (Φ) and day-time dark respiration (R_d). Values shown are *F*-values (degrees of freedom) for fixed effects (species [SPP], day of treatment [DOE], relative soil water content [RSWC], DOE X SPP, SPP X RSWC) and covariance parameter estimates for the random effect *bin*. Bold type indicates values are significant at the *P* < 0.05 level.

Variable	Fixed Effects					Random Effect
	SPP	DOE	RSWC	DOE X SPP	SPP X RSWC	Bin σ^2
A_{net}	**9.15 (3,38)**	**8.78 (2,38)**	0.30 (1,38)		**5.56 (3,38)**	0
E	**3.39 (3, 35)**	1.10 (2, 35)		2.32 (6, 35)		0.087
G_{sw}	**3.05 (3,37)**	0.19 (2, 37)	0.32 (1,37)		**3.92 (3, 37)**	0.000036
A_{net} : E	2.09 (3, 41)	1.13 (2, 41)	1.64 (1, 41)			0
A_{net} : G_{sw}	**9.35 (3, 40)**	**13.47 (2, 40)**	3.20 (1, 40)			86.4
A_{max}	**5.70 (3, 38)**	3.20 (3, 38)	0.28 (1, 38)		**3.22 (3, 38)**	0
Θ	0.47 (3, 41)	0.29 (2, 41)	0.11 (1, 41)			0
Φ	0.53 (3, 41)	0.98 (2, 41)	0.01 (1, 41)			0
R_d	1.91 (3, 41)	**7.69 (2, 41)**	1.65 (1, 41)			0

Table 1.14. Mixed effects model results for leaf-level gas exchange measurements and photosynthetic light-use efficiency parameters compared between species in the low-water treatment during the second dry-down.

Variables are net photosynthesis (A_{net}), transpiration (E), and stomatal conductance rates (G_{sw}), transpiration-based (A_{net} : E) and conductance-based (A_{net} : G_{sw}) water-use efficiency, light saturated photosynthesis (A_{max}), convexity (Θ), apparent quantum yield (Φ) and day-time dark respiration (R_d). Values shown are *F*-values (degrees of freedom) for fixed effects (species [SPP], day of treatment [DOE], relative soil water content [RSWC], DOE X SPP, SPP X RSWC) and covariance parameter estimates for the random effect *bin*. Bold type indicates values are significant at the $P < 0.05$ level.

Second Dry-down	Fixed Effects							Random Effect
Variable	SPP	DOE	RSWC	DOE X SPP	SPP X RSWC	$RSWC^2$	SPP X $RSWC^2$	Bin σ^2
A_{net}	**6.94 (3,47)**	**22.09 (3,47)**		**2.69 (9, 47)**				0
E	**11.75 (3, 46)**	**11.74 (3, 46)**	**7.42 (1, 46)**	**6.63 (9, 46)**				0.017
G_{sw}	**6.97 (3,47)**	**30.45 (3, 47)**		**4.35 (9,47)**				0.000069
A_{net} : E	**10.41 (3, 47)**	**6.60 (3, 47)**		**2.96 (9, 47)**				0.235
A_{net} : G_{sw}	**15.86 (3, 47)**	2.09 (3, 47)		**4.03 (9, 47)**				0
A_{max}	**8.41 (3, 56)**	**11.99 (3, 56)**	**6.32 (1, 56)**					0
Θ	**3.81 (3, 40)**	2.12 (3, 40)	**9.35 (1, 40)**	**4.39 (9, 40)**	**3.55 (3, 40)**	**9.28 (1, 40)**	**2.69 (3, 40)**	0
Φ	**20.79 (3, 49)**	**15.36 (3, 49)**	**31.05 (1, 49)**		**17.67 (3, 49)**	**25.79 (1, 49)**	**15.59 (3, 49)**	0
R_d	1.83 (3, 55)	0.38 (3, 55)	0.29 (1, 55)					0.165

Table 1.15. Mixed effects model results for pot relative soil water content (RSWC) compared between species in the low-water treatment during the initial and second dry-downs.

Values shown are *F*-values (degrees of freedom) for fixed effects (species [SPP], day of treatment and its quadratic term [DOE, DOE^2], and their interaction terms [SPP X DOE, SPP X DOE^2]) and covariance parameter estimates for the random effect *bin*. Bold type indicates values are significant at the $P < 0.05$ level. Italics indicate values are nearly significant at the $0.5 < P < 0.10$ level.

Dry-down	Fixed Effects					Random Effect
	SPP	DOE	DOE^2	SPP X DOE	SPP X DOE^2	Bin σ^2
Initial	0.41 (3, 39)	**374.29 (1, 39)**		*2.79 (3, 39)*		0.000027
Second	1.88 (3, 51)	**43.57 (1, 5)**	*3.91 (1,51)*	**4.12 (3, 51)**	4.30 (3, 51)	0.000331

Table 1.16. Mixed effect model results for pulse responses in the high-water and low-water treatments for leaf-level measured, calculated and estimated variables.

Variables are net photosynthesis (A_{net}), transpiration (E), and stomatal conductance rates (g_{sw}), transpiration-based (A_{net} : E) and conductance-based (A_{net} : g_{sw}) water-use efficiency, light saturated photosynthesis (A_{max}), convexity (Θ), apparent quantum yield (Φ) and day-time dark respiration (R_d). Each models' fixed effect was species and the random effect was bin. Values shown are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effect *bin*. Bold type indicates values are significant at the *P* < 0.05 level.

	High-water Treatment		Low-water Treatment	
Pulse Response	Fixed Effects	Random Effect	Fixed Effects	Random Effect
Variable	Species	Bin σ^2	Species	Bin σ^2
A_{net}	2.80 (3, 11)	0.0078	5.73 (3, 12)	0
E	2.06 (3, 12)	0	1.43 (3, 12)	0
G_{sw}	0.63 (3, 12)	0	2.63 (3, 12)	0
A_{net} : E	**4.48 (3, 11)**	0.1073	1.75 (3, 12)	0
A_{net} : G_{sw}	**4.48 (3, 11)**	0.1073	1.75 (3, 12)	0
A_{max}	2.85 (3, 12)	0	1.67 (3, 12)	0
θ	1.39 (3, 12)	0	0.67 (3, 12)	0
Φ	0.69 (3, 11)	0.01929	1.52 (3, 12)	0
R_d	0.77 (3,11)	0.1677	0.31 (3, 11)	0.08789

Table 1.17. Mixed effects model results for leaf-level and plant-level net photosynthesis (A_{net}) and transpiration rates (E) in the high-water and low-water treatments under dry (pre-pulse) and wet (post-pulse) soil conditions.

Fixed effect was species (SPP). Values shown are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effect *bin*. Bold type indicates values are significant at the *P* < 0.05 level. Italics indicate values are nearly significant at the 0.05 < *P* < 0.10 level.

		Dry (pre-pulse)		**Wet (post-pulse)**	
		Fixed Effects	**Random Effect**	**Fixed Effects**	**Random Effect**
Level	**Variable**	**SPP**	**Bin σ^2**	**SPP**	**Bin σ^2**
Leaf-level	**A_{net}**	1.10 (3, 12)	0	2.12 (3, 11)	33.79
	E	1.65 (3, 12)	0	1.10 (3, 11)	1.34
Plant-level	**A_{net}**	2.39 (3, 12)	0	*2.96 (3,12)*	0
	E	1.69 (3, 12)	0	1.57 (3, 11)	0

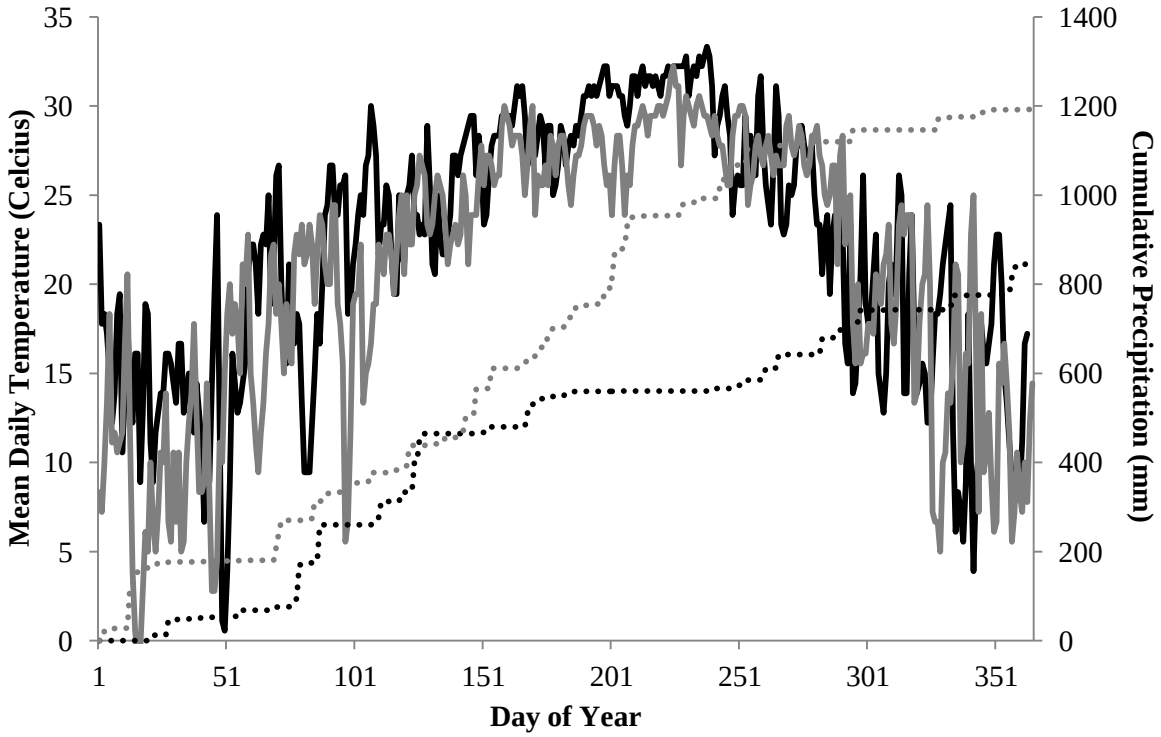

Figure 1.1. Cumulative precipitation and mean daily temperature at the WFC during 2006 and 2007.

Mean daily temperatures in 2006 (solid black lines) and 2007 (solid grey lines) and annual cumulative precipitation during 2006 (dashed black lines) and 2007 (dashed grey lines) for Austin, TX (NCDC, weather station data for Austin Bergstrom Airport, Austin, TX).

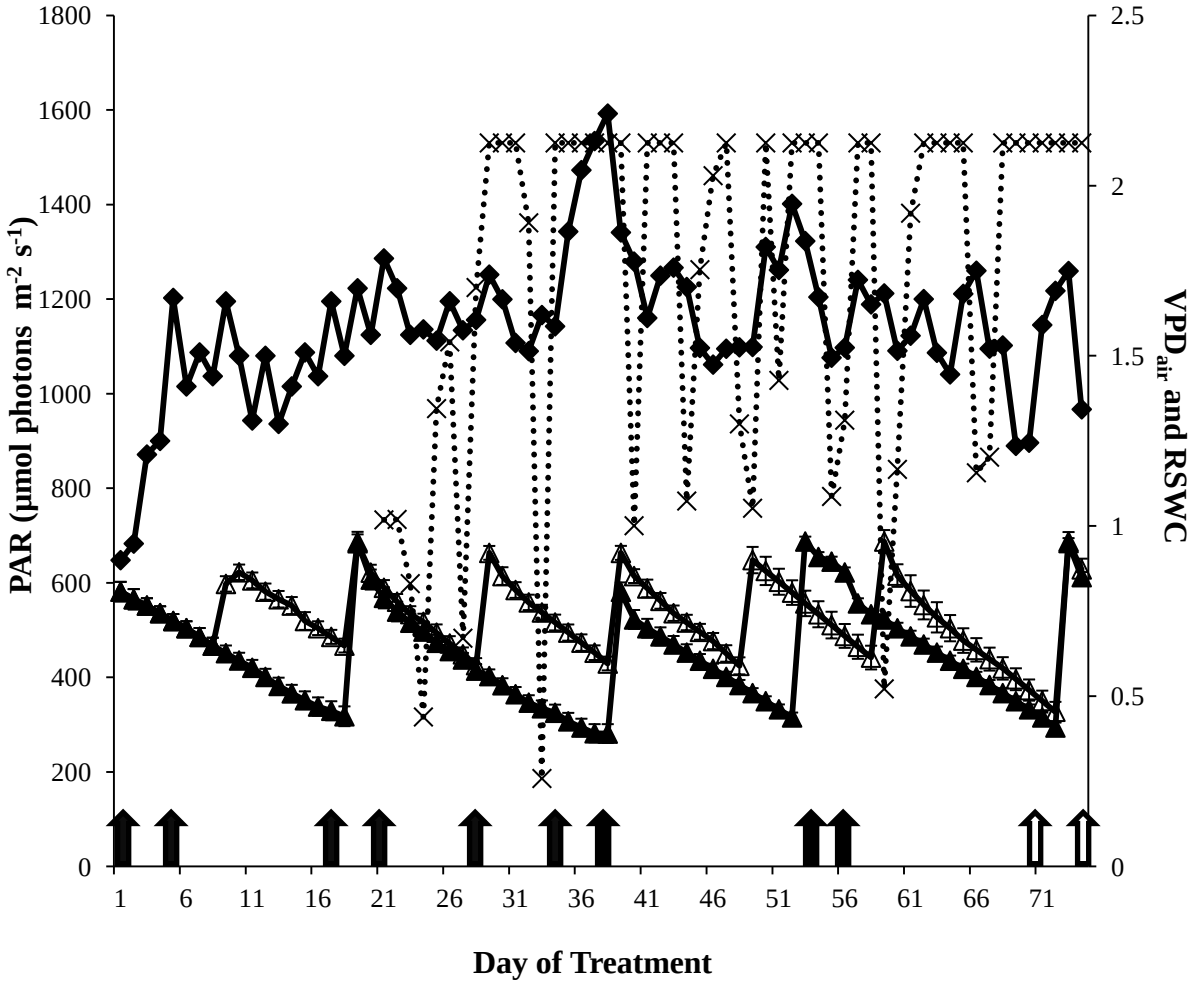

Figure 1.2. Environmental conditions during the greenhouse experiment.

Daily maximum photosynthetically active radiation (PAR; x, dotted line), daily average air vapor pressure deficit (VPD_{air}; solid black diamond) and daily relative soil moisture content (RSWC) for the low-water (solid black triangles) and high-water treatments (open triangles) during the greenhouse soil moisture pulse frequency experiment (values for RSWC are treatment means ± 1 SE). Days on which leaf-level photosynthetic measurements were conducted are indicated along the x-axis for low-water treatment (solid black arrows) and high-water treatment (white arows) plants.

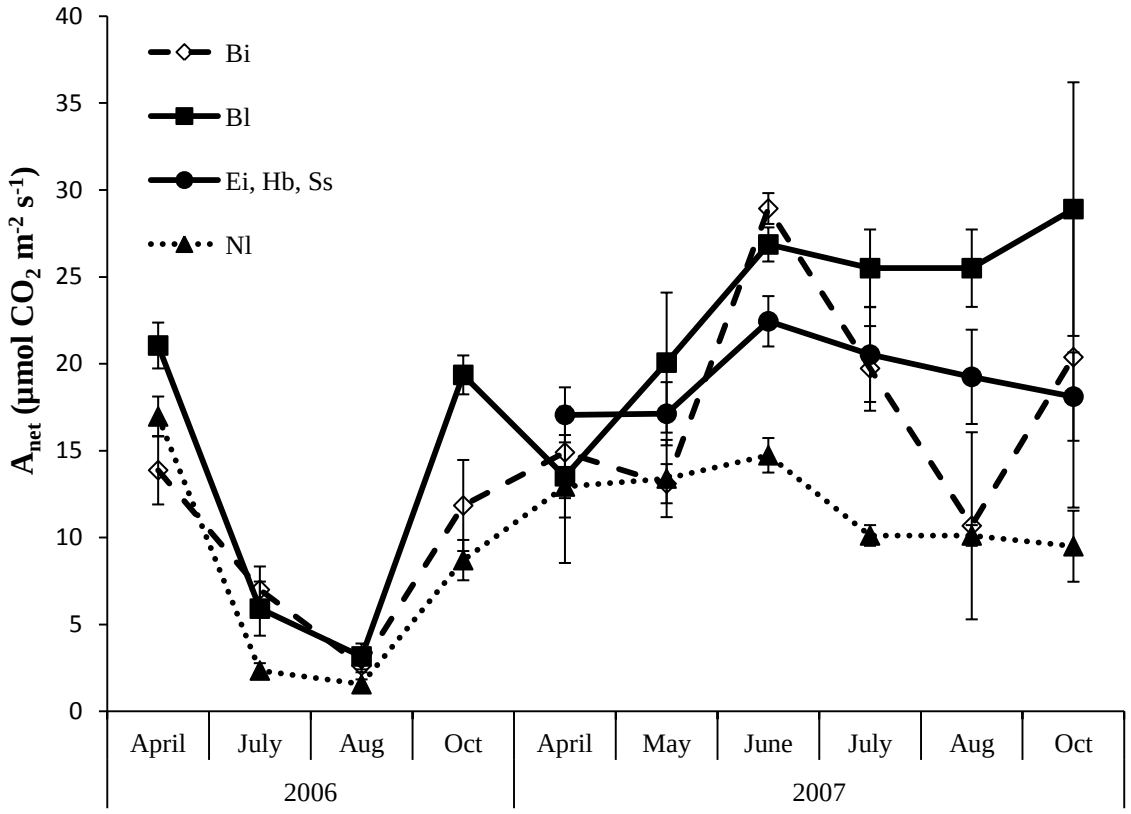

Figure 1.3. Net photosynthetic rates (A_{net}) measured in the field at the WFC.

A_{net} measured for the invasive C_4 grass, *B. ischaemum* (Bi; open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (Nl; solid triangle, dotted line), the native C_4 grass, *B. laguroides* (Bl; solid square, solid line) and the averaged values of the other native C_4 grasses (*E. intermedia [Ei]*, *H. belangeri [Hb],* and *S. scoparium [Ss]*) during the 2006 and 2007 growing seasons. Values are monthly means, error bars are ± 1 SE for 6 (in 2006) and 3 (in 2007) repeatedly measured individuals per species (N = 9 for the averaged native C_4 species in 2007).

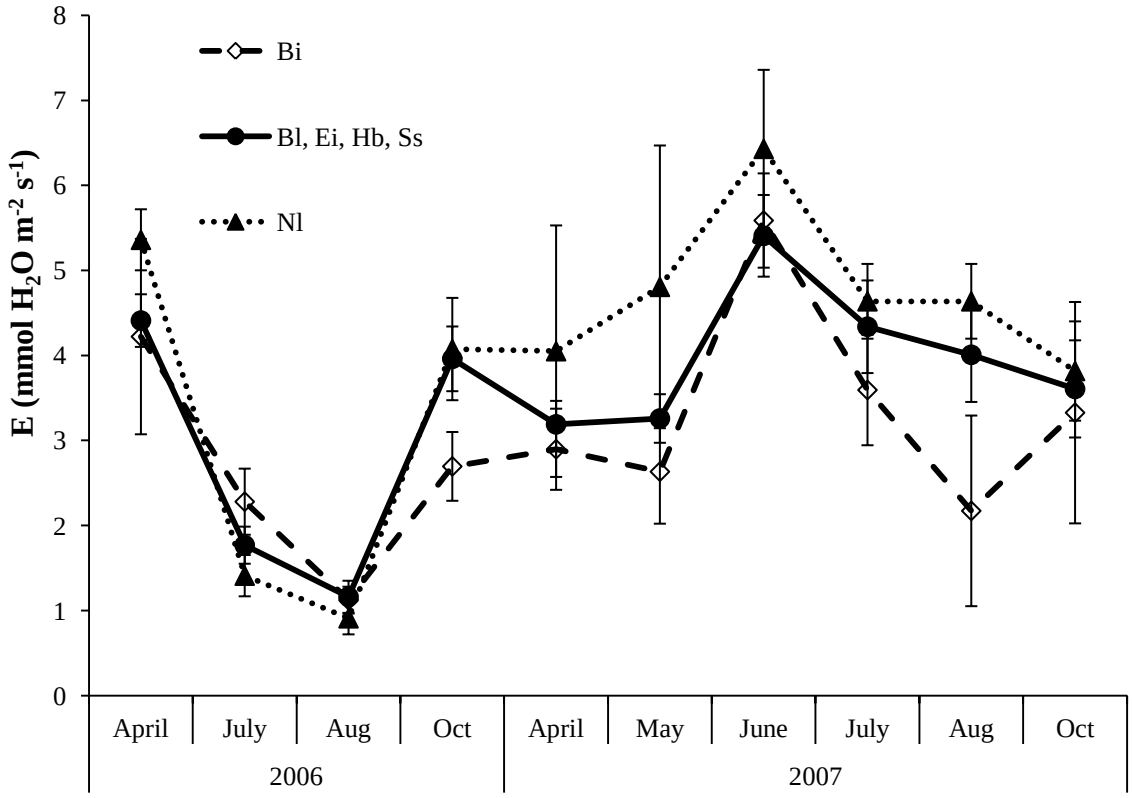

Figure 1.4. Transpiration rates (E) measured in the field at the WFC.

E measured for the invasive C_4 grass, *B. ischaemum* (Bi; open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (Nl; solid triangle, dotted line), and the averaged value of the native C_4 grasses (*B. laguroides* [Bl], *E. intermedia* [Ei], *H. belangeri*[Hb], and *S. scoparium* [Ss]) during the 2006 and 2007 growing seasons. Values are monthly means, error bars are ± 1 SE for 6 (in 2006) and 3 (in 2007) repeatedly measured individuals per species (N = 6 for the average of the native C_4 species in 2006; N = 12 for the average of the native C_4 species in 2007).

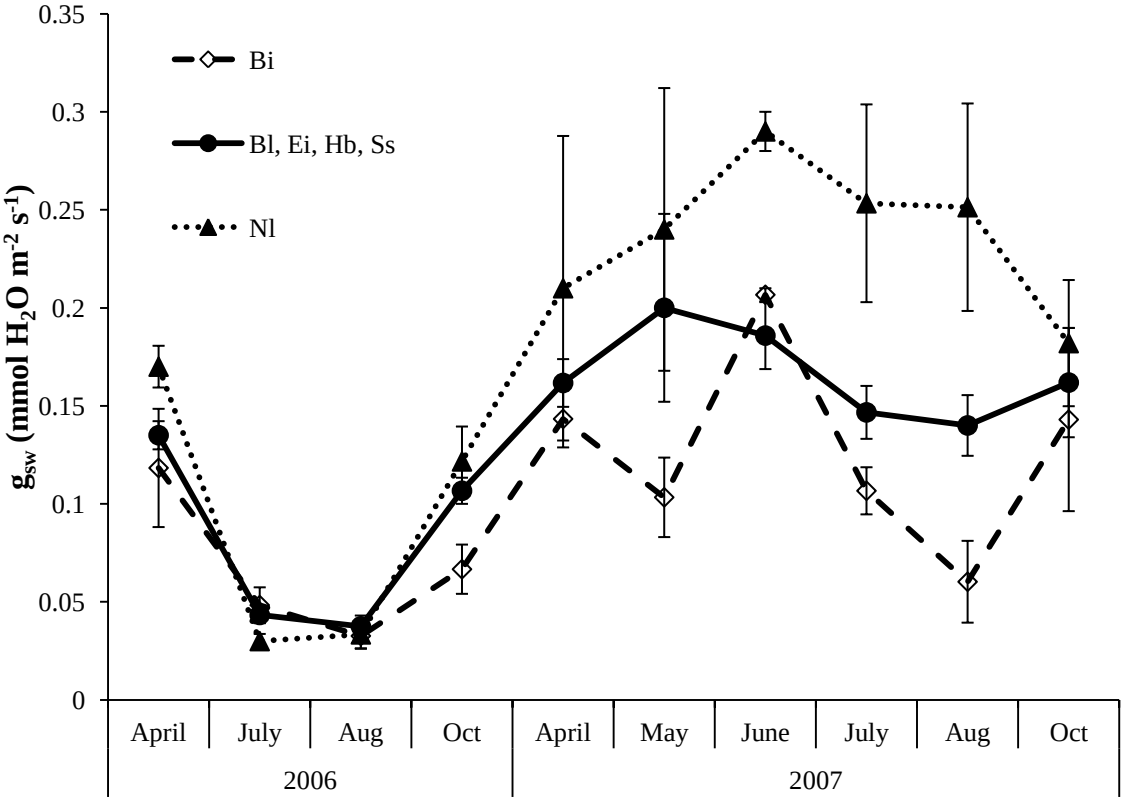

Figure 1.5. Stomatal conductance rates (g_{sw}) measured in the field at the WFC.

G_{sw} measured for the invasive C_4 grass, *B. ischaemum* (open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (solid triangle, dotted line), and the averaged value of the native C_4 grasses (*B. laguroides, E. intermedia, H. belangeri* and *S. scoparium*) during the 2006 and 2007 growing seasons. Values are monthly means, error bars are ± 1 SE for 6 (in 2006) and 3 (in 2007) repeatedly measured individuals per species (N = 6 for the average of the native C_4 species in 2006; N = 12 for the average of the native C_4 species in 2007).

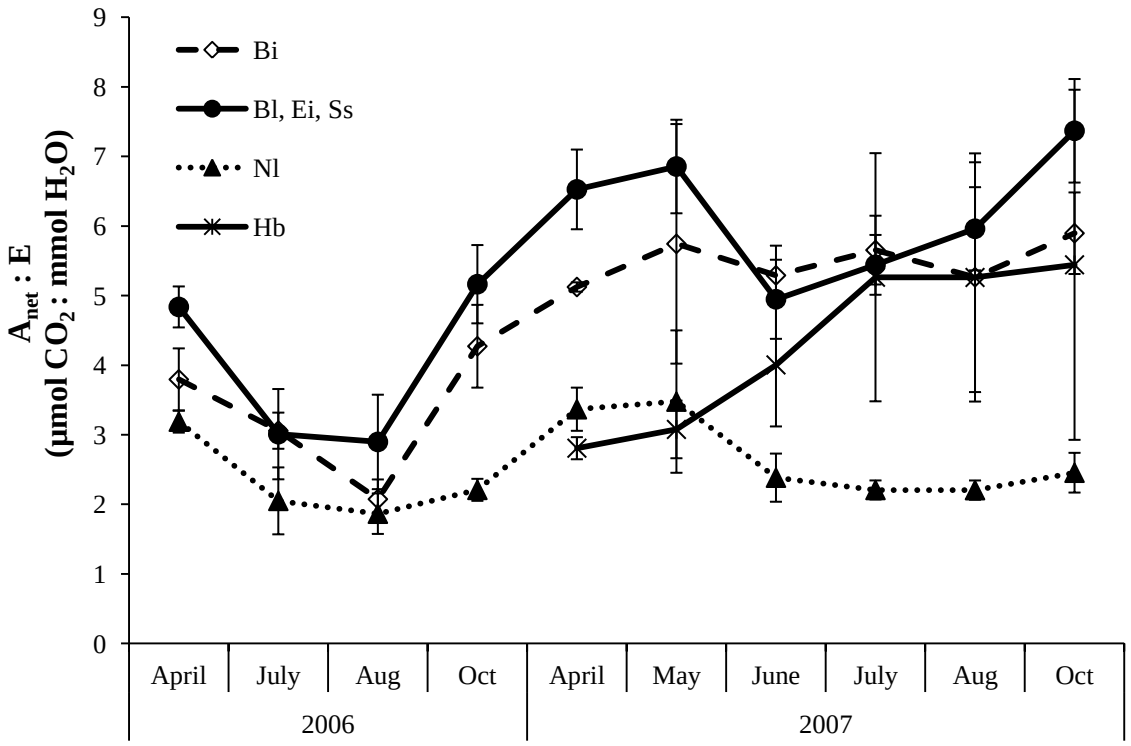

Figure 1.6. Transpiration-base water-use efficiency (A_{net}:E) measured in the field at the WFC.

A_{net}:E measured for the invasive C_4 grass, *B. ischaemum* (Bi; open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (Nl; solid triangle, dotted line), the native short C_4 grass, *H. belangeri* (Hb; asterisk, solid line) and the averaged value of the other native C_4 grasses (*B. laguroides* [Bl] in 2006, N = 6; *B. laguroides*[Bl], *E. intermedia* [Ei], and *S. scoparium*[Ss] in 2007, N = 9) during the 2006 and 2007 growing seasons. Values are monthly means, error bars are ± 1 SE for 6 (in 2006) and 3 (in 2007) repeatedly measured individuals per species.

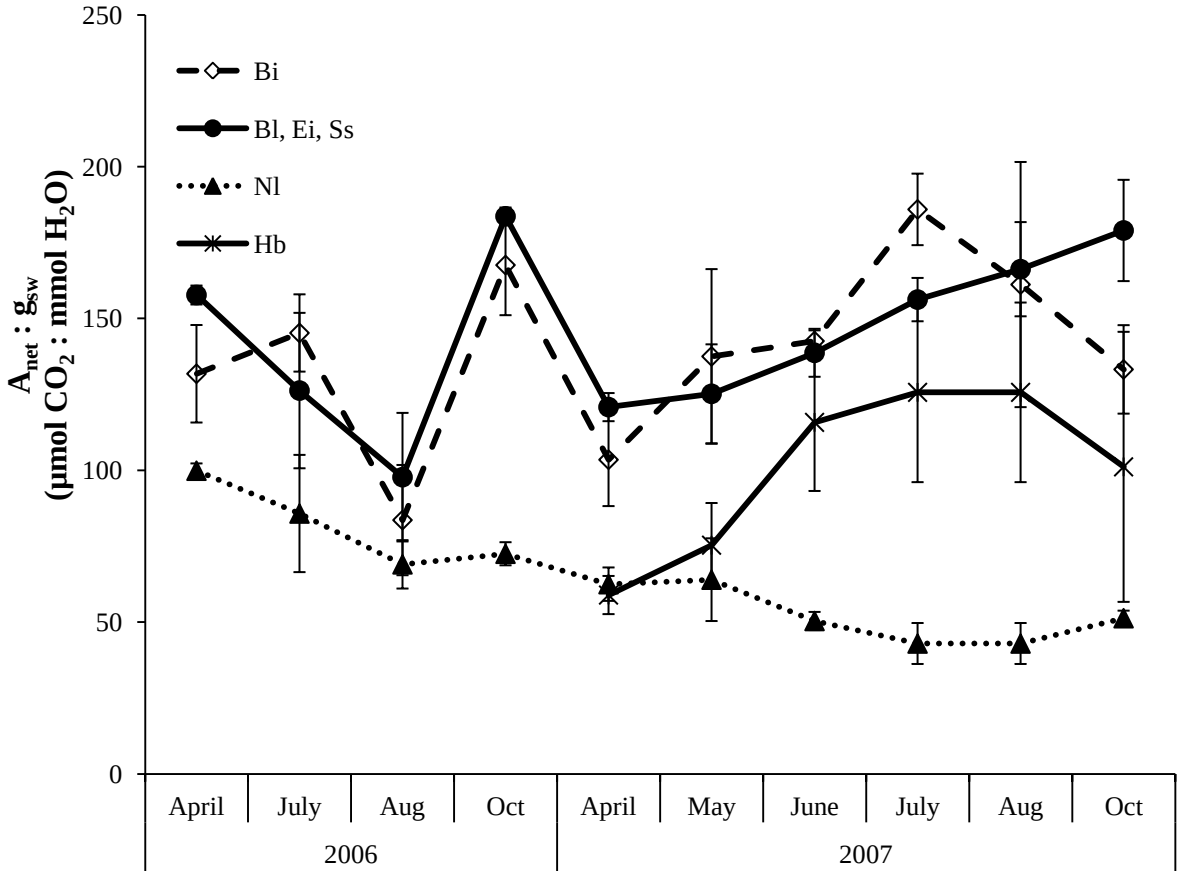

Figure 1.7. Conductance-base water-use efficiency (A_{net}:g_{sw}) measured in the field at the WFC.

A_{net}:g_{sw} measured for the invasive C_4 grass, *B. ischaemum* (Bi; open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (Nl; solid triangle, dotted line), the native short C_4 grass, *H. belangeri* (asterisk, solid line) and the averaged value of the other native C_4 grasses (*B. laguroides* in 2006, N = 6; *B. laguroides*, E. *intermedia*, and *S. scoparium* in 2007, N = 9) during the 2006 and 2007 growing seasons. Values are monthly means, error bars are ± 1 SE for 6 (in 2006) and 3 (in 2007) repeatedly measured individuals per species.

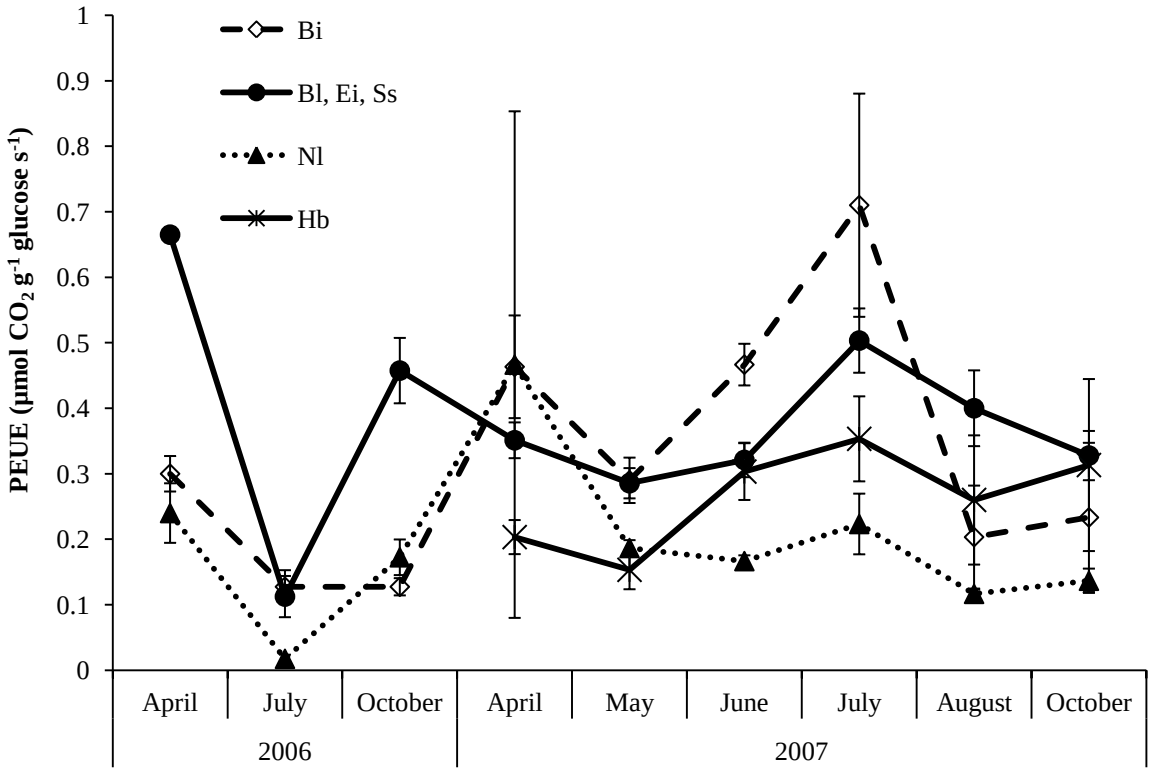

Figure 1.8. Photosynthetic energy-use efficiency (PEUE) measured in the field at the WFC.

PEUE measured for the invasive C_4 grass, *B. ischaemum* (Bi; open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (Nl; solid triangle, dotted line), the native short C_4 grass, *H. belangeri* (Hb; asterisk, solid line) and the averaged value of the other native C_4 grasses (*B. laguroides* [Bl] in 2006, N = 4; *B. laguroides* [Bl], E*. intermedia* [Ei], and *S. scoparium* [Ss] in 2007, N = 9) during the 2006 and 2007 growing seasons. Values are monthly means, error bars are ± 1 SE for 4 (in 2006) and 3 (in 2007) repeatedly measured individuals per species.

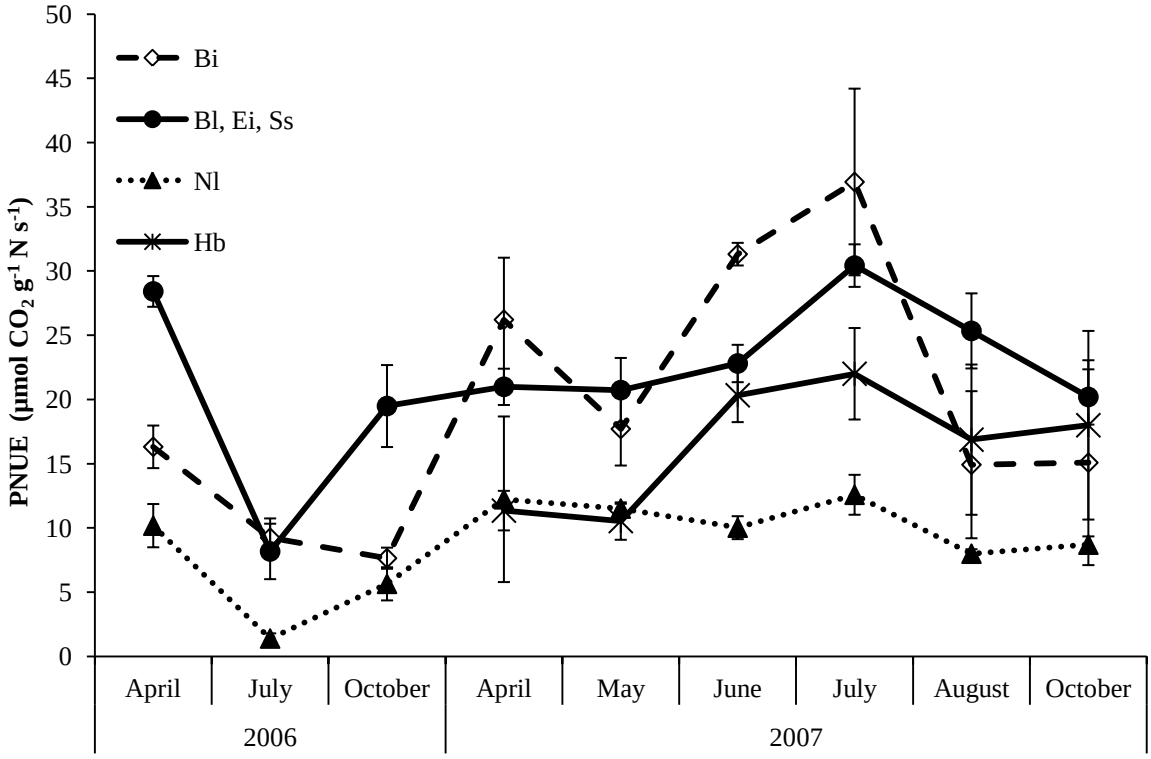

Figure 1.9. Photosynthetic nitrogen-use efficiency (PNUE) measured in the field at the WFC.

PNUE measured for the invasive C_4 grass, *B. ischaemum* (Bi; open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (Nl; solid triangle, dotted line), the native short C_4 grass, *H. belangeri* (Hb; asterisk, solid line) and the averaged value of the other native C_4 grasses (*B. laguroides* [Bl] in 2006, N = 4; *B. laguroides* [Bl], E*. intermedia* [Ei], and *S. scoparium* [Ss] in 2007, N = 9) during the 2006 and 2007 growing seasons. Values are monthly means, error bars are ± 1 SE for 4 (in 2006) and 3 (in 2007) repeatedly measured individuals per species.

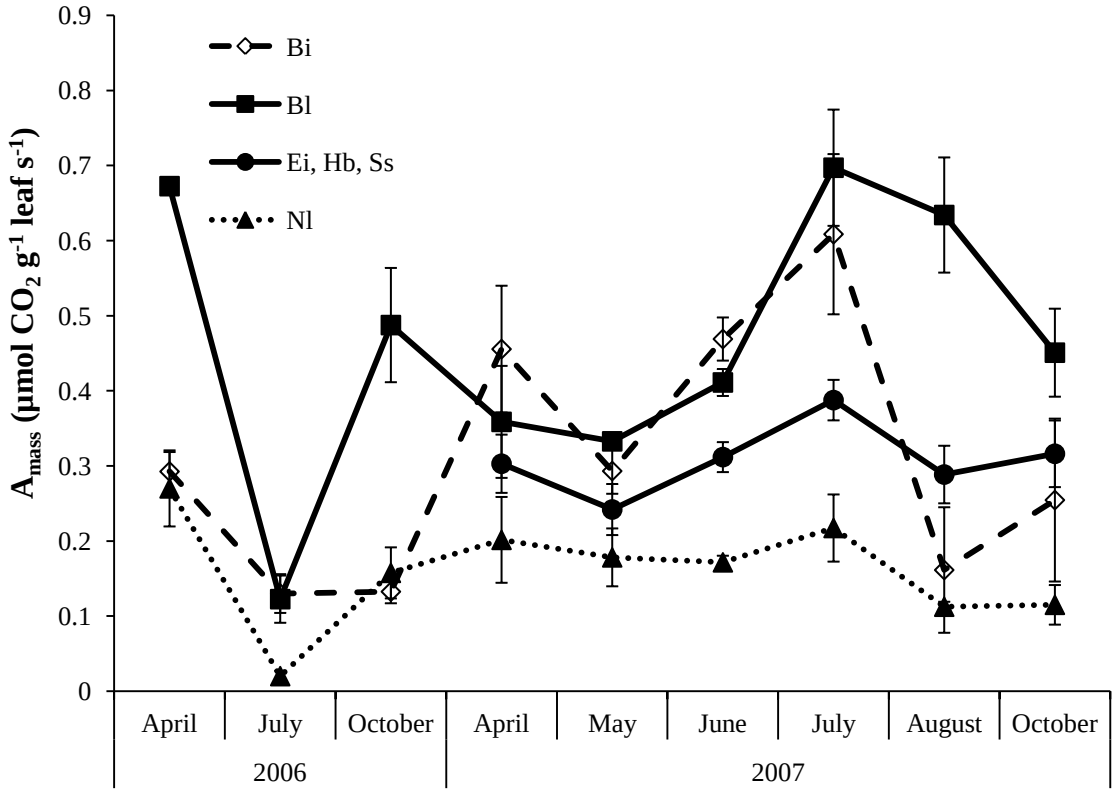

Figure 1.10. Mass-based photosynthetic rates (A_{mass}) measured in the field at the WFC.

A_{mass} measured for the invasive C_4 grass, *B. ischaemum* (Bi; open diamond and dashed lines), the native C_3 grass, *N. leucotricha* (Nl; solid triangle, dotted line), the native C_4 grass, *B. laguroides* (Bl; solid square, solid line) and the averaged values of the other native C_4 grasses (*E. intermedia* [Ei], *H. belangeri* [Hb], and *S. scoparium* [Ss]; N = 9 for the averaged native C_4 species) during the 2006 and 2007 growing seasons. Values are monthly means ± 1 SE for 4 (in 2006) and 3 (in 2007) repeatedly measured individuals per species.

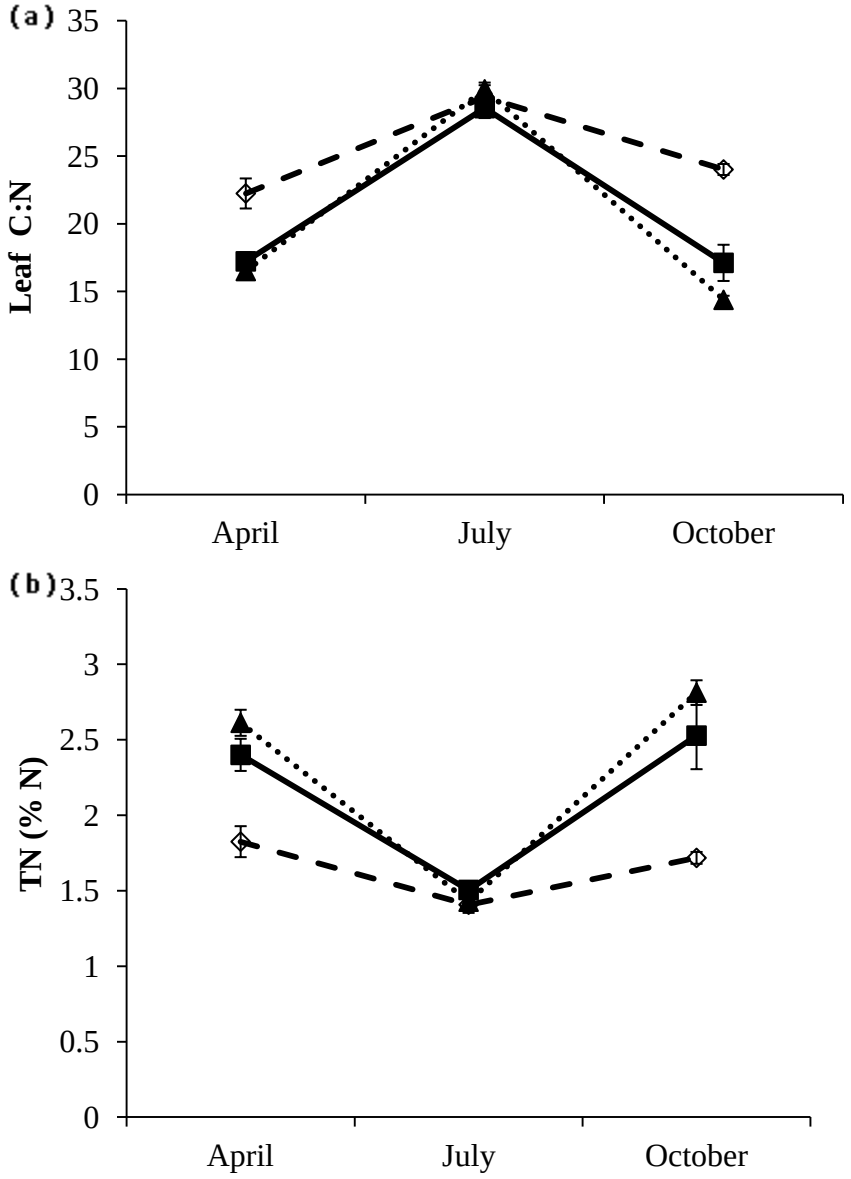

Figure 1.11. Seasonal changes in (a) leaf quality (C:N) and (b) nitrogen content (TN) measured at the WFC.

C:N (a) and TN (b) measured for leaves of the invasive C_4 grass, *B. ischaemum* (open diamond, dashed lines), the native C_3 grass, *N. leucotricha* (solid triangle, dotted line) and the native C_4 grass, *B. laguroides* (solid square, solid line) during the dry year 2006. Values are monthly means, error bars are ± 1 SE for 4 repeatedly measured individuals per species.

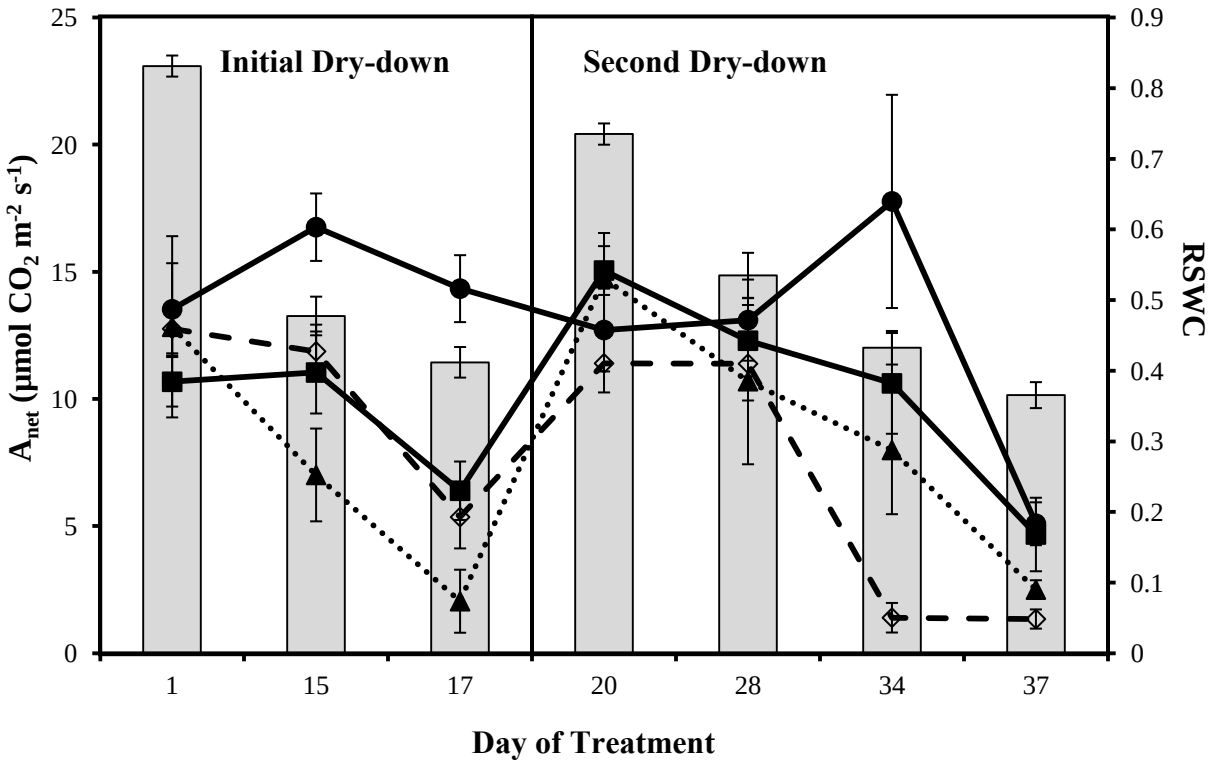

Figure 1.12. Light saturated net photosynthesis (A_{net}) measured during sequential dry-downs in the greenhouse.

Average relative soil water content (RSWC; grey bars; n = 16) and A_{net} as a function of day of treatment for the invasive, *B. ischaemum* (open diamonds, dashed lines), and three native species, *B. laguroides* (solid squares, solid line), *N. leucotricha* (solid triangles, dotted line), and *S. scoparium* (solid circles, solid line) over the course of two consecutive 20 day dry-down periods. Soil moisture pulses were applied on day 1 and day 20, of treatment. Values for A_{net} are means ± 1 SE for four replicates in the low-water treatment.

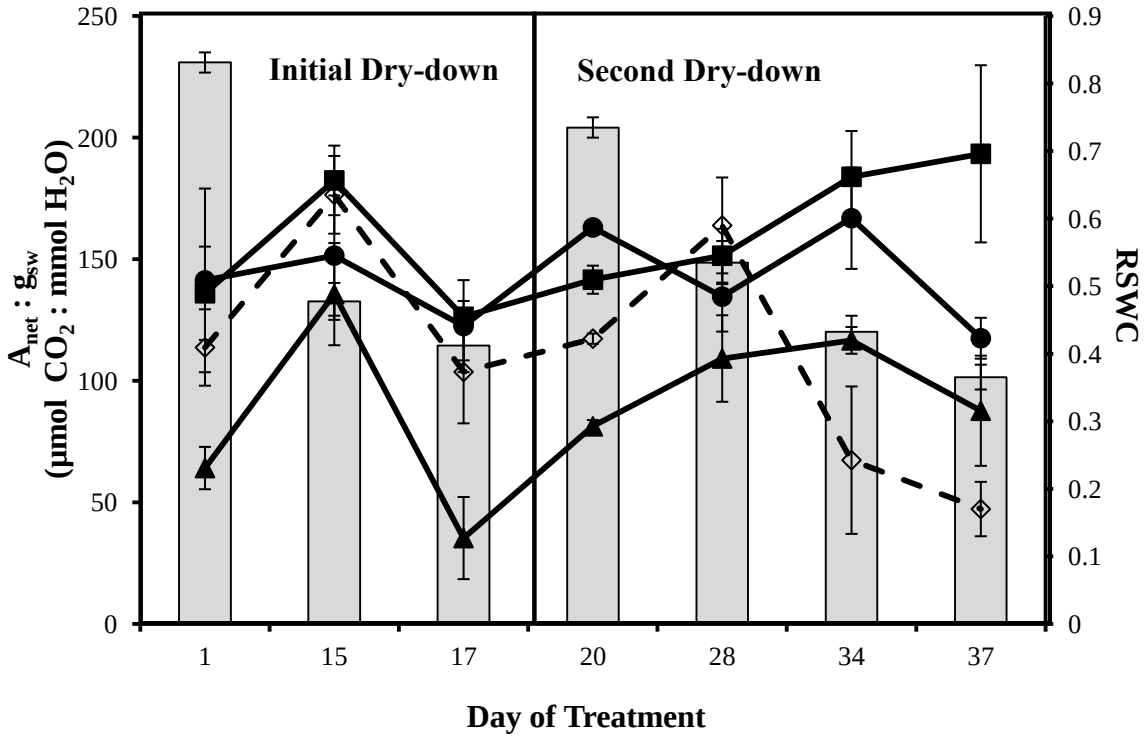

Figure 1.13. Leaf level conductance-based water-use efficiency (A_{net} : g_{sw}) measured during sequential dry-downs in the greenhouse.

Average relative soil water content (RSWC; grey bars; n = 16) and A_{net} : g_{sw} as a function of day of treatment for the invasive, *B. ischaemum* (open diamonds, dashed lines), and three native species, *B. laguroides* (solid squares, solid line), *N. leucotricha* (solid triangles, dotted line), and *S. scoparium* (solid circles, solid line) over the course of two consecutive 20 day dry-down periods. Soil moisture pulses were applied on day 1 and day 20, of treatment. Values for A_{net} : g_{sw} are means ± 1 SE for four replicates in the low-water treatment.

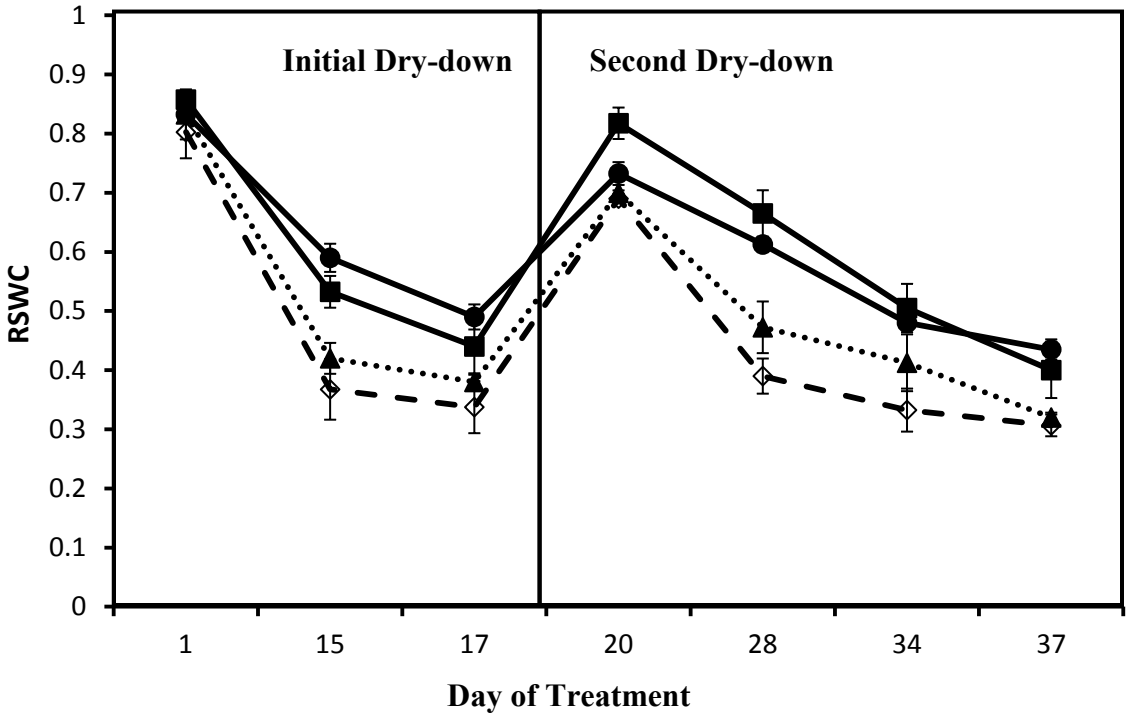

Figure 1.14. Relative soil water content (RSWC) as a function of day of treatment in the greenhouse pulse frequency experiment low-water treated pots for two consecutive dry-down periods.

RSWC measured in pots containing one individual plant, either the invasive, *B. ischaemum* (Bi), or one of three native species, *B. laguroides* (Bl), *N. leucotricha* (Nl) and *S. scoparium* (Ss) over the course of two 20 day dry-down periods. Soil moisture pulses were applied on days 1 and 20 of treatment. Values are means ± 1 SE for four replicates.

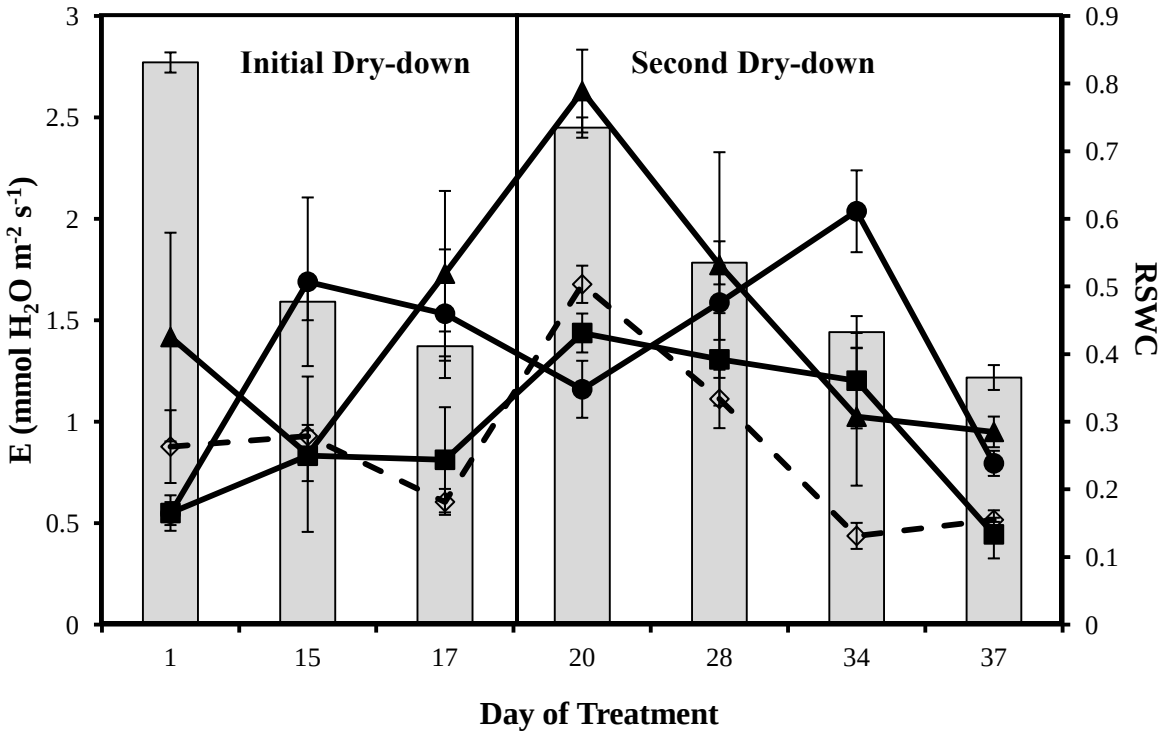

Figure 1.15. Leaf-level transpiration rates (E) during two consecutive dry-down periods in the greenhouse.

Average daily relative soil water content (RSWC; grey bars, n = 16) and E for the invasive, *B. ischaemum* (open diamonds, dashed lines), and three native species, *B. laguroides* (solid squares, solid line), *N. leucotricha* (solid triangles, dotted line), and *S. scoparium* (solid circles, solid line) over the course of two consecutive 20 day dry-down periods. Soil moisture pulses were applied on day 1 and day 20, of treatment. Values are means ± 1 SE for four replicates in the low-water treatment.

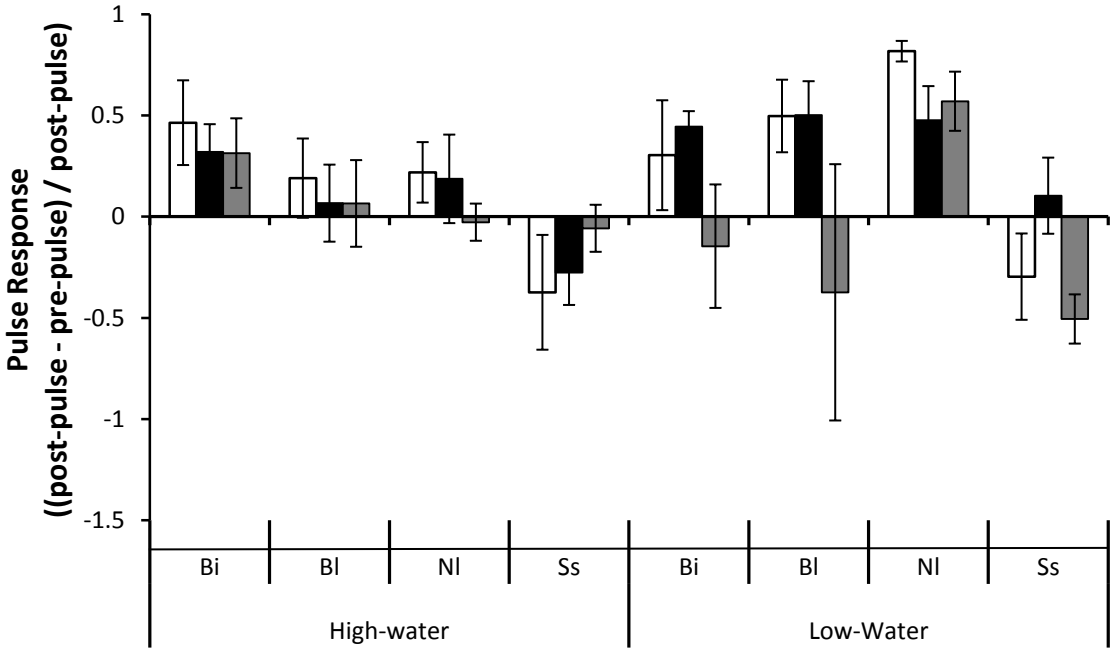

Figure 1.16. Pulse responses in leaf-level gas exchange variables during the greenhouse soil moisture pulse experiment.

Pulse responses in leaf-level light-saturated net photosynthesis (A_{net}; white bars), transpiration (E; black bars), and transpiration-based water use efficiency (A_{net}:E; dark grey bars) for high-water and low-water treatment plants. Pulse response was calculated as the difference between values two days after plants were watered to field capacity (post-pulse) and values after a 14-day dry-down (pre-pulse) divided by post-pulse values. Measurements were conducted on the invasive, *B. ischaemum* (Bi), and three native species, *B. laguroides* (Bl), *N. leucotricha* (Nl) and *S. scoparium* (Ss) during the greenhouse pulse experiment. Values are means ± 1 SE.

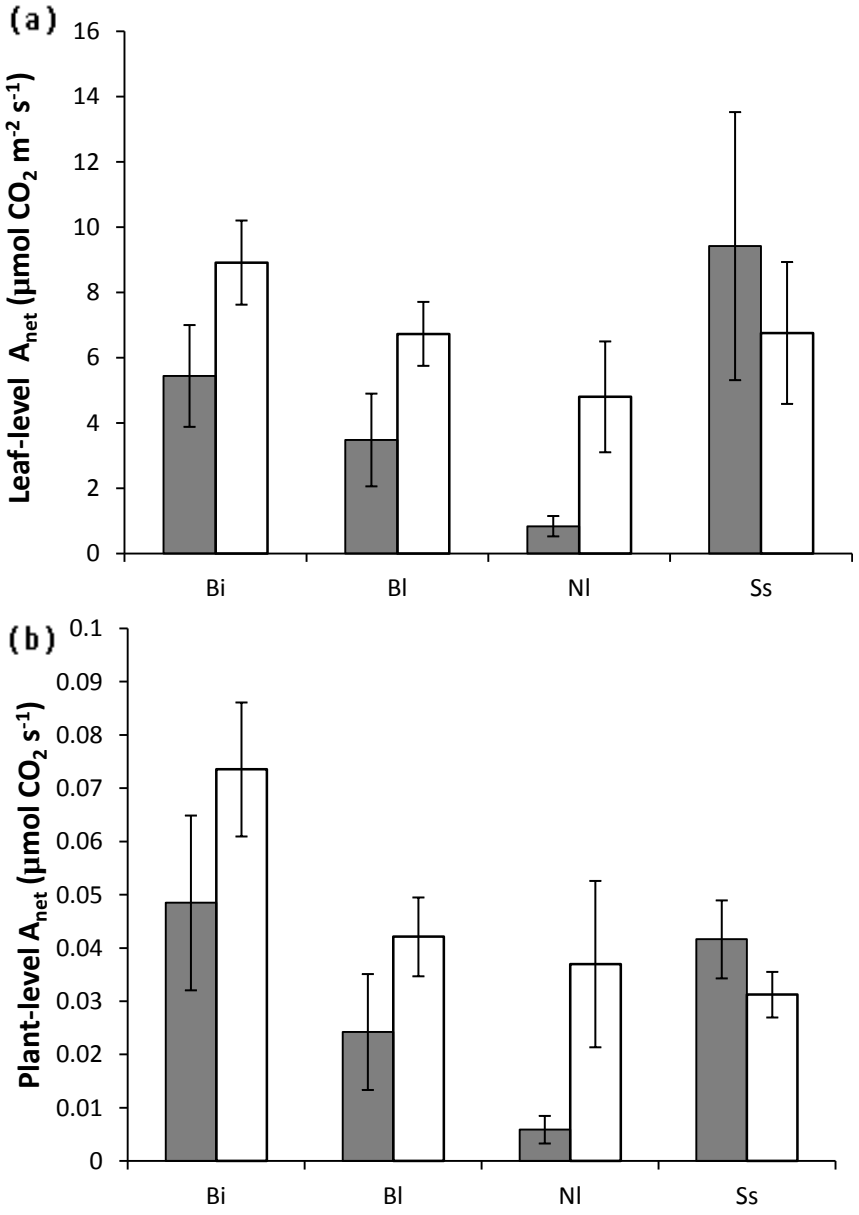

Figure 1.17. Final leaf-level and plant-level net photosynthetic rates (A_{net}) measured for greenhouse-grown plants.

A_{net} at the (a) leaf level and (b) the plant level for *B. ischaemum* (Bi), *B. laguroides* (Bl), *N. leucotricha* (Nl) and *S. scoparium* (Ss) in the low-water treatment under dry (pre-pulse; grey bars) and wet (post-pulse; white bars) soil conditions in the greenhouse soil moisture pulse experiment. Values are means ± 1 SE.

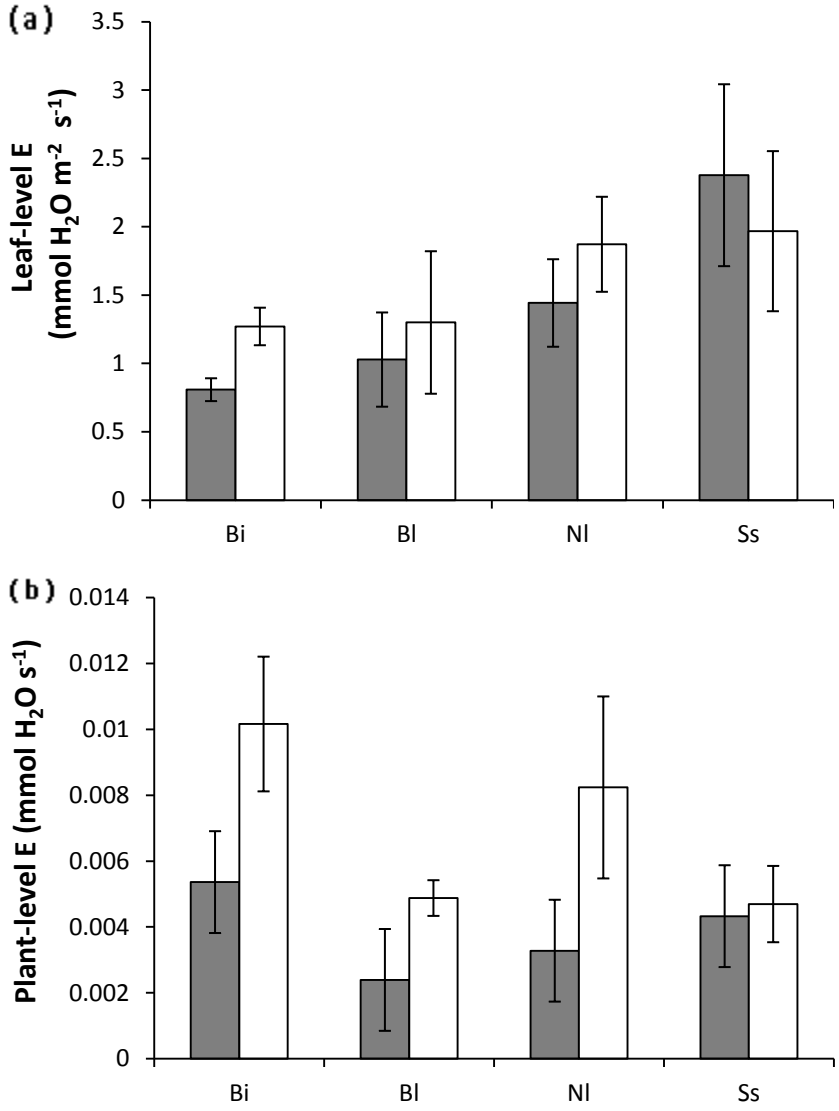

Figure 1.18. Final leaf-level and plant-level transpiration rates (E) measured for greenhouse-grown plants.

Transpiration rates (E) measured at the (a) leaf level and scaled up to (b) the plant level for *B. ischaemum* (Bi), *B. laguroides* (Bl), *N. leucotricha* (Nl) and *S. scoparium* (Ss) in the low-water treatment under dry (pre-pulse; grey bars) and under wet (post-pulse; white bars) soil conditions in the greenhouse soil moisture pulse experiment. Values are means ± 1 SE.

Chapter 2: The impacts of *B. ischaemum* invasion on plant input quality, soil Carbon and Nitrogen pools and litter decomposition

ABSTRACT

Introduced perennial C_4 grasses are invading large expanses of grassland and savanna ecosystems throughout the south-central U.S. Increased plant productivity and changes in plant input qualities associated these grass invasions have the potential to alter ecosystem nutrient cycling via processes mediated by soil microbial communities. We examined whether the invasion of central Texas mixed C_3/C_4 savanna grass-matrix by an introduced C_4 perennial grass, *Bothriochloa ischaemum*, alters soil carbon and nitrogen pools in invaded areas and whether changes in the quantity and quality of plant inputs to the soil microbial community provide a mechanism by which some of these alterations occur. We compared aboveground primary productivity (ANPP), fallen litter quality and quantity, standing dead plant material contributions to fallen litter, litter decomposition and soil nitrogen-cycling rates, and soil carbon and nitrogen pool sizes between *B. ischaemum*-invaded and native-dominated savanna grass-matrix areas. We found that ANPP was higher and fallen litter input quality was lower in *B. ischaemum*-invaded plots relative to native-dominated plots, but that fallen litter quantity did not differ between plot types. Although, fallen-litter input rates were similar between invaded and native areas, the timing of fallen-litter inputs in native areas occurred in higher quality pulses, but fallen-litter inputs were nearly continuous. We also found that soil C pools did not differ between invaded and native plots, but that root biomass N and soil plant available N were significantly lower in invaded plots. Litter decomposition and N-cycling rates did not differ between invaded and native plots, but standing dead contributions to fallen litter were slightly higher in invaded plots. Thus we conclude that the one of the mechanisms by which *B. ischaemum* invasion decreases soil nitrogen availability in

invaded areas may be by increasing plant material residence time in the standing dead pool which can alter plant canopy microhabitat by increasing shading and may result in a larger accumulation of nutrients aboveground. We suggest that decreased soil nitrogen availability may be one of the mechanisms by which this species excludes native species with lower nitrogen-use efficiency from invaded areas.

INTRODUCTION

Invasive introduced plant species are transforming ecosystem species composition and thus ecosystem function worldwide (Sharma et al. 2005). While the magnitude and direction of plant invasion impacts vary, plant invasions are generally associated with decreased native species diversity and enhanced primary productivity in invaded ecosystems (Vila et al. 2011), which can have profound implications for a wide array of ecosystem functions (Tilman 1997, Hooper and Vitousek 1998, Wiliams and Baruch 2000, Mack et al. 2001, Porazinska et al. 2003, Allison and Vitousek 2004, Drenovsky and Batten 2007, Litton et al. 2008, Urgenson et al. 2009, Wolkovich et al. 2010).

Increased plant productivity and changes in plant input qualities associated with invasive species have the potential to alter ecosystem nutrient cycling via processes mediated by soil microbial communities (Hawkes et al. 2005, Liao et al. 2008, Rossiter-Rachor et al. 2009, Ehrenfeld 2010). Changes in plant material quality may accelerate nutrient cycling rates when plant input quality increases as a result of invasion (Allison and Vitousek 2004), or slow them down when plant input quality decreases (Evans et al. 2001, Drenovsky and Batten 2007). As a result, changes in nutrient-cycling rates or alterations in the ratio of input (productivity) to output (decomposition/respiration) can alter ecosystem nutrient storage. For example, increased litter inputs and decreased decomposition rates resulting from grass invasion of shrublands have been shown to

increase carbon and nitrogen storage in invaded soils (Wolkovich et al. 2010). These changes in ecosystem function triggered by invasive species can create a plant-soil feedback system that favors the invasive species over native species, thus securing the dominance of invasive plants in the ecosystem (Kolb et al. 2002, Vinton and Goergen 2006).

While substantial shifts in dominant plant life form (e.g., the invasion of annuals into perennial ecosystems or shrubs into grasslands) are expected to result in substantial changes in ecosystem function (Gill and Burke 1999, Drenovsky and Batten 2007, Hooker et al. 2008, Mahaney et al. 2008), more subtle changes in plant community composition (e.g., the replacement of native perennial grasses by an invasive one) can have impacts of similar magnitude (Christian and Wilson 1999, Huxman et al. 2004, Reed et al. 2005, Hamerlynck et al. 2010, 2012a). Increased aboveground primary productivity and changes in plant input quality that result from an invasive grass replacing functionally similar native grasses have altered ecosystem function in invaded areas in a number of ways, including altered fire cycles and plant canopy structure, decreased soil nitrogen, and changes in ecosystem water and carbon cycling and storage (Christian and Wilson 1999, Wiliams and Baruch 2000, Huxman et al. 2004, Reed et al. 2005, Hamerlynck et al. 2010, Scott et al. 2010, Hamerlynck et al. 2012a, Ruffner et al. 2012).

We investigated the ecosystem-level impacts of shifts in dominant plant physiology that result from the invasion of mixed C_3/C_4 grasslands by the introduced C_4 grass, *Bothriochloa ischaemum var. songarica,* King Ranch Bluestem. *B. ischaemum*, an old world bluestem grass (OWB), is a C_4 perennial grass native to Eurasia where it is a climax species in arid and semi-arid environments (Akhani and Zeigler 2002, Wang 2003). It was released as a pasture improvement species in the 1930s (Gabbard and

Fowler 2007) and has since invaded a diverse array of habitat types throughout Texas and Oklahoma (Diggs et al. 1999, Turner et al. 2003, Gabbard and Fowler 2007). *B. ischaemum* is physiologically similar to many of the native C_4 grass species it displaces but it produces significantly more biomass than some of the native species it is replacing (Chapter 1). When *B. ischaemum* invades grassland and savanna ecosystems in Central Texas, it converts mixed C_3/ C_4 grasslands and savanna grass-matrices into dense, C_4-dominated monocultures and thus has the potential to significantly alter ecosystem function. The dense plant canopies associated with *B. ischaemum* invasion contain larger amounts of standing dead plant material which increases shading and alters plant-canopy microclimate (Chapter 3). These structural and microclimate changes, in conjunction with decreased plant input quality, have the potential to affect litter decomposition and nutrient cycling rates in invaded ecosystems.

We examined whether *B. ischaemum* invasion alters soil carbon and nitrogen pools in invaded areas relative to native savanna grass-matrix areas and whether changes in the quantity and quality of plant inputs to the soil microbial community provide a mechanism by which some of these alterations occur (Figure 2.1). We hypothesized that invaded areas would have higher biomass and litter production than native areas and that these products would be of much poorer quality (higher ratio of tissue carbon to nitrogen, C:N) than those found in native areas. We anticipated that poorer quality plant material in invaded areas would remain in standing dead pools longer and increase the contributions of standing dead plant material to fallen litter inputs. We also predicted that these poorer quality plant inputs would negatively impact decomposition and nutrient cycling in invaded areas, which would, in turn, reduce available soil nitrogen and increase soil carbon pool sizes. Such changes in ecosystem function have broad implications for ecosystem productivity and diversity, and a better understanding of the mechanisms

involved will contribute to a better understanding of invasion ecology and the fundamental ecological relationships between individuals and ecosystems (Hierro et al. 2005).

METHODS

Site description

Our research was conducted within the 279 acre Landscape Restoration Research Area at the Lady Bird Johnson Wildflower Center (WFC), a research unit of the University of Texas at Austin, Austin, Texas (N30 11'3",W97 52'27", 800' elevation). This property was managed for cattle production prior to its acquisition by the WFC in 1999. WFC is located in the central Texas *Quercus fusiformis* - *Juniperus ashei* savanna in the Texas Hill Country on the eastern edge of the Edwards Plateau. The grass matrix of the savanna at this site is characterized by C_4 grasses, including *Bothriochloa laguroides* subsp. *torreyana, Bothriochloa ischaemum* and *Hilaria belangeri,* C_3 grasses, including *Nassella leucotricha,* and over 200 species of forbs. The introduced grass, *B. ischaemum,* is rapidly becoming the dominant species in the WFC site where we worked, which is typical of its behavior in grassland and savanna systems throughout the region (Gabbard and Fowler 2007).

Soils at this site are limestone-derived thermic Lithic Argiustolls of the Speck Series, which range from nearly level stony clay loams to gravelly clays, 30 - 50 cm in depth (Survey Staff, NRCS, USDA 2009) . Rainfall and temperatures in the Austin area are highly variable, with a mean annual precipitation of 840 (± 250 sd) mm. The seasonality of plant activity in these savannas is highly variable and primarily dependent on water availability. The growing season in this area is often bimodal with a decline in activity during the hottest part of the summer (for all plants) (July - September) and (for

C_4 species) during the winter (January - February). In 2007, cumulative rainfall between January and December was 1192 mm and fell at regular intervals throughout the spring and into the early fall with relatively little rainfall after October.

Sampling design

The Research Area of the WFC, located in open *Quercus-Juniperus* savanna, is divided into 50 blocks, each approximately 0.75 ha in size, that were randomly assigned to burning, mowing and control treatments in 2001. We worked in six of the control blocks 0.18 - 0.85 km apart. We used an un-replicated block design to test whether biomass, fallen litter inputs, litter decomposition rates and soil C and N pools were similar between *B. ischaemum*-invaded ("invaded") and native-dominated ("native") grass-matrix areas within the savanna. Within each block, we established three 1 m^2 native plots and three 1 m^2 *B. ischaemum*-invaded plots. We designated one plot of each type (native or invaded) within a block for each of the following: (1) ongoing fallen litter collection, (2) ongoing fallen litter collection and biomass harvesting, or (3) the litterbag decomposition experiment. Ongoing fallen litter collection plots are hereafter referred to as "unclipped plots," ongoing fallen litter collection and biomass harvest plots are "clipped plots," and litter decomposition experiment plots are "decomposition plots." We randomly located native-dominated unclipped plots and clipped plots in native grassland areas within blocks using a gridded system. We randomly located *B. ischaemum*-invaded unclipped plots and clipped plots in previously delineated *B. ischaemum* monocultures within each block. We established decomposition plots next to unclipped plots in areas where grass species composition and canopy cover were similar to the mean composition and cover of the clipped plots. Plots were all located in open areas at least 5 m from any tree canopy. A list of all of the variables that we measured in

this study and the tables and figures in which they are reported is provided in Tables 2.1.a and 2.1.b.

Biomass harvest

We harvested aboveground biomass from the same clipped plots in early December 2006, and again in November 2007. This meant that there was no standing dead biomass from previous years in clipped plots when we collected biomass from them in 2007 and all of the standing dead plant material that we collected from clipped plots during the 2007 harvest was produced during the 2007 growing season. We separated standing dead from live biomass during collection but we included it as part of the total biomass harvested from each plot for analyses. Although fall senescence generally occurs between October and November in this ecosystem, warmer air temperatures and abundant rainfall in the fall of 2006 delayed senescence of most species until November - December.

Harvested biomass was separated by species into live and standing dead material, dried to a constant weight at 70 °C, and then weighed. We combined biomass collected at the end of 2007 from clipped plots with litter also collected from clipped plots during the 2007 growing season to compare estimated aboveground net primary productivity (ANPP) between native and invaded clipped plots.

Monitoring the microhabitat

In order to account for plant community differences in microhabitat, we installed HOBO mini-weather stations (Onset Computer Corp, Bourne, MA) equipped with soil moisture and temperature probes (0 - 5 cm) and relative humidity/temperature probes (placed above the grass canopy and within the grass canopy just above ground level) in

native and invaded plots within one block in the middle of the research area for the duration of the study.

Plant litter inputs

We collected fallen litter from clipped and unclipped plots monthly from December 2006 (after biomass was harvested) to November 2007. We used the litter collected from both *unclipped* plots (standing dead from previous years) and *clipped* plots (no standing dead from previous years) to estimate the amount of fallen litter derived from the previous years' standing dead biomass. Litter traps (0.05 m^2 in area) located at ground level within each plot were used to catch fallen litter in native and invaded unclipped and clipped plots in each block (n = 6). We constructed litter traps by cutting 1 m lengths of thick walled PVC pipe in half and attaching mesh at either end to prevent litter from escaping without trapping water. We dried fallen litter samples to a constant weight at 70 °C and picked them clean of non-plant materials (feces, frass, soil, etc.) and seeds before weighing them. Litter weights were converted to grams per unit area and compared (i) between invaded and native plots and (ii) between unclipped and clipped plots as seasonal input rates (fallen litter input rates, g m^{-2} day^{-1}) and cumulatively for the entire sampling period (cumulative fallen litter, g m^{-2}). We used comparisons between unclipped plots and clipped plots to test whether invaded and native plots differed in the amount of fallen litter from previous years' standing dead biomass (g m^{-2}).

Decomposition rates

We used aboveground biomass measurements from 2006 to choose native plant litter types to be included in the litter decomposition study. We calculated dominance as weight species / weight total biomass harvested from native plots and found that *B. laguroides, N. leucotricha,* and *H. belangeri* accounted for 26%, 11% and 6%,

respectively, of the total biomass sampled from all native plots. We used the pooled (across blocks) mean biomass of a species as a proportion of the pooled (across blocks) mean total of these three dominants to determine the proportions of each type of litter to be included in the mixed-native litterbags. *B. ischaemum* litter-bags contained 100% field-collected *B. ischaemum.*

The litterbags were 100 cm^2 and made of 2 mm UV-resistant fiberglass mesh containing either 1 g of mixed-native grass or 1 g of *B. ischaemum* plant material. We homogenized senescing biomass harvested from clipped plots in December of 2006 across blocks by species and cut it into 8 cm lengths before we distributed it into litterbags. We included leaves (blade + sheath) and stems such that the ratio of leaf to stem biomass in litterbags reflected that found for each species in the harvested biomass. Mixed-native litterbags contained 0.6, 0.25, and 0.15 g of *B. laguroides, H. belangeri*, and *N. leucotricha* plant material respectively, reflecting their relative biomass proportions in the 2006 harvested biomass. We determined initial litter chemistry by analyzing 5 subsamples each of homogenized litter from each species (*B. ischaemum, B. laguroides, H. belangeri* and *N. leucotricha*) and the mixture of native litter included in mixed-native litterbags for C and N content (Table 2.2). We coarse-ground subsamples in a coffee grinder for 30 seconds and then fine-ground them using a Mini-Beadbeater-96 (BioSpec Products, Inc., Bartlesville, OK) by shaking them for 10 min in sealed 7 mL polypropylene micro-vials with a mixture of 8 - 10 2.3 mm and 3.2 mm chrome-steel beads. Ground samples were analyzed for carbon and nitrogen at the University of Georgia Analytical Chemistry Lab, Athens, Georgia, using an NA1500 C/H/N Analyzer (Carlo Erba Strumentazione, Milan, Italy).

We placed litterbags in the field in the spring (March 26, 2007) when the majority of fall-senesced litter had already accumulated on the ground (as indicated by a decrease

in litter input rates from fall 2006). Twenty-four litterbags in direct contact with mineral soil were arranged on a 4X6 grid in each of the twelve 1 m^2 decomposition plots, with mixed-native litterbags in native plots and *B. ischaemum* litterbags in invaded plots. We collected two litterbags monthly from each plot and dried and picked them clean of non-plant materials (feces, frass, soil, etc.) and seeds before we weighed the decomposed litter. Values for individual litterbags collected at the same time from within a decomposition plot were averaged within the plot for analysis. We used litterbag mass over the course of the year to compare litter decay constants (k; see data analysis section below) and changes in the ratio litterbag mass at time = t to initial mass (M_t/M_0) between *B. ischaemum* and mixed-litter litterbags.

Litter-trap litter and decomposed litterbag litter from alternate months were processed and analyzed for C and N content using the methods described above for determining initial litter chemistry. Estimated litter chemistry for months in which trapped and decomposed litter were not analyzed for C and N (3 months) was assumed to be the average of the previous and following months' litter quality for the purposes of estimating fallen litter N and C input rates (g N m^{-2} day^{-1} and g C m^{-2} day^{-1} respectively); cumulative fallen litter C (g C m^{-2}), N (g N m^{-2}), and quality (C:N ratio); and changes in decomposing litterbag quality (C:N) and C (C_t/C_0) and N (N_t/N_0) content.

Soil carbon and nitrogen pools and processes

We quantified soil carbon and nitrogen pools associated with invaded and native areas within each block every three months during the decomposition experiments. We collected 10 cm soil cores using a 5 cm diameter, 15 cm long PVC pipe beveled at one end. Due to the destructive nature of soil core sampling, we collected soil cores from native and invaded areas outside of plots, within a 10 m radius of decomposition plots.

Three bulked cores were collected from the rooting zones of *B. ischaemum* individuals in invaded areas and three from the common rooting zones of *B. laguroides* and *N. leucotricha* individuals within native areas within each block. We sampled soils in late spring/early summer (May 23, 2007), mid-summer (August 24, 2007), late fall/early winter (December 7, 2007) and spring (March 20, 2008). We processed soil samples within 6 hours of collection and kept them cool until they were processed. We weighed entire wet samples and then hand-removed all visible roots before we divided them into subsamples to be analyzed for soil moisture and soil carbon and nitrogen pool. We rinsed roots removed from soil samples with distilled water. We then dried, weighed, and ground root samples before they were analyzed for C and N using the methods described above for litter samples. We converted root weights per gram of soil to root biomass and root C and N per unit area (g root cc^{-1}, g C cc^{-1}, and g N cc^{-1} respectively) using average measured bulk soil density (1.36 ± 0.04 g cc^{-1}), which matched well with published values for these soils (1.4 – 1.65 g cc^{-1}; Soil Survey Staff, NRCS, USDA 2009). Our measurements for bulk density did not differ when grouped by block or invaded/native status.

We measured plant-available inorganic nitrogen (N_{inorg}; μg N g^{-1} soil) and its components, ammonium (NH_4^+; μg NH_4^+ g^{-1} soil) and combined nitrite and nitrate (NO_2^- + NO_3^-; μg NO_2^- + NO_3^- g^{-1} soil), in soil samples by extracting 10 g of field moist soil in 50 mL of 2 M KCl for 1 hour on a shaker at 200 rpm. All 2 M KCl extractions were analyzed using spectrophotometric microplate analyses for quantification of [NH_4^+], [NO_2^-], and [NO_3^-] (Sims et al. 1995, Rhine et al. 1998, Sims 2006). N_{inorg} was calculated as the sum of [NH_4^+], [NO_2^-], and [NO_3^-] measured in extracts from each soil sample separately. During the Dec. 7, 2007 and March 20, 2008 sampling periods, we estimated potential net N-mineralization and nitrification rates over a 10 day period by incubating

50 g of soil with 5 mL of DI water at 23 °C in the laboratory and repeating 2 M KCl extractions on incubated soils. We calculated potential rates as the difference between fresh and incubated values.

We measured microbial biomass C (MBC; μg C g^{-1} soil) and N (MBN; μg N g^{-1} soil) in sampled soils using the chloroform fumigation method where soils were fumigated for 5 days (Brookes et al. 1985, Beck et al. 1997). We performed extractions of fresh and fumigated soils using 20 g soil in 80 mL 0.5 M K_2SO_4 for 1 hour shaken at 200 rpm. Soil 0.5 M K_2SO_4 extracts were analyzed for total dissolved organic C (TOC; μg C g^{-1} soil) and total dissolved N (TN; μg N g^{-1} soil) using a total organic carbon analyzer with a nitrogen analyzing unit (Shimadzu Scientific, Columbia, MD) at the Texas A&M University Soil Analysis Laboratory, College Station, TX. We calculated MCB and MNB as the difference in TOC and TN in extractions from fumigated (which contained lysed microbial cells) and fresh (in which microbial cells were intact) soils. We also used 0.5 M K_2SO_4 extracts from fresh soils to compare TOC and TN between invaded and native plots.

Data analysis

Aboveground net primary productivity (ANPP)

We tested whether *B. ischaemum* invasion increased aboveground productivity by comparing the effect of *plot type* (invaded or native) on total aboveground biomass and ANPP using ordinary least squares (OLS) models (GLM procedure in SAS 9.2, SAS Institute Inc., Cary, NC, USA). Total aboveground biomass and ANPP (biomass from clipped plots + cumulative fallen litter inputs from clipped plots) were analyzed separately. *Plot type* (native or invaded) was included in the model as a fixed-effect categorical variable. *Block* was included as a random-effect categorical variable; *F*-

values of differences among plot types were therefore calculated using the mean squares of the *plot type X block* term in the same model as the denominator (which was also the model error term).

Cumulative fallen litter and standing dead contributions to fallen litter

We tested whether *B. ischaemum* invasion increased cumulative fallen litter and the contribution of standing dead material to cumulative fallen litter by comparing cumulative fallen litter between invasive and native clipped and unclipped plots using an OLS model (SAS *proc glm*). We included *plot type* (invaded vs. native), *treatment* (unclipped vs. clipped) and their two-way interaction term (*plot type* X *treatment*) as categorical fixed effects and *block* as a random effect in the OLS model of cumulative fallen litter inputs. *F*-values of differences among plot types were calculated using the mean squares of the *plot type X block* term in the same model as the denominator. *F*-values of differences among treatments were calculated using the mean squares of the *treatment X block* term in the same model as the normalizing denominator. *F*-values of differences of *plot type X treatment* were calculated using the mean squares of the *plot type X treatment X block* term (the model error term) in the same model as the denominator.

Cumulative fallen litter quality

We tested whether *B. ischaemum* invasion decreased fallen litter quality, which was only examined for fallen litter collected from unclipped plots, by comparing the effect of *plot type* (invaded or native) on cumulative litter input C (g C m^{-2}), N (g N m^{-2}) and C:N from litter collected in the unclipped plots using OLS models (SAS *proc glm*). Cumulative litter C, N and C:N were analyzed separately. *Plot type* (native or invaded) was treated as a fixed-effect categorical variable and *block* was included as a random-

effect categorical variable. *F*-values of differences among species were therefore calculated using the mean squares of the *plot type X block* term in the same model as the denominator (which was also the model error term).

Fallen litter input rates

We used "mixed" models (SAS *proc mixed*) to assess the effects of *B. ischaemum* invasion on fallen litter input rates (g m^{-2} day^{-1}) and the contribution of standing dead material to fallen litter input rates (g m^{-2} day^{-1}). Input rates were compared between invasive and native unclipped (on-going fallen litter collection) and clipped (on-going fallen litter collection + biomass harvest) plots by including *plot type* (invaded vs. native), *treatment* (unclipped vs. clipped) and their interaction term (*plot type* X *treatment*) as fixed effects and *block* as a random effect in mixed models. The date on which each measurement was made (*doy*, Julian day-of-year) was also included in the model as a fixed-effect categorical variable, because there was no expectation of a linear relationship between the dates on which measurements were made and litter input rate. We included the interactions of *plot type, treatment* and date (*plot type X doy, treatment X doy, plot type X treatment X doy*) in the initial models in order to examine differences among plot types and treatments in their responses to season. Because fallen litter inputs were repeatedly measured on the same plots, individual plot as a function of *doy* was included in the model as a *repeated* statement.

Fallen litter quality over time

We also tested whether *B. ischaemum* invasion altered the timing of litter N and C inputs by comparing the effect of *plot type* (invaded or native) on fallen litter C and N input rates, g C m^{-2} day^{-1} and g N m^{-2} day^{-1} respectively, from litter collected in the unclipped plots using mixed models (SAS *proc mixed*). Litter C and N input rates were

analyzed separately. *Plot type* (native or invaded) and date (doy) were fixed-effect categorical variables in the model and *block* was a random-effect categorical variable. We included the interactions of *plot type* and date (*plot type X doy*) in models in order to examine differences among plot types in variable responses to season. Because fallen litter inputs were repeatedly measured on the same plots, individual plot was included in the model as a *repeated* statement.

Soil C and N pools and processes

We tested whether *B. ischaemum* invasion decrease soil nitrogen pools and increased soil carbon pools by comparing the effect of *plot type* (invaded or native) on soil pool sizes using OLS models (SAS *proc glm*). Each soil pool response variable (soil TOC, soil TN, soil N_{inorg}, soil $[NH_4^+]$, soil $[NO_3^- + NO_3^-]$, MBN, MBC, root biomass, root N, root C, and root biomass C:N) was analyzed separately. We also compared soil net nitrification rates and net N-mineralization rates between plot types for the two dates on which those variables were measured. *Plot type* (native or invaded) and sampling date (*date)* and their two-way interaction term (*plot type X date*) were included in the models as fixed-effect categorical variables. The date on which each measurement was made (*date*) was included in the model as a fixed-effect categorical variable, because there was no expectation of a linear relationship between the dates on which measurements were made and any response variable. We included the interaction *plot type X date* in models in order to examine differences between plot types in their responses to season. *Block* was considered a random-effect categorical variable in each of these models; therefore *F*-values of differences among species were calculated using the mean squares of the *plot type X block* term in the same model as the denominator.

Decomposition rates

The effect of *B. ischaemum* invasion on litter decomposition rates was tested by modeling litter decomposition using exponential decay curves fit at the individual decomposition plot nested within *block X plot type* level using non-linear mixed effects models (*nlme* function in the *nlme* package in R, R Development Core Team, 2008). We modeled decay constants (k) for decomposing litter weight using the equation, $M_t = M_0 e^{kt}$ (Olson 1963) where M_0 = initial mass or initial litter quality, M_t = mass or litter quality of the decomposing litter at sampling time "t", and t = sampling time in years. Initial values used for modeling were the initial weight of each litterbag. We compared decay constants for decomposing litter (k) between invaded and mixed-native decomposition litterbags using *nlme* models that included *individual plot* (*plot* nested within *type X block*) as a random effect and *plot type* (invaded or mixed-native) as the fixed effect. We tested model adequacy, whether models met modeling assumptions for normally distributed residuals and homoscedasticity, using standardized residuals versus fitted values plots and residuals autocorrelation and normal probability plots of with-in group residuals. *F*-tests were used to assess the significances of fixed-effect treatments on model parameters (Pinhero and Bates 2004).

We also compared litterbag mass loss (M_t/M_0), C loss (C_t/C_0), N retention (N_t/N_0) and litter quality ($C:N_t/C:N_0$) during decomposition between litterbag types (*B. ischaemum* and mixed-native). These ratios were compared between litterbag types over time using OLS models as described above for soil pools. Decomposed litterbag content M_t/M_0, N_t/N_0, C_t/C_0, and $C:N_t/C:N_0$ were all analyzed separately. Models using untransformed data met modeling assumptions for normally distributed residuals and homoscedasticity, so untransformed ratios were analyzed and reported.

RESULTS

Aboveground net primary productivity (ANPP)

B. ischaemum invasion significantly increased aboveground productivity in invaded areas (Figure 2.2, Table 2.3). ANPP was on average 26 ± 19 % higher in invaded areas than in native areas (comparison of clipped plots; Figure 2.2; Table 2.3. The proportion of ANPP derived from litter inputs was slightly higher in native clipped plots (19 ± 4 %) than invaded clipped plots (10 ± 2 %).

Microhabitat Characteristics

Although there was only one set of sensors installed in one native and one invaded area, we did observe differences in microhabitat characteristics that may influence litter decomposition and soil nutrient mineralization rates. The decrease in temperature from open air (above the grass canopy) to ground level (under the grass canopy) was larger where *B. ischaemum* formed the canopy than where native grasses did so (Table 2.4). Similarly, the increase in humidity from open air to ground level was larger in *B. ischaemum* stands (Table 2.4). Soil temperatures at 5cm depth, except in the coldest weeks, were higher under native canopies (Figure 2.3). Differences in soil moisture between *B. ischaemum*-dominated and native-dominated areas were small except in the fall, when native-dominated areas had higher soil moisture (Figure 2.4). These humidity and temperature data are what would be expected; *B. ischaemum*'s denser canopy created a cooler, moister sub-canopy microclimate than did the sparser canopy of the native grasses. However, soils in areas dominated by native species were wetter, which is probably related to the greater rate at which *B. ischaemum* removed water from the soil due to its greater total leaf area.

Cumulative fallen litter and standing dead contributions to fallen litter

Cumulative fallen litter was not significantly different between *B. ischaemum*-invaded and native areas (g m^{-2}; Figure 2.5a; Table 2.5). Higher productivity (Figure 2.2) without higher cumulative fallen litter may be due to *B. ischaemum* aboveground biomass remaining in the standing dead pool longer than most native biomass. While *B. ischaemum* invasion did not significantly increase the contribution of previous years' standing dead to cumulative fallen litter (g m^{-2}; Figure 2.5b; Table 2.5, standing dead contribution = differences between cumulative litter in clipped and unclipped plots), standing dead material contributed substantially to fallen litter in both native (estimated 55 ± 5 % of total fallen litter) and invaded (estimated 65 ± 7 % of total fallen litter) unclipped plots (Figure 2.5b).

Fallen litter quality and input rates

Cumulative fallen litter N (g N m^{-2}) was significantly higher in native areas and cumulative fallen litter quality was significantly lower (higher C:N) in *B. ischaemum*-invaded areas, but cumulative litter C (g C m^{-2}) did not differ between invaded and native areas (Tables 2.5, 2.6).

Although overall litter input rates were not significantly different in *B. ischaemum*-invaded plots (Table 2.7), we did observe significant differences in the timing of fallen litter inputs in comparison to native plots (g m^{-2} day^{-1}; significant type-date effect on fallen litter input rates in Table 2.7, Figure 2.6). Native-dominated plots received pulses of litter, the majority of which fell in the late spring and early summer (16 %) and late fall (53 %), while *B. ischaemum*-dominated received nearly continuous litter inputs (Figure 2.6). Litter input rates were higher in unclipped plots than in clipped plots, particularly in the late winter/early spring and the late fall indicating that standing dead material affected the timing of litter inputs (significant treatment and treatment-date

effects on fallen litter input rate in Table 2.7, Figure 2.6). There were also significant differences in the timing of carbon and nitrogen inputs between invaded and native plots (g C m^{-2} day^{-1} and g N m^{-2} day^{-1} respectively; significant type-date effects in Table 2.7; Figures 2.7a, 2.7b). *B. ischaemum*-dominated plots received lower quality litter throughout the year (C:N ratio, significant type effect in Table 2.7; Figure 2.7c).

Soil Carbon and Nitrogen Pools

B. ischaemum plots did not have larger soil carbon pools: total organic carbon (TOC; Table 2.8; Figure 2.8a), microbial biomass C (MBC; Table 2.8; Figure 2.9a), root biomass (Table 2.8; Figure 2.10a), and root C (Table 2.8; Figure 2.10c) were all similar between native and invaded soils. Soil TOC was slightly and non-significantly higher in native soils in the summer, but otherwise was similar between invaded and native soils (Figure 2.8a). MBC tracked plant activity, increasing throughout the growing season and decreasing during the cool season, but there were only small and non-significant differences in MBC between invaded and native soils (Figure 2.9a). There were only small and non-significant changes in root biomass and root C (Figures 2.10a, 2.10c).

While total soil N (TN; Table 2.8; Figure 2.8b) did not differ significantly between invaded and native soils, root N (Figure 2.10b), root quality (higher C:N; Figure 2.10d), and plant available inorganic nitrogen ($N_{inorg} = NO_3^- + NO_2^- + NH_4^+$; Figure 2.11a - 2.11c) were each significantly lower in invaded soils (significant type effects in Table 2.8). Higher root N and lower root quality (higher C:N) in invaded soils probably reflect poorer quality root exudates and root litter inputs from *B. ischaemum* roots to invaded soils. There were also seasonal differences in root N that indicate that *B. ischaemum* may reallocate or re-translocate less N belowground than native species do during the cool season (significant type-date effect in Table 2.8; Figure 2.10b).

Seasonal patterns of plant available inorganic N (N_{inorg}) differed between invaded and native plots, although the temporal differences did not reach significance (Table 2.8; Figure 2.11a). Differences in N_{inorg} were larger in the late spring (May), due to differences in soil [NH_4^+] (Figure 2.11b), and late fall/early winter (December), due mainly to significant differences in soil [NO_2^- + NO_3^-] (significant type-date effect in Table 2.8; Figure 2.11c). N_{inorg} peaked at different times in invaded and native plots: N_{iorg} peaked during the summer (August) in invaded soils and during the late fall (December) in native soils (Figure 2.11a). The peak in N_{inorg} in native soils occurred just after a pulse in fallen litter N, and coincided with increased Root N and decreased MBN in native soils. The peak in N_{inorg} in invaded soils was not obviously linked to any of the variables we measured.

We had anticipated significantly higher N immobilization in microbial biomass (as indicated by higher microbial N [MBN]) and lower N-cycling rates (N-mineralization and nitrification rates) in invaded soils. MBN was only higher in invaded plots briefly and not significantly during the late fall (December) sampling period (Figure 9b; Table 2.8). N-mineralization and nitrification rates were higher in lab-incubated native soils in the late fall, but overall differences in N-mineralization and nitrification rates were neither consistent nor significantly different between invaded and native soils (Figures 2.12a, 2.12b; Table 2.8). This may have been due to the limited number of incubations we conducted.

Decomposition

B. ischaemum invasion did not slow plant litter decomposition rates in invaded areas. Despite similar decomposing litter mass-loss rates (k and M_t/M_0 in Tables 2.9, 2.10 and Figures 2.13, 2.14a respectively), *B. ischaemum* litterbag litter lost carbon

(C_t/C_0; Figure 2.14b) (due to microbial respiration of plant material carbon) and increased in quality ($C:N_t/C:N_0$; Figure 2.14d) faster during the year in the field than the mixtures of native litter (significant type effects in Table 2.10). Final mass loss was ~33 % of both *B. ischaemum* and mixed-native litterbags. C content decreased by 9 % and 12 % of mixed-native and *B. ischaemum* litterbags respectively, and C:N in *B. ischaemum* litterbags decreased by 47 % versus a 24 % decrease in mixed-native litter bags. Higher nitrogen retention (N_t/N_0) in *B. ischaemum* litterbag litter, as indicated by larger increases in N content relative to C content, may indicate that native litter mixtures were more readily metabolized by the soil microbial community than was *B. ischaemum* litter (Table 2.10; Figure 2.14c). This was likely due to the breakdown of the higher quality *N. leucotricha* and *H. belangeri* portions of the mixed-native litterbags, which comprised less than half of the weight of these bags, leaving behind the significantly poorer quality *B. laguroides* material.

DISCUSSION

We predicted that the invasion of mixed C_3/C_4 native savanna grass-matrix by an invasive C_4 grass, *B. ischaemum*, would lead to an increase in the production of poorer quality plant material as a result of the displacement of higher quality, less productive native species. We also predicted that this increased productivity and decreased plant input quality would result in decreased decomposition and nitrogen-cycling rates and reduced soil nitrogen availability in invaded areas. We did find that aboveground productivity was significantly higher in invaded plots, but there was no parallel increase in productivity belowground (assessed by root biomass from soil cores) or cumulative amounts of fallen litter. The quality (measured by C:N ratio) of fallen-litter and belowground plant material were significantly lower in invaded areas, but the expected

indicators of depressed nutrient-cycling rates (slower litterbag decomposition [k], N-mineralization and nitrification rates, and higher microbial biomass N) were not significant. Thus, while there was evidence of lower plant-available nitrogen in invaded soils, we conclude that the primary mechanism by which this occurred was not depressed litter decomposition and nutrient-cycling rates.

Inter-specific differences in plant litter quality have been shown to be more important than environmental factors in determining soil carbon and nitrogen pool sizes and cycling rates (Dijkstra et al. 2006), and plant traits and impacts on soil microbial community structure strongly influence decomposition both above and below ground (Cortez et al. 2001, Quested et al. 2003, Fornara et al. 2009, Holly et al. 2009). In our study, *B. ischaemum* invasion was associated with significantly lower quality plant inputs to invaded soils: fallen litter quality was consistently higher in native areas. If we assume that higher-quality root biomass in native soils results in higher quality root exudates and root litter inputs (Jones et al. 2004), soil microbial communities in native plots received significantly higher quality plant inputs from both above- and belowground sources.

Lower quality plant inputs in invaded areas have the potential to slow both fast-cycling root exudates and slow-cycling soil organic matter (Kuzyakov 2010). In our study, however, we did not observe differences in litterbag decomposition rates or soil organic carbon pools (TOC and soil microbial biomass C [MBC]), and soil respiration rates were generally similar between invaded and native areas in this ecosystem (Chapter 3). Additionally, the differences that we observed in soil N processes (slightly higher N immobilization in microbial biomass [MBN] and slightly slower N-mineralization and nitrification rates) in invaded soils were not large enough to account for the significantly lower nitrogen availability measured in invaded soils. All of these factors indicate that decreased litter quality was probably not having a major impact on soil nutrient cycling

processes in invaded areas and therefore was not directly responsible for decreased available nitrogen in invaded soils.

Results from our litterbag experiment indicate that *B .ischaemum* invasion did not change decomposing litter mass-loss rates, which is contrary to our predictions and not what our other findings for soil pools and litter quality would indicate. While the quality of plant materials included in litterbags did not differ significantly between *B. ischaemum* and mixed-native litterbags initially, the quality of fallen litter collected in native plots was consistently higher (lower C:N) than that collected in invaded plots. Also, mixed-native litterbag-litter quality was lower than the average of native fallen litter collected in the field, but *B. ischaemum* litterbag-litter quality was similar to that of *B. ischaemum* fallen litter collected in the field. Therefore, the similarity in decomposition rates that we observed in our litterbag decomposition experiment may have been an artifact of our experimental design and not necessarily reflective of actual decomposition rates in this system.

In the absence of large differences in litterbag decomposition and N-cycling rates between invaded and native soils, it is likely that increased residence time in the standing dead pool in invaded plots was the primary mechanism causing lower soil nitrogen availability in invaded areas. Despite significantly higher aboveground productivity in invaded plots, the quantity of fallen litter collected in litter traps in invaded and native plots did not differ. This seems to be indicative of increased residence time of plant materials in the standing dead pool. There were also slightly larger differences in the total amount of fallen litter between clipped (no standing dead from previous growing seasons) and unclipped (standing dead from previous growing seasons) invaded plots than were seen in the native plots. These results indicate that contributions of fallen litter from standing dead vegetation from previous years were larger in invaded areas than they were

in native areas. This implies that the continuous input of fallen litter observed in invaded plots was due to fallen standing dead material from previous years and that one of the effects of invasion is increased residence time of plant products in standing dead pools. *B. ischaemum* invasion appears to create a litter reservoir in the standing dead pool that acts to regulate the flow of aboveground carbon to the decomposing litter pool at the soil surface and eliminates the pulses in fallen litter seen in native plots. This "damming" of litter reduces the natural temporal variability in litter input timing and quality and decreases the role of climatic variability in determining the timing and the quality of litter inputs in any given year.

Increased residence time in the standing dead pool has the potential to alter the quality and rhythm of fallen litter inputs in invaded areas and these alterations can negatively impact nutrient availability in invaded ecosystems. We did not investigate standing dead residence time or its effects on plant product quality in this work, but a preliminary study comparing flowering culm residence time in the standing dead pool between three native perennial grasses and *B. ischaemum* in this system indicate that *B. ischaemum* culms remain in the standing dead pool longer than those of native species *N. leucotricha* and *H. belangeri,* but not of *B. laguroides* (Basham and Poteet, *unpublished data*). Preliminary results from this study also indicate that residence time in the standing dead pool positively affects plant product quality (decreased C:N in plant material) of *N. leucotricha* and *H. belangeri*, but does significantly change that of the invasive or *B. laguroides* over the course of a year (Basham and Poteet, *unpublished data*). In ecosystems where an invasive is replacing native species with similar standing dead pool residence times, the effect of the invader might be less dramatic than in our study. Slower turnover of standing dead pools are commonly found in C_4-dominated grasslands (Sims and Singh 1978, Knapp and Seastedt 1986) and have been seen in other C_4-grass invaders

(Drenovsky and Batten 2007, Wolkovich et al. 2010). Increased residence time in the standing dead pool could decrease the rate of nutrient cycling by trapping nutrients in standing materials above ground, and may represent a decoupling of belowground and aboveground plant inputs because there is no belowground equivalent to aboveground standing dead pools. The role that changes in standing dead pool residence time play in nutrient cycling in these ecosystems remains to be investigated.

In addition to retaining nutrients aboveground, the increased standing dead pool residence time likely negatively impacts litter decomposition by altering plant canopy microhabitat conditions. Increased standing dead pools associated with plant invasions have been found to decrease decomposition rates in invaded grasslands due to both increased standing dead pool residence time (Drenovsky and Batten 2007) and as a result of decreased photodegradation due to increased shading (Wolkovich et al. 2010). Increased standing dead plant material also reduces inorganic-N inputs from rainfall (microbes on standing dead remove more inorganic N from and release more organic N to through-fall than living foliage does), decreases soil surface temperatures, and increases soil moisture content, all of which will impact decomposition rates at the soil surface (Knapp and Seastedt 1986). Photodegradation would be expected to play a significant role in soil surface decomposition in this semi-arid ecosystem, particularly in dry years (Austin and Vivianco 2006). Differences in canopy structure between native and invaded grasslands may also promote differences in non-microbial detritivore communities that can influence decomposition rates (Shadler and Brandl 2005). *B. ischaemum* invasion decreases light transmittance and increases shading within the plant canopy, which results in lower soil temperatures in invaded areas (Chapter 3). Decreased solar irradiance at the soil surface is also likely to decrease the role of photodegradation in plant litter decomposition in invaded areas. Lower soil temperatures in invaded areas

will tend to decrease litter decomposition rates, while higher soil moisture in invaded areas (Chapter 3) will increase decomposition rates. The net effect could be what we found in our litterbag study, which was no difference in decomposition rates between invaded and native areas.

Differences in microhabitat conditions are not uniform from year to year and appear to occur primarily when there are large differences in productivity and canopy structure between invaded and native areas (Chapter 3). If this is the case, the direction of invasion impacts on decomposition rates (and other ecosystem processes) may differ from year to year with climatic conditions, as has been seen in other studies (Ruffner et al. 2012). For example, decomposition rates may be similar between invaded and native areas in wetter years (like the one in which this study was conducted) when canopy light transmittance and soil temperatures are more similar and differences in soil moisture are larger between invaded and native areas, and higher in native plots, as we predicted, in drier years when solar irradiance and soil temperatures are higher in native areas, but soil moisture is similar between plot types. A longer-term study that tests the effects of microhabitat on decomposition rates is needed to unravel the effects of the interaction of *B. ischaemum* invasion and climate on these ecosystem processes.

While we did find significant differences in available soil nitrogen between invaded and native plots, this finding does not necessarily mean that these differences are biologically significant. We do not know to what degree *B. ischaemum* would have to affect soil nitrogen cycling and availability to influence the persistence of other species in these soils. The decline in cover of less nitrogen-use-efficient forb and C_3 grass species associated with *B. ischaemum* invasion (Chapter 3) does support the idea that nitrogen availability may play some role in the exclusion of native species form invaded areas. It is possible, however, that most of the species in this ecosystem are adapted to, or tolerant

of, low nitrogen availability, and that soil nitrogen availability does not play a large role in *B. ischaemum*'s success in this ecosystem. The role of nitrogen in determining *B. ischaemum*'s successful establishment and dominance in an area remains to be investigated.

B. ischaemum invasion increased aboveground productivity in invaded areas, but we did not find evidence that invasion also increased belowground productivity. The similarity in belowground biomass between invaded and native soils despite higher aboveground biomass production in invaded areas may be attributed to the tendency of *B. ischaemum* to have a lower root:shoot ratio than several of the native C_4 grasses that occurred in our plots (Wilsey and Polley 2006), a characteristic that is not uncommon in invasive plant species (Ehrenfeld 2003). While some other greenhouse studies have not found differences in root:shoot between *B. ischaemum* and native species (Coyne and Bradford 1985, Chapter 1), a study conducted in the Blackland Prairie of central Texas found that *B. laguroides, Schizachyrium scoparium* and *Bouteloua curtipendula* produce amounts of root biomass similar to those of *B. ischaemum* and other invasive C_4 grasses at shallower depths (0 – 20 cm), but significantly higher amounts of root biomass than these invaders at depths below 20 cm (Wilsey and Polley 2006). These native species accounted for 29 ± 5 % of the aboveground biomass in our native plots, so it is possible that had we sampled soils below 10 cm, we might have found higher root biomass in native areas. Whether belowground productivity remains the same or decreases with *B. ischaemum* invasion, shifting productivity from belowground to aboveground can decrease carbon storage in central Texas ecosystems by reducing inputs to slower cycling belowground soil carbon pools and increasing plant inputs to faster cycling aboveground pools (Gill and Burke 1999, 2002).

The increased productivity and differences in plant input quality that we found between invaded and native areas led us to expect to find differences in soil C pools. We did not, however, find significant differences in SOC or any of the other soil C pools examined in this study. As SOC can have a turnover time of decades to centuries (Davidson and Janssens 2006) the lack of differences in soil C pools may be a result of the relatively short time since *B. ischaemum* invaded the WFC (approximately 10 years prior to this study). Work in the Texas coastal prairie, where *B. ischaemum* and *Dichanthium annulatum* are replacing *S. scoparium* as the dominant species, did find higher SOC 10 - 20 cm, but not 0 - 10 cm deep, in soils that they estimated to have been invaded 8 - 10 years prior to their study (Ruffner et al. 2012). We sampled soils at the WFC to only 10 cm in depth, which may also account for our not finding differences in SOC. However, a comparison of C_3- and C_4-dominated restored prairies also failed to find differences in soil C pools 16 years after restoration despite large difference in productivity between the two systems (Cahill et al. 2009). There is also some evidence that faster cycling rates for C_4-derived than C_3-derived soil carbon may account for the missing increase in soil C in more productive C_4-dominated systems in that study and ours (Wynn and Bird 2007). Additionally, work along environmental gradients and on multiple soil types have shown that invader density, soil type, and other site characteristics can mediate an invader's impacts on soil carbon pools (Kramer et al. 2012, Ruffner et al. 2012), so our findings may be site-specific. Well-documented chronosequences of invasion compared among multiple sites would be a more appropriate way to investigate the impact of this species on longer-term carbon pools.

Bothriochloa spp. and many of the other perennial C_4 grasses that are now considered invasive in the central U.S. were selected for and widely introduced to the central plains of North America as forage species because of their ease of establishment,

high grazing tolerance, and high productivity (Coyne and Bradford 1985, Donahue 1999). These very traits are likely what make them successful invaders (Schmidt et al. 2008). Introduced *Bothriochloa* spp. and other Old World Bluestem grasses have been shown to increase aboveground biomass production in tall grass (Reed et al. 2005) and mid-grass prairies (Berg and Sims 1984, Ruffner et al. 2012). Although few other studies have examined the impacts of these species' invasions on ecosystem function, the ones that do so have concluded that whichever the direction of change in ecosystem function, the major factors instigating those changes are related to increased productivity and changes in plant input quality (Berg and Sims 1984, Reed et al. 2005, Ruffner et al. 2012). In tall-grass prairies, increased aboveground biomass has resulted in larger losses of nitrogen during burns, which has been exacerbated by poorer quality plant inputs from the invasive; together these have lowered nitrogen availability in already naturally low-nitrogen soils (Reed et al. 2005). In the coastal prairies of Texas, increased aboveground productivity and plant product quality that result from Old World Bluestem grass invasions contribute to increased decomposition and N-mineralization rates in invaded areas (Ruffner et al. 2012). In our mixed-grass system, where increased aboveground biomass of poorer quality can increase plant product residence time in standing dead pools and alter microhabitat characteristics, invasion results in lower soil nitrogen availability. In all three cases, higher aboveground productivity is not matched belowground, which has the potential to alter soil C dynamics in invaded areas. This shift in productivity from belowground to aboveground could have negative implications for ecosystem carbon storage, as was found to be the case for *Agropyron cristatum* in the northern-central plains (Christian and Wilson 1999). The reverse has been found for introduced African grasses that increase belowground productivity (Wiliams and Baruch 2000).

CONCLUSIONS

While the exact mechanism by which *Bothriochloa* spp. impact ecosystem function may vary from system to system, and even site to site within an ecosystem, increased aboveground productivity and changes in plant product quality are likely impacts of the introduction of all Old World Bluestem grasses into central US grasslands. The net effect of these invasions will be to change soil nitrogen availability and potentially to decrease soil carbon storage in invaded ecosystems. These alterations in ecosystem function can create plant-soil feedback that favors invasive species over native species, thus securing the dominance of the invasive plants in the ecosystem (Vinton and Goergen 2006).

Table 2.1.a. List of variables measured in Chapter 2 and the tables and figures in which they are reported.

Variable Type	Variable	Acronym	Units	Tables	Figures
Aboveground Productivity	Total biomass (live + standing dead)		$g\ m^{-2}$	2.3	2.2
	Aboveground net primary productivity (total biomass + litter)	ANPP	$g\ m^{-2}$	2.3	2.2
Microhabitat	Air temperature	T_{air}	°C	2.4	
	Relative humidity	RH	%	2.4	
	Soil temperature	T_{soil}	°C		2.3
	Soil moisture	θ	m^3 / m^3		2.4
Fallen Litter	Cumulative Fallen litter		$g\ m^{-2}$	2.5	2.5a
	Standing dead contributions to cumulative fallen litter		$g\ m^{-2}$	2.5	2.5b
	Cumulative fallen litter Carbon		$g\ C\ m^{-2}$	2.5, 2.6	
	Cumulative fallen litter Nitrogen		$g\ N\ m^{-2}$	2.5, 2.6	
	Cumulative fallen litter quality (C:N)			2.5, 2.6	
	Fallen litter input rates		$g\ m^{-2}\ day^{-1}$	2.7	2.6
	Fallen litter Carbon input rates		$g\ C\ m^{-2}\ day^{-1}$	2.7	2.7a
	Fallen litter Nitrogen input rates		$g\ N\ m^{-2}\ day^{-1}$	2.7	2.7b
	Fallen litter quality over time (C:N)			2.7	2.7c
Soil Pools and Processes	Total organic soil carbon	TOC	$\mu g\ C\ g^{-1}$ soil	2.8	2.8a
	Total soil nitrogen	TN	$\mu g\ N\ g^{-1}$ soil	2.8	2.8b
	Microbial Biomass Carbon	MBC	$\mu g\ C\ g^{-1}$ soil	2.8	2.9a
	Microbial Biomass Nitrogen	MBN	$\mu g\ N\ g^{-1}$ soil	2.8	2.9b

Table 2.1.b. List of variables continued.

Variable Type	Variable	Acronym	Units	Tables	Figures
Soil Pools and Processes (cont.)	Root biomass		g cc^{-1}	2.8	2.10a
	Root nitrogen		g N cc^{-1}	2.8	2.10b
	Root carbon		g C cc^{-1}	2.8	2.10c
	Root quality (C:N)			2.8	2.10d
	Plant availible inorganic nitrogen	N_{inorg}	µg N g^{-1} soil	2.8	2.11a
	Soil ammonium	NH_4^+	µg g^{-1} soil	2.8	2.11b
	Soil nitrite and nitrate	NO_2^-, NO_3^-	µg g^{-1} soil	2.8	2.11c
	Potential net nitrogen mineralization rates		µg N g^{-1} soil day^{-1}	2.8	2.12a
	Potential net nitrification rates		µg N g^{-1} soil day^{-1}	2.8	2.12b
Litter Decomposition	Litterbag decay constant	k	g yr^{-1}	2.9	2.13
	Litter bag mass loss	M_0/M^t		2.10	2.14a
	Litterbag C loss	C_0/C_t		2.10	2.14b
	Litterbag N retention	N_0/N_t		2.10	2.14c
	Litterbag quality (C:N)			2.10	2.14d

Table 2.2. Initial litter chemistry measured for plant material used in decomposition litterbags.

Two types of litterbags were included in the decomposition experiment: *B. ischaemum* and "mixed native". *B. ischaemum* decomposition litterbags contained 1 g of *B. ischaemum* plant material. Each mixed-native decomposition litterbag contained 0.6 g of *B. laguroides*, 0.25 g of *N. leucotricha* and 0.15 g of *H. belangeri* plant materials. Values are presented for separate species and for the mixture of native species material used in "mixed-native" litterbags. Values are means (± 1 SE) of 5 sub-samples from senescing biomass harvested the fall before in-field decomposition experiments were conducted. Values with different lower case letters beside them are statistically different (MANOVA, $F_{4,12} = 10.08$, $P < 0.0001$; Tukey HSD, $P < 0.05$).

Species	Total N (%)	Total C (%)	C/N Ratio
B. ischaemum	0.83 (0.08) a	43.23 (0.07) ab	53.67 (4.97) ac
B. laguroides	0.42 (0.02) b	45.55 (0.19) a	108.49 (6.43) b
H. belangeri	0.78 (0.05) a	39.87 (0.93) b	51.88 (2.78) ac
Mixed Native	0.69 (0.02) a	44.38 (0.21) a	64.36 (2.44) a
N. leucotricha	1.18 (0.05) c	44.71 (1.78) a	38.06 (1.22) c

Table 2.3. Ordinary least squares model results for total biomass and aboveground net primary productivity (ANPP) collected from clipped native and invaded plots at the WFC in 2007.

Total biomass included live and standing dead plant material but not litter. ANPP included total biomass and litter. Values are *F*-values (degrees freedom). Bold type indicates that the effect is significant ($P < 0.05$). The categorical covariates *type* (invaded or native) and block were included in the model as a fixed effect and a random effect respectively.

Variable	TYPE	BLOCK
Biomass	**14.46 (1, 5)**	2.13 (5, 11)
ANPP (Biomass + Litter)	**10.53 (1, 5)**	2.04 (5, 11)

Table 2.4. Seasonal differences in daily average air temperature and relative humidity between open air and below-canopy sensors.

Measurements were recorded every hour using sensors installed in one native and one invaded grassland area. Values are means (± 1 SE).

	Difference in Daily Average Air Temperatures		**Difference in Daily Average Relative Humidity**	
	Invaded	**Native**	**Invaded**	**Native**
Late Spring/ Early Summer (May - June)	-0.52 (0.07)	-0.32 (0.04)	4.07 (0.38)	0.87 (0.33)
Summer (July - August)	-0.51 (0.06)	0.01 (0.04)	4.47 (0.30)	-0.42 (0.23)
Late Summer/ Early Fall (September - October)	-0.85 (0.08)	-0.10 (0.06)	2.55 (0.64)	-0.10 (0.37)
Fall / Early Winter (November - December)	-0.73(0.14)	-0.38 (0.10)	2.79 (0.76)	2.01 (0.50)

Table 2.5. Results for ordinary least squares (OLS) models comparing cumulative fallen litter amounts, standing dead contributions to cumulative fallen litter, and cumulative fallen litter carbon and nitrogen content and quality (C:N) between clipped and unclipped and invaded and native plots.

Treatment (*trt*), plot type (*type*) and their interaction term (*trt X type*) were included as fixed effects in the model of cumulative fallen litter (Figure 2.5a). Plot type (*type*) was included as a fixed effect in models of standing dead contributions to cumulative fallen litter (Figure 2.5b) and cumulative fallen litter C, N and C:N (Table 2.6). *Block* was treated as a random effect in all of the models, therefore *F*-values of differences between treatments (*trt*) were calculated using the mean squares of the *trt X block* term. *F*-values of differences between plot types were calculated using the mean squares of the *type X block* term from the same model as the denominators. Values are *F*-values (degrees of freedom). Bold type indicates that values are significant at the $P < 0.05$. Italics indicate nearly significant values at the $0.5 < P < 0.10$. Standing dead contribution to fallen litter was calculated as the difference in cumulative litter between unclipped and clipped plots.

Variable	**TRT**	**TYPE**	**BLOCK**	**TRT X TYPE**	**TRT X BLOCK**	**TYPE X BLOCK**
Cumulative Fallen Litter ($g\ m^{-2}$)	**58.12 (1, 5)**	0.00 (1, 5)	0.48 (5, 5)	0.85 (1, 5)	0.28 (5, 5)	0.67 (5, 5)
Standing Dead Contribution to Fallen Litter ($g\ m^{-2}$)		1.93 (1, 5)	0.71 (5, 5)			
Cumulative Fallen Litter Carbon ($g\ C\ m^{-2}$)		1.57 (1, 5)	4.68 (5, 5)			
Cumulative Fallen Litter Nitrogen ($g\ N\ m^{-2}$)		**6.73 (1, 5)**	2.15 (5, 5)			
Cumulative Fallen Litter C:N		**11.04 (1, 5)**	0.81 (5, 5)			

Table 2.6. Cumulative fallen litter chemistry measured in native and invaded unclipped plots at the WFC.

Values are annual means (± 1 SE). Asterisks indicate significant differences between plot types (invaded vs. native) (* *P* < 0.05; ** *P* < 0.01; * *P* < 0.001).**

Variable	Invaded	Native	Significance
Cumulative litter C inputs ($g\ C\ m^{-2}$)	63.24 (4.31)	59.73 (3.28)	
Cumulative litter N inputs ($g\ N\ m^{-2}$)	1.36 (0.09)	1.75 (0.15)	*
Cumulative litter C:N	46.60 (3.02)	34.27 (1.65)	*

Table 2.7. Results for mixed effects models comparing seasonal trends in input rates for fallen litter mass, nitrogen and carbon content, and fallen litter quality (C:N).

Fallen litter input rates were compared between clipped and unclipped treatments (*trt*) and invaded and native plots (*type*); thus treatment (*trt*), plot type (*type*), sampling date (*doy*) and their two-way and three-way interaction terms (*trt X type, trt X doy, type X doy and trt X type X doy*) were included as fixed effects in the model for fallen litter input rates (Figure 2.6). Fallen litter C and N input rates and fallen litter C:N over time (Figures 2.7a – 2.7c) were compared between invaded and native plots (*type*); thus plot type (*type*), sampling date (*doy*) and their interaction term (*type X doy*) were included as fixed effects in models of fallen litter seasonal C and N input rates and fallen litter C:N over time. *Block* was treated as a random effect in all of the models. Because the same plots were repeatedly sampled, *doy* was also included in the model as a *repeated* statement. Values reported are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effect block. Bold type indicates that values are significant at the $P < 0.05$. Italics indicate nearly significant values for $0.05 < P < 0.10$.

Variable	Fixed Effects							Random Effect σ^2	Repeated Measure σ^2
	TRT	TYPE	TRT X TYPE	DOY	TRT X DOY	TYPE X DOY	TRT X TYPE X DOY	BLOCK	DOY
Litter input rates	**33.71 (1, 20)**	0.06 (1, 20)	0.00 (1, 20)	**11.17 (8, 160)**	**4.86 (8, 160)**	**3.97 (8, 160)**	1.32 (8, 160)	0	0.087
Litter N input rates		*4.73 (1, 10)*		**4.98 (8, 80)**		**3.21 (8, 80)**		0	0.000015
Litter C input rates		2.00 (1, 10)		**7.29 (8, 80)**		**2.89 (8, 80)**		0	0.01584
Litter Quality (C:N) over time		**27.21 (1, 10)**		**2.11 (8, 80)**		1.45 (8, 80)		7.62	128.02

Table 2.8. Results for ordinary least squares (OLS) models comparing seasonal trends in soil carbon and nitrogen pools and net nitrogen cycling rates between invaded and native soils.

Plot type (*type*), sampling date (*date*) and their interaction terms (*type X date*) were included as fixed effects in these models. Block was treated as a random effect in all of the models; *F*-values of differences between plot types were calculated using the mean squares of the *type X block* term from the same model as the denominator. Values are *F*-values (degrees of freedom). Bold type indicates that values are significant at the $P < 0.05$. Italics indicate nearly significant values at the $0.05 < P < 0.10$.

Soil Pools and Processes	TYPE	DATE	BLOCK	TYPE X DATE	TYPE X BLOCK	BLOCK X DATE
Total Organic Carbon (TOC)	0.82 (1, 5)	**82.53 (3, 15)**	1.22 (5, 15)	2.18 (3, 15)	1.65 (5, 15)	1.34 (15, 15)
Total Nitrogen (TN)	*5.59 (1, 5)*	**158.50 (3, 15)**	0.73 (5, 15)	*3.22 (3, 15)*	1.06 (5, 15)	1.06 (15, 15)
Microbial Biomass Carbon (MBC)	0.00 (1, 5)	**9.17 (3, 15)**	2.19 (5, 15)	0.58 (3, 15)	1.34 (5, 15)	2.04 (15, 15)
Microbial Biomass Nitrogen (MBN)	0.50 (1, 5)	**3.93 (3, 15)**	1.12 (5, 15)	1.56 (3, 15)	1.33 (5, 15)	**2.57 (15, 15)**
Root Biomass	1.14 (1, 5)	1.70 (3, 15)	**3.89 (5, 15)**	1.84 (3, 15)	1.22 (5, 15)	1.31 (15, 15)
Root Nitrogen	**9.10 (1, 5)**	**3.86 (3, 15)**	1.77 (5, 15)	**3.50 (3, 15)**	2.17 (5, 15)	**2.80 (15, 15)**
Root Carbon	1.55 (1, 5)	**1.96 (3, 15)**	**3.98 (5, 15)**	2.00 (3, 15)	1.20 (5, 15)	1.34 (15, 15)
Root C:N	**17.09 (1, 5)**	**12.54 (3, 15)**	**3.89 (5, 15)**	**0.15 (3, 15)**	1.47 (5, 15)	0.63 (15, 15)
Plant available inorganic nitrogen (N_{inorg})	**8.13 (1, 5)**	1.33 (3, 15)	1.20 (5, 15)	1.91 (3, 15)	1.27 (5, 15)	1.27 (15, 15)
Ammonium (NH_4^+)	**7.66 (1, 5)**	**11.37 (3, 15)**	**2.91 (5, 15)**	0.66 (3, 15)	0.44 (5, 15)	1.00 (15, 15)
Nitrite + Nitrate ($NO_2^- + NO_3^-$)	**10.13 (1, 5)**	**9.59 (3, 15)**	0.97 (5, 15)	**4.00 (3, 15)**	0.37 (5, 15)	**2.66 (15, 15)**
Potential Net N-Mineralization Rates	1.14 (1, 5)	*4.63 (1, 5)*	**6.67 (5, 5)**	*4.35 (1, 5)*	*3.97 (5 ,5)*	3.04 (5, 5)
Potential Net Nitrification Rates	0.66 (1, 5)	**19.72 (1, 5)**	**5.88 (5, 5)**	1.97 (1, 5)	1.90 (5, 5)	3.25 (5, 5)

Table 2.9. *F*-test results for the non-linear mixed-effects model comparing decay curve fits for mass loss (k) between mixed-native and *B. ischaemum* decomposed litterbags.

Variable	**df**	***F*-value**	***P*-value**
Intercept	1, 131	671.88	< 0.001
Type	1, 131	3.41	0.067

Table 2.10. Results for ordinary least squares (OLS) models comparing changes in litterbag-litter mass and chemistry between mixed-native and *B. ischaemum* litterbags during the in-field decomposition experiment at the WFC.

Models compared mass loss (M_t / M_0), changes in nitrogen content (N_t / N_0), carbon content (C_t / C_0) and carbon:nitrogen ($C:N_t$ / $C:N_0$) between mixed-native and B. ischaemum decomposed litterbags (type) over time (date). Plot type (type), sampling date (date) and their interaction terms (type X date) were included as fixed effects in models. Block was treated as a random effect in all of the models; *F*-values of differences between plot types were calculated using the mean squares of the type X block term from the same model as the denominators. Values are *F*-values (degrees freedom). Bold type indicates that values are significant at the $P < 0.05$. Italics indicate nearly significant values at the $0.5 < P < 0.10$.

Variable	TYPE	DATE	BLOCK	TYPE X DATE	TYPE X BLOCK	BLOCK X DATE
M_t / M_0	0.27 (1, 5)	**40.34 (6, 30)**	*2.26 (5, 30)*	1.42 (6, 30)	0.29 (5, 30)	1.29 (30, 30)
N_t / N_0	**100.02 (1, 5)**	**10.51 (6, 30)**	1.02 (5, 30)	1.80 (6, 30)	0.17 (5, 30)	1.12 (30, 30)
C_t / C_0	**25.22 (1, 5)**	**10.18 (6, 30)**	1.42 (5, 30)	1.71 (6, 30)	*2.29 (5, 30)*	1.15 (30, 30)
$C:N_t$ / $C:N_0$	**201.64 (1, 5)**	**9.63 (6, 30)**	1.08 (5, 30)	0.77 (6, 30)	0.38 (5, 30)	1.11 (30, 30)

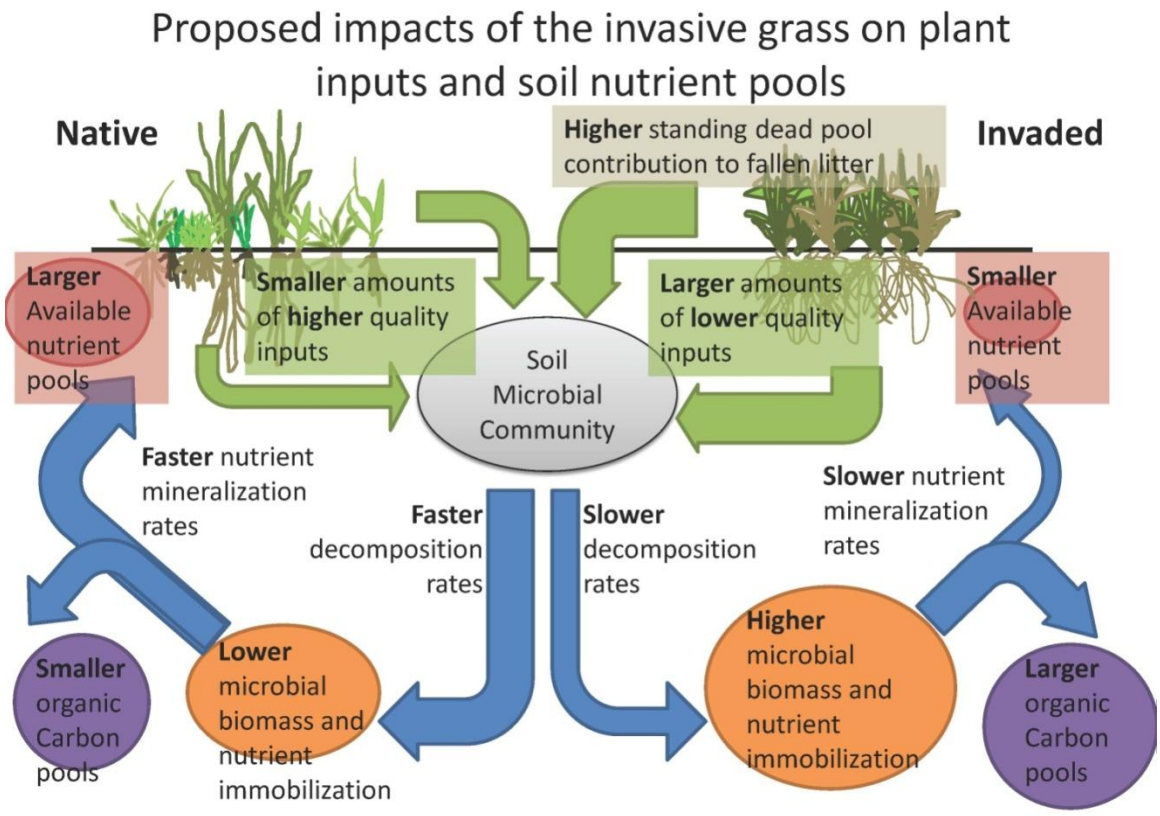

Figure 2.1. Proposed impacts of the invasive grass on plant inputs and soil nutrient pools and processes.

Invasive plants with lower nutrient tissue investment have the potential to decrease ecosystem nutrient cycling by contributing lower quality plant inputs to soil carbon pools (detritus and exudates). Lower quality substrates will alter soil microbial community activity and have the potential to alter soil carbon and nitrogen dynamics by slowing decomposition and mineralization rates. Suppressed nutrient cycling rates have the potential to decrease the size of available nutrient pools and to increase the size of soil organic carbon pools and soil carbon storage.

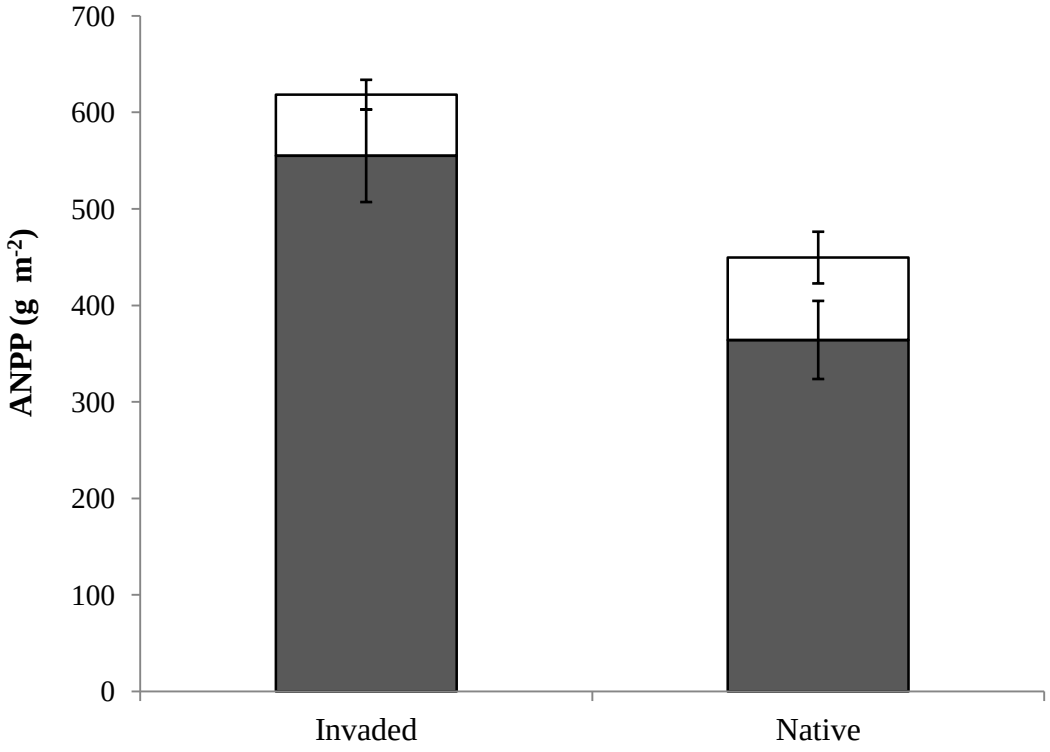

Figure 2.2. Aboveground net primary productivity (ANPP) measured in clipped plots at the WFC.

ANPP was comprised of total harvested biomass (grey portions of bars) plus cumulative fallen litter for the year (white portions of bars) in clipped plots. ANPP (total bar height) was significantly higher in invaded plots than in native plots. Average ANPP was 618 ± 49 g m^{-2} in invaded clipped plots and 450 ± 48 g m^{-2} in native clipped plots. Harvested biomass (height of gray bars) was significantly higher in invaded clipped plots, but cumulative fallen litter inputs (white portions of bars were not. Bar heights are means; error bars are ± 1 SE.

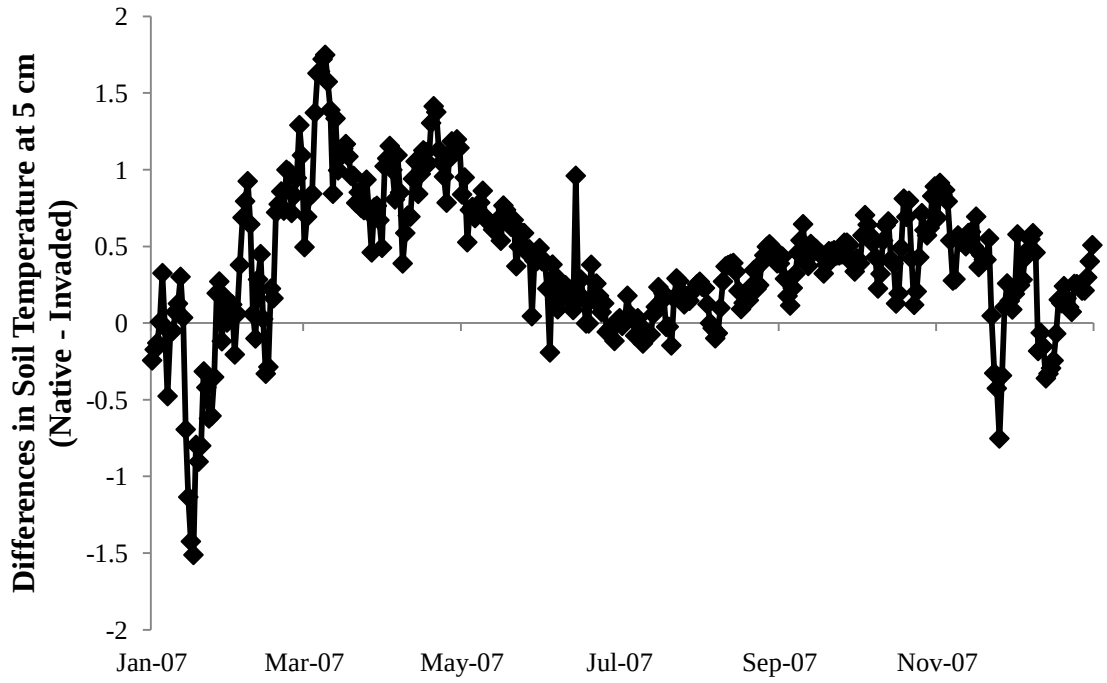

Figure 2.3. Seasonal differences in daily average soil temperature at 5 cm in depth between native and invaded grassland soils at the WFC.

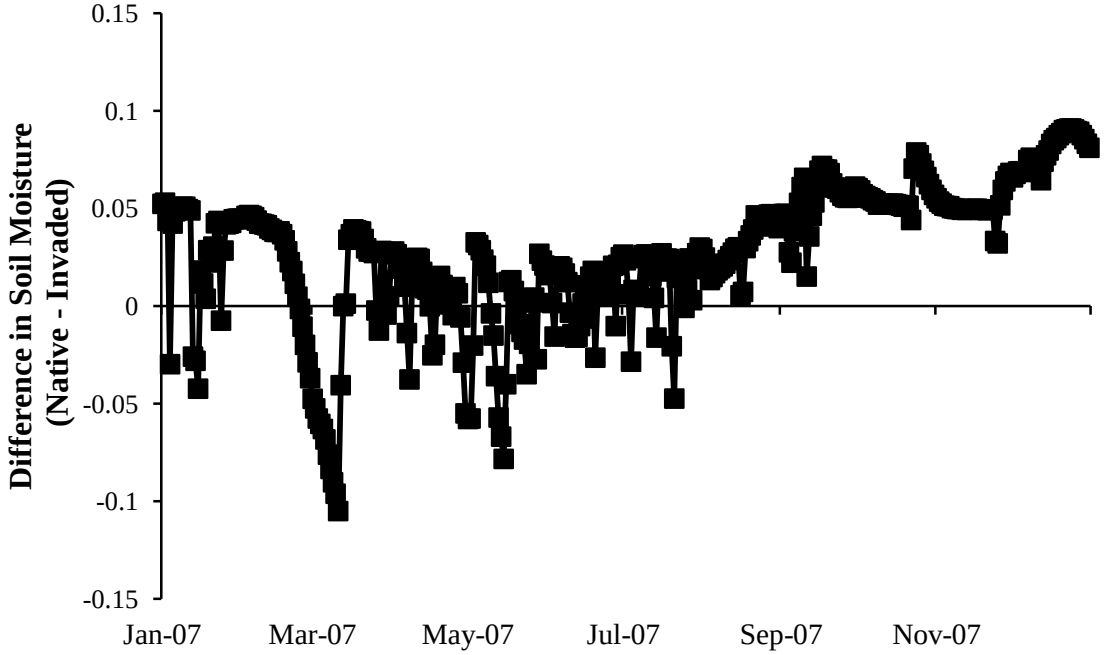

Figure 2.4. Seasonal differences in daily average soil moisture at 5 cm in depth between native and invaded grassland soils at the WFC.

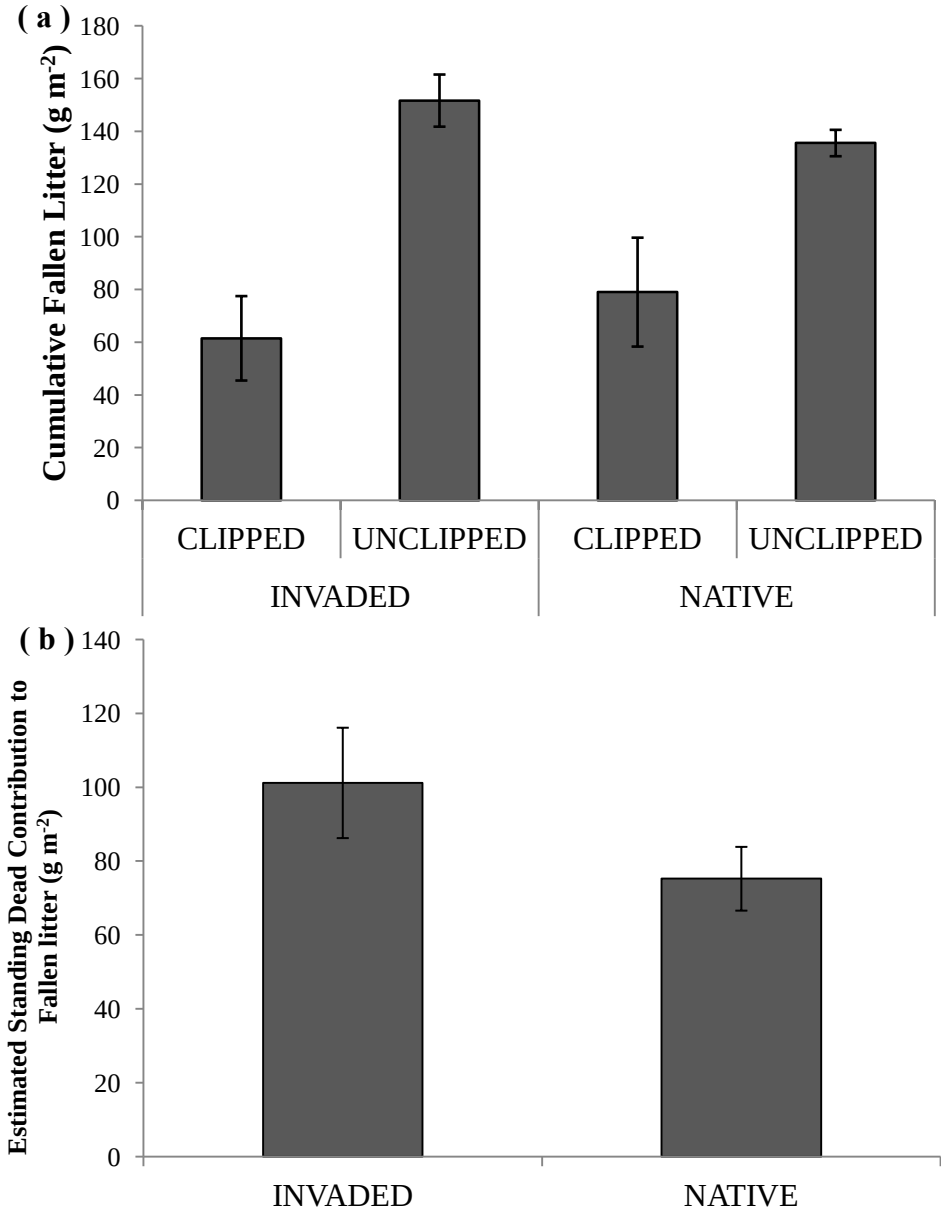

Figure 2.5. Cumulative fallen litter measured at the WFC and estimated standing dead contributions to fallen litter.

(a) Cumulative fallen litter in invaded and native *unclipped* (contained standing dead from previous years) and *clipped* (did not contain standing dead from previous years) plots. *Clipped* plots were harvested before and after litter collection commenced. Therefore, fallen litter collected in *clipped* plots fell from current growth not from previous years' standing dead. *Unclipped* plots are for samples not harvested for biomass and contained standing dead plant material from previous growing seasons. (b) The difference in cumulative fallen litter between *clipped* plots and *unclipped* plots represents the estimated contribution of previous years' standing dead material to fallen litter. Bar values are means ; error bars are ± 1 SE (n = 6).

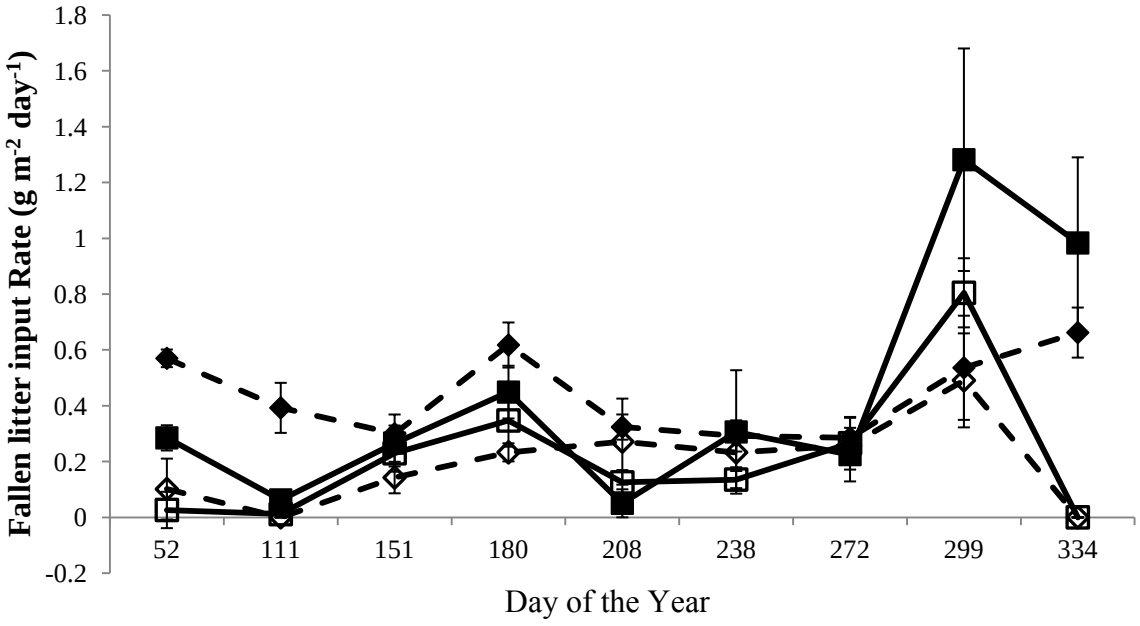

Figure 2.6. Fallen litter input rates measured in invaded and native clipped and unclipped plots at the WFC.

Fallen litter was collected from litter traps in native (solid black squares, solid black line) and invaded (solid black diamond, dashed line) *clipped* plots and litter traps in native (open black square, solid line) and invaded (open black diamond, dashed line) *unclipped* plots. *Clipped* plots, which were harvested for biomass in December 2006 and November 2007, did not contain standing dead plant material from previous years; *unclipped* plots contained standing dead plant material from previous growing seasons. Values are means; error bars are ± 1 SE (n = 6). Litter input rates were significantly higher in unclipped plots than clipped plots but did not differ between invaded and native plots (significant treatment term, *trt*, Table 2.7). There were also significant differences in the timing of litter inputs between unclipped and clipped plots (significant treatment-date term, *trt X doy*) and invaded and native plots (significant type-date term, *type X doy,* Table 2.7).

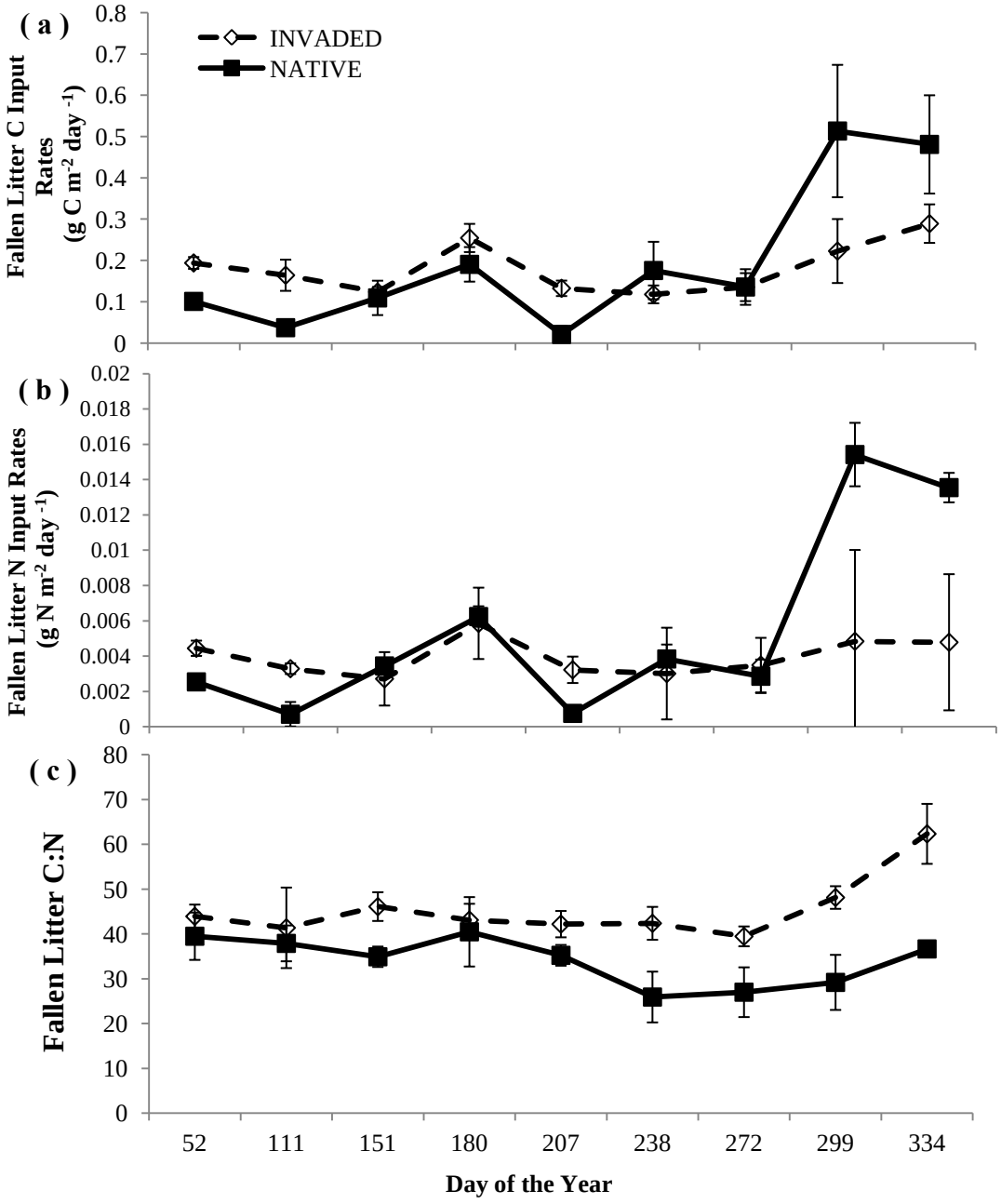

Figure 2.7. Seasonal trends in fallen litter C and N input rates and fallen litter C:N measured in invaded and native unclipped plots at the WFC.

(a) Carbon and (b) nitrogen input rates (g C m^{-2} day^{-1} and g N m^{-2} day^{-1} respectively) and (c) seasonal fallen litter quality (carbon:nitrogen) for fallen litter collected from litter traps in native (solid squares, solid line) and invaded (open diamond, dashed line) unclipped plots at the WFC. Values are means; error bars are ± 1 SE (n = 6). The rates of C and N litter inputs, but not C:N differ significantly among date-type combinations (significant type x doy term; Table 2.7).

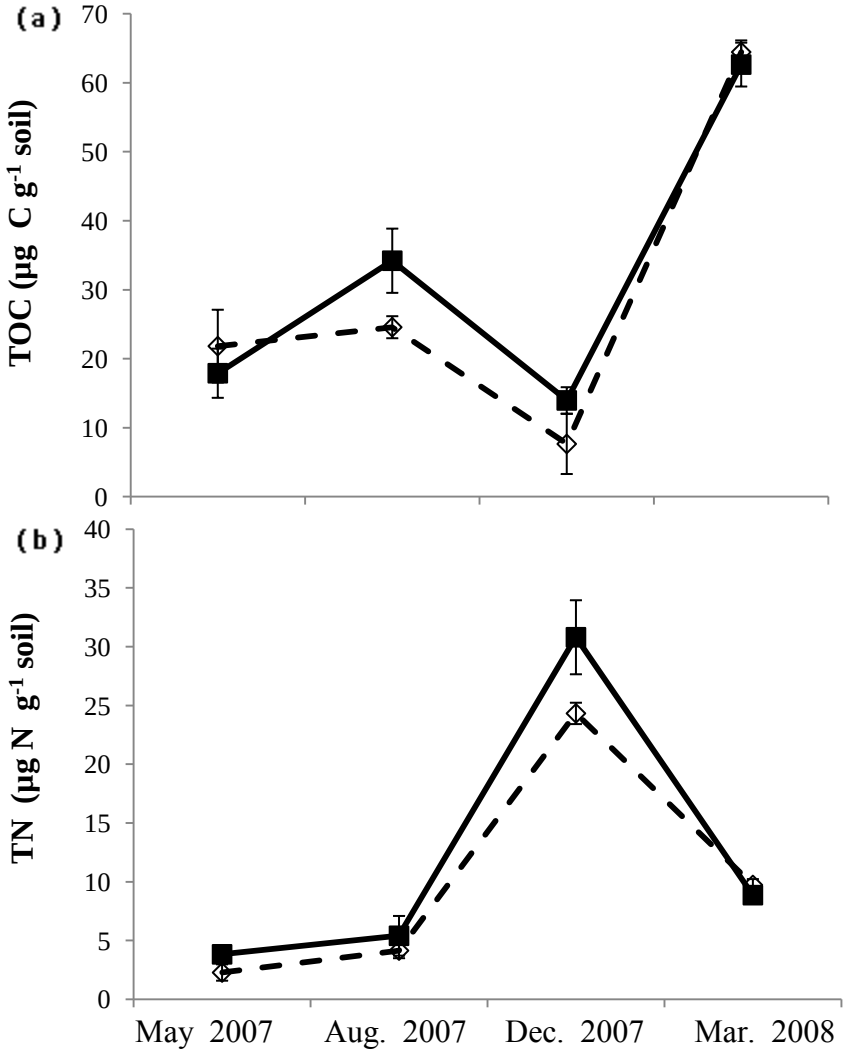

Figure 2.8. Seasonal trends in total organic carbon (TOC) and total nitrogen (TN) measured in soils collected at the WFC.

K_2SO_4 extractable (a) TOC and (b) TN extracted from soils collected in native (solid squares, solid line) and invaded (open diamonds, dashed line) areas from 0 - 10 cm depth at the WFC in the late spring (May 23, 2007), mid-summer (Aug. 24, 2007), late fall /early winter (Dec. 2, 2007) and early spring (Mar. 20, 2008). Error bars are ± 1 SE.

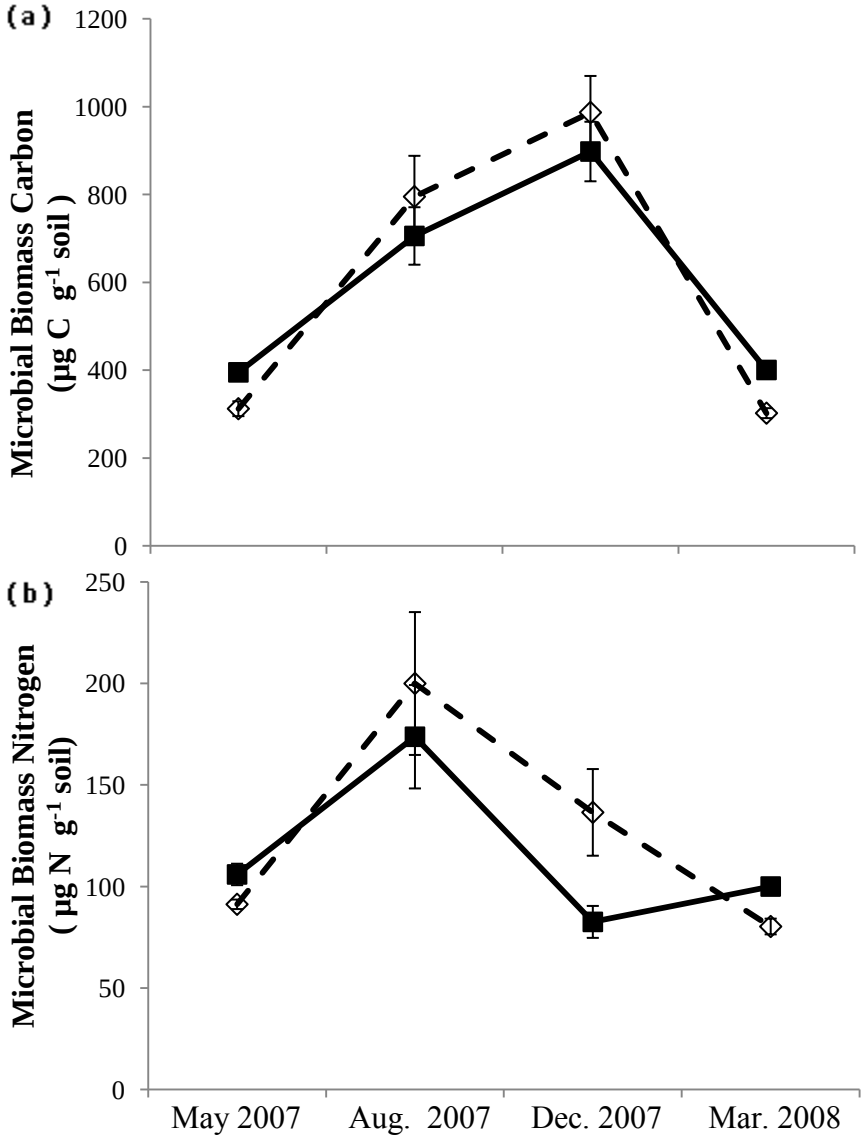

Figure 2.9. Seasonal changes in soil microbial biomass in soils collected at the WFC.

Microbial biomass (a) carbon (MBC) and (b) nitrogen (MBN) measured in native (solid squares, solid line) and invaded (open diamonds, dashed line) soils collected from 0 - 10 cm depth at the WFC in the late spring (May 23, 2007), mid-summer (Aug. 24, 2007), late fall/early winter (Dec. 2, 2007) and early spring (Mar. 20, 2008). Values are means ± 1 SE.

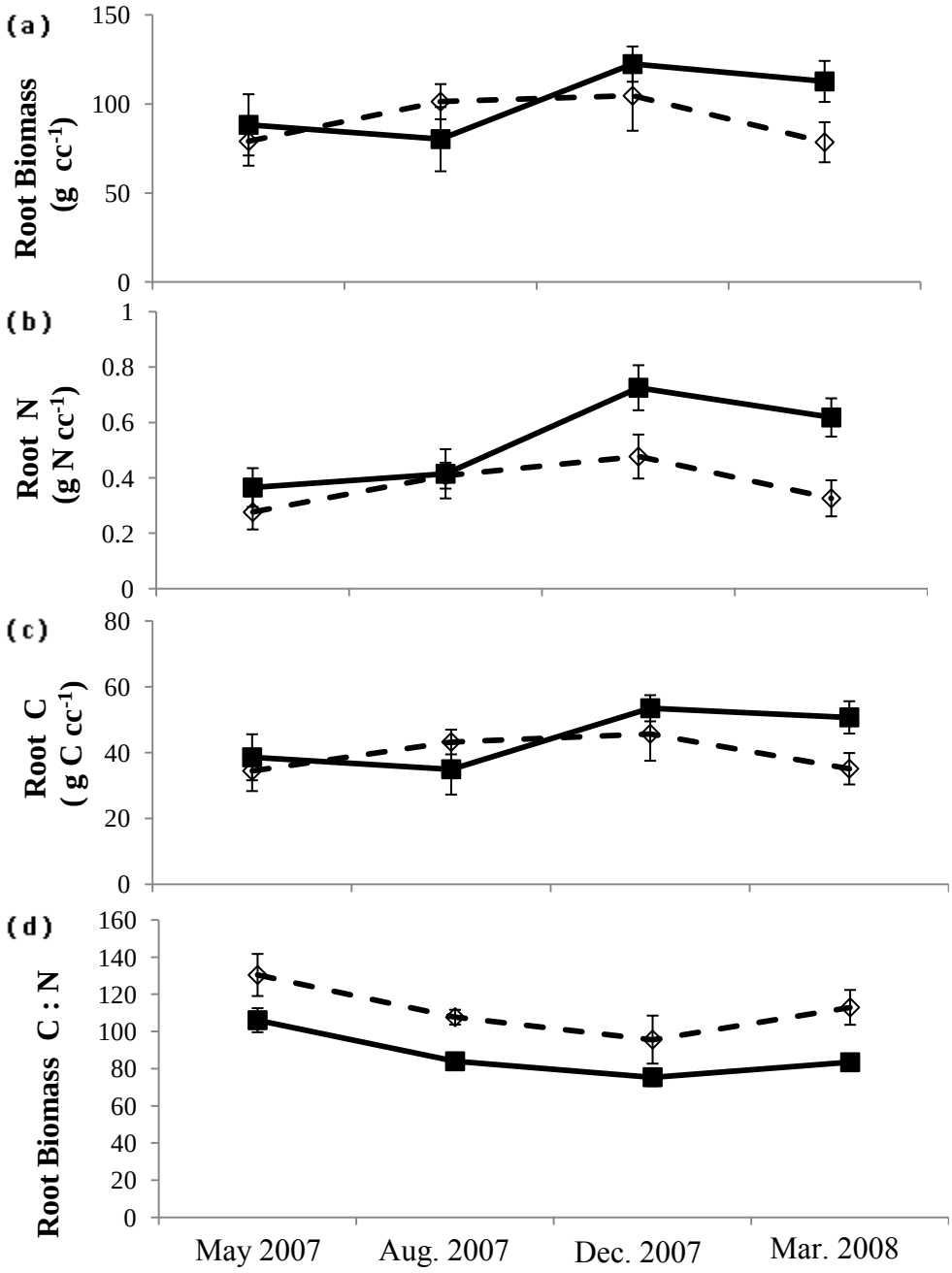

Figure 2.10. Seasonal changes in root biomass and root C and N content in soils collected at the WFC.

Total root biomass (a), root biomass nitrogen (b) and carbon (c) content, and (d) quality (C:N) measured in soils collected from 0 – 10 cm in native (solid squares and lines) and invaded (open diamonds, dashed lines) areas at the WFC in the late spring (May 23, 2007), mid-summer (Aug. 24, 2007), late fall /early winter (Dec. 2, 2007), and early spring (Mar. 20, 2008). Values are means ± 1 SE. Root N and C:N (significant *type* terms) and seasonal trends in root N were (significant type-date term, *typeXdoy*) significantly different between invaded and native soils (Table 2.8).

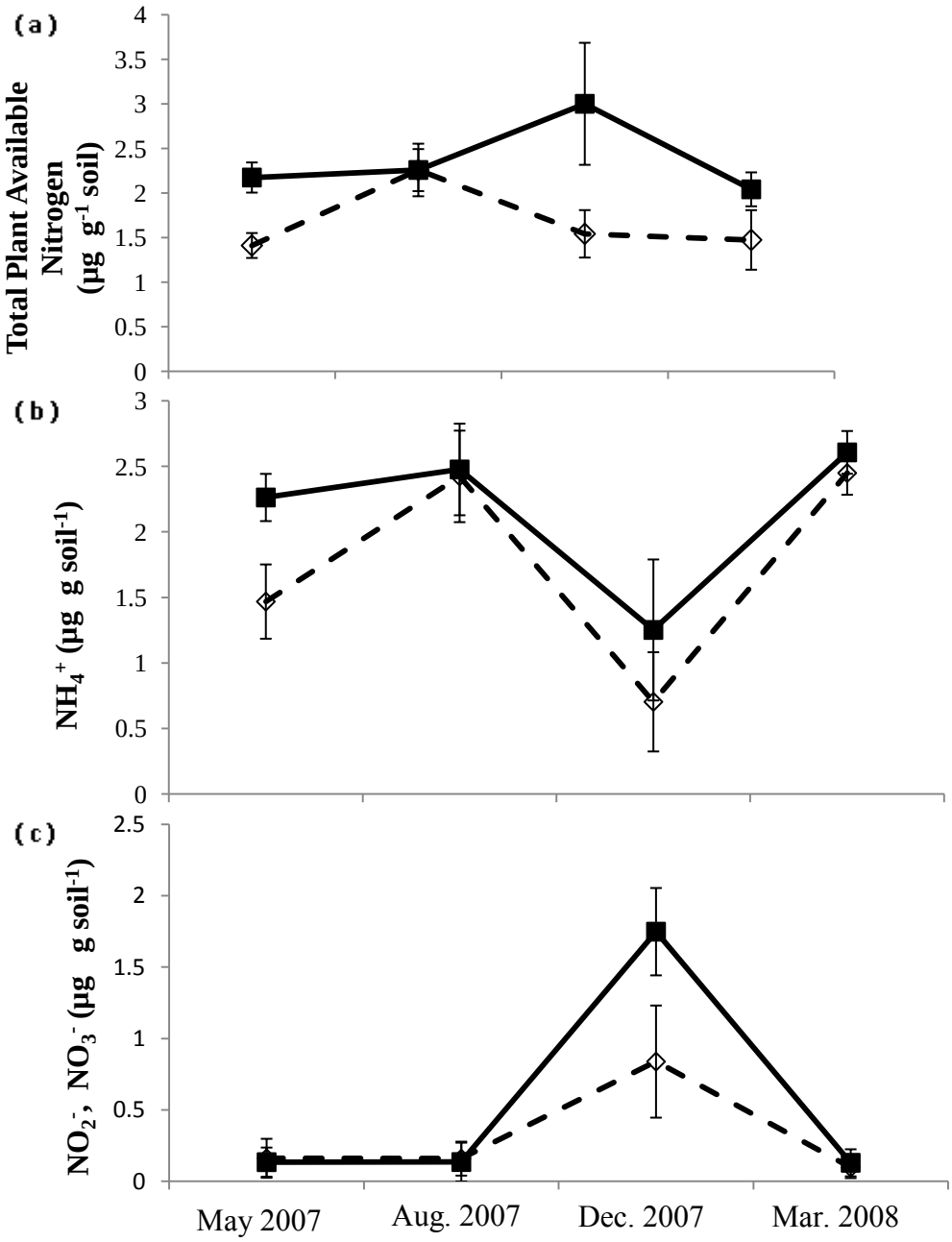

Figure 2.11. Seasonal trends in soil inorganic nitrogen availability at the WFC.

Seasonal changes in KCl-extractable (a) total plant-available inorganic nitrogen (NO_3^-, NO_2^- and NH_4^+), (b) ammonium (NH_4^+) and (c) nitrite + nitrate (NO_2^-, NO_3^-) in native (solid black squares, solid line) and invaded (open black diamonds, dashed line) soils collected from 0 - 10 cm depth at the WFC in the late spring (May 23, 2007), mid-summer (Aug. 24, 2007), late fall /early winter (Dec. 2,2007), and early spring (Mar. 20, 2008). Values are means ± 1 SE. Seasonal differences between invaded and native soils were only significant for [NO_2^-+NO_3^-], significant type-date term in Table 2.8.

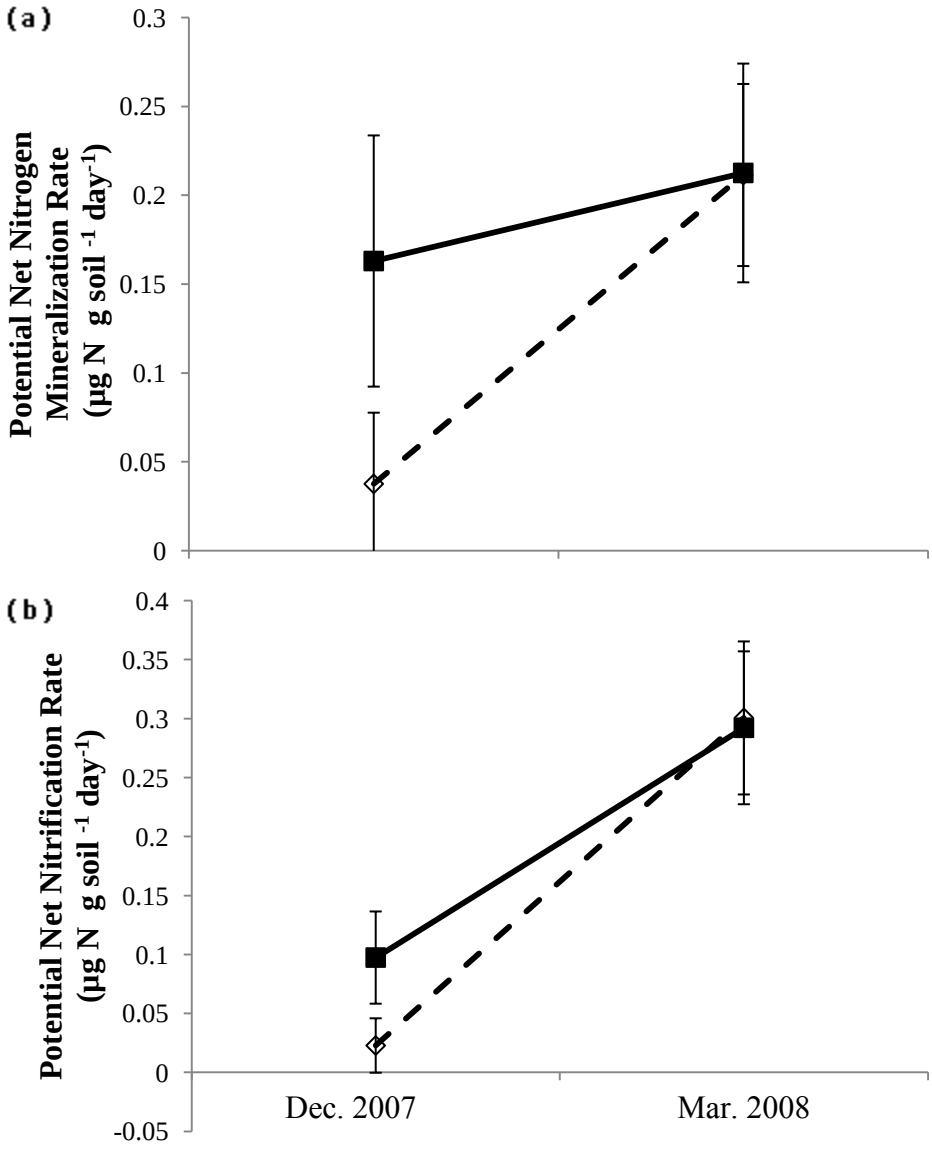

Figure 2.12. Nitrogen transformation rates in incubated soils collected from the WFC.

(a) Potential net nitrogen mineralization and (b) net nitrification rates estimated for soils collected from native (solid squares and lines) and invaded (open diamonds, dashed lines) grassland areas at the WFC from 0 – 10 cm depth in late fall /early winter (Dec. 2, 2007) and early spring (Mar. 20, 2008) and then incubated for 10 days at 23 C. Values are means ± 1 SE.

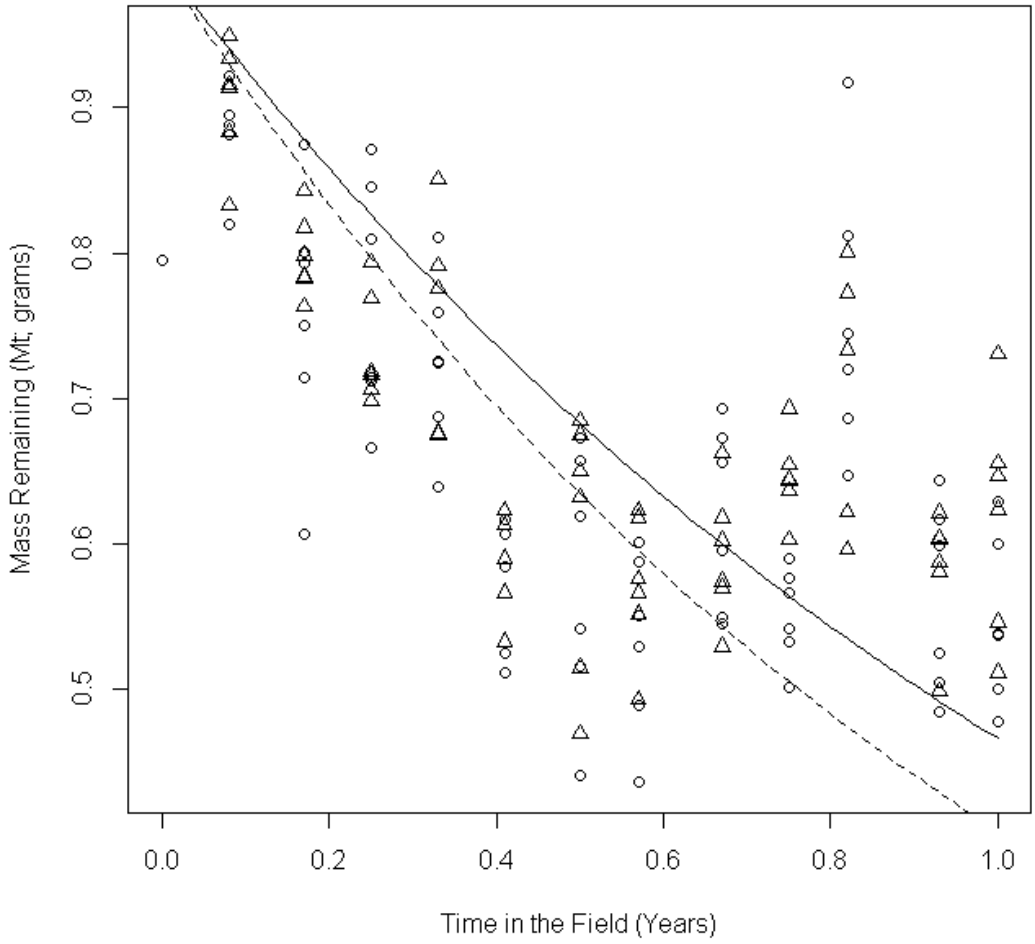

Figure 2.13. Litterbag mass remaining (grams) modeled as a function of time in the field (years).

Circles are values for *B. ischaemum* litterbags decomposed in invaded plots; triangles are values for mixed-native litterbags incubated in native plots at the WFC. Lines are fit to exponential decay curves. Invaded: dashed line, $M_t = M_0e^{-0.81t}$; Native: solid line, $M_t = M_0e^{-0.71t}$. $F_{1,131} = 3.41$, $P = 0.067$.

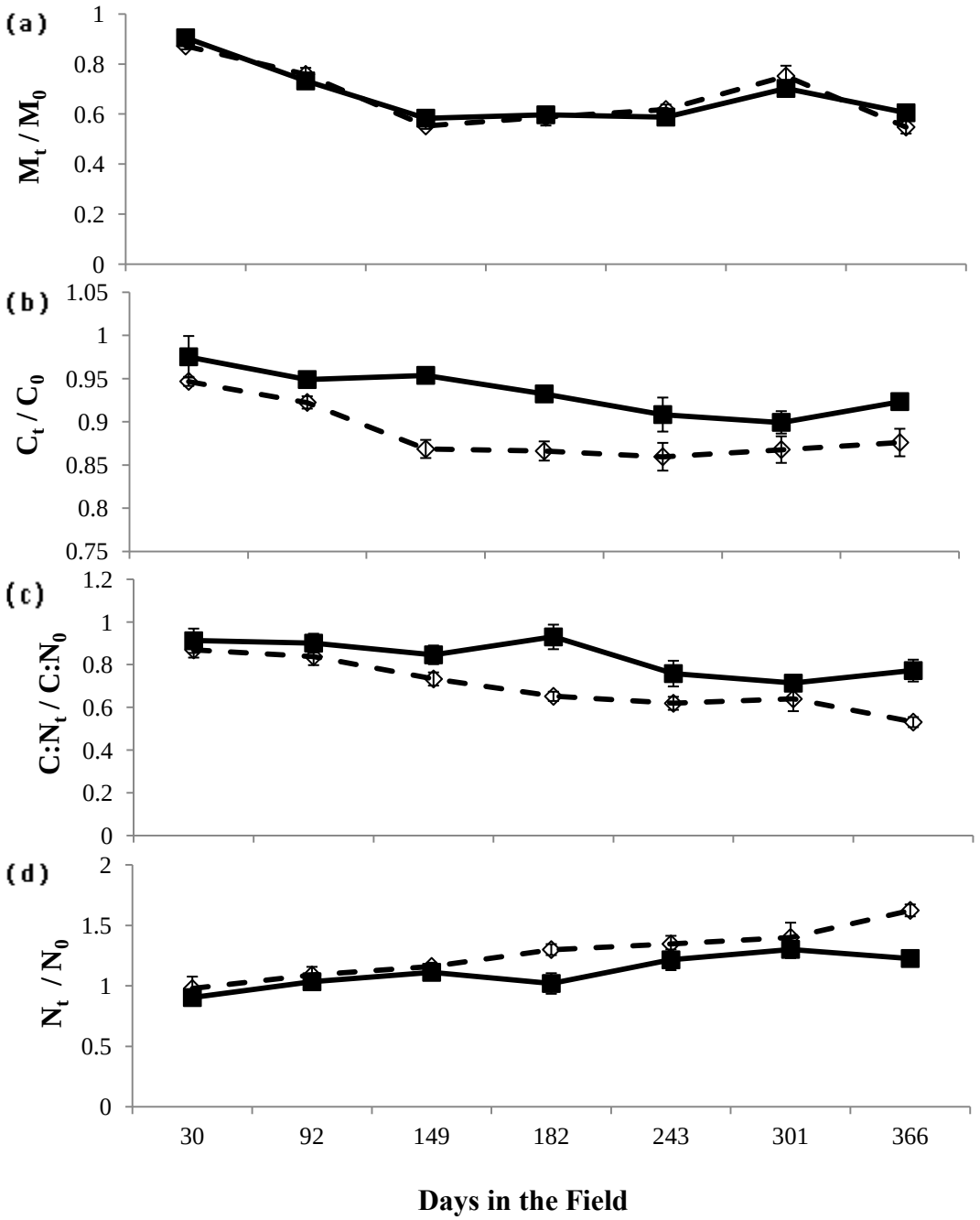

Figure 2.14. Changes in litterbag mass and C and N content during the decomposition experiment.

Changes in mixed-native (solid squares, solid lines) and *B. ischaemum* (open diamonds, dashed lines) decomposed litterbag (a) mass loss, (b) C loss, (c) N retention and (d) change in C:N over the course of the litter decomposition experiment in the field at the WFC. Values are means ± 1 SE of the ratio of litterbag mass, C, N, or C:N at sampling time = t to initial values. NOTE: In figure 2.15b, the x-axis scale starts at 0.75, not at 0.

Chapter 3: Impacts of *B. ischaemum* invasion on Net Ecosystem Carbon Exchange (NEE)

ABSTRACT

The introduction of alien perennial grasses into grassland and savanna ecosystems for forage improvement and soil erosion control is a global phenomenon. A number of these introduced grasses have become invasive in semi-arid and arid ecosystems where subtle differences in phenology and ecophysiology between themselves and the natives species that they displace have the potential to affect ecosystem response to climate variability and net ecosystem carbon exchange (NEE). We investigated the ecosystem-level effects of shifts in dominant plant physiology that result from the invasion of mixed C_3/C_4 savanna grass-matrices by an invasive C_4 perennial grass, *Bothriochloa ischaemum*. We examined whether the decreased ratio of C_3:C_4 grasses in savanna grass-matrix composition that accompanies *B. ischaemum* invasion altered ecosystem carbon uptake and its response to precipitation availability in an invaded ecosystem in central Texas. We compared vegetation characteristics and ecosystem carbon fluxes between native-dominated and *B. ischaemum*-invaded savanna grass-matrix areas during a dry year with a pronounced summer drought and a bimodal growing season and a wet year with a continuous growing season. We found that standing dead cover and green leaf area index were higher and total live vegetation cover, canopy light transmittance, and soil temperatures were lower in *B. ischaemum*-invaded plots than in native-dominated plots. Ecosystem and soil respiration did not differ significantly between invaded and native plots, but net carbon uptake from the atmosphere was higher in invaded plots at higher light levels and under hotter, drier conditions. Although *B. ischaemum* invasion altered the timing and conditions under which C-uptake occurred in this ecosystem, greater C-uptake during the summer and under drier conditions compensated for a shorter growing

season in invaded areas. Cumulative annual NEE was similar in invaded and native areas, in both the dry and the wet years. Overall, *B. ischaemum* impacts on NEE were small at this site, which indicates that this species may not have large effects on C-sequestration in the mixed C_3/C_4 grass systems it invades in this region. We anticipate, however, that *B ischaemum* invasion will positively impact net ecosystem C-uptake as atmospheric [CO_2] increases and climatic conditions change.

INTRODUCTION

Invasive introduced plant species are transforming species composition and thus ecosystem function worldwide (Sharma et al. 2005). While the magnitude and direction of plant invasion impacts vary, plant invasions are generally associated with decreased native species diversity and enhanced primary productivity in invaded ecosystems (Vila et al. 2011), which can have profound implications for a wide array of ecosystem functions (Tilman et al. 1997, Wiliams and Baruch 2000, Mack et al. 2001, Porazinska et al. 2003, Allison and Vitousek 2004, Drenovsky and Batten 2007, Liao et al. 2008, Litton et al. 2008, Urgenson et al. 2009, Ehrenfeld 2010, Wolkovich et al. 2010). Although substantial shifts in dominant plant life form (e.g., the invasion of annuals into perennial ecosystems or shrubs into grasslands) are expected to result in substantial changes in ecosystem function (Gill and Burke 1999, Drenovsky and Batten 2007, Hooker et al. 2008, Mahaney et al. 2008), more subtle changes in plant community composition (e.g., the replacement of native perennial grasses by an invasive one) can have impacts of similar magnitudes (Christian and Wilson 1999, Huxman et al. 2004, Reed et al. 2005, Hamerlynck et al. 2010, 2012a).

In the case of perennial grasses introduced into grasslands and savannas for forage improvement and soil erosion control, species were specifically selected for their ease of establishment, forage quality, grazing and drought tolerance, and high productivity (Donahue 1999). A number of these introduced grasses have become invasive in semi-arid and arid ecosystems where subtle differences in phenology and ecophysiology between themselves and the native grass species that they are displacing have affected ecosystem response to climate variability and net ecosystem carbon exchange (Wiliams and Baruch 2000, Huxman et al. 2004, Hamerlynck et al. 2010, Scott et al. 2010, Hamerlynck et al. 2012a, 2012b). Plant invasions in these ecosystems have been shown to both increase (Hamerlynck et al. 2012a) and decrease (Wolkovich et al. 2010) inter-annual variability in net ecosystem carbon exchange in response to variable precipitation. Given that many arid and semi-arid ecosystems are predicted to experience increased variability in precipitation with less frequent, more intense precipitation events as a result of global climate change (Easterling et al. 2000; Diffenbaugh et al. 2005; Leung and Gustafson 2005), understanding what role climate variability plays in invasive species' impacts on ecosystem function is vital (Dukes and Mooney 1999).

Net ecosystem carbon exchange (NEE) refers to the movement of carbon in the form of CO_2 between the land surface and the atmosphere. NEE is defined as the difference between the total carbon coming into the ecosystem through photosynthesis, i.e., gross ecosystem productivity (GEP), and the total carbon lost to the atmosphere through ecosystem respiration (R_{eco}) over a given period of time. R_{eco} is the sum of carbon losses due to both autotrophic (R_A) and heterotrophic (R_H) respiration. The rate at which carbon accumulates or is sequestered in an ecosystem, i.e., net ecosystem production (NEP), is determined by the ratio of total inputs (photosynthesis) to total outputs (R_{eco} plus losses of carbon due to soil leaching, volatilization, etc.) over a given

period of time. Changes in species composition associated with the invasion of introduced perennial grasses into grassland and savanna ecosystems have the potential to alter the timing, magnitude, and direction of net ecosystem carbon exchange in invaded ecosystems, and thus net ecosystem production. This is particularly likely when the plant invasion results in changes in the ratio of C_3 to C_4 plant species within the ecosystem. Large functional differences between C_3 and C_4 physiologies (Tilman and Wedin 1991, Knapp and Medina 1999, Craine et al. 2002, Dijkstra et al. 2006, Taylor et al. 2012) mean that shifts in the ratio of C_3 : C_4 physiologies in an ecosystem can greatly affect ecosystem function (Mahaney et al. 2008, Cahill et al. 2009). Also, while C_4 grasses are commonly grouped into a single functional group, there are significant ecophysiological differences among C_4 sub-types and taxa (Ghannoum et al. 2001, 2002, 2005, Taylor et al. 2012) that can also result in changes in ecosystem function when an introduced C_4 perennial grass displaces native C_4 grasses in an ecosystem (Huxman et al. 2004, Reed et al. 2005, Potts et al. 2006a, 2006b, Hamerlynck et al. 2010, 2012a).

Bothriochloa ischaemum var. songarica, King Ranch Bluestem, is a C_4 perennial grass native to Eurasia where it is a climax species in arid and semi-arid environments (Akhani and Zeigler 2002, Wang 2003). In the 1930's, *B. ischaemum* was introduced in the United States for pasture improvement and soil stabilization (Gabbard and Fowler 2007) and has since invaded a diverse array of habitat types throughout Texas and Oklahoma (Diggs et al. 1999, Turner et al. 2003, Gabbard and Fowler 2007). *B. ischaemum* invasion in central Texas is associated with an average 65 ± 13% decrease in the ratio of C_3 to C_4 grass aboveground biomass (g m^{-2}) and significant decreases in both short and mid-height native C_4 grass biomass in invaded areas (Basham and Poteet *unpublished data*). When *B. ischaemum* invades central Texas ecosystems, it replaces both native C_3 and C_4 grasses and converts C_3/C_4 mixed grasslands and savanna grass-

matrices into dense, C_4-dominated *B. ischaemum* near-monocultures, and thus has the potential to significantly alter ecosystem function.

B. ischaemum is physiologically similar to many of the native C_4 grasses it displaces in central Texas ecosystems, except that it produces significantly more biomass, has greater leaf area per plant, and is more sensitive to decreased water availability (Chapter 1). Furthermore, *B. ischaemum* has higher photosynthetic rates under warm, wet conditions and a shorter growing season than the native C_3 grasses it replaces in these ecosystems (Chapter 1). We suggest that these ecophysiological and phenological differences between the invading *B. ischaemum* and the native species it displaces have the potential to alter net ecosystem carbon sequestration in these mixed C_3/C_4 savanna grass-matrices by altering both the total carbon uptake through photosynthesis and carbon lost through respiration and the sensitivity of these processes to changes in climate.

Based on our previous results (Chapter 1, Chapter 2) we specifically hypothesize that *B. ischaemum* invasion would alter net ecosystem exchange relative to the mixed C_3/C_4 savannas it replaces in the following ways (Figure 3.1):

(1) change the seasonal dynamics of net ecosystem exchange largely due to a change in the sensitivity of CO_2 uptake to temperature and soil moisture. The resulting monoculture of a C_4 grass should have a more limited growing season concentrated in the summer months, compared to the mixed C_3/C_4 savannas it replaces. We also predicted *B. ischaemum* invasion would decrease the sensitivity of net ecosystem carbon uptake to higher temperatures, because it is in part replacing less heat-tolerant C_3 species (the grass *Nassella leucotricha* and various forbs; Chapter 1). However *B. ischaemum* invasion should also increase the sensitivity of ecosystem C-uptake to water availability, because it is in part replacing more drought-tolerant C_4 grass species, e.g., *B. laguroides* and *Schizachyrium scoparium* (Chapter 1).

(2) reduce overall net carbon uptake through photosynthesis in these ecosystems. Although *B. ischaemum* has higher leaf area per plant than many native species and leaf-level photosynthesis is generally similar between *B. ischaemum* and native species (Chapter 1), invaded areas typically have a more shaded plant canopy and standing dead cover (Chapter 2), which can negatively impact net carbon uptake.

(3) increase ecosystem respiration. Ecosystem respiration (R_{eco}) should be higher in *B. ischaemum*-invaded areas because higher aboveground plant biomass (Chapter 2) would result in higher aboveground autotrophic respiration (R_A). Although a more shaded plant canopy should decrease soil temperature and increase soil moisture in invaded areas, we expect soil respiration (R_{soil}) (i.e., belowground heterotrophic [R_H] plus autotrophic [R_A; root] respiration) to be similar between invaded and native areas because belowground root and microbial biomass do not differ significantly between invaded and native soils in this ecosystem (Chapter 2).

(4) decrease ecosystem carbon sequestration (NEP) in the current climate due to decreased carbon coming in through photosynthesis and higher carbon lost through respiration.

In the present study, we tested these hypotheses by comparing vegetation characteristics and ecosystem carbon fluxes (NEE, R_{eco}, R_{soil}, and GEP) between native-dominated and *B. ischaemum*-invaded savanna grass-matrix areas during a year with a pronounced summer drought and a bimodal growing season (2006) and a wet year with a continuous growing season (2007).We use our results to discuss the future impacts of this invasive species on ecosystem carbon exchange under the influences of climate change.

METHODS

Site description

Our research was conducted within the 279 acre Landscape Restoration Research Area at the Lady Bird Johnson Wildflower Center (WFC), a research unit of the University of Texas at Austin, Austin, Texas (N30 11'3",W97 52'27", 800' elevation). This property was managed for cattle production prior to its acquisition by the WFC in 1999. WFC is located in the central Texas *Quercus fusiformis* - *Juniperus ashei* savanna in the Texas Hill Country on the eastern edge of the Edwards Plateau. The grass matrix of the savanna at this site is characterized by C_4 grasses, including *Bothriochloa laguroides* subsp. *torreyana, Bothriochloa ischaemum* and *Hilaria belangeri,* C_3 grasses, including *Nassella leucotricha,* and over 200 species of forbs. The introduced grass, *B. ischaemum,* is rapidly becoming the dominant species in the WFC site where we worked, which is typical of its behavior in grassland and savanna systems throughout the region (Gabbard and Fowler 2007).

Soils at this site are limestone-derived thermic Lithic Argiustolls of the Speck Series, which range from nearly level stony clay loams to gravelly clays, 30 - 50 cm in depth (Soil Survey Staff, NRCS, USDA 2009). Rainfall and temperatures in the Austin area are highly variable, with a mean annual precipitation of 840 (± 250 sd) mm. The growing season in this area is often bimodal with a decline in activity during the hottest part of the summer for all plants (July-September) and, primarily for C_4 species during the winter (January-February). However, the seasonality of plant activity is highly variable and primarily dependent on water availability. Annual rainfall and temperatures differed greatly between the two years of our study (Figure 3.2). In 2006, cumulative annual rainfall was 860 mm, the majority of which (82 %) fell before the end of June. Temperatures were high and highly variable in 2006. As a result, 2006 had distinct wet

and dry seasons and a bimodal growing season in which the majority of plant activity occurred March to June and October to December. In 2007, cumulative rainfall was 1192 mm and fell at regular intervals throughout the spring and into the early fall with relatively little rainfall after October. Temperatures were also more moderate and less variable in 2007. As a result, 2007 had a continuous growing season that did not end until the fall brought cooler weather. These two years represent a "dry year" (2006) and a "wet year" (2007) but neither would be considered extreme with regards to amount or distribution of precipitation for this environment (Figure 3.3).

Sampling design

The Research Area of the WFC, located in open *Quercus-Juniperus* savanna, is divided into 50 blocks, each approximately 0.75 ha in size, that were randomly assigned to burning, mowing and control treatments in 2001. Our work was conducted in six of the control blocks 0.18 - 0.85 km apart. We used a replicated block design to test whether vegetation characteristics (aerial cover, leaf area index), canopy microclimate (canopy light transmittance, soil temperature and moisture), and carbon fluxes (net ecosystem exchange, ecosystem respiration, soil respiration) of the savanna grass-matrix were similar between *B. ischaemum*-invaded and native-dominated areas. Within each block, we established two 0.64 m^2 (0.9 m in diameter) round plots in native-dominated areas ("native" plots) and two 0.64 m^2 (0.9 m in diameter) round plots in *B. ischaemum*-invaded areas ("invaded" plots). We randomly located native plots in native-dominated areas within blocks using a gridded system. We randomly located invaded plots in previously delineated *B. ischaemum* monocultures within each block. Plots were all located in open areas at least 5 m from any tree canopy.

Custom-constructed aluminum bases measuring 91 cm in diameter and 10 cm in depth and beveled on one side were installed in each plot (two native and two invaded plots) in each of the six blocks (for a total of 12 invaded and 12 native plots across the 6 blocks). The bases were hammered into the soil to a depth of 5 cm. One soil collar, a 5 cm section of 3" (7.62 cm) inner diameter Schedule 40 polyvinyl chloride (PVC) pipe beveled from the outer to the inner edge on one end, was installed in the ground to a depth of 4.5 cm in un-vegetated soil within each plot (inside the area enclosed by the aluminum base). Bases and collars were installed in plots in July 2005, 6 months before measurements commenced. The week prior to each round of measurements, base and collar stability in the ground were checked and loose bases or collars were reinstalled to prevent leaks and reduce measurement error.

Plots were sampled for C fluxes (net ecosystem exchange [NEE] and soil respiration [R_{soil}]), vegetation cover, leaf area index (LAI), and soil moisture and temperature nine times in both 2006 (February 3 - 4, March 25, April 11 - 12, June 18 - 19, July 12, 24, September 15 - 16, October 12 - 13, and December 2) and 2007 (January 8, April 26, May 17, June 12, July 13, August 9 - 10, September 15, October 12 - 13, and November 16). Due to instrument failure, R_{soil} was not measured in January, 2007. Canopy light transmittance in plots was measured five times in 2006 and four times in 2007. Measurements were made in only five of the six blocks in 2006 (a total of 20 plots) but in all six blocks (a total of 24 plots) in 2007. Diurnal changes in C-fluxes (NEE and R_{soil}) were measured in one block (a total four plots) on June 23, 2006, and two blocks (for a total of 8 plots) on July 16, and October 1, 2006. In 2007, day-time ecosystem respiration (R_{eco}) was measured in one native and one invaded plot in each of the six blocks during six of the nine sampling periods. Soil moisture and temperature and photosynthetically active radiation (PAR) data were collected concurrently with C-flux

measurements. During each sampling period (approximately monthly), we collected C-flux measurements from all sampled blocks in 1 - 2 days. Vegetation cover, LAI, and canopy light transmittance data were collected within a week of C-flux measurements. We provided a list of variables measured in this study and the tables and figures in which they are reported in Table 3.1.

Vegetation assessment

During our study, we assessed seasonal changes in plant canopy composition and structure by recording relative percent cover and ceptometer-measured leaf area index (LAI_{cept}; m^2 leaf surface area / m^2 ground surface area). We estimated relative percent cover following Daubenmire (1959). The relative aerial percent cover of each grass species separately, of forbs as a functional group, of standing dead plant material and of bare ground were estimated in each plot. The number of tillers of each grass species and the number of stems of each forb species were recorded. LAI_{cept} and light transmittance (i.e., the ratio of below-canopy photosynthetically active radiation [PAR] to above-canopy PAR) in each plot were measured at the top of aluminum bases 5 cm above ground-level using an ACCUPAR LP-80 ceptometer (Decagon Devices, Pullman, WA).

We corrected LAI_{cept} for the presence of standing dead material in plots by estimating live leaf area within plots from field-collected samples of grass tillers and dominant forbs combined with our stem and tiller counts. Three living (green) tillers of each grass species found in plots (9 species) and three living (green) stems of the three seasonally dominant forb species were collected from outside of plots in each block approximately every four months during the study for scanning. After separating leaves from stems, leaves were scanned at 800 dpi using a desktop scanner (HP Deskjet F300 All-in-One Series, Hewlett Packard) and the resulting leaf images were analyzed using

ImageJ (Wayne Rasband, Research Services Branch, NIH, Bethesda, MD, USA) to measure leaf surface area. For grasses, leaf blades were separated from leaf sheathes and leaf sheathes were included as stem biomass because preliminary measurements indicated that photosynthetic rates were more similar between grass sheaths and stems than they were between grass leaf blades and sheathes. Scanned leaf area index (LAI_{scan}) was estimated for each plot by multiplying leaf surface area by the appropriate grass tiller count or forb stem count. Leaf area per stem for un-sampled forb species was assumed to be the average of that for all sampled forb species. Linear regression between ceptometer-measured (LAI_{cept}) and scanned LAI (LAI_{scan}) estimates was used to develop a correction factor for LAI_{cept} to account for standing dead biomass in plots. The relationship between LAI values derived using the two methods differed significantly between native and invaded plots in 2006, but not in 2007, so we used separate regression equations to correct LAI_{cept} from native and invaded plots in 2006, but one equation to correct measurements from 2007 (equations Native 2006: $LAI_{corr} = (LAI_{cept} - 0.96)/ 0.77$; $R_2 = 0.63$, $F_{1,107} = 215.99$, $P < 0.0001$; Invaded 2006: $LAI_{corr} = (LAI_{cept} – 1.29)/ 0.83$; $R_2 = 0.64$, $F_{1,215} = 221.05$, $P < 0.0001$; Native 2007: $LAI_{corr} = (LAI_{cept} - 0.96)/ 0.77$; $R_2 = 0.63$, $F_{1,209} = 215.99$, $P < 0.0001$; Invaded 2007: $LAI_{corr} = (LAI_{cept} – 0.1)/ 1.23$; $R_2 = 0.98$, $F_{1,209} = 4967$, $P < 0.0001$). All leaf area index values reported in the results are corrected for standing dead biomass, LAI_{corr}.

Carbon flux estimates

The term carbon flux refers to the movement of carbon, primarily in the form of CO_2 or organic carbon, from one pool, e.g., plants, soil, or soil microbial community, to another within an ecosystem, between ecosystems, or into the atmosphere. By convention, ecosystem removal of CO_2 from the atmosphere is negative and ecosystem

output of CO_2 to the atmosphere is positive. Therefore when net ecosystem carbon exchange (NEE) is negative, gross ecosystem productivity (GEP) is greater than ecosystem respiration (R_{eco}) and vice versa when NEE is positive. When cumulative daily NEE is negative (GEP > R_{eco}), the ecosystem is described as being a carbon "sink". When cumulative daily NEE is positive (GEP < R_{eco}), the ecosystem is described as being a carbon "source".

We measured ecosystem-level or canopy-level CO_2 fluxes (NEE and R_{eco}; µmols CO_2 m^{-2} s^{-1}) using a custom-made cylindrical canopy chamber that was 90 cm in diameter by 1 m tall and was covered in tightly sewn clear polyethylene greenhouse film. Rubber weather-stripping at the bottom of the chamber ensured a tight seal between the chamber bottom and the aluminum bases. The canopy chamber was plumbed to a portable closed-system infrared gas analyzer (LI-6400, LI-COR, Lincoln, Nebraska, USA) using the single outlet manifold accessory for the lower leaf chamber manifold of the sensor head (part # 9964-053, LI-COR, Lincoln, Nebraska, USA). Air was pumped from the chamber at a flow rate of 500 mmol m^{-2} s^{-1} into an external buffer volume and then into the Li-6400 sensor head before being returned to the chamber using an external electric pump powered by a 12 V battery. The 12 V battery, pump, LI-6400 sensor head, buffer volume, and electrical connector strips for system wiring were mounted in a carrying box to protect equipment and make the system portable. Four fans inside the chamber ensured thorough mixing of air within the chamber. A quantum flux sensor (LI-190SA quantum sensor, LI-COR, Lincoln, Nebraska, USA) mounted 2 cm below the top of the chamber measured PAR levels within the chamber. Relative humidity (RH; %) and temperature (T_{air}; °C) within the chamber were monitored using a Humitter 50Y integrated relative humidity and temperature sensor (Vaisala, Woburn, MA, USA) suspended from the top center within the chamber. Chamber-mounted sensors were connected to the LI-6400 via

the auxiliary port which allowed conditions within the chamber to be easily logged during flux measurements.

Ecosystem C fluxes were estimated using changes in CO_2 and H_2O concentration within the chamber over a two-minute-long interval and closed-system flux software for the LI-6400 (LI-COR, Lincoln, Nebraska, USA). Software estimates of fluxes were quality-checked by hand and recalculated using equations provided in the Closed-System Flux Software Manual (issue date 28 April 2004, LI-COR, Lincoln, Nebraska, USA). This allowed us to discard measurements with insufficient or unstable light conditions, potential leaks or when chamber CO_2, temperature, or humidity diverged from ambient levels enough to impact the rate of CO_2 fluxes. The numbers of discarded measurements are reported in table 3.1.

Light-saturated net ecosystem exchange (NEE_{LS}; µmols CO_2 m^{-2} s^{-1}) measurements were made at ambient light levels when PAR ≥ 900 µmols photon m^{-2} s^{-1} between 10:00 and 16:00 during the day by fitting the chamber to the base and monitoring the change in [CO_2] within the chamber for two minutes. Between measurements, the canopy chamber was covered using a tightly fitting, reflective, and insulted cover and vented to ambient air until chamber CO_2, temperature, and relative humidity stabilized.

In 2006, in addition to light-saturated NEE, we conducted measurements of diurnal changes in NEE on three dates: June 23, July 16, and October 1. On June 23, 2006, we measured NEE six times, 05:00 – 06:00, 08:00 – 09:00, 10:00 – 11:00, 13:00 – 14:00, 15:00 – 16:00, and 17:00 – 18:00, on two invaded and two native plots in one block. On July 16 and October 1, we measured NEE and R_{soil} three (0:00 - 2:00, 11:00 - 13:00 and 15:00 - 17:00) and four (0:00 - 02:00, 10:00 - 12:00, 13:00 - 15:00, and 16:00 - 18:00) times respectively on two invaded and two native plots in two blocks, the same

block measured on June 23, plus the one nearest it. Diurnal NEE measurements were combined with light-saturated NEE (NEE_{LS}) and non-light-saturated NEE measurements from the other nine sampling periods to develop the multiple regression model used to estimate daily and annual NEE for 2006 (see below). Non-light saturated NEE measurements were measurements from the other nine sampling periods that met stability criteria for chamber CO_2, temperature, and relative humidity, but during which PAR < 900 µmols photon m^{-2} s^{-1} and therefore did not meet criteria for light saturation.

We did not use night-time dark NEE measurements made in 2006 to partition day-time NEE into ecosystem respiration (R_{eco}) and gross ecosystem productivity (GEP) because this method has been found to over-estimate day-time R_{eco} (Reichstein et al. 2005). Therefore instead of conducting diurnal measurements in 2007, we measured day-time R_{eco} immediately after measuring NEE_{LS} on one invaded and one native plot in each of the six blocks during six of the nine sampling periods. After measuring NEE_{LS} at ambient light levels the chamber was removed from the base, covered, and vented with ambient air. The covered chamber was then replaced on the base and allowed to shade the plot for approximately two minutes before day-time R_{eco} was measured. We used these paired NEE_{LS} and R_{eco} measurements to estimate GEP for these six sampling periods using the equation GEP = -1 * (NEE - R_{eco}). R_{eco} measurements were also combined with light-saturated NEE (NEE_{LS}) and non-light-saturated NEE measurements from the nine sampling periods to develop the multiple regression model used to estimate daily and annual NEE for 2007 (see below).

Concurrent with canopy-level C-flux measurements, soil respiration (R_{soil}; µmols CO_2 m^{-2} s^{-1}) was measured using a soil CO_2 flux chamber (Li6400-09, LI-COR, Lincoln, Nebraska, USA) connected to a portable infrared gas analyzer (LI-6200, LI-COR, Lincoln, Nebraska, USA) per Norman *et al.*(2003). Soil respiration (R_{soil}) is CO_2 gas

exchange at the soil surface including heterotrophic respiration (R_H) from soil communities and autotrophic respiration from plant roots (R_A). Ambient CO_2 levels were measured at the soil surface by resting the chamber bottom open at the edge of the soil collar for several minutes. The soil chamber was then placed on the soil collar and CO_2 was filtered from air inside the chamber until CO_2 within the chamber was 20 - 30 ppm below ambient. Soil CO_2 flux was measured as CO_2 concentrations within the chamber returned to ambient levels.

Monitoring environmental drivers

We recorded environmental conditions during our study using a combination of hand-collected point measurements and sensor-collected continuous measurements. Soil moisture, soil and air temperature and PAR were measured concurrently with C-flux measurements. Soil moisture was measured in a 0 - 10 cm soil core collected adjacent to each plot in a pre-weighed metal container. The container and soil samples were immediately weighed and dried for three days at 70 C and weighed again to determine the gravimetric soil moisture content (g water g^{-1} soil) of the soil samples. Gravimetric soil moisture was converted to volumetric soil moisture (θ) using previously determined soil bulk density for each site. Ambient air temperature (T_{air}; °C) and soil temperatures at 2 ($T_{soil\ 2;}$ °C) and 5 ($T_{soil\ 5}$; °C) cm from the soil surface were measured using type K thermocouple probes and a hand held dual input, high accuracy datalogger/thermometer (HH506A, Omega Engineering, Inc., Stamford, Connecticut, USA). Above canopy PAR (µmols photons m^{-2} s^{-1}) was recorded during measurements using an ACCUPAR LP-80 ceptometer (Decagon Devices, Pullman, WA).

Continuous sensor-collected measurements were collected for soil temperature ($T_{soil\ 5}$) and moisture (θ), air temperature (T_{air}) and relative humidity (RH), and ambient

irradiance (PAR). Soil moisture and temperature were continuously monitored throughout the study in one native and one invaded area in two blocks. Soil moisture probes (S-SMC-M005, ECH$_2$O probe, Decagon Devices, Inc., Pullman, WA, USA and Onset Computer Corp, Pocasset, MA, USA) were installed vertically from 0 - 10 cm. This provided an integrated measurement of soil moisture (θ) within the rooting zone that coincided with the sampling depth of our manually-collected soil moisture data. Soil temperature probes (S-TMA-M006, Onset Computer Corp, Pocasset, MA, USA) were installed at 5 cm ($T_{soil\ 5}$) from the surface within the soil profile. All soil probes were interfaced with HOBO Micro Station data loggers (H21-002, Onset Computer Corp, Pocasset, MA, USA). Ambient irradiance (PAR), air temperature and relative humidity were monitored using a Li190sb quantum sensor (LI-COR, Lincoln, Nebraska, USA and Campbell Scientific, Inc. Logan, UT, USA) and a HMP 45C relative humidity and temperature sensor (Campbell Scientific, Inc. Logan, UT, USA) interfaced with a CR23X datalogger (Campbell Scientific, Inc. Logan, UT, USA). Relative humidity (RH; %) and air temperature (T_{air}; °C) were used to calculate air vapor pressure deficit (VPD_{air}). Gaps in continuous environmental data were filled with data collected using similar equipment at a site 22 miles away in San Marcos, TX and publicly available data from the Texas ET Network (TAMU Agricultural Extension Service, http://texaset.tamu.edu). Soil data from the San Marcos site were compared with data from WFC over periods of simultaneous measurements using linear regression models to derive correction coefficients for gap-filling calculations.

Data analysis

Seasonal trends in, and treatment effects on, repeated variables

Seasonal trends and plot *type* (invaded or native) effects on variables that were repeatedly measured on the same plots (i.e., vegetation cover, LAI, canopy transmittance, and carbon fluxes) were compared between invaded and native plots using repeated measures mixed models (MIXED procedure in SAS 9.2, SAS Institute, Cary, NC, USA). *Type*, sampling date (*doy*, Julian day-of-year), and their interaction term (*type X doy)* were included in models as fixed effects. *Block* and individual plots (*plotid*) nested within *type X block* combinations were included as random effects. Individual plots (*plotid*) were also identified as the subject of repeated measures. Sampling date (*doy*) was considered to be a fixed-effect categorical variable because there was no expectation of a linear relationship between the dates on which measurements were made and the response variables. The interaction of *type* and date *(type X doy*) was included in the models to examine differences between plot *types* in their responses to season. Each response variable was analyzed for each of the two years (2006 and 2007) separately.

Seasonal trends in, and treatment effects on, non-repeated variables

Seasonal trends and plot *type* (invaded or native) effects on variables that were not repeated measurements (i.e., hand-collected soil moisture and temperature) were compared between invaded and native plots using ordinary least squares (OLS) models (GLM procedure in SAS). Plot *type*, sampling date (*doy),* and their interaction term (*type X doy*) were included in the models as fixed-effect categorical variables. The date on which each measurement was made (*doy*) was included in the model as a fixed-effect categorical variable because there was no expectation of a linear relationship between the dates on which measurements were made and any response variable. The interaction

term, *type X doy*, was included in models in order to examine differences between invaded and native plots in their responses to season. *Block* was considered a random-effect categorical variable in each of these model; therefore *F*-values of differences between plot *types* were calculated using the mean squares of the *type X block* term in the same model as the denominator. Each response variable was analyzed for each of the two years (2006 and 2007) separately.

Effects of environmental variables on C-flux variables

To analyze the effects of environmental variables on C-flux variables (NEE_{LS}, GEP, R_{eco} and R_{soil}) and to compare them between invaded and native plots, we constructed repeated measures mixed models. In these models, *type* (invaded or native) was a fixed effect, as were up to five different environmental variables and their five squared values. If NEE_{LS} or GEP was the response variable, the initial environmental variables were PAR, and PAR^2, T_{air}^2, etc. If R_{eco} was the response variable, PAR and PAR^2 were never included; only T_{air}, $T_{soil\ 5}$, RH, and volumetric soil moisture (θ), and their squared values were tested. If R_{soil} was the response term, $T_{soil\ 5}$, volumetric soil moisture (θ), and their squared values were tested. Green leaf area index (LAI_{corr}), but not its interaction term with *type*, was also tested in models in order to account for differences in vegetation effects that were independent of plot type. *Block* and *plotid* nested within *type* x *block* were included in each model as random effects. Date (*doy*) was included as a repeated measure with *plotid* (a unique plot identifier) as its subject. We included the squared values of each environmental variable in the initial models because the environmental variables can have non-linear effects on the response variables.

We also tested the possibility that the relationship between each response variable and each environmental variable would differ between plot *types*. Due to limited sample sizes, we had to test this for each environmental variable separately. For example, one initial model had, in addition to all the terms listed above, terms to compare the effects of PAR and PAR^2 on NEE between invaded and native plots (*type*); another initial model had terms to compare the effect of T_{air} and T_{air}^2 on NEE between invaded and native plots (*type*); and so on. These are coded as "interaction" terms in SAS; e.g., *type X* T_{air}, *type X* T_{air}^2. If any of these "interaction" terms were significant, they were retained in all subsequent models, as were the corresponding main effects. If an "interaction" term was not significant, it was dropped. Once all of these "interaction" terms had been tested, a single model with all environmental variables, all their squared values, and the significant "interaction" terms was constructed. Quadratic terms (e.g., PAR^2) that were not significant in this model were dropped, and another new model constructed without them. Finally, if neither its "interaction" terms nor its quadratic term was significant, and the main effect of an environmental variable was non-significant, that environmental variable was dropped entirely from the final model. Each response variable was analyzed for each of the two years (2006 and 2007) separately.

Developing predictive models for annual C-flux estimates

To develop predictive models for the purpose of comparing estimated daily and annual NEE between native and invaded plots, we used multiple regression models of NEE as a function of environmental variables (*PAR,* θ*,* $T_{soil\ 5}$*,* and either T_{air} and *RH* or VPD_{air}), *type* and green leaf area index (LAI_{corr}) separately for the two years (2006 and 2007) fitted with the MIXED procedure of SAS. The initial models included *type*, LAI_{corr}, environmental variables, each environmental variable squared, and its linear and

quadratic interaction terms with *type* (coded as "interaction" terms in SAS, e.g., *type X* T_{air}, *type X* T_{air}^2). A unique identifier for each plot (*plotid*) was included in models as a random effect to account for the unbalanced nature of the dataset (uneven numbers of measurements per plot) and for the fact that measurements were repeatedly conducted on the same plots and therefore not independent. If a quadratic interaction term was non-significant, it was deleted from the model and the model re-run with only the corresponding linear interaction term. If the linear interaction term was not significant in this second model, it was also removed, and the model re-run with only the covariate and its square. If the squared covariate was non-significant, it was also dropped, and the model re-run. Finally, if the linear covariate was non-significant it was also dropped.

The resulting multiple regression models were then used to estimate daily diurnal NEE for the two plot *types* using hourly averages of continuously measured environmental variables for each year separately. Because we found significant differences between invaded and native plots for soil temperature (T_{soil5}) and moisture (θ), continuous measurements of T_{soil5} and θ measured in invaded and native plots were used to estimate NEE (µmols CO_2 m^{-2} s^{-1}) for invaded and native plots respectively. We used a linear regression model (MIXED procedure in SAS) that included *type* as a categorical fixed effect and sampling date (*doy*) and its squared (*doy*^{2}) and cubic (*doy*^{3}) terms as continuous fixed effects to estimate daily green leaf area that was then used in estimating NEE (Table 3.2). Interaction terms between *type* and *doy*, *doy*^{2}, and *doy*^{3} were also tested in the model of LAI_{corr} (coded as "interaction" terms in SAS, e.g., *type X doy*, *type X doy* ^{2}). Daily estimates of NEE were summed for each year to compare annual carbon exchange between invaded and native plots (*type*) on an area basis. We calculated daily and annual sums of CO_2 using a code containing a nested loop constructed with an inner loop of 24 steps and an outer loop of 365 steps that was written in Visual Basic.

The Visual Basic code read and wrote values directly to an Excel spreadsheet. We converted [CO_2] (μmol m^{-2} s^{-1}) calculated using the multiple regression models to g m^{-2} hr^{-1} using the following formula:

[CO_2] (g m^{-2} hr^{-2}) = [CO_2] (μmol m^{-2} s^{-1}) x 0.000001 (mol μmol^{-1}) x 12.011 (g C mol_{CO2}^{-1}) x 3600 (s hr^{-1}).

RESULTS

B. ischaemum invasion impacts on cover and leaf area

B. ischaemum-invaded plots had on average lower live cover and higher standing dead cover than native-dominated plots (Tables 3.3, 3.4). This was particularly true during the winter and early spring when C_4 grasses, including *B. ischaemum*, were dormant (Figure 3.4). Invaded plots also had significantly lower aerial cover (live) for each of the native functional groups we monitored: C_3 grasses, C_4 short-grasses, C_4 mid-grasses, and forbs (Figure 3.4; Tables 3.3, 3.4). Native plots varied in composition, but were primarily composed of native C_3 grasses (mainly *N. leucotricha*) and forbs, with relatively small amounts of native C_4 short- and mid-grasses, including *Bouteloua curtipendula*, *Bouteloua rigidiseta*, *B. laguroides*, *H. belangeri* and *S. scoparium* (Table 3.4). *B. ischaemum*-invaded plots had a *B. ischaemum* and standing dead over-story with a native C_3 grass (mainly *N. leucotricha*) and forb understory; both the C_3 grass cover and forb cover were, however, less than they were in the native-dominated plots (Table 3.4). Green leaf area index (LAI_{corr}) was significantly higher in invaded plots during the dry year (2006)(Tables 3.3; Figure 3.5). During the winter and early spring of the second year (2007), when C_4 grasses were dormant, LAI_{corr} was higher in native areas; during drier, hotter periods in the late summer that year, when C_3 grasses and forbs were less active,

LAI_{corr} was higher in invaded areas (Figure 3.5; significant type-date term for both years, Table 3.3).

B. ischaemum invasion impacts on plant canopy microclimate

The microclimate in the plant canopy of *B. ischaemum*-invaded plots was more insulated from ambient conditions than those found in native-dominated plots. Perhaps because of their higher amounts of standing dead biomass, invaded plots had lower canopy light transmittance (Table 3.5; Figure 3.6). Although native-dominated and invaded plots had significant differences in some soil variables, the magnitudes of the differences were small (Table 3.6, Figure 3.7a).

B. ischaemum invasion impacts on net ecosystem carbon exchange and its components

Net ecosystem carbon exchange (NEE; μmol CO_2 m^{-2} s^{-1}) showed a strong seasonal cycle in both native-dominated and the *B. ischaemum*-invaded plots. As expected, substantial light-saturated C-uptake (indicated by negative NEE_{LS}) began in the spring (see day 102 in 2006 and 116 in 2007 in Figure 3.7b) and continued until the summer drought in the dry year (see day 205 in 2006 in Figure 3.7b) and fall senescence during the wet year (see day 285 in 2007 in Figure 3.7b). During the dry year, C-uptake was highest when soil moisture was moderate and lower when soil moisture was high (see days 170 and 263 in 2006 in Figures 3.7a, 3.7b). This was likely due to precipitation-induced pulses in soil respiration (R_{soil}; see days 170 and 263 in 2006 in Figure 3.7c). During the wet year, C-uptake was fairly continuous throughout the growing season (Figure 3.7b). The seasonal pattern of NEE was modified in two primary ways by the invasion of *B. ischaemum*: (1) net C-uptake began later in *B. ischaemum*-invaded plots (see days 8 and 116 in 2007 in Fig 3.7b) and (2) light-saturated NEE was higher (more

negative) in invaded areas than in native areas during dry periods in the spring and the summer. Higher C-uptake under hot, dry conditions in invaded plots was evident in both the dry (see days 102, 193, and 206 in 2006, Figure 3.7b; significant type-date term in Table 3.7) and the wet year (see day 258 in 2007, Figure 3.7b; significant type-date term in Table 3.7). Both plot types switched from being C sinks to being C sources at higher temperatures during the wet year than they did during the dry year.

Overall, soil respiration (R_{soil}; μmol CO_2 m^{-2} s^{-1}) was similar between invaded and native plots during both years (Figures 3.7c; Table 3.7). One exception was that R_{soil} was higher in native areas during the spring and early summer of the wet year (2007; significant type-date term in Table 3.7). Higher soil temperatures and plant activity (i.e., higher root respiration and more available labile carbon in the form of root exudates to fuel heterotrophic respiration) in native areas likely account for this difference.

Diurnal measurements taken during the dry year indicated that night-time ecosystem respiration generally was higher in invaded areas, but that day-time carbon uptake remained higher (NEE was more negative) in invaded areas as soil moisture availability declined during the summer dry period (Figure 3.8). Ecosystem respiration (R_{eco}) was similar between invaded and native areas during 2007 (Figure 3.9a; Table 3.7).

Although we only measured GEP a few times during the wet year, we did not see evidence that gross ecosystem productivity (GEP) was lower in invaded plots than in native plots. Instead, GEP was generally similar between invaded and native plots (Figure 3.9b; Table 3.7). GEP was briefly higher in native areas during the cool season but these differences were non-significant (Figure 3.9b; Table 3.7).

***B. ischaemum* invasion impacts on ecosystem response to environmental drivers**

In general, as *B. ischaemum* invaded, the sensitivity of net ecosystem carbon exchange (NEE) to environmental drivers changed largely along the lines of what would be expect as a former mixed C_3/C_4 savanna approaches a C_4 monoculture. As both temperature and PAR increased and relative humidity decreased, the plots dominated by *B. ischaemum* had more negative NEE, indicating higher rates of net CO_2 uptake. The modeled response of light-saturated net ecosystem carbon exchange (NEE_{LS}; μmol CO_2 m^{-2} s^{-1}) to environmental drivers indicated that NEE_{LS} peaked at higher relative humidity (Table 3.8; Figure 3.10) and lower air temperatures in native plots than it did in invaded plots (Table 3.8; Figure 3.11). The multiple regression models developed to estimate daily and annual NEE, which included all canopy-level chamber measurements made during each year separately, also indicated that C-uptake started at lower soil temperatures ($T_{soil\ 5}$) in native plots (~ 8°C in native plots and ~ 12°C in invaded plots) (Table 3.9; Figures 3.12, 3.13). Native plots also switched from being a C sink to being a C source at lower soil temperatures (~ 28 °C in 2006 and ~ 31°C in 2007) than invaded plots (~ 32 °C in 2006 and ~ 35 °C in 2007) did during both years (significant T_{soil} *X type* interaction terms for both 2006 and 2007 in Table 3.9; Figures 3.12, 3.13). The multiple regression models, which included canopy-level chamber measurements of NEE at PAR ranging 0 - 2100 μmol photons m^{-2} s^{-1}, indicated that invaded areas were more light-use efficient (i.e., fixed more carbon per unit increase in PAR) and fixed more carbon at higher light levels than native areas (2006, significant *PAR X type* interaction term in Table 3.9; Figure 3.14). However, native plots switched from being a source of C to being a sink for C from the atmosphere at a lower PAR (~ 300 μmol photons m^{-2} s^{-1}) than invaded plots (~ 550 μmol photons m^{-2} s^{-1}) (Figure 3.14).

GEP, R_{eco}, and R_{soil} in native and invaded plots responded similarly to environmental drivers (Tables 3.10, 3.11).

***B. ischaemum* invasion impacts on cumulative annual ecosystem C fluxes**

Model-estimated daily and annual NEE indicated that the growing season was shorter in invaded areas and that daily C-uptake was higher in invaded areas when conditions were hot and dry (Figure 3.15). Although invaded areas lost less C to the atmosphere than native areas during the summer of 2006, native areas lost less C than invaded areas did in the early part of the year (late winter and early spring) and in the fall of 2006 (Figure 3.15). Estimated annual NEE was 1023.78 g C m^{-2} in native areas and 986.32 g C m^{-2} in invaded areas in 2006, indicating that invaded areas lost slightly less C to the atmosphere than native areas during the dry year (2006). During the wet year (2007), native areas switched from being a C source to being a C sink earlier in the year than invaded areas (early February, day 34, Figure 3.15). Mean daily C uptake, however, was higher (i.e., daily NEE was more negative) in invaded areas during the peak of the growing season (days 116 – 285): mean estimated daily NEE during the peak of the growing season was - 2.07 ± 0.51 sd g C m^{-2} day^{-1} in native areas and - 3.08 ± 0.51 sd g C m^{-2} day^{-1} in invaded areas in 2007. Overall, in 2007, the wet year, native areas were a slightly greater carbon sink than invaded areas: estimated annual NEE was - 613.63 g C m^{-2} in native areas and - 572.21 g C m^{-2} in invaded areas.

Estimated cumulative NEE for the two years suggests that both invaded and native areas were a net source for carbon to the atmosphere over the course of the two years and that cumulative NEE over the two years did not differ between native (410.15 g C m^{-2}) and invaded areas (414.10 g C m^{-2}; Figure 3.16).

DISCUSSION

B. ischaemum invasion altered plant canopy composition, structure, and microhabitat characteristics of our central Texas C_3/C_4 mixed savanna grass-matrix study area. The net impacts of these alterations, however, did not result in large changes in net annual ecosystem C exchange (NEE; g m^{-2}) in invaded areas. *B. ischaemum* invasion altered the ecosystem's response to light availability and temperature: C-uptake was higher in native areas at lower light levels and temperatures, and higher in invaded areas at higher light levels and temperatures. These shifts in ecosystem response to environmental drivers shortened the growing season in invaded areas, but this was compensated for by increased C-uptake under higher temperatures and lower water availability. Despite these differences between *B. ischaemum*-invaded and native-dominated areas in the season and conditions when C-uptake occurred, net annual ecosystem carbon exchange did not differ greatly between invaded and native areas over the course of our study.

We anticipated that phenological and ecophysiological differences between *B. ischaemum* and the native species it displaces in central Texas ecosystems would cause *B. ischaemum* invasion to increase variability in ecosystem responses to climate variability and decrease overall ecosystem carbon uptake. We expected that differences between C-fluxes during a dry year and a wet year would be greater in invaded than native areas. These hypotheses were primarily based on two observations: (1) that *B. ischaemum* is active during a shorter period of the year than the dominant native C_3 grass, *N. leucotricha*, and thus unable to take advantage of available water during the cool season and (2) leaf-level photosynthetic measurements in a greenhouse experiment indicated that *B. ischaemum* is more sensitive to decreased soil moisture availability than two native C_4 species in this ecosystem, *B. laguroides* and *S. scoparium* (Chapter 1). We anticipated

that during years with a pronounced summer dry season, a combination of greater water availability during the cool season when C_3 species were active in native areas and lower sensitivity in native C_4 grasses to drying soil conditions would result in greater annual carbon uptake in native areas than in invaded areas. However, the winter of 2005 - 2006 was not wet enough to give C_3 species an advantage, and only a few of the native C_4 grass species that *B. ischaemum* is replacing are more drought tolerant than itself at this site.

The direction and size of carbon exchanges between the atmosphere and semi-arid mixed C_3/C_4 grasslands are largely driven by precipitation availability (Aires et al. 2008), and in years in which a pronounced summer dry season is followed by a wet or average cool season, C-uptake during the cool season can be considerable in these ecosystems (Kjelgaard et al. 2008). The winter of 2005 – 2006 was a dry winter following a drier than average summer in central Texas (Figure 3.3). Compared with the winter of 2006 – 2007, total vegetation cover was very low at the WFC in early 2006, indicating that the plant community was largely dormant during the winter of 2005 - 2006. Therefore there was very little cool season C-uptake in native areas in early 2006 to compensate for low C-uptake during the dry spring and summer of 2006. Invaded areas were a slightly smaller C source than native areas in 2006 because of larger C-uptake under hot, dry conditions during the summer. In dry years with a wetter cool season, native areas may be a smaller C source (or a slight sink) than invaded areas despite higher C-uptake under dry summer conditions in invaded areas. In wet years with a wetter cool season, like 2007, native areas could be greater carbon sinks than invaded areas because C-uptake could be similar between invaded and native areas during the majority of the growing season. We suggest that winter precipitation availability may be the deciding factor that

determines whether annual C-uptake differs substantially between invaded and native areas in this ecosystem.

The direction and degree of an invasive plant's impacts on ecosystem function at a particular site are influenced by initial species composition and ecophysiological characteristics of the ecosystem before invasion (Kramer et al. 2012). We assumed that *B. ischaemum* replaces a large proportion of native C_4 grasses that are less sensitive than it is to dry conditions in the ecosystems it invades. At the WFC where native areas are comprised of approximately 60 and 20%, respectively of C_4 and C_3 grass biomass, with *B. laguroides* and *S. scoparium* accounting for approximately half of native C_4 grass biomass (Basham and Poteet *unpublished data*), it seemed reasonable to predict that ecosystem C-uptake under dry conditions would be negatively impacted by *B. ischaemum* invasion. Our results do not support this hypothesis and there are several possible explanations: (1) exchanging native C_4 grasses for an introduce C_4 grass is a less substantial change in net ecosystem physiology than exchanging a C_3 grass for a C_4 grass; (2) *B. ischaemum* is replacing a variety of native C_4 grasses that respond in a variety of ways to drought, and the net drought response of that community of native C_4 grasses is similar to that of *B. ischaemum*; and (3) the leaf-level phenomenon we observed in the greenhouse was not representative of what occurs at the ecosystem level in the field. In ecosystems where *B. ischaemum* is displacing a larger proportion of native C_4 grass species that are less sensitive to drought, invasion may result in larger changes in ecosystem response to precipitation availability and decreased C-uptake under drier conditions; however, that was not the case at our site.

Continuous eddy flux measurements at another *B. ischaemum*-invaded grassland 22 miles from the WFC on the eastern edge of the Edwards Plateau indicated that a similar mixed C_3/C_4 grassland was a small carbon sink in 2006 (Kjelgaard et al. 2008).

Differences in annual NEE measurements at that site and our estimates for annual NEE at the WFC may be due to over-estimation of night-time respiration by our model simulations and/or higher rainfall at that site during the fall. Lower standing dead plant material at that site, which is grazed by cattle, may also account for differences in NEE between the two sites. High standing dead cover in un-grazed grasslands can reduce ecosystem carbon uptake below that of grazed sites by increasing canopy shading (Delgado-Balbuena et al. 2013). *B. ischaemum* invasion increases standing dead cover (this study) and residence time (Chapter 2), and it is probable that increased standing dead material negatively impacts ecosystem carbon uptake in invaded areas.

Warm-season lengths and the duration of prolonged summer dry periods are increasing in Texas and other parts of the south-central US (Groisman and Knight 2008) where *B. ischaemum* is invading. Arid and semi-arid ecosystems are predicted to experience increased variability in precipitation and prolonged extreme hot periods as a result of global climate change (Easterling et al. 2000, Diffenbaugh et al. 2005, Leung and Gustafson 2005). Increased warm-season lengths should shorten the differences in growing season length between native and invaded areas. Higher C-uptake in invaded areas under hot, dry conditions will likely increase the differences in annual C-uptake between native and invaded areas.

B. ischaemum responds positively to increases in atmospheric [CO_2] (Anderson et al. 2001), benefiting primarily from increased water-use efficiency and decreased water deficits under drought conditions (Polley et al. 2002). Thus increasing atmospheric [CO_2] could help this invader to cope with drier climatic conditions. However, the invader will not be the only species in this ecosystem to benefit from increasing atmospheric [CO_2]: the C_3 (Reich et al. 2001) and many of the C_4 species in this system also have the capacity to respond positively to increasing atmospheric [CO_2] (LeCain and Morgan

1998). *N. leucotricha,* which possesses heat and water-deficit tolerance similar to some C_4 species in this system (Hicks et al. 1990), may be able to take advantage of increasing atmospheric [CO_2] despite higher temperatures and less frequent rainfall.

While it is difficult to predict the net effect of changing climatic and atmospheric conditions on any ecosystem, based on our results we anticipate that increasing [CO_2] and temperature and decreasing water availability will result in increased differences in annual C-uptake between invaded and native areas in this ecosystem. As differences in growing season length decrease and the importance of performance under hot, dry conditions increases we anticipate that net annual C-uptake will regularly become higher in invaded areas.

CONCLUSIONS

The degree and direction of *B. ischaemum*'s impacts on ecosystem carbon dynamics depend largely on two factors: (1) timing and variability of precipitation and (2) the initial species composition of the invaded ecosystem. Thus the impacts of this invasive species will vary from year to year and may be site-specific. Although, *B. ischaemum* invasion shifted ecosystem C-uptake from being nearly year-round to occurring predominantly in the summer, greater C-uptake during the summer and under drier conditions compensated for a shorter growing seasons in invaded areas. Overall, *B. ischaemum* impacts on annual net ecosystem carbon exchange were small at this site which indicates that this species may not have large impacts on C sequestration in the mixed C_3/C_4 grass systems it invades in this region. We anticipate, however, that *B ischaemum* invasion will positively impact net ecosystem C-uptake as atmospheric [CO_2] increases and climatic conditions change.

The savanna in this study is not typical of *B. ischaemum*-invaded grassland and savanna ecosystems in this region because it is not grazed by cattle. A multi-site comparison of ecosystems that vary in native species composition and includes cattle grazing and measures the impacts of increased standing dead on ecosystem C-uptake would be helpful in further determining the effects of this species on net ecosystem carbon exchange.

Table 3.1.a. List of variables measured or estimated in Chapter 3 and the tables and figures in which they are reported.

Type of Variable	Variable	Acronym/ Symbol	Units	Tables	Figures
Vegetation	Aerial vegetation cover		%	3.3, 3.4	3.4
	Green leaf area index	LAI_{corr}	m^2 leaf m^{-2} ground	3.2, 3.3	3.5
Microhabitat	Canopy light transmittance		below-canopy PAR : above-canopy PAR	3.5	3.6
	Soil temperature at 2 cm	$T_{soil\ 2}$	° C	3.6	3.7a
	Soil temperature at 5 cm	$T_{soil\ 5}$	° C	3.6	3.7a, 3.12, 3.13
	Volumetric soil moisture	θ	$m^3\ m^{-3}$	3.6	3.7a
Carbon Fluxes	Light-saturated NEE	NEE_{LS}	µmol CO_2 $m^{-2}\ s^{-1}$	3.7, 3.8	3.7b
	Soil respiration	R_{soil}	µmol CO_2 $m^{-2}\ s^{-1}$	3.7, 3.11	3.7c
	Ecosystem respiration (2007 only)	R_{eco}	µmol CO_2 $m^{-2}\ s^{-1}$	3.7, 3.10	3.9a
	Gross ecosystem productivity (2007 only)	GEP	µmol CO_2 $m^{-2}\ s^{-1}$	3.7, 3.10	3.9b
	Diurnal changes in net ecosystem productivity (2006 only)	NEE	µmol CO_2 $m^{-2}\ s^{-1}$		3.8
	Estimated daily and annual net ecosystem exchange	NEE	g C m^{-2} day^{-1}; g C m^{-2}	3.9	3.15, 3.16
Environmental Drivers	Photosynthetically active radiation	PAR	µmol photons $m^{-2}\ s^{-1}$		3.8, 3.14
	Relative humidity	RH	%		3.10
	Air temperature	T_{air}	° C		3.7a, 3.11

Table 3.1.b. List of variables measured in Chapter 3 (continued).

Listed are the number of dates, blocks, and plots in which variables were sampled during the 2006 growing season. Also listed are the number of samples dropped (see text for criteria) and the total number of samples analyzed for each variable.

Type of Variable	Variable	Symbol	2006				
			Dates	Blocks	Plots	Dropped	Total
Vegetation	Aerial vegetation cover		9	5	20	0	180
	Green leaf area index (corrected for standing dead)	LAI_{corr}	9	5	20	0	180
Microhabitat	Canopy light transmittance		5	5	20	0	100
	Soil temperature at 2 cm	$T_{soil\ 2}$	9	5	20	0	180
	Soil temperature at 5 cm	$T_{soil\ 5}$	9	5	20	0	180
	Volumetric soil moisture	θ	9	5	20	0	180
Carbon Fluxes	Light-saturated NEE	NEE_{LS}	9	5	20	24	180
	Soil respiration	R_{soil}	9	5	20	0	180
	Diurnal changes in net ecosystem exchange	NEE	3 (3 - 6 measurements $plot^{-1}$ day^{-1})	1 - 2	4 - 8	6	50
	Estimated daily/annual net ecosystem productivity	NEE	Compiled light saturated and non-light saturated NEE measurements from all sampling dates to develop a multiple regression model used to estimate daily and annual NEE.				254
Environmental Drivers	Photosynthetically active radiation	PAR	9	5	20	0	Hand-collected: 254; Sensor-collected: 8, 760
	Air temperature	T_{air}	9	5	20	0	
	Relative humidity	RH					Sensor-collected: 8, 760

Table 3.1.c. List of variables measured in Chapter 3 (continued).

Listed are the number of dates, blocks, and plots in which variables were sampled during the 2007 growing season. Also listed are the number of samples dropped (see text for criteria) and the total number of samples analyzed for each variable.

Type of Variable	Variable	Symbol	2007				
			Dates	Blocks	Plots	Dropped	Total
Vegetation	Aerial vegetation cover		9	6	24	0	216
	Green leaf area index (corrected for standing dead)	LAI_{corr}	9	6	24	0	216
Microhabitat	Canopy light transmittance	tau	4	6	24	0	96
	Soil temperature at 2 cm	$T_{soil\ 2}$	9	6	24	0	216
	Soil temperature at 5 cm	$T_{soil\ 5}$	9	6	24	0	216
	Volumetric soil moisture	θ	9	6	24	0	216
Carbon Fluxes	Light-saturated NEE	NEE_{LS}	9	6	24	0	216
	Soil respiration	R_{soil}	8	6	24	0	192
	Ecosystem respiration	R_{eco}	6	1 , 6	4 , 12	7	57
	Gross ecosystem productivity	GEP	6	1 , 6	4 , 12	7	57
	Estimated daily/annual net ecosystem productivity	NEE	We compiled NEE_{LS}, R_{eco}, and non-light saturated NEE measurements from all sampling dates to develop a multiple regression model used to estimate daily and annual NEE.				281
Environmental Drivers	Photosynthetically active radiation	PAR					Hand-collected: 254; Sensor-collected: 8, 760
	Air temperature	T_{air}					
	Relative humidity	RH					Sensor-collected: 8, 760

Table 3.2. Mixed model results for models used to predict daily live green leaf area index (LAIcorr) values used in the multiple regression model simulations to estimate daily and annual net ecosystem carbon exchange (NEE) reported in Figures 3.15 and 3.16.

Model fixed effects were plot *type* (invaded or native), sampling date (*doy*), sampling date squared and sampling date cubed, and interaction terms between type and sampling date and its polynomials (i.e., *type X doy*, *type X doy*^{2}, and *type X doy*^{3}). Interaction terms were only retained in the model when they were significant. *Block* and *plotid* (unique plot identifier) nested within *block X type* were included in models as random effects. Values reported for fixed effects are model fit coefficients, standard error (SE), degrees of freedom (DF), *F*-values, and *P*-values. Values for model intercepts are coefficients, standard error (SE), degrees of freedom (DF), *t*-values, and *P*-values. Covariance parameter estimates are reported for random effects.

LAI_{corr}		Effect	Estimate	SE	DF	*F*-value	*P*-value
2006	Fixed Effects	Intercept	1.1569	0.07902	1, 4	14.64	0.0001
		TYPE	0.3304	0.1117	1, 14	8.74	0.0104
		DOY	0.01109	0.000583	1, 156	891.93	<.0001
		DOY X TYPE	0.002425	0.000824	1, 156	8.66	0.0038
		DOY^2	-0.00004	1.54E-06	1, 156	1406.27	<.0001
		DOY^2 X TYPE	-7.01E-06	2.18E-06	1, 156	10.33	0.0016
	Random Effects	BLOCK				0	
		PLOTID (TYPE X BLOCK)				0.04	
2007	Fixed Effects	Intercept	0.7958	0.0961	1, 5	8.28	0.0004
		TYPE	-0.7309	0.1259	1, 17	33.72	<.0001
		DOY	-0.00441	0.002342	1, 186	4.45	0.0362
		DOY X TYPE	0.001832	0.003312	1, 186	0.31	0.5809
		DOY^2	0.000079	0.000018	1, 186	64.97	<.0001
		DOY^2 X TYPE	0.000043	0.000025	1, 186	2.99	0.0854
		DOY^3	-1.32E-07	0	1, 186	13.46	0.0003
		DOY^3 X TYPE	-1.28E-07	0	1, 186	6.32	0.0128
	Random Effects	BLOCK				0.008	
		PLOTID (TYPE X BLOCK)				0.009	

Table 3.3. Mixed effects model results for vegetation cover variables and leaf area index (LAI) measured at the WFC in 2006 (dry year) and 2007 (wet year).

Model fixed effects were plot *type* (invaded or native), Julian day-of-the-year (*doy*) and their interaction term (*type X doy*). Model random effects were *plotid* (plot unique identifier) nested within *type X block* and *block*. *Doy* was included in the models as a *repeated* statement with *plotid* as its subject. Values are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effects and the repeated measure. Bold type indicates that values are significant at the $P < 0.05$. *Italics* indicate nearly significant values for $0.05 < P < 0.10$. Total vegetation cover is comprised of native short C_4, mid-C_4, and C_3 grass, *B. ischaemum*, and forb covers.

Year	Plant Canopy Characteristics	Fixed Effects			Random Effects σ^2		Repeated Measure σ^2
		TYPE	DOY	TYPE X DOY	BLOCK	PLOTID (TYPE X BLOCK)	
2007	**Standing Dead**	**51.72 (1, 22)**	**130.21 (8, 176)**	**29.35 (8, 176)**	2.08	19.1	32.66
	Bare	0.40 (1, 22)	**13.87 (8, 176)**	**2.51 (8, 176)**		4.38	10.16
	Total Vegetation	**32.17 (1, 22)**	**71.05 (8, 176)**	**16.19 (8, 176)**		35.05	69.59
	Native Short C_4 Grasses	**12.37 (1, 22)**	1.42 (8, 176)	1.42 (8, 176)	1.89	5.18	27.18
	Native Mid-C_4 Grasses	**20.36 (1, 22)**	**8.01 (8, 176)**	**8.01 (8, 176)**		54.7	26.64
	B. ischaemum	**1024 (1, 22)**	**207.39 (8, 176)**	**206.72 (8, 176)**	1.32	10.54	10.6
	Native C_3 Grasses	**91.43 (1, 22)**	0.27 (8, 176)	**4.20 (8, 176)**	5.02	60.66	24.82
	Native Forbs	**26.99 (1, 22)**	**13.52 (8, 176)**	1.40 (8, 176)		20.72	22.38
	LAI	*4.18 (1, 22)*	**418.04 (8, 176)**	**15.1 (8, 176)**	0.008	0.01	0.056
2006	**Standing Dead**	**31.88 (1, 18)**	**106.23 (8, 144)**	**14.61 (8, 144)**		4.6467	51.0557
	Bare	0.12 (1, 18)	**4.17 (8, 144)**	*1.87 (8, 144)*		5.1161	6.0108
	Total Vegetation	**30.61 (1, 18)**	**101.40 (8, 144)**	**16.52 (8, 144)**		6.0301	49.7828
	Native Short C_4 Grasses	**6.44 (1, 18)**	**2.51 (8, 144)**	**2.51 (8, 144)**	0.07	2.3	1.16
	Native Mid-C_4 Grasses	**22.18 (1, 18)**	**15.29 (8, 144)**	**15.31 (8, 144)**	3.32	15.42	12.23
	B. ischaemum	**665.93 (1, 18)**	**68.58 (8, 144)**	**64.89 (8, 144)**	3.14	5.04	22.92
	Native C_3 Grasses	**430.15 (1, 18)**	**28.14 (8, 144)**	**22.86 (8, 144)**	23.44	4.08	23.08
	Native Forbs	**23.68 (1, 18)**	**17.83 (8, 144)**	**5.15 (8, 144)**		6.61	6.64
	LAI	**16.14 (1, 18)**	**126.00 (8, 144)**	**7.46 (8, 144)**			0.03

Table 3.4. Annual mean aerial cover (%) measured in invaded and native plots at the WFC during the 2006 and 2007 growing seasons.

Values are adjusted means from the mixed models (± 1 SE). Total live cover was comprised of native C_3, native C_4 short- and mid-grasses, *B. ischaemum*, and forb cover. Bold type indicates significant differences between plots types within each year.

Aerial Cover (%)	2006		2007	
	Invaded	Native	Invaded	Native
Open	4.15 (1.27)	3.78 (0.86)	4.01 (1.47)	3.41 (1.06)
Standing Dead	**57.34 (5.99)**	**49.23 (5.45)**	**35.38 (5.8)**	**21.38 (2.67)**
Total Live	**38.51 (5.75)**	**46.93 (5.46)**	**59.95 (6.75)**	**75.10 (2.90)**
Native Short C_4 Grasses	**0 (0)**	**1.77 (0.83)**	**0 (0)**	**4.11 (2.39)**
Native Mid-C_4 Grasses	**0.05 (0.06)**	**8.68 (2.99)**	**0 (0)**	**13.99 (3.90)**
B. ischaemum	**32.08 (5.74)**	**0.29 (0.34)**	**45.09 (5.53)**	**0.37 (0.40)**
Native C_3 Grasses	**3.65 (1.83)**	**27.55 (3.99)**	**6.56 (2.39)**	**37.65 (2.98)**
Native Forbs	**2.73 (1.00)**	**8.63 (1.67)**	**9.48 (2.12)**	**19.69 (2.06)**

Table 3.5. Mixed effects model results comparing plant-canopy light transmittance measured in invaded and native plots at the WFC in the dry (2006) and wet (2007) years.

Model fixed effects were plot *type* (invaded or native), Julian day-of-the-year (*doy*), and their interaction term (*type X doy*). Model random effects were *plotid* (plot unique identifier) nested within *type X block* and *block*. *Doy* was included in the models as a *repeated* statement with *plotid* as its subject. Values are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effects and the repeated measure. Bold type indicates that values are significant at the *P* < 0.05.

Seasonal Comparisons		Fixed Effects			Random Effects σ^2		Repeated Measure σ^2
Variable	YEAR	TYPE	DOY	TYPE X DOY	BLOCK	PLOTID (TYPE X BLOCK)	
Canopy Light Transmittance	2006	**19.01 (1, 18)**	**10.73 (4,72)**	0.87 (4, 72)	0.001	0	0.011
	2007	**7.20 (1, 22)**	**51.96 (3, 66)**	0.14 (3, 66)	0.002	0.001	0.003

Table 3.6. Ordinary least squares (OLS) model results for soil characteristics, soil temperature at 5 cm and 2 cm depth, and volumetric soil moisture (θ), measured at the WFC during the 2006 (dry) and 2007 (wet) growing seasons.

Plot *type*, sampling date (*doy*), and their interaction terms (*type X doy*) were included as fixed effects in these models. *Block* was treated as a random effect in all of the models; therefore *F*-values of differences between plot *types* were calculated using the mean squares of the *type X block* term from the same model as the denominator. Values are *F*-values (degrees of freedom). Bold type indicates that values are significant at the $P < 0.05$. Italics indicate nearly significant values at the $0.05 < P < 0.10$.

Soil Character-istics	Year	TYPE	BLOCK	DOY	TYPE X Block	TYPE X DOY	BLOCK X DOY	TYPE X BLOCK X DOY
Soil Temp (5 cm)	2006	**24.19 (1, 4)**	**2.80 (4, 90)**	**189.81 (8, 32)**	**0.97 (4, 90)**	**2.90 (8, 90)**	**3.79 (32, 90)**	0.87 (32, 90)
	2007	*4.97 (1, 5)*	**3.95 (5, 108)**	**106.22 (8, 40)**	1.67 (5, 108)	**4.17 (8, 108)**	**8.27 (40, 108)**	**2.41 (40, 108)**
Soil Temp (2 cm)	2006	**37.74 (1, 4)**	**2.56 (4, 90)**	**544.55 (8, 32)**	0.74 (8, 90)	**2.64 (8, 90)**	**3.79 (32, 90)**	0.78 (32, 90)
	2007	**15.12 (1, 5)**	**2.51 (5, 108)**	**88.21 (8, 40)**	1.00 (5, 108)	**2.41 (8, 108)**	**8.10 (32, 108)**	1.24 (40, 108)
Soil Moisture	2006	0.69 (1, 4)	**18.98 (4, 90)**	**116.63 (8, 40)**	0.67 (4, 90)	**3.52 (8, 90)**	**2.24 (32, 90)**	1.16 (32, 90)
	2007	**16.62 (1, 5)**	**11.90 (5, 108)**	**213.75 (8, 40)**	**2.16 (5, 108)**	**3.16 (8, 108)**	**1.61 (40, 108)**	**1.75 (40, 108)**

Table 3.7. Results for mixed effects models testing for treatments effects (invaded versus native) on carbon fluxes measured in the field at the WFC.

Light saturated net ecosystem exchange (NEE_{LS}) and soil respiration (R_{soil}) were measured during the 2006 and 2007 growing seasons and gross ecosystem productivity (GEP) and ecosystem respiration (R_{eco}) were measured during the 2007 growing season at the WFC. Model fixed effects were *type* (invaded or native), Julian day-of-the-year (*doy*), and their interaction term (*type X doy*). Model random effects were *block* and *plotid* (plot unique identifier) nested within *type X block*. *Doy* was included in the models as a *repeated* statement with *plotid* as its subject. Values are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effects and the repeated measure. Bold type indicates that values are significant at the $P < 0.05$. Italics indicate nearly significant values for $0.05 < P < 0.10$.

Seasonal Comparisons		Fixed Effects			Random Effects σ^2		Repeated Measure σ^2
Variable	YEAR	TYPE	DOY	TYPE X DOY	BLOCK	PLOTID (TYPE X BLOCK)	
NEE_{LS}	2006	**15.54 (1, 18)**	**70.83 (8, 144)**	**7.16 (8, 144)**	0.02		1.77
	2007	0.0 (1, 22)	**68.94 (8, 173)**	**5.87 (8, 173)**	0.04	0.38	3.4
R_{soil}	2006	1.93 (1, 18)	**164.44 (8, 144)**	1.44 (8, 144)		0.006	0.17
	2007	0.33 (1, 22)	**133.91 (7, 154)**	**3.50 (7, 154)**		0.22	0.88
GEP	2007	0.16 (1, 20)	**37.47 (5, 25)**	1.15 (5, 25)			10.98
R_{eco}	2007	0.0 (1, 20)	**38.12 (5, 25)**	0.47 (5, 25)			2.64

Table 3.8. Mixed effects model results for models comparing light saturated net ecosystem exchange (NEE_{LS}) responses to environmental drivers between native and invaded plots.

Environmental drivers included in final models were soil ($T_{soil\ 5}$) and air temperature (T_{air}), relative humidity (*RH*), and volumetric soil moisture (θ). Model fixed effects were plot *type* (invaded or native), environmental variables, environmental variables squared, and two-way interaction terms between *type* and environmental variables and their linear and quadratic terms. Model random effects were *block* and *plotid* (plot unique identifier) nested within *type X block*. *Doy* was included in the models as a *repeated* statement with *plotid* as its subject. Values are model-fit coefficients (standard error), *F*-values (degrees of freedom) for fixed effects, and covariance parameter estimates for the random effects and the repeated measure. Bold type indicates that values are significant at the *P* < 0.05. Italics indicate nearly significant values for 0.05 < P < 0.10. See Figures 3.10, 3.11.

Environmental Drivers	NEE_{LS}				
	YEAR	2006		2007	
	Variable	Coefficient (SE)	*F*-value (DF)	Coefficient (SE)	*F*-value (DF)
Fixed Effects	Intercept	38.62 (4.76)	**8.11 (1, 18)**	37.0223 (6.5199)	**5.68 (1, 5)**
	TYPE	5.74 (2.29)	**6.30 (1, 18)**	8.216 (2.0246)	**16.47 (1, 17)**
	$T_{soil\ 5}$	-1.08 (0.28)	**15.53 (1, 166)**	- 0.1849 (0.0900)	**4.22 (1, 186)**
	$T_{soil\ 5}^{\ 2}$	0.03269 (0.00655)	**25.5 (1, 166)**		
	T_{air}	-1.19 (0.26)	**21.11 (1, 166)**	- 2.14 (0.42)	**27.73 (1, 186)**
	$T_{air}^{\ 2}$	0.01491 (0.003993)	**14.04 (1, 166)**	0.0356 (0.0062)	**33.41 (1, 186)**
	RH	-0.4429 (0.0951)	**76.10 (1, 166)**		
	RH^2	0.004123 (0.00125)	**8.77 (1, 166)**		
	θ			- 39.65 (7.66)	**26.80 (1, 186)**
	θ^2			44.35 (15.74)	**7.94 (1, 186)**
	T_{air} X TYPE			- 0.2295 (0.0583)	**15.49 (1, 186)**
	RH X TYPE	-0.3936 (0.1372)	**8.36 (1, 166)**		
	RH^2 X TYPE	0.005479 (0.001872)	**8.77 (1, 166)**		
Random Effects σ^2	BLOCK		0.04		0.13
	PLOTID (TYPE X BLOCK)				0.07
Repeated Measure σ^2			3.56		5.83

Table 3.9. Multiple regression model results for models used to predict daily and annual values of net ecosystem exchange (NEE) from environmental drivers and green leaf area index (LAI_{corr}).

Environmental drivers included in the final model were photosynthetically active radiation (*PAR*), soil ($T_{soil\ 5}$) and air (T_{air}) temperature, relative humidity (*RH*), and volumetric soil moisture (θ). Model fixed effects were *type* (invaded or native), LAI_{corr}, environmental variables, and linear and quadratic terms of environmental variables. Interaction terms between *type* and environmental variables and their polynomial terms were also tested. A unique plot identifier (*plotid*) was included in models as a random effect. Values reported are model fit coefficients, standard error (SE), degrees of freedom (DF), *F*-values, and *P*-values. Values reported for model intercepts are coefficients, standard error (SE), degrees of freedom (DF), *t*-values, and *P*-values. See Figures 3.12 – 3.14 for graphs of significant *type* interactions with environmental drivers. Daily and cumulative net ecosystem carbon exchange (NEE) estimated using these models are reported in Figures 3.15 and 3.16 respectively.

YEAR	Fixed Effect	Coefficient	SE	DF	*F*-value	*P*-value
2006	Intercept	7.8508	1.2342	1, 18	6.36	<.0001
	TYPE	3.4802	1.0592	1, 224	10.8	0.0012
	PAR	-0.003468	0.000889	1, 224	22.78	0.0001
	PAR^2	0.000001394	4.299E-07	1, 224	10.51	0.0014
	PAR X TYPE	-0.001429	0.04696	1, 224	9.26	0.0026
	θ	8.766	1.587	1, 224	30.52	<.0001
	$T_{soil\ 5}$	0.3072	0.03963	1, 224	53.91	<.0001
	$T_{soil\ 5}$ X TYPE	-0.09493	0.03583	1, 224	7.02	0.0086
	T_{air}	-0.2039	0.0397	1, 224	26.37	<.0001
	RH	-0.3319	0.02832	1, 224	137.42	<.0001
	RH^2	0.002861	0.000274	1, 224	109.36	<.0001
	LAI_{corr}	-0.7167	0.3962	1, 224	3.27	0.0718
2007	Intercept	7.388	2.2946	22	3.22	0.0039
	TYPE	3.855	1.5056	251	6.56	0.011
	PAR	-0.00646	0.000331	251	380.9	< 0.0001
	$T_{soil\ 5}$	-0.8578	0.2595	251	13.39	0.003
	$T_{soil\ 5}^2$	0.02172	0.006239	251	12.12	0.0006
	$T_{soil\ 5}$ X TYPE	-0.187	0.06448	251	8.41	0.0041
	VPD_{air}	1.0619	0.1566	251	45.96	< 0.0001
	LAI_{corr}	0.6026	0.2552	251	5.58	0.019

Table 3.10. Mixed effects model results for models comparing gross ecosystem productivity (GEP) and ecosystem respiration (R_{eco}) responses to environmental drivers between invaded and native plots.

Environmental drivers included in the final version of models were relative humidity (*RH*) and volumetric soil moisture (θ). Model fixed effects were plot *type* (invaded or native), environmental variable linear and quadratic terms, and two-way interaction terms between *type* and environmental variables and their polynomials. Model random effects were *block* and *plotid* (plot unique identifier) nested within *type X block*. *Doy* was included in the models as a *repeated* statement with *plotid* as its subject. Values are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effects and the repeated measure. Bold type indicates that values are significant at the $P < 0.05$.

Environmental Drivers	2007	GEP	R_{eco}
Fixed Effects	TYPE	0.11 (1, 5)	0.16 (1, 5)
	θ	**18.45 (1, 48)**	**7.89 (1, 47)**
	θ^2		**13.59 (1, 47)**
	RH	**11.78 (1, 48)**	**10.21 (1, 47)**
Random Effects σ^2	BLOCK	5.87	0.21
	PLOTID (TYPE X BLOCK)		
Repeated Measure σ^2		17.82	4.99

Table 3.11. Mixed effects model results for models comparing soil respiration (R_{Soil}) responses to environmental drivers between invaded and native plots.

Environmental drivers tested in the models were soil temperature ($T_{soil\ 5}$) and volumetric soil moisture (θ). Model fixed effects were plot *type* (invaded or native), green leaf area index (LAI_{corr}), environmental variables, and the linear and quadratic terms of environmental variable. Two-way interaction terms between *type* and environmental variables and their polynomial terms were also tested. Model random effects were *block* and *plotid* (plot unique identifier) nested within *type X block*. *Doy* was included in the models as a *repeated* statement with *plotid* as its subject. Values are *F*-values (degrees of freedom) for fixed effects and covariance parameter estimates for the random effects and the repeated measure. Bold type indicates that values are significant at the $P < 0.05$.

Environmental Drivers	R_{soil}	YEAR	
	Variable	2006	2007
Fixed Effects	TYPE	**12.41 (1, 18)**	0.39 (1, 22)
	$T_{soil\ 5}$	**16.30 (1, 156)**	**141.19 (1, 164)**
	$T_{soil\ 5}^{\ 2}$	**6.52 (1, 156)**	
	θ	**2151.05 (1, 164)**	**13.95 (1, 164)**
	$\theta^{\ 2}$		**10.33 (1, 164)**
	LAI_{corr}	**38.88 (1, 156)**	**19.98 (1, 164)**
Random Effects σ^2	BLOCK	0.06	
	PLOTID (TYPE X BLOCK)	0.001	0.03
Repeated Measure σ^2		0.41	2.5

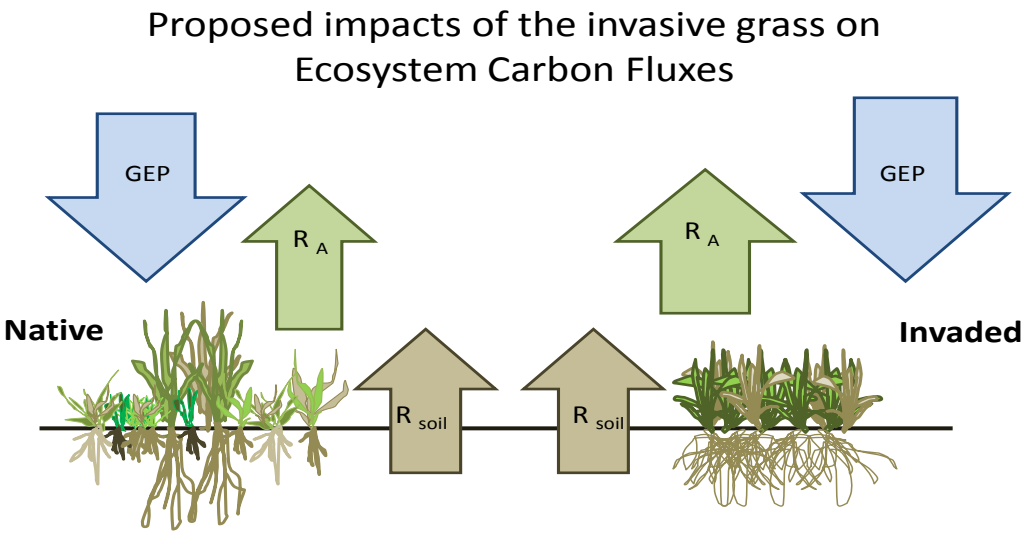

Figure 3.1. Predicted impacts of *B. ischaemum* invasion on ecosystem carbon fluxes.

We predicted that lower gross ecosystem productivity (GEP) and higher ecosystem respiration rates (R_{eco}; the sum of soil respiration, R_{soil}, and aboveground autotrophic respiration, R_A) would result in lower net ecosystem carbon uptake (NEE = GEP - R_{eco}) in invaded areas.

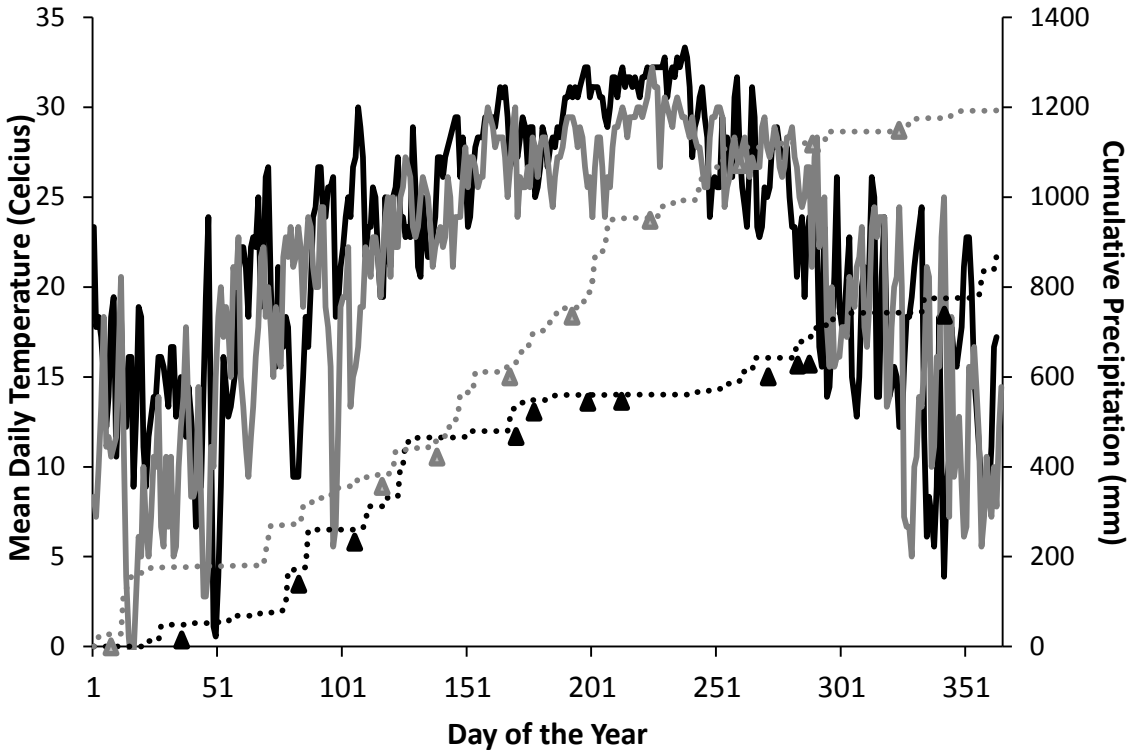

Figure 3.2. Mean daily temperature and cumulative precipitation during the study.

Mean daily temperatures in 2006 (solid black lines) and 2007 (solid grey lines) and annual cumulative precipitation during 2006 (dashed black lines) and 2007 (dashed grey lines) for Austin, TX (NCDC, weather station data for Austin Bergstrom Airport, Austin, TX). Dates of net ecosystem exchange (NEE) and soil respiration (R_{soil}) chamber measurements are indicated by solid black triangles for 2006 and solid grey triangles for 2007.

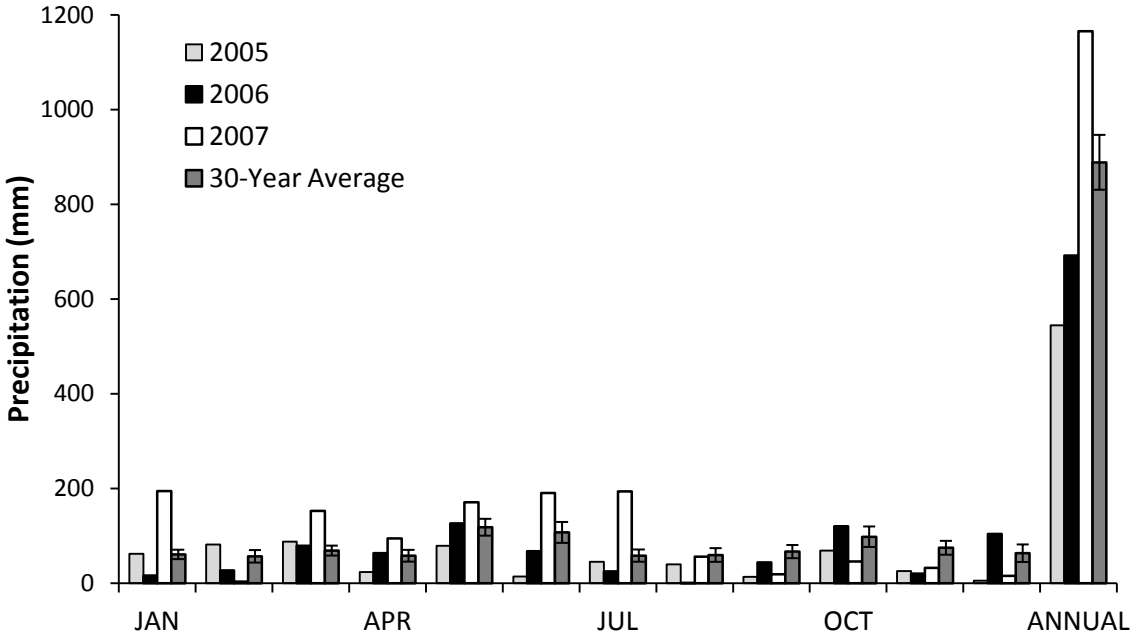

Figure 3.3. Total monthly and annual precipitation

Total monthly and annual precipitation recorded in 2005 (light grey bars), 2006 (black bars), and 2007(white bars) and averaged over 30 years (dark grey bars; 1978-2008) from data collected at Austin Bergstrom International Airport, Austin, TX. Error bars are ± 1 SE. The precipitation distribution was bimodal in 2006 and continuous in 2007. Both precipitation distribution patterns are common in this ecosystem.

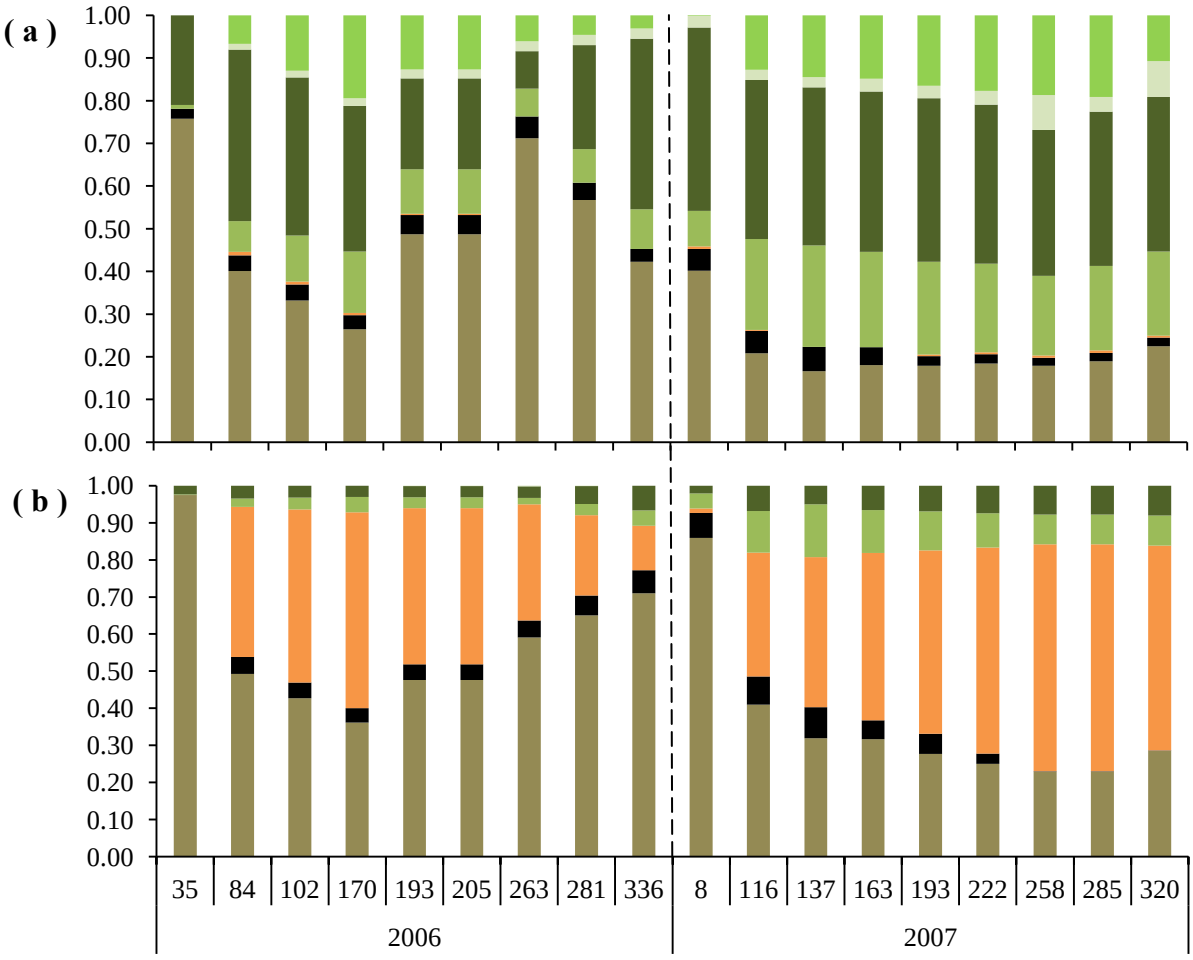

Figure 3.4. Seasonal changes in aerial cover in invaded and native plots at the WFC.

Aerial cover presented as proportions in (a) native and (b) invaded savanna grass-matrix plots at the WFC during the dry (2006) and wet (2007) growing seasons at the WFC. Values are sampling date averages for native mid-C_4 grass ( ), native short C_4 grass ( ), native C_3 grass ( ), forb ( ), *B. ischaemum* ( ), bare ground ( ), and standing dead ( ) aerial cover.

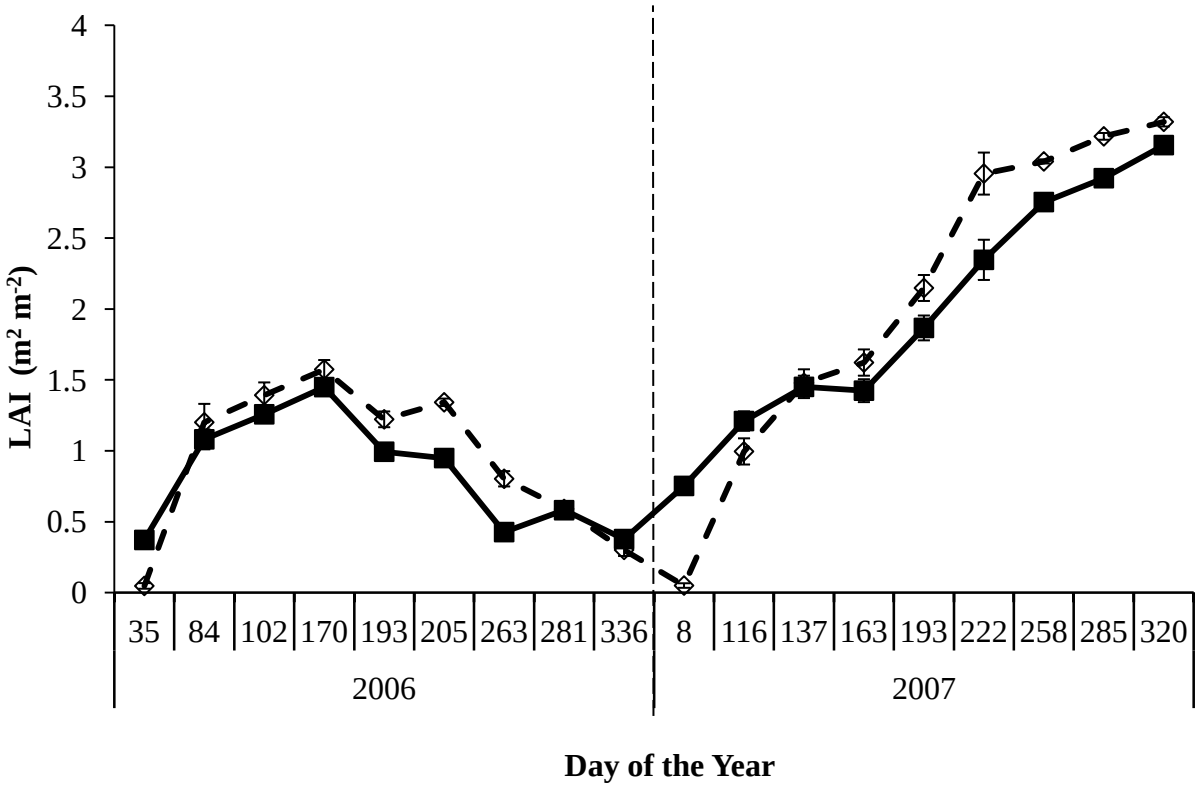

Figure 3.5. Leaf area index measured in invaded and native plots during 2006 and 2007.

Leaf are index (LAI; m^2 leaf m^{-2} ground) in invaded (open diamonds, dashed lines) and native (solid squares, solid line) plots as a function of Julian day-of-the-year during the 2006 (dry) and 2007 (wet) growing seasons at the WFC. Values are sampling date averages; error bars are ± 1 SE.

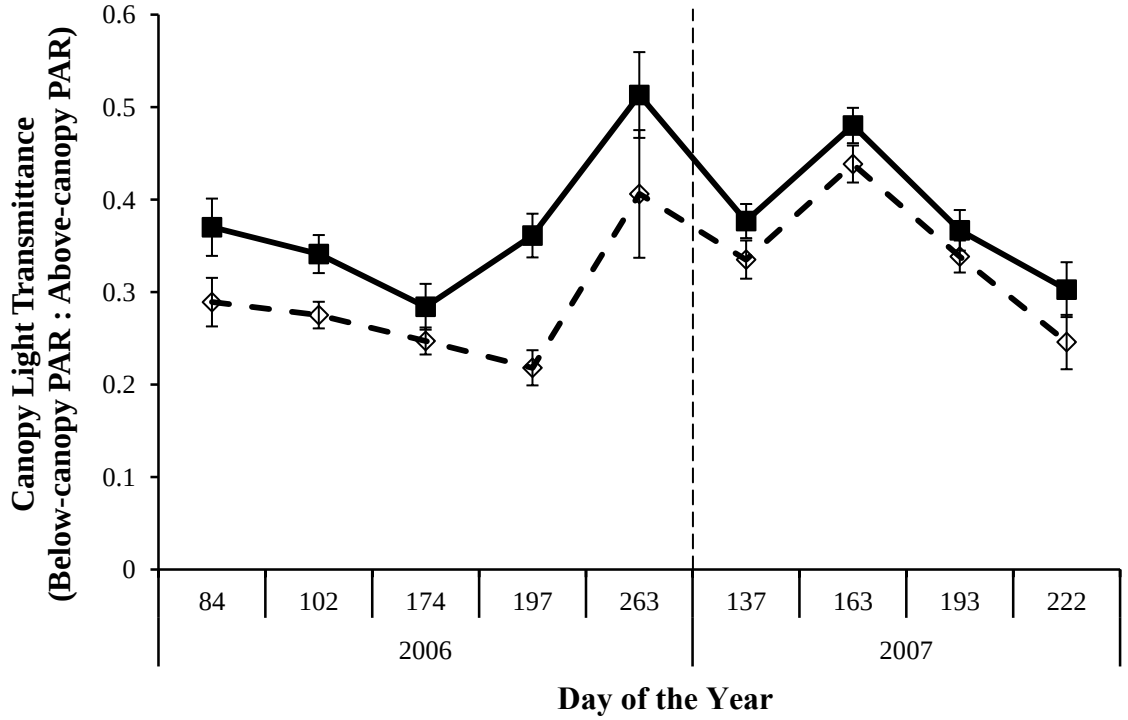

Figure 3.6. Plant canopy light transmittance measured in invaded and native plots.

Plant canopy light transmittance measured in invaded (open diamonds, dashed line) and native (solid squares, solid line) plots during the dry (2006) and wet (2007) growing seasons at the WFC. Values are sampling date means ± 1 SE.

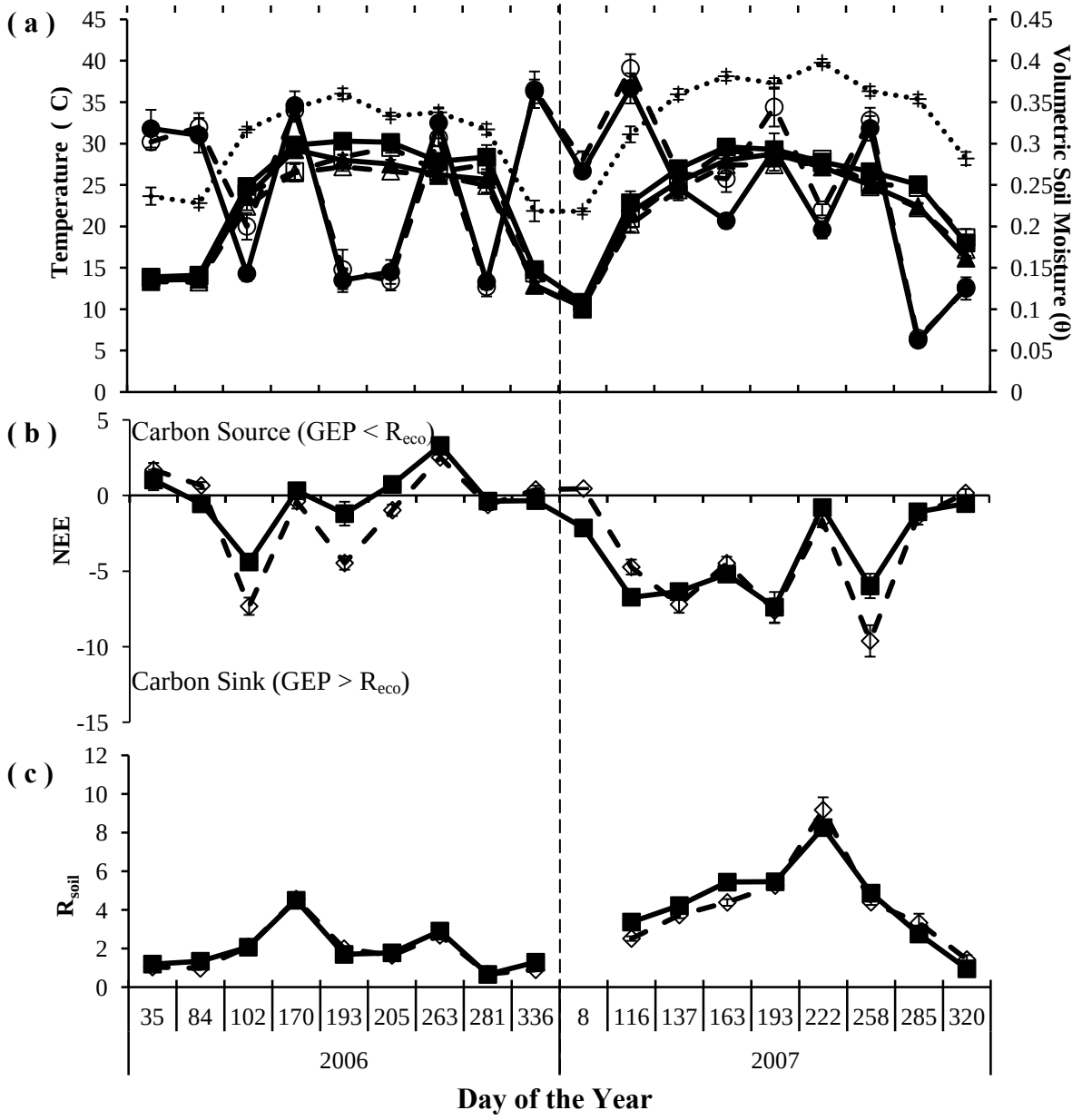

Figure 3.7. Environmental drivers, soil respiration and net ecosystem carbon exchange in native and invaded plots at the WFC during 2006 and 2007.

Environmental drivers (a) air temperature (°C; +, dotted line), soil temperature at 2 (°C; squares, solid line) and 5 (°C; triangles, solid line) cm, and volumetric soil moisture (θ; circles) from 0 - 10 cm in invaded (open symbols, dashed line) and native (solid symbols, solid lines) plots at WFC during the dry (2006) and wet (2007) years. (b) Net ecosystem exchange (NEE; µmol CO_2 m^{-2} s^{-1}) and (c) soil respiration (R_{soil}; µmol CO_2 m^{-2} s^{-1}) in invaded (diamonds, dashed lines) and native (squares, solid lines) plots. Negative NEE values indicate net uptake of CO_2 (photosynthesis > respiration). Values are means ± 1 SE.

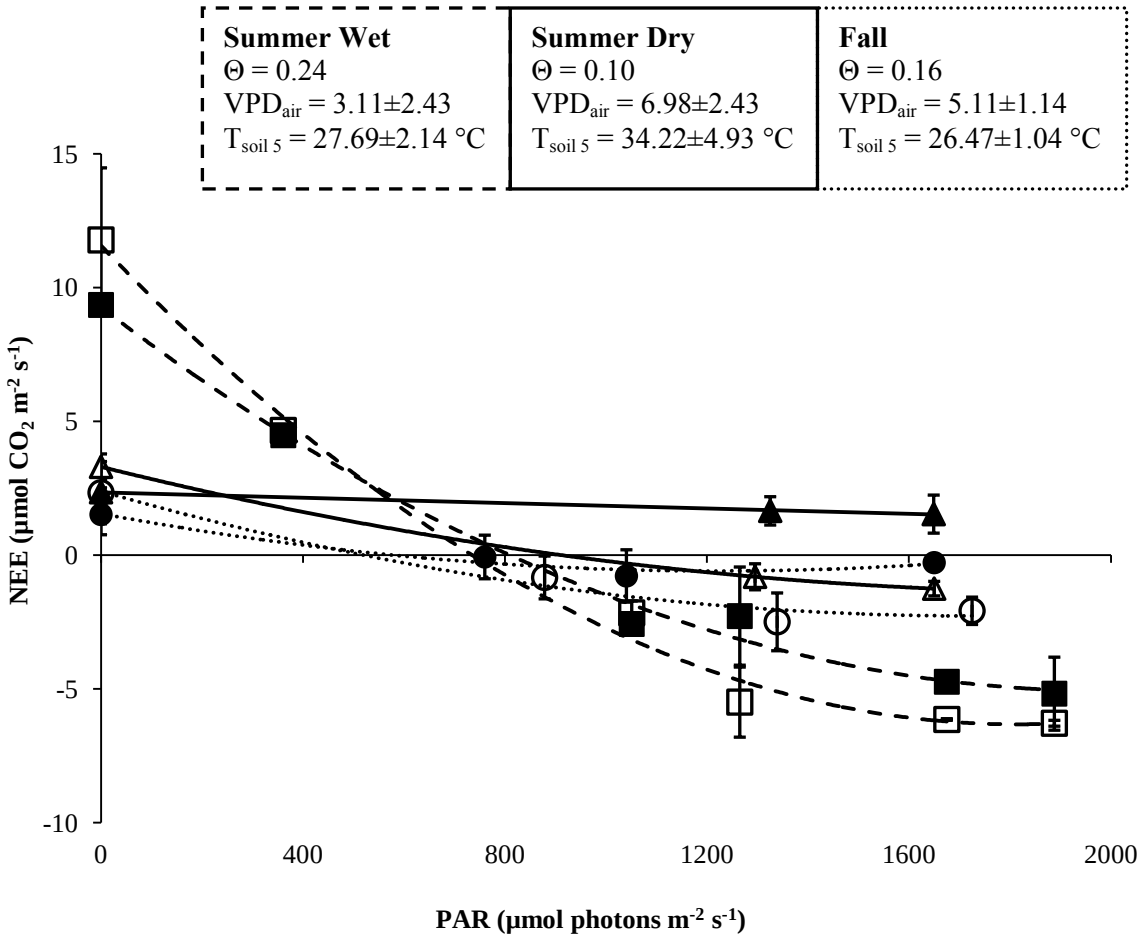

Figure 3.8. Diurnal net ecosystem exchange (NEE) measurements presented as a function of photosynthetically active radiation (PAR).

Diurnal changes in NEE as a function of photosynthetically active radiation (PAR) for three dates: summer wet season (June 23, 2006; Native = solid squares; Invaded = open squares; dashed lines), summer dry season (July 16, 2006; Native = solid triangles; Invaded = open triangles, dashed line) and early fall (October 1, 2006; Native = solid circles; Invaded = open circles, dotted line). Environmental conditions for each set of measurements are reported in the boxes located at the top of the graph. Negative NEE values indicate net uptake of CO_2 (photosynthesis > respiration).

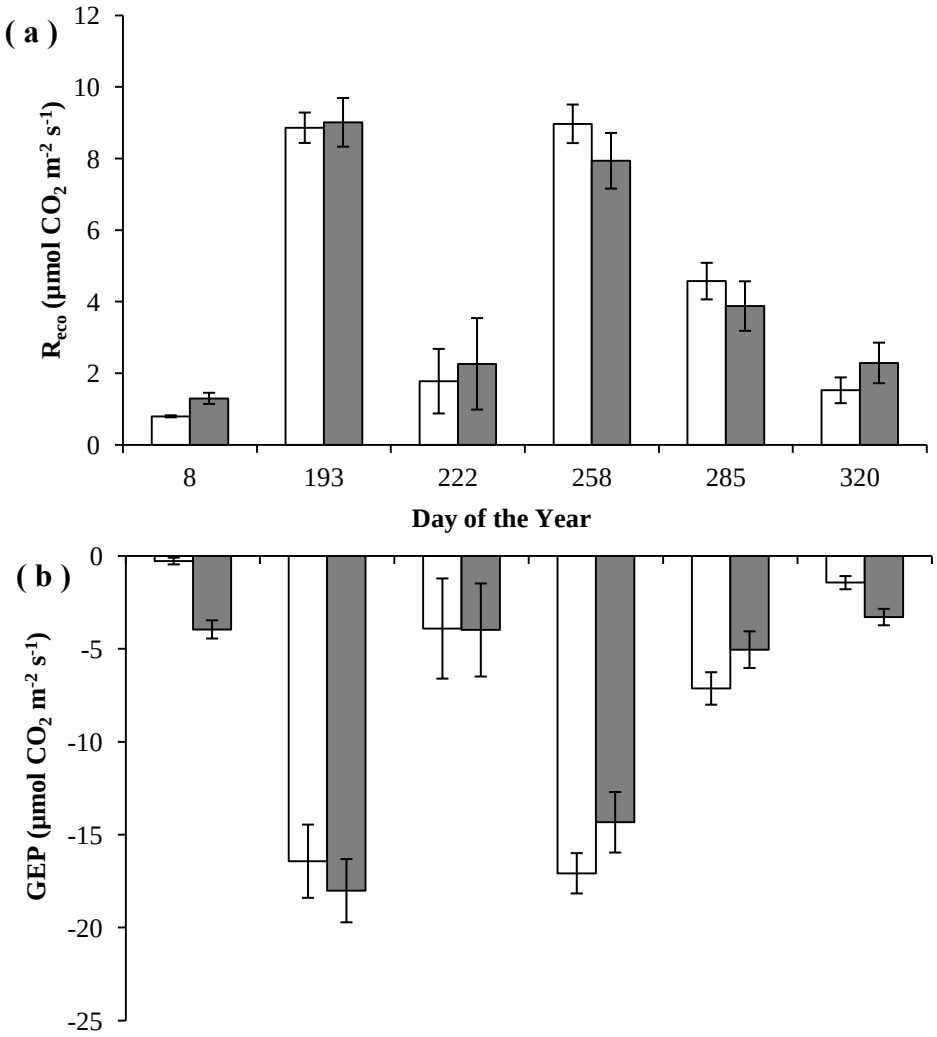

Figure 3.9. Day-time ecosystem respiration and gross ecosystem productivity measured in invaded and native plots during 2007.

Measured day-time (a) ecosystem respiration (R_{eco}) and (b) estimated gross ecosystem productivity (GEP) in invaded (white bars) and native (dark grey bars) plots at the WFC during the 2007 growing season. Values are sampling date means ± 1 SE. N = 6.

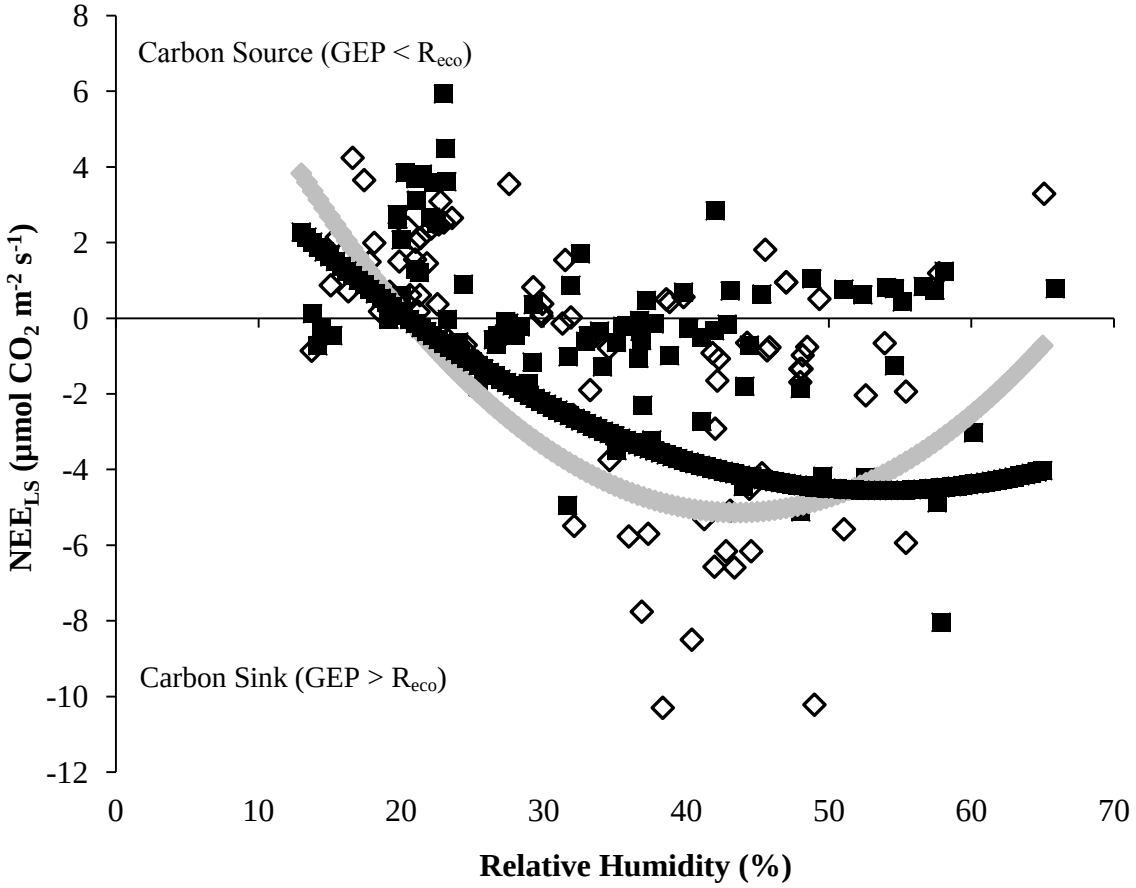

Figure 3.10. Light-saturated net ecosystem exchange (NEE_{LS}) measured at the WFC in 2006 as a function of relative humidity (RH).

NEE_{LS} in invaded (open diamonds, gray line) and native (solid squares, black line) plots as a function of RH for measurements made during the 2006 growing season. Lines are model fit equations (Table 3.8) solved using plot *type* mean values for air (T_{air}) and soil ($T_{soil\ 5}$) temperature. Negative NEE values indicate net uptake of CO_2 from the atmosphere (photosynthesis [GEP] > respiration [R_{eco}]).

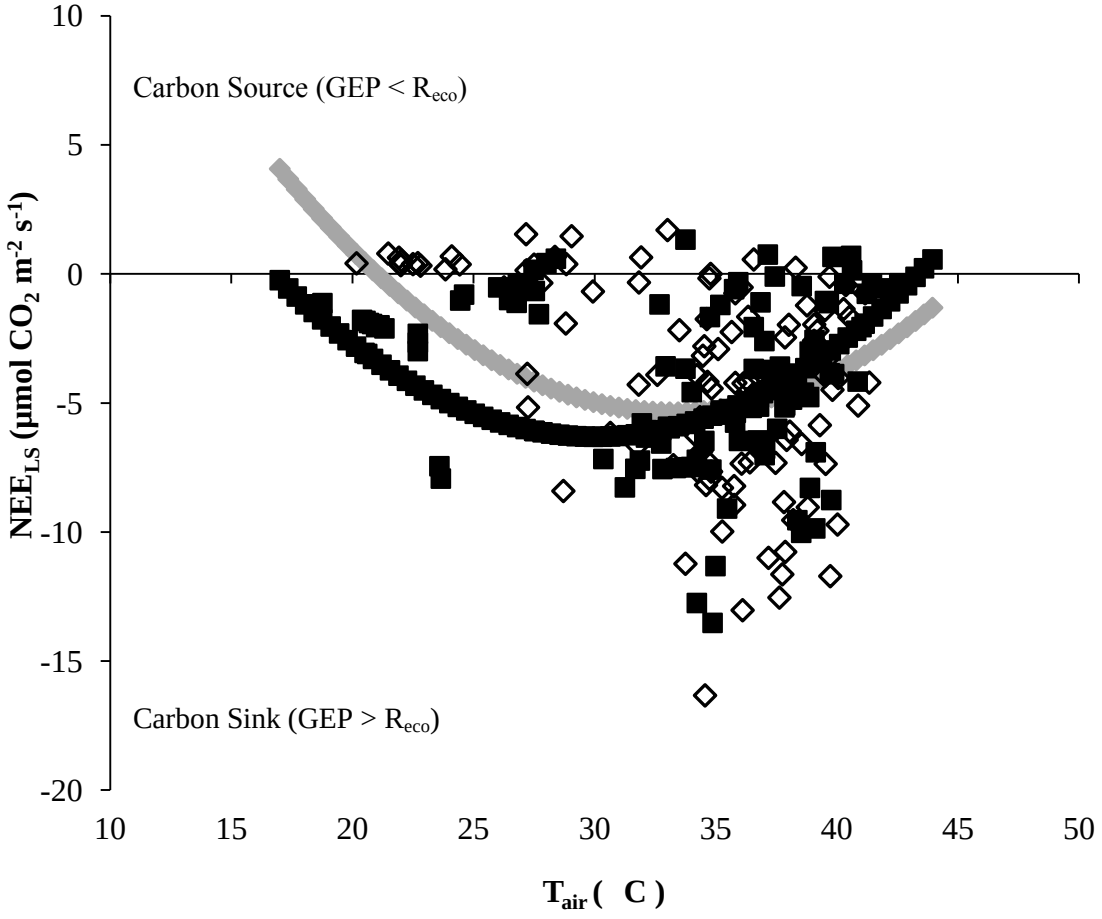

Figure 3.11. Light-saturated net ecosystem exchange (NEE_{LS}) measured at the WFC in 2007 as a function of air temperature (T_{air}).

NEE_{LS} in invaded (open diamonds, gray line) and native (solid squares, black line) plots as a function of T_{air} for measurements made during the 2007 growing season. Lines are model fit equations (Table 3.8) solved using mean values for soil temperature ($T_{soil\ 5}$) and volumetric soil moisture (θ). Negative NEE values indicate net uptake of CO_2 from the atmosphere (photosynthesis [GEP] > respiration [R_{eco}]). NOTE: X-axis starts at 10 °C not at 0.

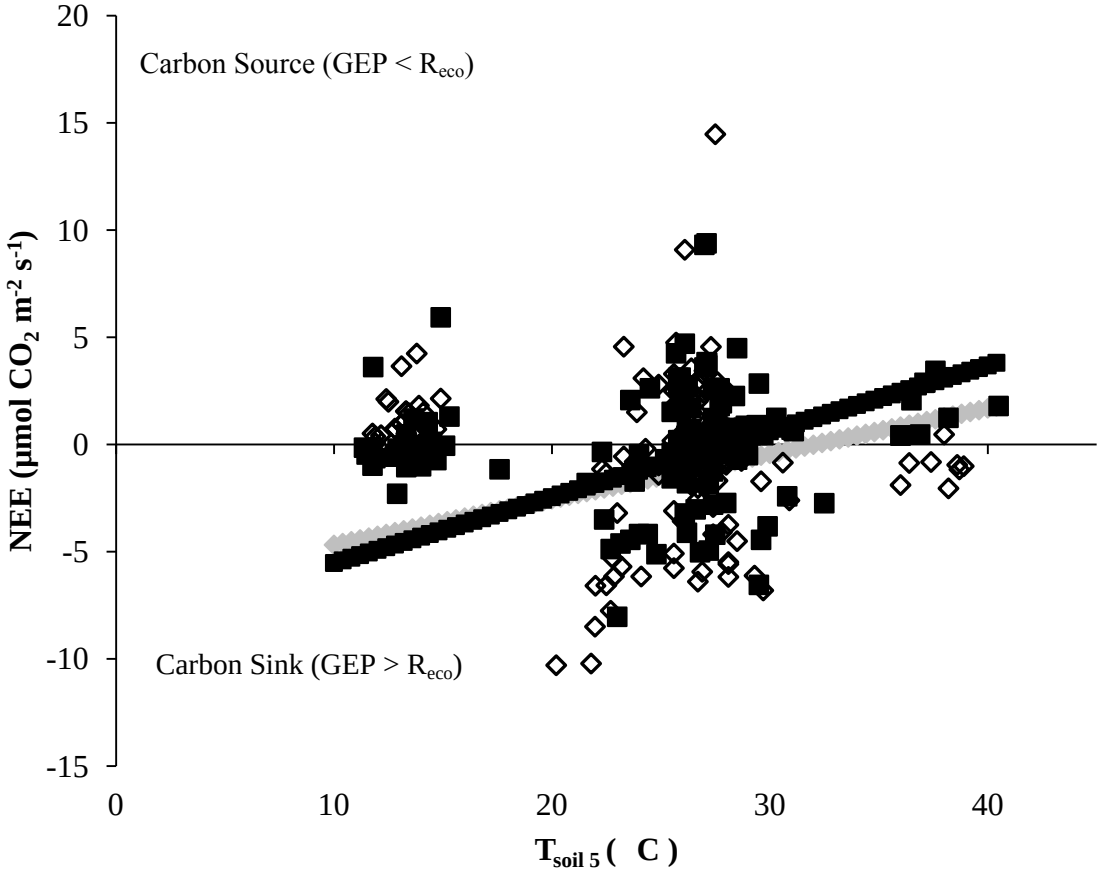

Figure 3.12. Net ecosystem exchange (NEE) measured at the WFC in 2006 as a function of soil temperature at 5 cm ($T_{soil\ 5}$).

NEE in invaded (open diamonds, gray line) and native (solid squares, black line) plots as a function of $T_{soil\ 5}$ for all measurements (light-saturated and not) made during the 2006 growing season. Lines are model fit equations (Table 3.9) solved using plot type mean values for photosynthetically active radiation (PAR), air temperature (T_{air}), volumetric soil moisture (θ), relative humidity (RH), and green leaf area index (LAI_{corr}). Negative NEE values indicate net uptake of CO_2 from the atmosphere (photosynthesis [GEP] > respiration [R_{eco}]).

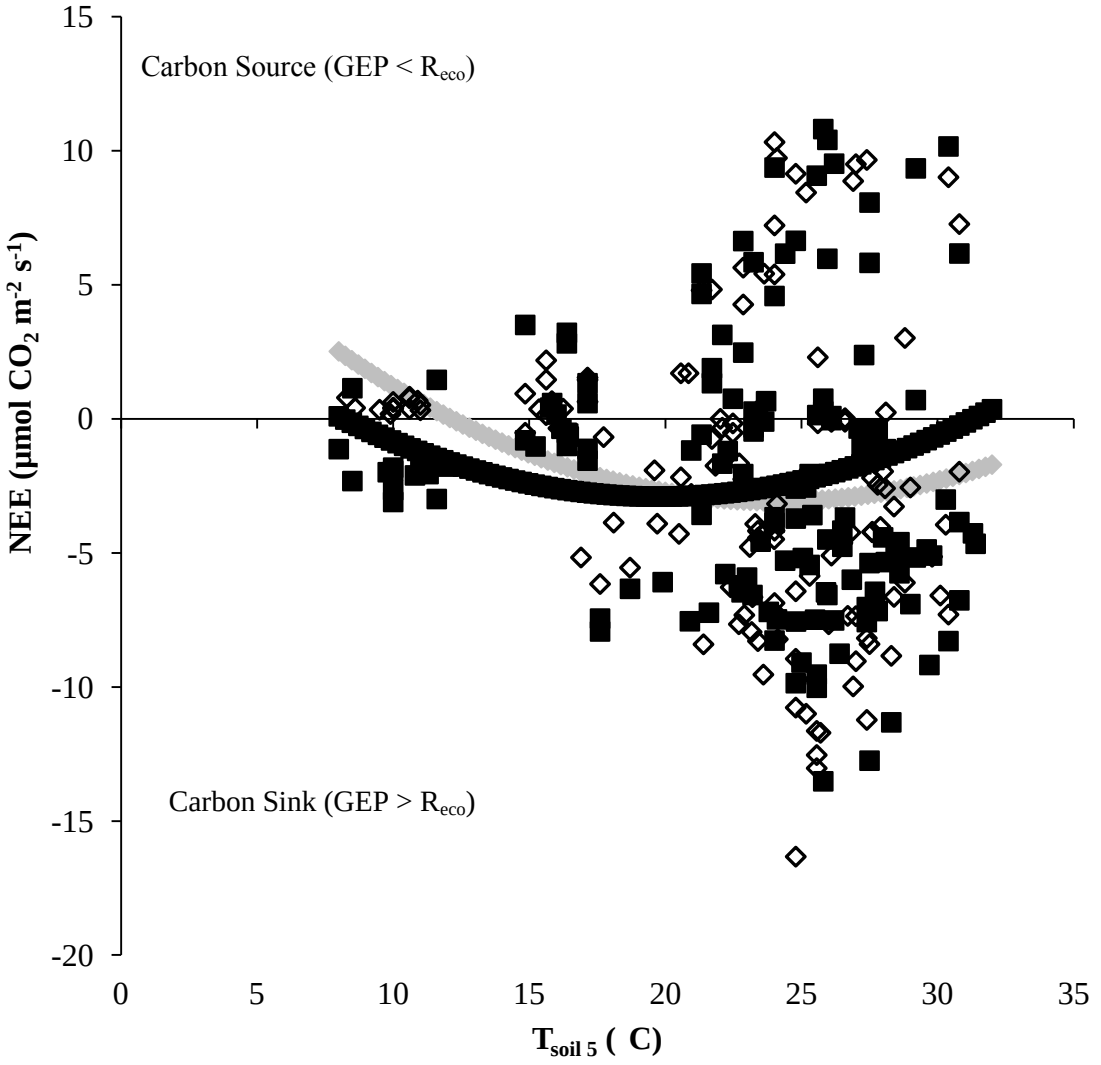

Figure 3.13. Net ecosystem exchange (NEE) measured at the WFC in 2007 as a function of soil temperature at 5 cm ($T_{soil\ 5}$).

NEE in invaded (open diamonds, gray line) and native (solid squares, black line) plots as a function of $T_{soil\ 5}$ for all measurements (light-saturated and not) made during the 2007 growing season. Lines are model fit equations (Table 3.9) solved using plot type mean values for photosynthetically active radiation (PAR), air vapor pressure deficit (VPD_{air}), volumetric, and green leaf area index (LAI_{corr}). Negative NEE values indicate net uptake of CO_2 from the atmosphere (photosynthesis [GEP] > respiration [R_{eco}]).

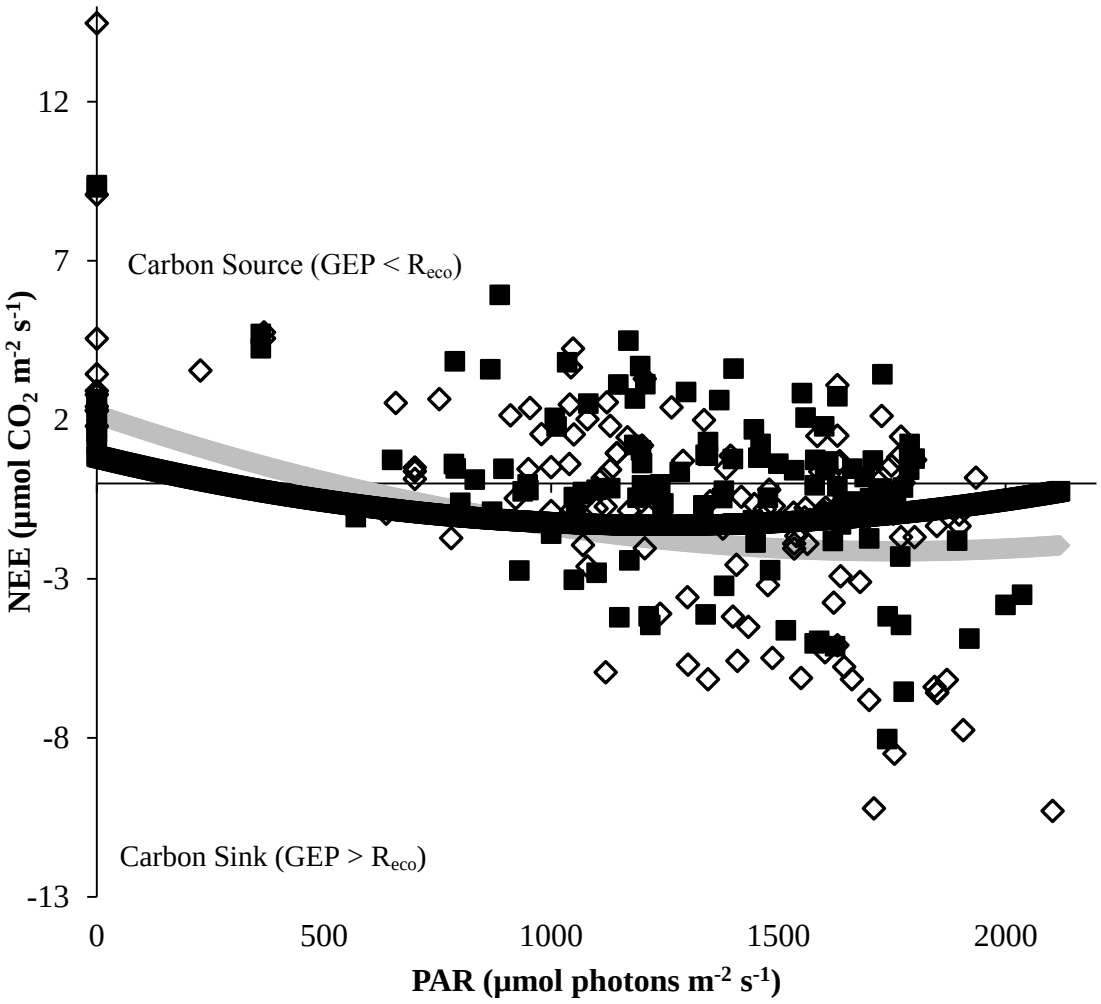

Figure 3.14. Net ecosystem exchange (NEE) measured at the WFC in 2006 as a function of photosynthetically active radiation (PAR).

NEE in invaded (open diamonds, gray line) and native (solid squares, black line) plots as a function of PAR for all measurements (light-saturated and not) made during the 2006 growing season. Lines are model fit equations (Table 3.9) solved using plot type mean values for soil ($T_{soil\ 5}$) and air (T_{air}) temperature, volumetric soil moisture (θ), relative humidity (RH), and green leaf area index (LAI_{corr}). Negative NEE values indicate net uptake of CO_2 from the atmosphere (photosynthesis [GEP] > respiration [R_{eco}]).

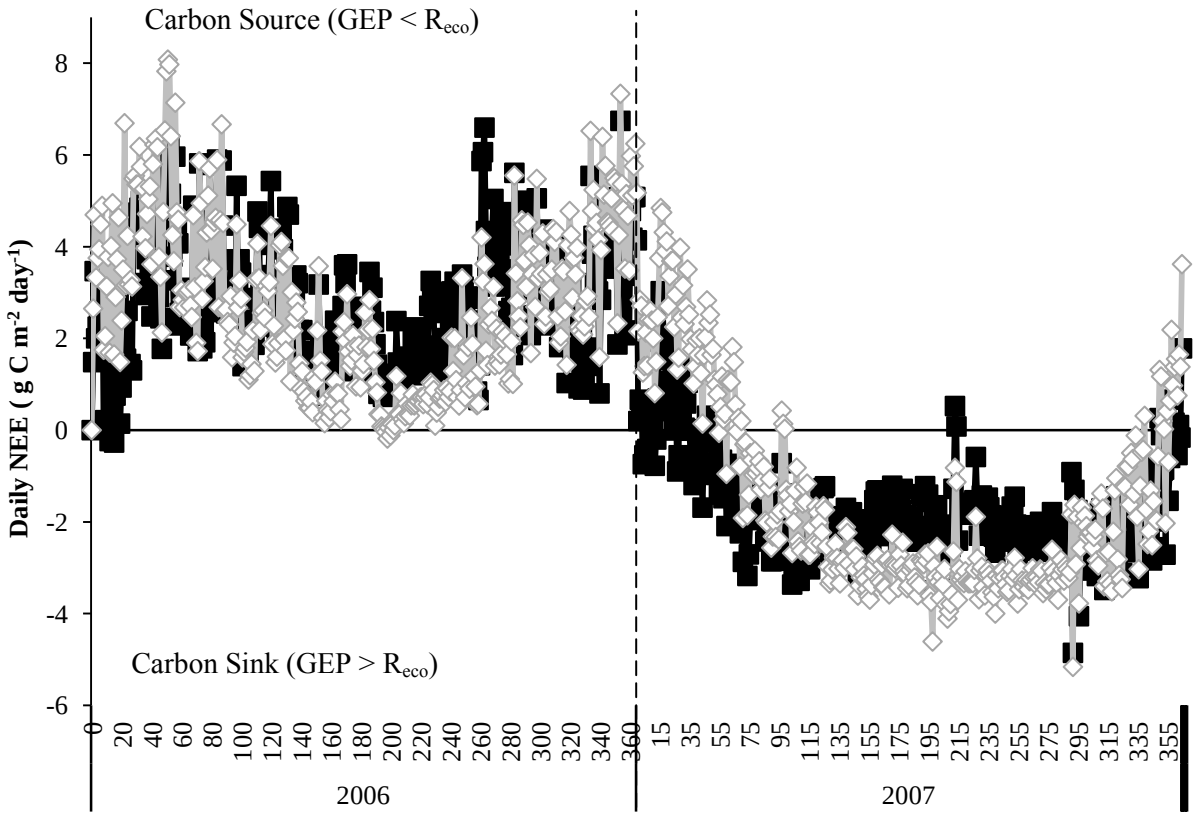

Figure 3.15. Daily net ecosystem carbon exchange (NEE) estimated for 2006 and 2007.

Estimated daily NEE as a function of day of the year for native (black squares, black line) and invaded (white diamonds, gray lines) areas at the WFC for 2006 and 2007. Negative NEE values indicate net uptake of CO_2 from the atmosphere (photosynthesis [GEP] > respiration [R_{eco}]). Daily NEE values were estimated using multiple regression models reported in Table 3.9.

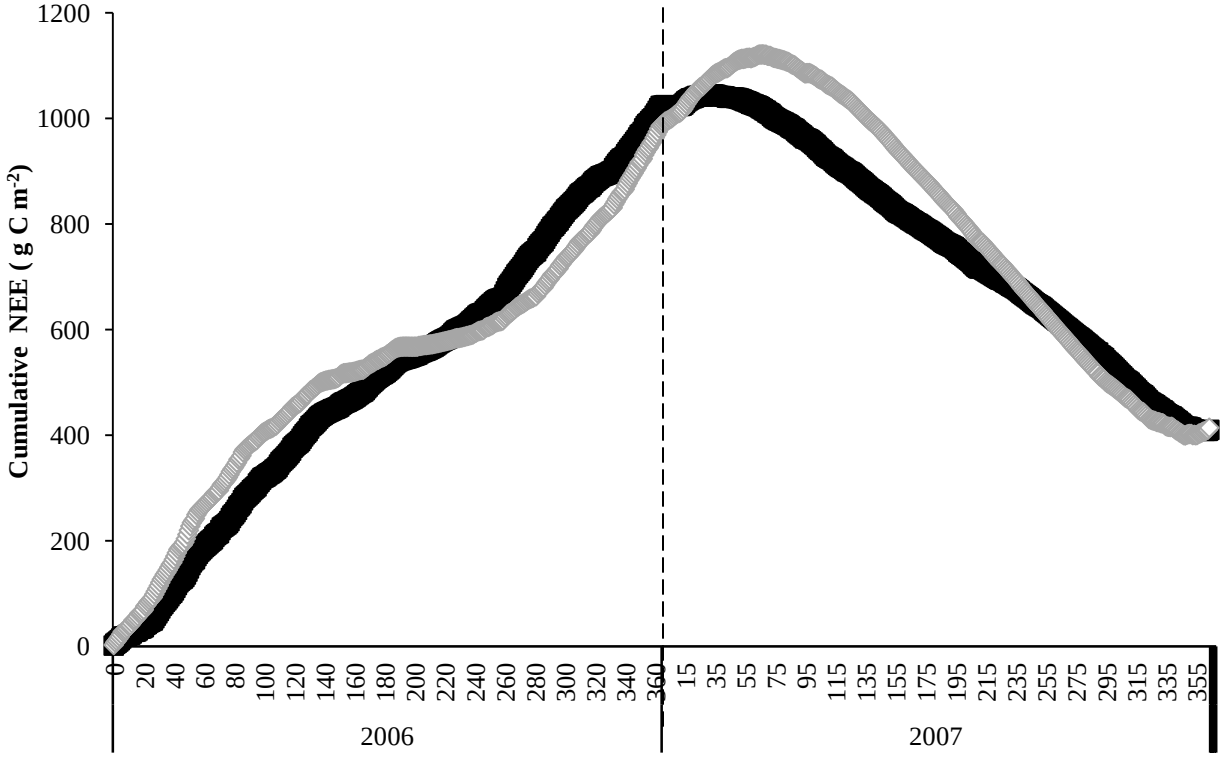

Figure 3.16. Cumulative net ecosystem exchange (NEE) estimated for invaded and native areas at the WFC over a two-year period (2006 – 2007).

Estimated cumulative NEE as a function of day of the year for native (black squares, black line) and invaded (white diamonds, gray lines) areas at the WFC summed over the dry year (2006) and the wet year (2007). Negative NEE values indicate net uptake of carbon (photosynthesis > respiration). Cumulative NEE is the sum of daily NEE estimates over the course of the two years. Daily NEE values were estimated using continuously recorded environmental data, linear regression model estimated green leaf area index (LAI_{corr}; Table 3.2), and the multiple regression models reported in Table 3.9 and.

Discussion

Old World Bluestem grasses and many of the other perennial C_4 grasses that are now considered invasive in the central U.S. were selected for and widely introduced to the central plains of North America as forage species and for soil erosion control because of their ease of establishment, high grazing tolerance, and high productivity (Coyne and Bradford 1985, Donahue 1999). These very traits likely contribute to their success as invaders (Schmidt et al. 2008). Although *B. ischaemum's* success as an invader is not directly related to its ability to cope with precipitation variability and availability, its ability to rapidly produce large amounts of biomass may allow it to directly out-compete native species (Chapter 1). Additionally, its impacts on ecosystem function, e.g., decreased nitrogen availability (Chapter 2), and plant-canopy microhabitat, e.g., decreased grass-canopy light transmittance (Chapter 3), may allow it to exclude native species from invaded areas.

Regardless of how they become dominant in an ecosystem, introduced *Bothriochloa* spp. and other Old World Bluestem grasses have been shown to increase aboveground biomass production in tall grass (Reed et al. 2005) and mid-grass prairies (Berg and Sims 1984, Ruffner et al. 2012). Although few other studies have examined the impacts of these species' invasions on ecosystem function, the ones that do so have concluded that whichever the direction of change in ecosystem function, the major factors instigating those changes are related to increased productivity and changes in plant input quality (Berg and Sims 1984, Reed et al. 2005, Ruffner et al. 2012). In tall-grass prairies, increased aboveground biomass has resulted in larger losses of nitrogen during burns, which has been exacerbated by poorer quality plant inputs from the invasive; together these have lowered nitrogen availability in already naturally low-

nitrogen soils (Reed et al. 2005). In the coastal prairies of Texas, increased aboveground productivity and plant product quality that result from Old World Bluestem grass invasions contribute to increased litter decomposition and N-mineralization rates in invaded areas (Ruffner et al. 2012). In our mixed-grass system, where increased aboveground biomass of poorer quality can increase plant product residence time in standing dead pools and alter microhabitat characteristics, invasion results in lower soil nitrogen availability (Chapter 2). In all three cases, higher aboveground productivity is not matched belowground, which has the potential to alter soil C dynamics in invaded areas. This shift in productivity from belowground to aboveground could have negative implications for ecosystem carbon storage, as was found to be the case for *Agropyron cristatum* in the northern-central plains (Christian and Wilson 1999). The reverse has been found for introduced African grasses that increase belowground productivity (Wiliams and Baruch 2000).

While the exact mechanism by which *Bothriochloa* spp. impact ecosystem function may vary from system to system, and even site to site within an ecosystem, increased aboveground productivity, changes in plant product quality, and shifts in the seasonality of nutrient and carbon cycling are likely impacts of the introduction of all Old World Bluestem grasses into central US grasslands. The degree and direction of *Bothriochloa* spp. impacts on ecosystem carbon and nitrogen cycling depend largely on two factors: (1) timing and variability of precipitation and (2) the initial species composition of the invaded ecosystem. Thus the impacts of these invasive species will vary from year to year and may be site-specific.

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