**Cover Sheet for Proposal to the National Science Foundation**

**Program Announcement/Solicitation No./Closing Date:** Not in response to a program announcement/solicitation enter NSF 04-23

**PD 04-7381**  
**01/09/05**

**For Consideration by NSF Organization Unit(s):** DEB - Ecosystem Science Cluster

**Division Assigned:**

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<th>Number of Copies</th>
<th>Division Assigned</th>
<th>Fund Code</th>
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**Employer Identification Number (EIN) or Taxpayer Identification Number (TIN):** 846000545

**Name of Organization to Which Award Should Be Made:** Colorado State University

**Awardee Organization Code (If Known):** 0013508000

**Address of Awardee Organization, Including 9 Digit Zip Code:**  
Colorado State University  
Fort Collins, CO. 805232002

**Title of Proposed Project:** Collaborative Research: Convergence and contingencies in savanna grasslands

**Requested Amount:** $452,672  
**Proposed Duration (1-60 Months):** 36 months  
**Requested Starting Date:** 09/01/05  
**Show Related Preliminary Proposal No. If Applicable:**

**Check Appropriate Box(es) If This Proposal Includes Any of the Items Listed Below:**

- Beginning Investigator (GPG I.A)
-Disclosure of Lobbying Activities (GPG II.C)
-Proprietary & Privileged Information (GPG I.B, II.C.1.d)
-Historic Places (GPG II.C.2.i)
-Small Grant for Explor. Research (SGER) (GPG II.D.1)
-Vertebrate Animals (GPG II.D.5) IACUC App. Date

**PI/PD Department:** Department of Biology  
**PI/PD Postal Address:**  
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Ft. Collins, CO 80523  
United States

**PI/PD Fax Number:** 970-491-0649

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**Show High Resolution Graphics/Other Graphics Where Exact Color Representation Is Required for Proper Interpretation (GPG I.E.1):**

**Electronic Signature:**

0516094
**Title of Proposed Project:** Collaborative Research: Convergence and contingencies in savanna grasslands

**Requested Amount:** $76,732

**Proposed Duration:** 36 months

**Requested Starting Date:** 09/01/05

**SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE**

**CHECK APPROPRIATE BOXES IF THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW**

- BEGINNING INVESTIGATOR (GPG I.A)
- DISCLOSURE OF LOBBYING ACTIVITIES (GPG II.C)
- PROPRIETARY & PRIVILEGED INFORMATION (GPG I.B, II.C.1.d)
- HISTORIC PLACES (GPG II.C.2.i)
- SMALL GRANT FOR EXPLOR. RESEARCH (SGER) (GPG II.D.1)
- VERTEBRATE ANIMALS (GPG II.D.5) IACUC App. Date

- HUMAN SUBJECTS (GPG II.D.6) Exemption Subsection
- INTERNATIONAL COOPERATIVE ACTIVITIES: COUNTRY/COUNTRIES INVOLVED (GPG II.C.2.g.(iv).(c))
- HIGH RESOLUTION GRAPHICS/OTHER GRAPHICS WHERE EXACT COLOR REPRESENTATION IS REQUIRED FOR PROPER INTERPRETATION (GPG I.E.1)

**Department of Biology**

**PI/PD Department**

**PI/PD Fax Number**

**PI/PD Name**

**PI/PD Postal Address**

**Names (Typed)**

**Telephone Number**

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**Scott L Collins**

**PhD**

**1981**

**505-277-6303**

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**Collaborative research: Convergence and contingencies in savanna grasslands**

**Requested Amount**: $267,021  
**Proposed Duration (1-60 months)**: 36 months  
**Requested Starting Date**: 09/01/05  
**Show Related Preliminary Proposal No. If Applicable**

- Beginning Investigator (GPG I.A)
- Disclosure of Lobbying Activities (GPG II.C)
- Proprietary & Privileged Information (GPG I.B, II.C.1.d)
- Historic Places (GPG II.C.2.i)
- Small Grant for Explor. Research (SGER) (GPG II.D.1)
- Vertebrate Animals (GPG II.D.5) IACUC App. Date
- Human Subjects (GPG II.D.6) Exemption Subsection or IRB App. Date
- International Cooperative Activities: Country/Countries Involved (GPG II.C.2.g.(iv).(c))
- High Resolution Graphics/Other Graphics Where Exact Color Representation Is Required For Proper Interpretation (GPG I.E.1)
- Small Business
- For-Profit Organization
- Minority Business
- Woman-Owned Business
- If This Is a Preliminary Proposal Then Check Here

**PI/PD Department**: Ecology and Evolutionary Biology  
**PI/PD Postal Address**: New Haven, CT 065208337 United States

**PI/PD Name**: Melinda Smith  
**High Degree**: PhD  
**Year of Degree**: 2002  
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**Cover Sheet for Proposal to the National Science Foundation**

**Program Announcement/Solicitation No./Closing Date:**

**PD 04-7381**

**Date Received:** 01/09/05

**For Consideration by NSF Organization Unit(s):** DEB - Ecosystem Science Cluster

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**Name of Organization to Which Award Should Be Made:**

Kansas State University

**AWardee Organization Code (If Known):** 001928100

**Name of Performing Organization, If Different From Above:**

Kansas State University

**Address of Performing Organization, If Different, Including 9 Digit Zip Code:**

2 Fairchild Hall
Manhattan, KS. 665061103

**Performing Organization Code (If Known):**

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**Title of Proposed Project:**

Collaborative Research: Convergence and Contingencies in Savanna Grasslands

**Requested Amount:** $185,662

**Proposed Duration (1-60 Months):** 36 months

**Requested Starting Date:** 09/01/05

**Check Appropriate Box(es) If This Proposal Includes Any of the Items Listed Below:**

- [ ] Beginning Investigator (GPG I.A)
- [ ] Disclosure of Lobbying Activities (GPG II.C)
- [ ] Proprietary & Privileged Information (GPG I.B, II.C.1.d)
- [ ] Historic Places (GPG II.C.2.i)
- [ ] Small Grant for Explor. Research (SGER) (GPG II.D.1)
- [ ] Vertebrate Animals (GPG II.D.5) IACUC App. Date

**Check Appropriately If This Proposal Includes Any of the Items Listed Below:**

- [ ] Human Subjects (GPG II.D.6) Exemption Subsection or IRB App. Date
- [ ] International Cooperative Activities: Country/Countries Involved (GPG II.C.2.g.(iv).c) SF
- [ ] High Resolution Graphics/Other Graphics Where Exact Color Representation Is Required for Proper Interpretation (GPG I.E.1)

**PI/PD Name:**

John M Blair Ph.D. 1987 785-532-7065 jblair@ksu.edu

**Division of Biology**

---

**Electronic Signature**
Collaborative Research: Convergence and contingencies in savanna grasslands.

Savanna grassland distribution, structure and function are a product of three interacting drivers - fire, grazing by large herbivores, and extreme climatic fluctuations. Although all savanna grasslands share these drivers, evidence suggests that fire and grazing affect ecosystem structure and function in fundamentally different ways in southern Africa (South Africa (SA), in particular) and North America (NA). These differences have been attributed to the contingent factors of greater age, longer evolutionary history, lower soil fertility, and greater diversity of plants and large herbivores in SA. An alternative hypothesis is that differences in methods and approaches used to study these systems, and a strong NA bias in the number of studies of savanna grasslands, has led to differing perspectives on the role of these drivers. It’s important to differentiate between these alternatives. If the impacts of shared and fundamental ecosystem drivers - fire and grazing regimes, which are being extensively altered by humans worldwide - truly differ with age and evolutionary history, this calls into question our basic understanding of savanna grasslands and our ability to forecast change and maintain ecosystem services. Thus, our goal is to quantify, in directly comparable ways, ecosystem and community responses to fire and grazing in savanna grasslands of SA and NA, and to identify those ecological processes that are similar (convergent), despite potential contingent factors of differing evolutionary history, herbivore diversity and soil fertility. To address this goal most powerfully requires experiments in SA and NA savanna grasslands in which fire and grazing are manipulated similarly and responses are measured at comparable spatial and temporal scales. We propose such experiments, building on three ongoing long-term (20-50+ yr) manipulations of fire and grazing in both NA and SA. These long-term experiments form the centerpiece of our research and provide an unprecedented resource for comparative research, ensuring that the ecological context for interpreting responses is similar. This is a rare opportunity in ecological research at this inter-continental scale, one that to our knowledge exists in no other biome in the world. We will test specific hypotheses related to responses of ecosystem processes (ANPP, N and C cycling) and plant community structure (richness, diversity and dominance) and dynamics (compositional change, species turnover, species associations) to manipulations of 1) fire regime, 2) grazing and fire/grazing interactions, and 3) megaherbivore diversity (1 vs. 14 species). New manipulations and identical sampling approaches in the context of these long-term experiments will allow us to test the general prediction that fire and grazing will differ in their effects on plant community structure and dynamics in NA and SA savanna grasslands - driven by evolutionary diversification of the grasses and the diverse array of megaherbivores extant in SA. However, we expect convergence in responses of ecosystem processes due to shared traits among the consistently dominant C₄ grasses. Thus, we predict that divergence in responses at the community level is not inconsistent with convergence in responses at the ecosystem level. Intellectual Merit: The focus on ecological responses at both the ecosystem and community levels sets our research apart from previous studies. Convergence in structure in unrelated organisms or in distant ecosystems subjected to similar selective regimes has long been of interest to ecologists. However, comparisons of ecological processes and dynamics at more than one hierarchical level in ecosystems with similar structure are required to determine if convergence in function exists. Our research will allow us to identify ecological processes in savanna grasslands that are convergent and those in which underlying differences in age, evolutionary history, and megaherbivore diversity act as contingent factors. Such an assessment, even in a moderate number of ecological processes, will advance our understanding of the functional determinants of savanna grassland ecosystems far beyond that of most biomes. Broader Impacts: Effective conservation and management of savanna grasslands requires an understanding of the fundamental similarities and differences in the impacts of shared drivers, such as fire and grazing, on ecosystem structure and function. Conservation biologists and land managers grapple with how to distill information from disparate studies, thus the synthetic understanding gained through our research can guide the development of management strategies for savanna grasslands worldwide. Our research will provide training and important global and cultural experiences for NA and SA postdoctoral associates, graduate students and undergraduates. Data management and sharing protocols adopted from the LTER program will ensure that information is readily available to our SA colleagues, the scientific community, the general public and educators through a dedicated project web page, as well as through proposed web-based educational activities.
C. Project Description

1. Response to previous reviews

This proposal was submitted to the Ecosystems program (July 2004), but was not reviewed by the panel. Ad hoc reviews were positive, but suggested four major alterations: 1. better justification for site selection, 2. stronger conceptual rationale for predicted differences in community vs. ecosystem level responses, 3. recognition that only two continents were being compared (N. America vs. Africa) which limits generalizations possible, and 4. inclusion of measurements of aboveground NPP in grazed sites. The proposal has been revised to satisfy these concerns and address other minor suggestions. In addition, the budget request has been reduced.

2. Introduction and statement of goals

From a global perspective, the structure and dynamics of most ecosystems are generally determined by one or two abiotic drivers (e.g., Holdridge 1967, Whittaker 1975, Walter 1985). Grassland and savanna ecosystems (hereafter savanna grasslands, see below) are unique in that the interplay of three drivers - fire, grazing by megaherbivores and extreme climatic fluctuations - are recognized as major historic and present-day determinants of their distribution, structure and function (Walker 1985, Archer 1995, Scholes & Archer 1997, Knapp et al. 1998, Oesterheld et al. 1999, Scholes et al. 2003a). Today, human alterations of these drivers are dramatically changing savanna grassland ecosystems worldwide (McPherson 1997, Vitousek et al. 1997, Sala et al. 2000).

Of the drivers important for savanna grasslands, fire and grazing regimes have been most extensively altered (Archer 1989, Eckhardt et al. 2000, van Wilgen et al. 2000, Hoch et al. 2002, Bond et al. 2003). These changes have occurred directly via management (i.e., replacing diverse native herbivores with single grazers or eliminating fire) and indirectly due to landscape fragmentation, shifts in socio-political attitudes/policy, and the extinction of megaherbivores (Reid & Ellis 1995, Leach & Givnish 1996, Hoch et al. 2002, Fuhlendorf & Engle 2001). As a result, many savanna grasslands are endangered (Archer 1989, Sampson & Knopf 1994, Frank et al. 1998, Anderson et al. 1999). A more comprehensive understanding of how these drivers regulate the functioning of these systems is needed to maintain ecosystem services and forecast changes in savanna grasslands in the face of future alterations in these drivers (du Toit et al. 2003, Palmer et al. 2004).

When ecologists attempt to forecast the impacts of changes in ecosystem drivers, the benchmarks used for comparison are the ways in which these drivers determine pattern and processes in “natural” or “pristine” systems – recognizing that no ecosystem is free from human impacts (Vitousek et al. 1997, Palmer et al. 2004). A critical, and usually untested assumption of this paradigm is that these drivers have broadly consistent impacts throughout the biome, allowing for inference beyond specific study sites or geographic regions (Thompson et al. 2001, Dynesius et al. 2004). Scholes et al. (2003a) and others (M. Scholes 2003b, Lusk & Bellingham 2004, Uys et al. 2004) have questioned this assumption for savanna grasslands on a global scale. They argue that although all savanna grasslands share common drivers, the ways in which fire and grazing influence ecosystem structure and function are fundamentally different in southern Africa (South Africa (SA), in particular) as compared to North America (NA) and elsewhere. Differences are attributed to the longer evolutionary history with fire and grazing in SA, reduced soil fertility in these ancient ecosystems, and greater diversity of large herbivores present today in SA (Fig. 1, Scholes et al. 2003a,b, Bond et al. 2003).

Our current understanding of the role of fire, large herbivores and their interactions in savanna grasslands is based on hundreds of ecological studies. There are numerous syntheses of these, usually focused on a particular site or region (Booysen & Tainton 1984, Cole 1986, Collins & Wallace 1990, Scholes & Walker 1993, Knapp et al. 1998, Frank et al. 1998, Milchunas et al. 1988, McNaughton 1983, 1985, du Toit et al. 2003). But such syntheses often fall short of their goals because most studies are conducted independently with methods and approaches that differ considerably (Knapp et al. 2004). This is of particular concern in SA where there is a distinct founder effect in ecological perspective caused by a relatively small scientific community (Scholes et al. 2003a).

Thus, comparisons among studies are difficult if not impossible; especially for ecological attributes that are strongly scale and sampling dependent (e.g., diversity, Scheiner et al. 2000). An additional problem is that studies of savanna grasslands are biased geographically (the Northern Hemisphere
has been more extensively studied - at least in terms of papers published - than the Southern Hemisphere, and the most comprehensive studies have been in the US (former IBP and current LTER sites, Risser et al. 1981, Archer et al. 1988, Knapp et al. 1998, Tilman et al. 2001, Scholes et al. 2003a). The Serengeti is a notable exception where herbivory, but not fire, has been intensively studied (McNaughton 1983, 1985).

This raises important questions about our understanding of savanna grasslands around the world. Is our knowledge of fire and grazing sufficiently general to enable us to make accurate predictions of how ecosystem structure and function will change as these key drivers are altered? Put another way, how much of what we know about savanna grasslands is biased by the North American view? Are the different methods and approaches used in other regions responsible for differing perspectives on the role of these drivers? Or, are the impacts of the drivers on ecological processes truly different in systems with different evolutionary histories (such as NA and SA)? The goal of our research is to quantify, in directly comparable ways, ecosystem and community responses to key ecological drivers (fire and grazing) in savanna grasslands in South Africa and North America, and consequently, to identify those ecological processes that are similar (convergent), despite potential contingent factors of differing evolutionary history, herbivore diversity and soil fertility.

Comparisons of ecological traits in organisms or ecosystems that have been subjected to similar selective regimes in geographically distinct regions have long been of interest to ecologists (Pielou 1979). Convergence - when organismal traits or structural characteristics are similar - is commonly found in these comparisons (Orians & Solbrig 1977, Cody & Mooney 1978, Price et al. 2000), although the evolutionary basis for some well-known examples (e.g., plant traits in Mediterranean ecosystems) has been questioned (Barbour & Minnich 1990, Verdu et al. 2003). Nonetheless, similarity in traits of organisms, communities and ecosystems with different evolutionary histories are common when environments in distant regions are analogous (Cody & Mooney 1978, Mares 1980, Price et al. 2000, Bond & Midgley 2001, Ojeda et al. 2001, Meserve et al. 2003). Far less common are comparative assessments of ecological processes and dynamics, particularly at more than one hierarchical level (i.e., community and ecosystem), in regions where ecosystem structure is convergent. Milchunas et al. (1988) hypothesized that ecological processes should be sensitive to differences in evolutionary history, whereas Paruelo et al. (1998) presented evidence for convergence in ecological processes (i.e., determinants of productivity) in North and South American grasslands.

The focus of our research is on detecting convergence (or divergence) in ecological processes and dynamics at the community and ecosystem level. This distinguishes our approach from previous comparative studies that focus on pattern and structure. Initially, we will constrain our research to comparisons of savanna grassland sites in NA and SA. However, our results will have implications for generalizing across ecosystems with similar physiognomy and drivers, and can serve as a springboard for future comparative studies in other savanna grasslands with divergent evolutionary histories (e.g., South America, Austin & Sala 2002).

There are additional compelling reasons for focusing our comparisons on savanna grasslands in SA and NA. First, the existence of similar, long-term (20-50+ yr) manipulative studies of fire and grazing in both regions (see below) provides an unprecedented resource for comparative research, one that to our knowledge exists in no other biome. Long-term experiments are critical for assessing ecological processes (Brown et al. 2001, Meserve et al. 2003) and to the success of short-term (<5 yr) comparative studies, because they ensure that the ecological context of sites being compared is
known and consistent, a rare phenomenon in ecology. Second, the separate and interactive effects of fire and grazing are not well known in Africa, despite a wealth of research on these drivers independently. Third, collaborations between SA ecologists and the PI’s of this proposal have been established and will be strengthened by the proposed activities (Knapp et al. 2004, see letters of support); such working relationships increase the likelihood of success in such large-scale studies. Finally, from an ecosystem services and conservation perspective, savanna grasslands encompass as much as 40% of the terrestrial land surface, sequester huge deposits of soil C, are economically important as grazing lands, and house much of the world’s remaining great megafauna (Owen-Smith 1988, Schimel et al. 1994, Allen-Diaz 1996, Amthor et al. 1998, Fuhlendorf & Engle 2001). To effectively conserve and manage these ecosystems globally, we must know if there are fundamental differences in the processes that determine ecosystem structure and function, particularly in response to shared drivers such as fire and grazing. This will allow us to determine if management and conservation strategies based on detailed knowledge from intensively studied regions is generally applicable (Lawton 1999) to savanna grasslands worldwide.

Below we briefly compare and contrast savanna grassland structure and function in NA and SA, describe two exceptional long-term (>50 yr) experiments in SA that form the centerpiece of our proposed research, and detail new experiments and data collection that will use directly comparable methods and approaches to integrate SA studies with long-term (> 20 yr) experiments at the Konza Prairie Biological Station (KPBS) in the US, a site with a long history of fire and grazing studies (Knapp et al. 1998).

3. Grasslands, savannas and savanna grasslands

Grasslands and savannas span a broad climatic gradient on most continents, and overlap considerably in structure and function (Walter 1985, Scholes & Archer 1997, Lauenroth et al. 1999, Oesterheld et al. 1999). Indeed, more than one author has noted that their distinction as separate biomes is “fuzzy” (Scholes & Walker 1993, McPherson 1997, Oesterheld et al. 1999), since as precipitation increases in these systems that lie between deserts and forest, herbaceous plant cover and biomass, and the density and height of shrubs and trees, increases until forest occurs. In NA, ecologists differ in their recognition of savanna as a separate biome (Anderson et al. 1999) with some assigning ecosystems with continuous grass cover and scattered trees (the common definition of savanna) as grasslands or open woodlands, avoiding the term savanna altogether (Barbour & Billings 1988). Others map most of the southwest, intermountain and southeastern US as present-day or potential savanna (McPherson 1997). In regions such as Africa, savanna (or “bush”) – ecosystems with clear shrub/grass coexistence – occurs over vast areas, grading from xeric shrublands to woodland to forest. These African ecosystems are strikingly similar to the mesic grasslands of the central US (Photo 1), which also have a significant woody plant component (shrubs or trees). Thus, although these ecosystems are commonly distinguished as separate biomes, structurally they are quite similar (Oesterheld et al. 1999). We will refer to these ecosystems as savanna grasslands (sensu Scholes & Archer 1997, i.e., a continuous grass layer with scattered shrubs and trees). Tallgrass prairie in the US fits this definition (Photo 1), with the exception of sites burned annually for many years where woody plants are much reduced (Briggs et al. 2002). Not surprisingly, woody plant density is also strongly reduced in annually burned savannas in SA (Enslin et al. 2000), thus, these could also be described as grasslands.

The rationale for considering savannas and grasslands as a single ecological unit is strengthened further by three shared determinants of their ecological properties and dynamics: climate and climate
variability, periodic fire, and herbivory by large mammals (Fig. 1, Scholes 1993, Knapp et al. 1998, Frank et al. 1998, Scholes et al. 2003a, Bond et al. 2003). Historically, herbivores included a diverse array of grazers (graminoid consumers) and browsers (consumers of forbs and woody plants; Axelrod 1985, du Toit 2003), but these now are often reduced to a subset or a single grazer (Hobbs & Huenneke 1992, Olf et al. 2002, but see Keesing 2000 and Howe et al. 2002 for the role of small mammals). The relative importance of fire varies from dry to mesic savanna grasslands, with fire frequency increasing as precipitation and fuel loads increase (Anderson 1990, Oesterheld et al. 1999), whereas climatic variability and grazing are important throughout.

The focus of this proposal is the mesic portion of the grassland/savanna continuum (precipitation >600 mm) where all three drivers are important separately and interactively, often in complex ways. However, of the three drivers, climate and climatic variability appear to have the most consistent impact (Knapp et al. 2002, Scholes et al. 2003a), producing similar responses to interannual variation in rainfall in both NA and SA (Sala et al. 1988, Snyman 2000), and with droughts and floods recognized as important events ecologically and evolutionarily (Tilman & El-Haddi 1982, Hayden 1998, du Toit et al. 2003). Therefore, our proposed research focuses on fire and grazing. As described below, it is the opportunity to manipulate fire and grazing independently and in tandem that will allow us to expand upon previous ground-breaking studies of large ungulate herbivory in savanna grasslands (McNaughton 1983, 1985, Frank et al. 1998).

4. Fire and grazing as determinants of ecosystem processes and structure in NA and SA

Given our overarching goal of comparing how fire and grazing impact ecosystem processes and community dynamics in SA vs. NA mesic savanna grasslands, a brief review of key attributes of these systems is warranted. For brevity, we summarize similarities (Table 1) and differences (Table 2), and then note important disparities reported in responses of NA and SA savanna grasslands to fire and grazing. It is these differences that have led to the notion that these drivers impact ecosystems differently in SA.

Annual precipitation amounts and patterns are strikingly similar between NA and SA savanna grasslands (Fig. 2), with most inputs (75%) occurring during the growing season (Hayden 1998, Scholes et al. 2003a). Growing season temperatures also are similar (Fig. 2). The primary differences occur in the dormant season where temperature and the environmental cues that initiate spring growth differ (i.e., temperature in NA vs. rainfall in SA), as expected in temperate vs. sub-tropical systems (Fig. 2).

Responses of woody plants to climate, fire and grazing are also quite similar in NA and SA mesic savanna grasslands. On both continents, where annual precipitation is >600 mm, dominance by woody plants occurs if fire is suppressed (Hoch et al. 2002, Titshall et al. 2000, Bond et al. 2003). Trees and shrubs in both regions are capable of resprouting after fire (Higgins et al. 2000, Briggs et al. 2002) though if fire is excluded for long periods, fire sensitive species may invade (Knight et al. 1994, Morris & Tainton 2002, Bond et al. 2003). Grazing may hasten bush or forest encroachment by reducing fuel loads and decreasing fire intensity (Roques et al. 2001, Hoch et al. 2002). Only in SA, where elephants impact large trees, are there major differences between regions in the controls of woody plants (Trollope et al. 1998, Eckhardt et al. 2000). Thus, from a structural perspective, responses to fire and grazing in NA and SA ecosystems differ much less in the woody plant than the herbaceous plant component (our research focus below).

Arguments that fire and grazing affect ecosystem processes and community structure and

<table>
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<th>Ecological attribute or response</th>
<th>NA</th>
<th>SA</th>
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<tr>
<td>Climate</td>
<td>Drought and climate variation is a key driver</td>
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<td></td>
<td>Precipitation limits ANPP</td>
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<tr>
<td>Fire</td>
<td>Systems are fire maintained</td>
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</tr>
<tr>
<td></td>
<td>Reduced fire frequency increases woody plants</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Absence of fire results in conversion to forest</td>
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<td></td>
<td>Burned systems are N limited, but P limited</td>
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<tr>
<td>Grazing</td>
<td>Grazing by large herbivores is a key driver</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Grazers are attracted to burned sites</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>C₄ grass dominated with abundant C₃ trees/shrubs</td>
<td></td>
</tr>
<tr>
<td></td>
<td>ANPP limited by multiple factors (N, light, etc.)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>N addition increases ANPP</td>
<td></td>
</tr>
<tr>
<td></td>
<td>N addition shifts plant species composition</td>
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dynamics in fundamentally different ways in the Southern vs. Northern hemispheres (Scholes et al. 2003a, Lusk & Bellingham 2004, Uys et al. 2004) may seem surprising given this strong consensus regarding their importance (Table 1, Collins & Wallace 1990, Frank et al. 1998, du Toit 2003, Bond et al. 2003). But the histories of these systems differ considerably; NA ecosystems are young, having been glaciated in the recent geologic past, whereas SA savanna grasslands are much older (Bond et al. 2003, Table 2). Other key differences are: 1) a lack of recent historic megafaunal extinction events in SA (Table 2) reflected today in greater richness in the SA megaherbivore guild, 2) lower soil nutrient availability and altered key soil properties (e.g., exchange capacity) in the more highly weathered soils of SA, despite the presence of potentially N-fixing trees in SA (Scholes et al. 2003b), and 3) higher plant species richness (particularly in grasses) due, perhaps, to greater niche diversification in SA (Scholes et al. 2003a). Greater endemism in the flora and fauna of the savanna grasslands of SA vs. NA is often cited as a manifestation of the greater age of SA ecosystems (Axelrod 1985, Bond et al. 2003).

It is these historical differences that are thought to underlie purported disparities in responses of community structure and ecosystem processes to fire and grazing in NA and SA savanna grasslands. These include reported differences in the responses of primary production and soil N to fire (Risser et al. 1981, Briggs & Knapp 1995, Frank & Evans 1997) in NA vs. (Tainton et al. 1978, Morris & Fynn, Morris & Tainton 2002 in SA) and a remarkable divergence in responses of plant community structure and dynamics to both fire and grazing (Collins & Glenn 1991, Hartnett et al. 1996, Collins et al. 1998, Collins 2000 in NA vs. Morris et al. 1992, Morris & Tainton 1996, Martens et al. 1996, Titshall et al. 2000, Fynn et al 2004, Uys et al. 2004 in SA). It is important to emphasize that the interactions of fire and grazing have not been experimentally assessed in Africa, despite intensive study of these in NA (Collins & Wallace 1990, Knapp et al. 1998). Typically, herbivory in Africa is studied via exclusion plots with fire excluded or with a variable fire regime (McNaughton et al. 1982, Young et al 1998). Alternatively, fire is manipulated without concurrent manipulation or control of herbivores (Tainton et al. 1978, Biggs & Potgieter 1999, Morris & Fynn 2001). Thus, rigorous comparisons of responses with NA systems are not currently possible.

Our proposed research will focus on important ecosystem (ANPP and nutrient cycling) and community (plant species richness, diversity and turnover) patterns and processes purported to differ between NA and SA. This emphasis is particularly timely given the considerable interest in linkages between community structure and ecosystem function in grasslands (Tilman 1984, Tilman & Downing 1994, Hector et al. 1999, Tilman et al. 2001, Smith & Knapp 2003).

Table 2. Differences in attributes of NA and SA savanna grasslands.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>NA</th>
<th>SA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (rise of biome)</td>
<td>5-7 mya</td>
<td>40-60 mya</td>
</tr>
<tr>
<td>Age of extant community</td>
<td>8-10,000 yrs</td>
<td>4.6 million yrs</td>
</tr>
<tr>
<td>Historic megaherbivore richness</td>
<td>49 species</td>
<td>45 species</td>
</tr>
<tr>
<td>Current megaherbivore richness</td>
<td>2 species</td>
<td>33 species</td>
</tr>
<tr>
<td>Plant diversity (3)</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Soil nutrients (3)</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Climate</td>
<td>Temperate</td>
<td>Sub-tropical</td>
</tr>
<tr>
<td>Dormant season</td>
<td>Winter (cold)</td>
<td>Winter (drought)</td>
</tr>
</tbody>
</table>

(1) Data from Martin (1984) for all megafauna of North America and Africa.
(2) Data for SA specific to Kruger Park and in NA for Konza Prairie (Kaufman et al. 1998).
(3) From Scholes et al. 2003a,b
5. Conceptual framework, research approach, questions and predictions

How do we determine if hypothesized differences in effects of fire and grazing on ecosystem processes and community dynamics arise from contingent factors (Fig. 1, Price et al. 2000) or reflect research bias and methods that are not comparable? Are the assumptions that underlie many of these purported differences - greater plant and megaherbivore diversity and more nutrient limited soils in SA - valid? To address these questions most efficiently and powerfully requires experiments in which fire and grazing are manipulated independently and in tandem on both continents and responses are measured at comparable spatial and temporal scales. This is particularly true for plant community data, which are strongly scale and sampling dependent (Gross et al. 2000, Scheiner et al. 2000, Chase & Leibold 2002), but also for soil nutrient status which depends on past fire and grazing regime (Blair 1997, Venter et al. 2003), and for ANPP estimates which are based on mechanized mowing in SA (Fynn, pers. comm.) vs. clipping of small plots in NA (Knapp et al. 1998).

Our research approach will utilize identical sampling methods and take advantage of long-term manipulations of fire frequency (annual and intermediate fire frequency and complete fire exclusion) in large replicated plots in two SA sites (with and without native herbivores). These will be compared with similar experiments in NA at the Konza Prairie LTER site. The two sites in SA are ca. 400 km apart and broadly representative of the most common mesic savanna grasslands in the region - comprising 66.8% of southern Africa (south of Angola and Zambia, Cowling et al. 1997).

Hypotheses we will test can be grouped into those related to the impacts of 1) fire, 2) grazing and fire/grazing interactions, and 3) differences in megaherbivore diversity. Hypotheses related to megaherbivore diversity are the most challenging to address because the historically diverse megaherbivore guild in NA is now extinct (Table 2; only bison (Bos bison) and deer (primarily browsers of woody plants) remain). However, Kruger National Park (KNP), where one set of long-term experimental plots is located, has a diverse native large herbivore assemblage (maximum = 14 megaherbivores). KNP also has a large enclosure containing a single native herbivore, Cape buffalo (Syncerus caffer), which is functionally similar in terms of diet (du Toit 2003) to bison, a generalist graminoid consumer in NA ecosystems (Knapp et al. 1999). Thus, we can directly compare the effects of differences in megaherbivore diversity in SA, as well as responses to grazing by a single functionally similar herbivore between SA and NA. The co-location of the fire experiments and enclosures facilitates hypotheses testing and integration of results.

Below, we articulate general predictions and specific questions that are based on our general expectation that when measured comparably, fire and grazing will be broadly convergent in their effects on ecosystem processes in NA and SA savanna grasslands, but plant community responses (structure and dynamics) to fire and grazing will differ markedly, reflecting the divergent evolutionary histories and resultant differences in plant and herbivore composition in the two regions (Fig. 3). In other words, we predict that the impacts of fire and grazing on ecosystem processes (such as ANPP, N and C cycling) will be similar in NA and SA sites, although the magnitude of responses may differ due to differences in soil fertility. In contrast, we expect divergent effects of fire and grazing on plant communities (diversity, compositional dynamics), both in direction and magnitude, in SA vs. NA savanna grassland. Impacts of megaherbivore diversity on ecosystem processes vs. communities will follow similar paths. With comparable moderate grazing intensities, we predict that reductions in megaherbivore diversity to a single grazer species will have little effect on ecosystem processes in SA, but will cause substantial plant community change. In all cases, null hypotheses are that despite the contingent factors of evolutionary history, megaherbivore diversity, and age, there will be no difference in ecosystem and community responses to fire and grazing between NA vs. SA, indicating that historic research bias and different sampling/measurement techniques are responsible for previously reported differences.

The conceptual basis for predictions of divergence in community vs. convergence in ecosystem responses is rooted in the ways in which evolutionary history and the resultant assemblage of species and traits are manifest at these two hierarchical levels. C_4 grasses are the most abundant herbaceous species in both SA and NA, and as a consequence, these dominant species contribute most to community structure and ecosystem function. In both NA and SA, changes in abundance of these species can have important consequences for community structure (diversity), dynamics (turnover) and species associations (competitive interactions) in response to fire and grazing (McNaughton...
A long evolutionary history in SA has allowed for extensive diversification of \( \text{C}_4 \) grasses (Scholes et al. 2003a). By contrast, only a few generalist \( \text{C}_4 \) grasses dominate in the younger communities in NA. We expect this difference in the diversity of dominant \( \text{C}_4 \) grasses will contribute to divergence in community responses to fire and grazing in NA and SA. Differences in megaherbivore diversity between NA and SA also are important. Bison in NA have been shown to preferentially consume \( \text{C}_4 \) grasses, reducing their competitive impacts and increasing species diversity (Vinton and Hartnett 1992, Collins et al. 1998). We predict that community structure and dynamics will respond differently to grazing in SA because the diverse array of megaherbivores will consume both grasses and forbs regardless of fire regime, contributing to divergence in community responses to fire and grazing between NA and SA. However, because \( \text{C}_4 \) grasses are always dominant and their functional traits (e.g., C uptake, water use efficiency, N requirements, litter quality) are similar, responses of ecosystem processes to fire and grazing should be convergent. Thus, an important idea we will test is that divergence of community structure (richness, diversity and dominance) and dynamics (compositional change, species turnover, species associations) is not inconsistent with convergence in ecosystem function.

Support for this convergence/divergence dichotomy is provided by comparative studies focused on each hierarchical level independently. For example, structural-functional relationships driving ecosystem processes (C uptake) may be strongly convergent across diverse biomes with different evolutionary history (Reich et al. 1997, 1999). Within biome types, structural and functional convergence at the ecosystem level have been documented (Cody & Mooney 1978, Paruelo et al. 1998). Convergence in community dynamics (e.g., succession) also occurs with common species pools and phylogenetic histories (Inouye & Tilman 1988, 1995). However, when evolutionary history differs, community structure may diverge because different taxa possess traits and life-history attributes that determine community dynamics (Kelt et al. 1996). We know of no studies that have assessed ecosystem and community pattern and process simultaneously to test this important convergence/divergence dichotomy. But if this prediction for SA vs. NA savanna grasslands is supported, a logical next step would be to extend studies to the savanna grasslands (cerrados) of Brazil, where herbivory also strongly influences ecosystem processes, but grazer (primarily rodents) and plant communities differ markedly (Oliveira & Marquis 2002).

Research questions and predictions

A. Ecosystem processes, community dynamics and fire

a. Are ecosystem responses to long-term fire regimes (in the absence of megaherbivores), specifically herbaceous ANPP, root biomass and tissue N, and pools and dynamics of soil C and N, convergent in NA and SA?

With annual fire in NÁ, ANPP, root biomass and soil CO\(_2\) flux increases, root tissue N concentration decreases (greater C:N ratio), and N availability and mineralizable N pools are reduced compared to unburned sites in the absence of megaherbivores (Hobbs et al. 1991, Blair 1997, Knapp et al. 1998). We predict similar ecosystem responses in SA. However the magnitude of responses may be muted due to greater nutrient limitations such that ANPP, root biomass and soil CO\(_2\) flux will...
be less responsive to fire in SA. Convergence in mechanisms also will be evident. Greater light limitation in unburned canopies will reduce ANPP of C₄ grasses more than the C₃ forbs (Knapp & Seastedt 1986) and soils will be drier in burned sites, reducing N availability (Blair 1997). In sites burned after several years of fire exclusion (infrequently burned treatments), ANPP is stimulated above that in annually burned sites in NA (Knapp et al. 1998). We expect a similar response in SA, but because this “fire history” response is driven by transient periods of high N availability (Blair 1997), this response is predicted to be greater in the more nutrient limited soils of SA. Alternatively, species with different resource use efficiencies and the potential for other soil nutrients to limit responses in SA may mute this response.

b. Do plant community structure and dynamics (richness, diversity, turnover in dominant species, composition) respond differently to long-term fire regimes in NA and SA?

Richness and diversity is lowest with annual fire, intermediate in the absence of fire and highest with intermediate fire frequency for savanna grassland in NA (Collins et al. 1998), whereas community change exhibits an opposite pattern (Collins 2000). We predict divergence in community responses to fire in SA; plant community richness and diversity will not be affected by fire regime in SA (Uys et al. 2004). Mechanistically, we posit that trait diversity in the species rich pool of SA C₄ grasses will maintain strong grass dominance (leading to functional stability) and result in competitive suppression of the high N-requiring C₃ forbs regardless of fire regime in SA. In contrast, only a few C₃ grasses are available to dominate in NA savanna grassland, and in the absence of fire, reduced grass dominance and increased N availability allow forb abundance to increase (Collins & Steinauer 1998). Consequently, forb species will play a much larger role in influencing community dynamics and diversity in response to fire regime in NA than SA. By sampling identically, we will also test the underlying assumption that savanna grasslands in SA are more species rich at the local scale than in NA.

c. Does N limitation affect ecosystem and plant community processes differently in SA than NA?

Long-term fertilization experiments are ongoing in both SA and NA and these consistently indicate N, but not P, limitation to most ecological processes (although evidence for P limitation in N fertilized sites is greater in SA than NA, Blair et al. 1998, Fynn & O’Conner 2004). In NA, N limitation is more pronounced with frequent fire (Turner et al. 1997), but no comparable data exist for SA. Although leguminous trees and shrubs in SA are putative N-fixers, the most abundant trees in nutrient poor sites are from the subfamily Caesalpinioideae, which typically do not fix N, and even in savanna grassland with woody species from the Mimosaceae, N fixation has not been confirmed (Scholes & Walker 1993). Based on this evidence, we will focus initially on N as a primary limiting nutrient in both NA and SA, and quantify differences in relative N limitation to ANPP between burned and unburned sites with similar fine texture, high clay content soils. We predict N limitation to ANPP will be strong, particularly in annually burned sites, in SA enhanced by inherently lower soil nutrients. But responses to N fertilization may be muted relative to NA responses (Seastedt et al. 1991) due to other soil nutrients becoming limiting (such as P or base cations) or due to species traits that limit short-term responses to high N. Thus, NA savanna grassland may respond more to N addition than SA in the short-term, but community shifts may occur more rapidly (during the 3-yr study period) in SA due to the potentially greater pool of species traits and number of species capable of responding positively to increased N availability.

B. Ecosystem and community responses to grazing and fire/grazing interactions

a. Does grazing by native megaherbivores affect key ecosystem processes and properties including ANPP, N and C cycling and soil pools similarly in NA and SA?

In NA savanna grasslands, grazing by native megaherbivores consistently increases N cycling and availability (Frank & Evans 1997, Johnson and Matchett 2001). We predict similar responses in SA. With comparable, moderate grazing intensity, ANPP will be stimulated, soil N availability will be increased, and soil CO₂ flux and root biomass decreased in both annually burned and unburned sites (McNaughton et al. 1998, Johnson & Matchett 2001) relative to sites (exclosures) without grazers. However, the responses in soil CO₂ flux and root biomass may be less in SA, consistent with the longer evolutionary history of this savanna grassland with megaherbivores.

b. Do plant communities respond differently to native megaherbivore grazing in SA vs. NA?
Native megaherbivores in NA savanna grassland strongly influence overall plant community structure and dynamics because the primary herbivore (Bos bison) consumes mainly the dominant C₄ grass species, reducing their abundance and leading to large changes in composition. The diverse forb flora, in turn, responds positively thereby increasing diversity (Hartnett et al. 1996, Collins et al. 1998). We predict that plant community diversity will be relatively insensitive to grazing by the diverse megaherbivore assemblage in SA across all fire regimes, due to maintenance of C₄ grass dominance and suppression of the less abundant forbs by the large number of forb browsers (du Toit 2003). We expect, however, that composition will change significantly (compared to the grazing exclosures) as a result of turnover of the dominant grasses from those susceptible to grazing to those that are more tolerant (decreasers and increasers, Martens et al. 1996). Despite decreases in cover, there is little turnover of grass dominance in NA savanna grasslands with moderate grazing (Collins et al. 1998), and thus compositional changes will be driven primarily by the forb component.

c. Do interactions between fire and grazing affect ecosystem processes and plant community dynamics differently in SA vs. NA?

Again, we predict convergence in fire-grazing interactions at the ecosystem level. Reductions in N pools (mineralizable soil N) and cycling (in situ N availability) in annually burned, ungrazed sites are offset if grazers are present in NA, due to increased N turnover with herbivory (Frank & Evans 1997, Johnson & Matchett 2001). We predict a similar response in SA. In NA, fire and grazing interact to influence plant community diversity and composition (Collins et al. 1998). When sites are both grazed and burned, diversity increases as a result of heavy utilization of the dominant grasses by herbivores. Thus, annually burned, grazed sites are as diverse as unburned sites and generally contain a similar suite of forb species. Because fire and grazing have not been simultaneously manipulated in SA, there is little basis for prediction. However, interactions are not expected to have strong effects on overall plant community diversity, as fire and grazing are predicted to have little effect separately. In contrast, within the diverse grass component in SA, interactions are more likely, and thus fire and grazing are likely to impact composition in complex ways.

C. Megaherbivore diversity and the structure and function of savanna grasslands

a. How does herbivory by a diverse suite of megaherbivores affect ecosystem processes and plant communities compared to grazing by a single megaherbivore?

At moderate grazing intensity, we predict little measurable effect of megaherbivore diversity on ecosystem processes in annual or infrequently burned SA savanna grassland, as long as herbivores are present that feed primarily on the dominant grass component (true grazers sensu du Toit 2003). In contrast, if specialist forb browsers (McNaughton & Georiadis 1986) are absent from the megaherbivore guild, then plant species diversity will increase in response to herbivory by a single megaherbivore that consumes mainly graminoid species (i.e., Cape buffalo). The mechanism for the increase in diversity will be an increase in forb abundance, similar to that documented in NA ecosystems (Collins et al. 1998).

b. Does grazing by a single megaherbivore affect plant and soil nutrient cycling and plant communities similarly in SA and NA?

Grazing by bison (NA) and Cape buffalo (SA) (both primarily graminoid consumers, Knapp et al. 1998, du Toit 2003) will have similar ecosystem effects (increased N availability, reduced root biomass and soil CO₂ flux) regardless of fire regime in both NA and SA. Community responses will be divergent however (see a) with greater turnover of the dominant grasses in SA vs. NA.

c. Will ecosystem processes and plant community structure and dynamics be affected similarly if diverse vs. single species of megaherbivores are removed from savanna grassland?

We predict that removal of megaherbivores from savanna grassland (via exclosures) will have similar effects in NA and SA at the ecosystem level, regardless of the diversity of megaherbivores removed (1 vs. 14). ANPP will be reduced initially compared to long-term ungrazed sites, but as root/shoot ratios, belowground carbohydrate and nutrient reserves are reestablished (Vinton & Hartnett 1992), ANPP will recover by the second growing season. If ANPP does not recover, compensation by small consumers may be responsible (Keesing 2000, Howe et al. 2002) and can be tested with small mammal exclosures. We also predict that the magnitude of effects of
megaherbivore loss on C and N cycling will be similar regardless of megaherbivore diversity. In NA, loss or removal of a single large grazer (bison) causes diversity to decline (Collins et al. 1998). Since bison selectively feed on the dominant grasses, dominance by a few C₄ grass species will increase, and consequently abundance of forbs will decrease. The decline is expected to be more rapid with annual vs. infrequent burning. With removal of the diverse suite of megaherbivores in SA, the dominant grasses are expected to turnover to more grazing intolerant species, irrespective of fire frequency, whereas forb species should remain low in abundance due to competitive suppression from the grasses. In contrast, we expect that removal of a single herbivore in SA will cause diversity to decline, similar to responses in NA.

The hypotheses presented above are, by necessity, somewhat descriptive. There are two reasons for this. First, purported differences that may be caused by contingent factors (age, evolutionary history, megaherbivore diversity) need to be examined rigorously. This requires that we quantify ecosystem and community responses in comparable ways, controlling for ecological context and measurement/sampling bias. This will allow us to eliminate non-ecological explanations related to differences in methods and techniques. Thus, the initial thrust of our research must be to evaluate key ecosystem processes and community responses to fire and grazing with a directly comparable experimental design. Second, ecosystem age and evolutionary history are impossible to manipulate as ultimate causal factors, but comparative studies can distinguish between evolutionary and ecological mechanisms and have proven quite powerful (Losos 1996). This approach requires that one or several ecological variables (e.g., ANPP) be measured in the same way on two continents, as well as across habitats or treatments (fire, grazing experiments) within each continent. If “treatment” variables explain a significant proportion of the variance relative to “continent” or the “continent x treatment” interaction, then convergence is supported (Schluter & Ricklefs 1993). This approach is implicitly phylogenetic in that it assumes species are more closely related to each other on the same continent than between continents (Losos 1996). Further, by focusing on more mechanistic (process level) as well as structural variables, we can provide insight into ultimate causation, as we have done with the Konza Prairie LTER program (Knapp et al. 1998, Collins et al. 1998).

Although not detailed in this proposal, established mechanisms from NA research will be tested in SA savanna grasslands when appropriate and as resources permit. For example, after convergence or divergence in responses in ANPP is confirmed, the role of light and water limitations can be assessed (Knapp & Seastedt 1986). Or trait-based rather than taxon-based analyses can be used to provide additional mechanistic understanding of system responses. Species traits reflect evolutionarily derived trade-offs for resource capture, grazing tolerance, etc. (Suding et al. 2003, Suding et al. submitted), which ultimately influence community structure and ecosystem processes (Shaver & Chapin 1980, Grime 2001, Diaz & Cabido 2001).

6. Long-term experiments as research platforms

The questions and predictions above will be addressed with three long-term experiments in which fire and grazing are manipulated, one in NA and two in SA. The PI’s of this proposal have made six planning visits to SA (2000-04), initially to help decide the future of the long-term fire experiments and more recently to plan for this collaborative research.

Konza Prairie LTER Experimental Watersheds.

The Konza Prairie Biological Station (KPBS) is a 3,487 ha C₄-dominated savanna grassland ecosystem. The herbaceous vegetation is composed primarily of native (>90%) perennial C₄ grasses such as Andropogon gerardii and Sorghastrum nutans that account for the majority of herbaceous primary productivity (Knapp et al. 1998). Numerous sub-dominant grasses, forbs, shrubs and trees contribute to the floristic diversity of the site (Towne 2002). The climate is continental (Fig. 2), with mean monthly air temperature in July of 27°C. Annual precipitation averages 820 mm/year, with 75% falling as rain during the Apr-Oct growing season. Soils are fine textured, silty clay loams (Ransom et al. 1998).

KPBS includes fully replicated watershed-level fire and fire/grazing experiments, in place since 1977 and 1987, respectively. Replicate watersheds (mean size ~60ha) are burned at 1-, 2-, 4-, 10- and 20-yr intervals, mainly in the spring, to encompass a range of likely natural fire frequencies and management practices. To address the role of native grazers and fire/grazing interactions (Hobbs et
al. 1991, Johnson & Matchett 2001), bison (~260 individuals) were reintroduced to KPBS in a 1000-ha fenced area that includes replicate watersheds burned in the spring at 1-, 2-, 4- and 20-year intervals. The overall grazing intensity is considered moderate (Knapp et al. 1999).

Within long-term study watersheds (grazed and ungrazed), permanent sampling transects are replicated at various topographic positions (n=4/topographic position/watershed), where ANPP, plant species composition, plant and consumer populations, and soil properties are measured. The collection of diverse data from common sampling locations facilitates synthesis and integration of research. In addition, there are 32 25-m² permanent exclosures within the grazed watersheds that are identical to the exclosures to be erected as part of this proposal. These will provide important context for interpreting results and will allow us to compare the influence of bison grazing at small-scales (inside and outside of exclosures) and at the watershed scale.

**Kruger National Park Experimental Burn Plots and Herbivore Enclosures.**

Kruger National Park (KNP), is a 2 million ha protected area of savanna grassland located in NE South Africa. The park includes many of the large herbivores that evolved in the savanna grasslands of southern Africa (du Toit et al. 2003), with 12-14 megaherbivores commonly observed in the plots described below. The extant abundance and grazing intensity of herbivores in KNP is considered moderate for regional savanna grasslands (Trollope, pers. comm.). Due to the large size of KNP, climatic gradients are substantial, but in the south-central region where our research will take place, rainfall ranges from 600 - >800 mm (Venter et al. 2003) with most falling during the growing season (October-April). The dormant season is mild, dry and frost free, and summers are warm with mean monthly maximum air temperature = 28.9°C in January.

Because of the importance of fire in this savanna grassland ecosystem (Trollope 1982, Biggs & Potgieter 1999), the Experimental Burn Plot (EBP) experiment was initiated in 1954 to examine the effects of fire frequency (control-no fire, 1-, 2-, 3-, 4- and 6-yr return interval) and season [early spring (Aug), spring (Oct), mid-summer (Dec), late summer (Feb), and fall (Apr)] on vegetation communities in the park (Biggs et al. 2003). It is one of the longest fire ecology experiments in Africa. Four blocks of 12 plots (two were later split for the 4- and 6-yr trts), each ~7 ha (370 x 180 m) in size, were established in four primary vegetation types covering the two major soil types (granites and basalts) and spanning the precipitation gradient in the park. Each plot has 50+ years of known fire history, and native herbivores have had unrestricted access, thus fire and grazing effects are combined. Although KNP scientists have maintained these treatments faithfully over the years, assessments of responses have been limited to pre-treatment and intermittent surveys of graminoid and woody plants from a management perspective (Trollope 1982; Trollope et al. 1998; Enslin et al. 2000). For our research, we will focus on those EBPs located near Satara (Photo 1) where precipitation, soil type, and the mix of herbaceous and woody plants are similar to Konza.

Adjacent to one of the Satara blocks is the Cape buffalo enclosure, erected in 2000 for veterinary purposes. The 200 ha permanent enclosure contains 65-80 animals and is divided into 4 blocks burned on a rotational basis. The grazing intensity inside is comparable to the moderate levels imposed in the park and at KPBS. Two blocks will be burned annually for the duration of the study with others left unburned to represent the infrequently (4-yr) burned treatment. Additionally, 4 other permanent exclosures are present in KNP that we can sample to provide context for the grazing studies. Thus, KNP offers sites with known long-term fire history, gradients of megaherbivore diversity from 0 to 1 to 14 species, and with permission to erect additional exclosures and the logistical assistance of KNP scientists (see letters of support), the ability to assess fire and grazing effects independently and interactively in Africa for the first time.

**Ukulinga Long-term Fire and Mowing Plots.**

The Ukulinga Research Farm (URF) of the University of KwaZulu-Natal is located in Pietermaritzburg, SA (Morris & Fynn 2001). The area has been described as dense grassland with scattered trees (Morris & Tainton 2002). Mean annual precipitation is 790 mm, mostly as convective storms during summer (October - April, Fig. 2). Summers are warm with a mean monthly maximum of 26.4 °C in February, and winters are mild with occasional frost. Soils are derived from shales and are fine textured. There is no grazing at this site.
Long-term experimental plots were established at URF in 1950 with the objective of determining the optimal fire and/or summer cutting regime to maximize hay production. The experiment is a randomized block (three replicates) split-plot design with four whole-plot utilization treatments (no haying, one early or late summer haying, and two summer hayings) and eleven subplot fire or mowing treatments. These include annual fire in spring or winter, 2-yr burn in spring, winter or fall, 3-yr burn in spring, winter or fall, unburned, mowed once in winter, or mowed once in spring. Subplot sizes are 13.7 x 18.3 m.

As with the KNP EBPs, the treatments in this experiment have been maintained for 50+ years, but data collection has been sporadic (see Morris & Tainton 2002) and interest in these experiments has shifted from a management focus to their basic ecological value (Morris & Tainton 2002, Dr. K. Kirkman, U. Kwazulu-Natal, see letter of support). Although the replicate number (n=3/trt) is small, the treatment duration is extensive and there are striking visible differences among treatments. Further, Keesing (2000) reported significant treatment effects in African savanna grassland with n = 3.

7. Specific studies

We will utilize the long-term research platforms at KPBS, KNP, and URF to address the questions and specific hypotheses described above. For all the proposed studies, we will establish equal numbers of identically sized permanent plots (as already in place at URF or KNP) at KPBS (Fig. 4; A: N=9/site; B: N=12/site) and in the Buffalo enclosure (N=8). Permanent exclosures will be established with adequate space (25 m²) for destructive and nondestructive measurements (n=5/plot, B: N=60/site, C: N=40/site; Fig. 4), as well as moveable 1x1 m exclosures for ANPP estimates in grazed plots. These exclosure sizes will minimize damage from most SA megaherbivores, which tend to travel around small obstructions, but through large fences (J. duToit, pers. com.). The use of identical sampling methods will ensure seamless integration among studies and between regions. It is important to note that new measurements will be made at all three sites to ensure identical spatial and temporal scales of inference. New measurements at KPBS are particularly critical, since many of the LTER sampling protocols for large experimental watersheds are not appropriate for the scale of the 7 ha and smaller plots in SA. However, past LTER data will provide invaluable context.

A. The role of long-term fire regimes (without megaherbivores)

Long-term experiments in which fire frequency is directly manipulated are already in place at KPBS and URF. At URF, measurements will be made in replicate plots (not hayed) burned every 1 and 3 yr in the spring, and those left unburned (Fig. 4). At KPBS, measurements will be made in permanent plots (same size as at URF) established in ungrazed watersheds that are burned every 1 and 4 yr in the spring and where fire is excluded (Fig. 4). For fire effects on ecosystem processes, we will focus primarily on 1-yr and unburned treatments since fire effects on ANPP, root biomass and N...
and C content, soil N pools (mineralizable and total), N availability (resin bags), and soil CO₂ flux are manifest most strongly in NA at these extremes (Seastedt et al. 1991, Blair 1997). The infrequent fire treatment will be used primarily to assess fire history effects on ANPP and N limitation. For fire effects on plant community structure and dynamics, all three fire treatments (1-yr, 4-yr and fire exclusion) will be used, since changes in community structure in NA have been observed across a range of fire regimes (Collins & Steinauer 1998). We will sample (see detailed methods below) over 3 growing seasons except for root C and N and biomass, which will only be measured in a representative year (based on the normalcy of the rainfall pattern that year).

To address N limitation questions at KPBS and URF, we will add nitrogen (10 gN/m²/yr as ammonium nitrate; Seastedt et al. 1991) to subplots within 1-yr, infrequently burned, and unburned plots (Fig. 4) and measure herbaceous ANPP and soil N availability in 1-yr and unburned subplots, and plant community composition in all fire treatments over three growing seasons.

B. Importance of grazing and grazing/fire interactions

Long-term experiments in which native megaherbivore grazers are present and fire frequency is directly manipulated are in place at KPBS and KNP. To assess the effects of grazing and fire/grazing interactions, we will construct exclosures (5x5 m x 2 m tall with wire covers) in the Satara EBPs burned every 1 and 3 yr in the spring, and in fire exclusion plots (N = 60). Permanent (unenclosed) sampling plots will be established adjacent to the exclosures (Fig. 4). At KPBS, we will establish permanent plots (same size as the EBPs) in the 1-yr, 4-yr, and unburned watersheds grazed by bison, and within each plot we will construct exclosures with matching unenclosed plots (N = 60/site). In each exclosure and in adjacent unenclosed plots we will sample soil N availability (resin bags), soil CO₂ flux, and plant community composition (in permanent subplots) over three growing seasons. ANPP will be measured at the end of each growing season in the exclosures and throughout the growing season in grazed areas. Root biomass and C and N content will be measured initially and after 3 yrs of excluding grazers. In addition, we will add N over three growing seasons to subplots within exclosures in all fire treatments in KPBS and KNP (Fig. 4) to assess N limitation. In each N addition subplot, we will measure herbaceous ANPP and soil N availability (in 1-yr and unburned plots) and plant species composition (all treatments) each year.

C. The role of megaherbivore diversity

To assess the effects of megaherbivore diversity, ANPP, soil N availability, soil CO₂ flux, and plant community composition will be measured over three growing seasons in unenclosed plots in the 1- and 3-yr burned Satara EBPs (14 megaherbivore species), and same sized plots established in the 1- and 4-yr burn blocks of the Cape Buffalo enclosure (single grazer species; Fig. 4). Potential interactions between megaherbivore diversity and megaherbivore loss will be assessed in plots located inside and outside of exclosures placed in the 1- and 3 or 4-yr burned plots in the Satara EBPs, KPBS, and the Buffalo enclosure (Fig. 4). These will be used to measure ANPP, N availability, soil CO₂ flux, and plant community composition over three growing seasons, and responses in root biomass after 3 yrs of exclosure.

8. Detailed methods

For all studies, fire is the whole-plot treatment and grazing and/or nitrogen addition is the subplot treatment (Fig. 4). There are three fire treatments (1-yr, 3/4-yr, and unburned), three grazing treatments (0, 1 or 12-14 megaherbivores), and two nitrogen treatments (-N, +N). Sub-plots, exclosures, and quadrats will be randomly located within the larger treatment plots, but since our interest is focused on herbaceous-layer responses, these will be located to avoid trees and large shrub patches within the large plots. To assess (A) the long-term effects of fire frequency (in the absence of megaherbivores) and (C) the effects of herbivore diversity on the suite of ecosystem and community response variables measured, we will use repeated measures ANOVA. To assess (A & B, Fig. 4) N limitation with long-term fire and grazing and (B & C) the effects of grazing and the interaction between grazing and fire frequency, we will use split-plot (repeated measures) ANOVAs. In addition to these general analytic procedures, additional question-specific analyses will be conducted. For example, time-lag analysis will be used to quantify rates of species compositional change over time (Collins 2000, Collins et al. 2000) and species turnover will be calculated. Although three years may seem like a short time period for quantifying dynamics, NA savanna grasslands respond rapidly to
grazing and N manipulations (Steinauer and Collins 2001). From these measures, we can infer other community level mechanisms, such as competition. Regression analyses also will be used to assess relationships among changes in soil N availability, productivity, plant species diversity and other response variables. All analyses will be conducted using SAS statistical software.

**Response variables:**

**Aboveground NPP:** Herbaceous ANPP will be estimated from end-of-season harvests of 0.1 m² quadrats in ungrazed treatments (A: n=10/plot, N=90/site; B & C: n=3/subplot, N=360 or 240/site; N addition plots: n=1/subplot, N=12-20/trt; Fig. 4). In grazed treatments, small, moveable exclosures will be sampled at 3-wk intervals throughout the growing season (n=3/subplot, N=60/trt; McNaughton *et al.* 1996). Biomass will be sorted into dominant grass, dominant forb, other graminoid, other forb, current year’s dead, and previous year’s dead components. For burned sites, all biomass represents ANPP. For the infrequently and unburned sites, ANPP is all but previous years dead biomass. Plant tissue will be ground and analyzed for C and N content using a Carlo-Erba NA 1500 C/N analyzer. Ground samples will be archived for future analyses (i.e., lignin content).

**Belowground biomass:** Soil cores (5 cm diam x 20 cm deep; A: 10/plot; B & C: 2/subplot, N=20/trt) will be collected to quantify root biomass at the end of the growing season. The cores will be washed and the roots collected on screens for biomass and C and N determinations.

**Soil C and N pools and fluxes:** Soil samples (2 cm diam. x 10 cm deep cores, 10/plot or exclosure, or 2/subplot) will be collected at the beginning, middle and end of the growing season. Samples will be split, and a portion dried, ground, and analyzed for total C and N content. Mineralizable (labile) C and N fractions (C₀ and N₀) will be assessed by long-term laboratory incubations (Robertson *et al.* 1999). Soil samples will be archived for assessment of any additional long-term changes in soil properties. Resin bags (10/plot or exclosure, or 2/subplot) will be buried and incubated *in situ* over a growing season to provide an integrated index of NO₃ and NH₄ availability (Baer *et al.* 2003). Soil CO₂ flux will be measured at 2–4 wk intervals during the growing season using a Li-COR 6200 portable infrared gas analyzer fitted with an 850-cm² soil respiration chamber (Knapp *et al.* 1998).

**Plant species composition:** Each permanent 2 x 2 m subplot (n=2/subplot, A: N=18/site, B & C: N=120 or 80/site) will be divided into 4 1 x 1m plots in which canopy cover of each species will be visually estimated as in Knapp *et al.* (2002) and Collins and Smith (unpubl). These measures will be repeated twice during the growing season to sample early and late season species. Maximum cover values of each species will be used to determine richness, diversity and dominance and changes in composition, species turnover, and species associations over time.

**9. Project management and South African collaborators (also see Budget Justification)**

Overall project management will be shared by Knapp (ecosystem) and Smith (community responses, Table 4). The logistics of working in SA can be challenging in many ways, particularly with the SA growing season occurring during the academic year in the US. Thus, we will rely on two post-doctoral associates to assist in accomplishing our research goals. One will be based in SA at URF (Dr. Richard Fynn) and the 2nd at the KNP (Dr. Catherine Burns). Post-docs will be responsible for studies related to plant community responses and megaherbivore diversity and logistical support (Table 4). Blair, along with a graduate student will take primary responsibility for nutrient cycling and belowground sampling, whereas Collins will focus on the fire/grazing interactions and temporal community dynamics hypotheses. Collins and the information Manager (IM) at the Sevilleta LTER site will provide leadership in data management, access, and web page development (Table 4).

In addition to Dr. Fynn, other SA colleagues that have agreed to collaborate include Drs. Kevin Kirkman (Chair, Grassland Science) and Craig Morris, U. Kwazulu-Natal (Ukulung Plots), and Dr. Harry Biggs (Systems Ecologist) and Ms. Navashni Govender (Fire Ecologist & manager of the EBP’s), KNP. They have provided their CV’s as supplemental documents in this proposal.

**10. Significance of proposed research**

The value of individual long-term field experiments has been amply demonstrated in ecology (Brown & Heske 1990, Likens *et al.* 1996, Brown *et al.* 2001, Hobbie *et al.* 2003). But the research opportunities afforded by these three long-term studies with similar manipulations of drivers is truly unprecedented. With a comparative research approach based on similar experimental designs and
identical sampling protocols in both NA and SA, our research will provide a rigorous assessment of the cumulative effects of long-term fire and grazing regimes, as well as responses to short-term manipulations of resources and herbivores, for a suite of important ecosystem and community properties. The congruence in ecological attributes (i.e., growing season length and climate, productivity, growth form dominance and structure) of these NA and SA savanna grasslands will provide the backdrop from which we can discern the importance of contingencies, such as age, evolutionary history, and herbivore diversity. This will allow us to resolve concerns about NA and SA savanna grasslands responding to fire and grazing in fundamentally different ways and ascertain the kinds of inferences that can be made from one region to another. The identification of those ecological processes that are convergent across systems, despite contingent factors, as well as those that are divergent, will provide a basis for more focused comparative studies in other ecosystems – our long-term goal (Knapp & Smith 2001, Knapp et al. 2004). Ultimately this understanding will allow us to improve savanna grassland models that include fire and grazing effects on both community and ecosystem processes (i.e., SAVANNA, Coughenour 1993). Such an assessment, even in a moderate number of ecological processes, will advance our general understanding of the structural and functional determinants of savanna grasslands far beyond that of most biomes.

II. Broader Impacts

The proposed research will provide unique educational, cultural and research experiences for both SA and NA undergraduates, graduate students and post-docs. Although we can only directly support US students, SA students will be involved through our SA collaborators and we will actively recruit SA students for graduate assistantships. Moreover, all PI’s will incorporate results from these studies into course content. We are currently collaborating with Dr. Charlene D’Avanzo (Hampshire College) to develop online TIEE (Teaching Issues & Experiments in Ecology, NSF/ESA supported) course material based on KPBS data. A webpage describing the research and results will be maintained at the Sevilleta LTER site with links to the Konza Prairie LTER and all PIs webpages. Data will be available on-line to scientists, educators and the general public in accordance with LTER policies. Results will also be of value to the SA ecological community and regional managers (see letters of support). Conservation biologists and land managers grapple with problems of distilling information from disparate studies, thus the synthetic understanding gained through our research should help guide the development of conservation and management strategies for savanna grasslands worldwide (Brooks et al. 2001). Finally, we hope that our results will serve as a basis for designing future research to elucidate the mechanisms responsible for divergent responses in these and other ecosystems.

III. Results from Prior Support


The Konza Prairie LTER Program is a comprehensive, interdisciplinary research program designed to further our understanding of ecological processes in mesic savanna grassland and contribute to the advancement of ecological knowledge and theory. The focal site for this research is the KPBS in NE Kansas. Since 1981, the Konza LTER program has encompassed studies from the organismal through landscape levels, linked via an overarching theme that includes fire, grazing and climate as essential and interactive drivers responsible for the structure and function of this system. Studies during LTER IV focused on ecological responses to fire, grazing, and the natural climatic variability characteristic of this system. We (1) continued the long-term, watershed-level experiments on fire and grazing by large, native ungulates (Bos bison) that form the core of the Konza LTER experimental design, (2) continued several long-term, plot-level experiments (e.g., Irrigation Transects), (3) initiated several new long-term experiments (e.g., the Fire Treatment Reversal Experiment), and (4) broadened our research program by the addition of new investigators. From 1996-2002, the Konza Prairie LTER program produced 265 publications (164 refereed journal articles, 1 book, 40 book chapters, 43 dissertations and theses, and 17 miscellaneous publications). In addition, several major synthetic works were produced during LTER IV, including publication of the first book in the Oxford Press LTER Site Synthesis series (Knapp et al. 1998). A complete listing of LTER publications is available at (www.konza.ksu.edu/general/publications/pub.html).
References Cited


