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TITLE OF PROPOSED PROJECT Collaborative Research: Convergence and Contingencies in Savanna Grasslands						
REQUESTED AMOUNT \$ 160,259	PROPOSED DURATION (1-60 MONTHS) 36 months		REQUESTED STARTING DATE 02/01/09		SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE	
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COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

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NAME OF ORGANIZATION TO WHICH AWARD SHOULD BE MADE Colorado State University			ADDRESS OF AWARDEE ORGANIZATION, INCLUDING 9 DIGIT ZIP CODE 601 S Howes St Fort Collins, CO 80523-0001			
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TITLE OF PROPOSED PROJECT Collaborative Research: Convergence and Contingencies in Savanna Grasslands						
REQUESTED AMOUNT \$ 248,546	PROPOSED DURATION (1-60 MONTHS) 36 months		REQUESTED STARTING DATE 02/01/09		SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE	
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<input type="checkbox"/> SMALL GRANT FOR EXPLOR. RESEARCH (SGER) (GPG II.D.1)						
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Collaborative Research: Convergence and Contingencies in Savanna Grasslands

The distribution, structure and function of mesic savanna grasslands are a product of three interacting drivers - fire, grazing by large herbivores, and extreme climatic fluctuations. Some ecologists have argued that fire and grazing influence savanna grassland structure and function differently in South Africa (SA) compared to North America (NA). These differences have been attributed to the contingent factors of greater biome age, longer evolutionary history with fire and grazing, reduced 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 bias in the number of studies in NA, has led to differing perspectives on the role of these drivers. If the impacts of shared ecosystem drivers truly differ between NA and SA, this calls into question the generality of our understanding of these ecosystems and our ability to forecast how changes in key drivers will affect savanna grasslands globally. In 2005, we initiated a comparative research program **to determine the degree of convergence in ecosystem (productivity, N and C cycling) and herbaceous community responses (composition, diversity, dynamics) to fire and grazing in savanna grasslands in SA and NA.** Our research takes advantage of a unique research platform consisting of three long-term (20-50+ yr) experimental manipulations of fire and grazing at the Kruger National Park (KNP) and Ukulinga Research Farm (URF) in SA and the Konza Prairie Biological Station (KPBS) in NA. At these sites, we are conducting a suite of studies using identical experimental designs and methods to address hypotheses related to: 1) the role of long-term fire regimes (without megaherbivores), 2) the importance of grazing and fire-grazing interactions, and 3) the impacts of reductions in megaherbivore diversity. At KBPS and KNP we have erected 168 permanent megaherbivore exclosures in sites subjected to different fire return intervals (1-yr, 3-4 yr and unburned) and single vs. a diverse suite of megaherbivores to assess in directly comparable ways the interactive effects of fire regime, grazing and megaherbivore diversity on herbaceous plant community and ecosystem processes. Results thus far suggest convergence in ANPP and soil N responses as a function of fire frequency and N manipulations, and divergence in herbaceous plant community responses to fire and grazing in SA vs. NA. However, the steep trajectories of change in many response metrics over the initial 2.5 yrs have precluded resolution of many of our hypotheses. **The purpose of this renewal proposal is to request funding to complete those studies included in our original proposal and to assess the mechanisms driving differential community-level responses via trait diversity and phylogenetic constraints.** Renewal funding will allow us to maintain the substantial investment in infrastructure in place in NA and SA, to complete the considerable ongoing data collection activities, and to conduct the new mechanistic studies. These activities are crucial for testing our general prediction that ecosystem responses to fire and grazing will be broadly convergent in NA and SA, but plant community responses will diverge, reflecting key contingencies, such as differences in evolutionary history and species diversity. **Intellectual Merit:** Our research is designed to address an important question about our understanding of savanna grasslands globally: Is our knowledge of fire and grazing sufficiently general to enable us to predict how these ecosystems will respond to changes in these drivers over time? While convergence of structure and function in similar biomes has long been of interest to ecologists, rigorous comparisons of *ecological processes* at more than one hierarchical level are rare. However, such comparisons are crucial to forecast the future of these important ecosystems. Our research differs from previous studies in that the separate and interactive impacts of key drivers on ecosystem and community processes are being examined in geographically distinct but structurally similar systems. This allows us to assess those ecological processes that are similar across savanna grasslands in SA and NA, and those in which underlying differences in age, evolutionary history, and species diversity may cause divergent responses. Such an assessment, even in a moderate number of ecological processes, will significantly advance our general understanding of the structural and functional determinants of savanna grasslands far beyond that of most biomes. **Broader Impacts:** Our research provides diverse training and global and cultural experiences for young scientists in SA and NA. Further, our project has achieved considerable public outreach in KNP through educational signage at our study sites, SA media attention, wildlife tours, and collaborations with Park staff, including job training. Results and data will be made publicly available via PIs webpages and will be of particular value to the SA ecological community and natural resource managers. Conservation biologists and land managers grapple with problems of distilling information from disparate studies, thus the synthetic understanding gained through our research will help guide the development of conservation and management strategies for savanna grasslands worldwide.

C. Project Description

1. Response to Previous Reviews

This renewal proposal was submitted to the Ecosystem Studies Program in January 2008 (fund if possible) and co-reviewed by the Geography and Regional Science Program (fund, medium priority). Overall, the reviews were positive (1 E, 1 E/VG, 5 VG). Reviewers were enthusiastic about our comparative approach to assessing responses of North American (NA) and South African (SA) savanna grasslands to fire and grazing, using existing long-term manipulations of fire frequency, matched manipulations of large herbivore presence/absence, and directly comparable sampling methods. They also felt the intellectual merit of the proposal was high and that a considerable amount of progress had been accomplished to date. Although the panelists concluded that the proposed research represents 'a golden opportunity to advance our understanding of the controls over grassland ecosystems', three major concerns were raised: 1) the proposed studies did little to address the mechanisms that might underlie differences in plant community and ecosystem responses between NA and SA, such as differences in evolutionary histories of plant species; 2) too much attention was given to background data and conceptual underpinnings at the expense of details about the continuing and new studies that will be supported with the renewal (including statistical analyses); and 3) not enough detail was provided about what projects will be funded by the renewal request and how the funds would be used. Because the panel placed high priority on continuing the core studies focused on the long-term effects of fire, fire-grazing interactions, and megaherbivore diversity but not the new studies begun in the previous funding period (e.g., size-dependent herbivore exclusion), we have removed these from our proposed research plan (those co-PIs will pursue funding from other sources). We now focus our renewal activities on the core studies described in our original proposal, we provide greater methodological detail, and we have added studies examining phylogenetic community structure and species traits to assess potential mechanisms underlying differential responses at the community and ecosystem-level between NA and SA. As a result of these changes, our requested budget has decreased by 33%.

2. Introduction and Research Goals

Grassland and savanna ecosystems are unique in that the interplay of three drivers - fire, grazing by megaherbivores, and extreme climatic fluctuations - are recognized as major determinants of their distribution, structure and function (Walker 1985, Archer 1995, Scholes & Archer 1997, Knapp *et al.* 1998a, Oesterheld *et al.* 1999, Scholes *et al.* 2003a). Of these, fire and grazing regimes have been most extensively altered by humans (Archer 1989, 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 domestic grazers or eliminating fire altogether) and indirectly due to landscape fragmentation, shifts in socio-political attitudes/policy, and the extinction of megafauna (Reid & Ellis 1995, Leach & Givnish 1996, Fuhlendorf & Engle 2001, Hoch *et al.* 2002). From an ecosystem services and conservation perspective, grasslands and savannas encompass as much as 40% of the terrestrial land surface, sequester large amounts 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). If we are to maintain the critical services these ecosystems provide as well as forecast changes in these ecosystems worldwide in the face of increasing human impacts (Newmark 2008), a more comprehensive understanding of how these drivers regulate ecosystem structure and functioning is required (du Toit *et al.* 2003, Palmer *et al.* 2004).

Grasslands and savannas span broad climatic gradients on most continents (Walter 1985, Scholes & Archer 1997, Lauenroth *et al.* 1999, Oesterheld *et al.* 1999). The focus of our research is on the mesic portion of the grassland/savanna continuum (precipitation >500 mm) where fire and grazing are important separately and interactively. Hereafter, we collectively refer to these mesic grasslands and savannas as *savanna grasslands* (*sensu* Scholes & Archer 1997) because 1) they are structurally very similar, i.e., both are characterized by a continuous grass layer with scattered shrubs and trees, and 2) they share common determinants of their ecological properties and dynamics (Scholes 1993, Knapp *et al.* 1998a, Frank *et al.* 1998, Bond *et al.* 2003). Despite these common features, many have argued that the ways in which fire and grazing influence savanna grassland structure and function are fundamentally different in southern Africa (SA) compared to NA and elsewhere (see below). Differences are posited to be due to the

longer evolutionary history with fire and grazing, reduced soil fertility in these ancient ecosystems, and a greater diversity of plants and megaherbivores (Scholes *et al.* 2003a,b, Bond *et al.* 2003).

Our current understanding of the role of fire, megaherbivores and their interactions in these savanna grasslands is based on hundreds of ecological studies. There are numerous syntheses of these, usually focused on a particular site or region (Booyesen & Tainton 1984, Cole 1986, Collins & Wallace 1990, Scholes & Walker 1993, Knapp *et al.* 1998a, 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 site-based studies are conducted independently with methods and approaches that differ considerably (Knapp *et al.* 2004). This is of particular concern in SA where there may be 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, 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.* 1998a, 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 forecast how ecosystem structure and function will change as these key drivers are altered? Are the different methods and approaches used between systems responsible for differing perspectives on the role of these drivers? Or, are the impacts of the shared drivers on ecological processes truly different in systems with different evolutionary histories, such as NA and SA? **The goals of our ongoing research are to quantify, in directly comparable ways, community and ecosystem responses to alterations in key ecological drivers (fire and grazing) in savanna grasslands in SA and NA, allowing us to identify those ecological processes that are divergent or site-specific and those that are convergent or similar, despite the potential contingent factors of differing evolutionary history, megaherbivore diversity and soil fertility.**

Although comparative studies are common in ecology, most have focused on pattern and structure, often at a single hierarchical level (Cody & Mooney 1978, Mares 1980, Price *et al.* 2000, Bond & Midgley 2001, Ojeda *et al.* 2001, Meserve *et al.* 2003, Knapp *et al.* 2006). Our research is unique in that we are focused on detecting convergence or divergence in *ecological processes and dynamics* at the community and ecosystem level. To date and by logistical necessity, we have constrained our research to comparisons of savanna grassland sites in NA and SA. However, our results will have implications for generalizing across other ecosystems with similar physiognomy and drivers, and our longer-term vision is for our current studies to serve as a springboard for expansion into other mesic savanna grasslands (e.g., South America, Austin & Sala 2002, Overbeck & Pfenner 2007; Australia, Beringer *et al.* 2007).

At this stage, there are several compelling reasons to continue to focus our comparisons on SA and NA. *First*, we have well-established collaborations with SA ecologists (see letters of support) and these relationships have been crucial in garnering permission and the local scientific support required to initiate, maintain and sample the experiments in SA. *Second*, the existence of similar, long-term (20-50+ yr) manipulative studies of fire regimes in both regions 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 shorter-term comparative studies, because they ensure that the ecological context of sites being compared is known and consistent. *Third*, the interactive effects of fire and grazing are not well known in Africa, despite a wealth of research on these drivers independently. It is our ability to manipulate fire and grazing in tandem that allows us to expand upon previous ground-breaking studies of large ungulate herbivory in savanna grasslands (McNaughton 1983, 1985, Frank *et al.* 1998).

Below we 1) briefly compare and contrast fire and grazing as determinants of savanna grassland structure and function in NA and SA, 2) present our conceptual framework, research approach and the questions and hypotheses we are addressing with our ongoing research, 3) describe the exceptional long-term experiments in SA and NA that form the centerpiece of our research, 4) detail our core studies and

provide a brief overview of results to date, and 5) describe the data collection activities and new mechanistic studies to be supported by this renewal proposal.

3. Fire and Grazing as Determinants of Ecosystem Structure and Function in NA and SA

Given our overarching goal of comparing how fire and grazing impact savanna grasslands in SA vs. NA, we summarize similarities and differences in key attributes of these systems, and then note important disparities that have led to the notion that mesic savanna grassland ecosystems in NA and SA differ fundamentally in their responses to fire and grazing (Scholes *et al.* 2003a).

Mesic savanna grasslands in NA and SA have similar climates (Fig. 1); growing season temperatures and annual precipitation amounts and patterns are comparable, with most inputs (75%) occurring during the growing season (Hayden 1998, Scholes *et al.* 2003a). The primary differences occur in the dormant season where temperature and the environmental cues that start spring growth differ (i.e., temperature in NA vs. rainfall in SA), as expected in temperate vs. sub-tropical systems (Fig. 1).

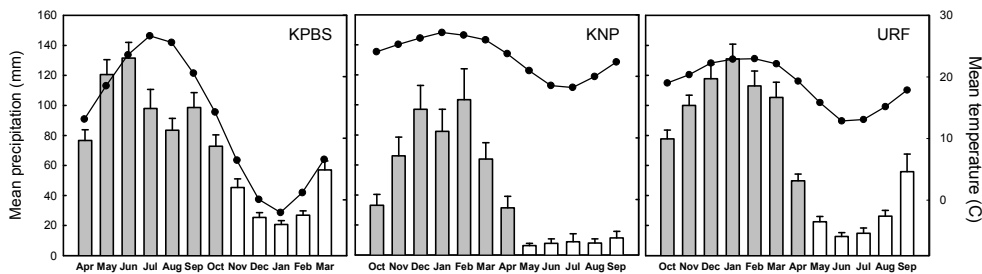


Fig. 1. Long-term (20+ yr) patterns of air temperature (lines) and precipitation (bars) for savanna grassland in South Africa and North America. Grey bars = growing season precipitation. Data are from Konza Prairie (KPBS), the Satara region of the Kruger National Park (KNP), and the Ukulinga Research Farm (URF).

Responses of woody plants to climate, fire and grazing are also quite similar. On both continents, where annual precipitation is >500 mm, dominance by woody plants occurs if fire is excluded (Enslin

et al. 2000, Titshall *et al.* 2000, Hoch *et al.* 2002, Bond *et al.* 2003, Sankaran *et al.* 2005, Higgins *et al.* 2007). Trees and shrubs in both regions are capable of resprouting after fire (Higgins *et al.* 2000, Briggs *et al.* 2002), and grazing may hasten woody encroachment by reducing fuel loads and fire intensity (Roques *et al.* 2001, Hoch *et al.* 2002, Sankaran *et al.* 2008). 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 than in the *herbaceous plant component* - our research focus.

Arguments that fire and grazing affect ecosystem processes and community structure and dynamics in fundamentally different ways in SA vs. NA (Scholes *et al.* 2003a, Lusk & Bellingham 2004, Uys *et al.* 2004) may seem surprising given the strong consensus regarding their importance in both systems (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 (5-7 million yrs), having been glaciated in the recent geologic past, whereas SA savanna grasslands are much older (40-60 million yrs, Bond *et al.* 2003). Other key differences are: 1) a lack of recent historic megafaunal extinction events in SA (Martin 1984), such that current megaherbivore richness in KNP is 33 species vs. 2 at KPBS (Kaufman *et al.* 1998), 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 (Scholes *et al.* 2003a,b), and 3) higher plant species richness (particularly in grasses) 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 disparate 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 independent and interactive effects of fire and grazing have not been experimentally assessed in Africa, despite intensive study of these in NA (Collins & Wallace 1990, Knapp *et al.* 1998a). Typically, effects of herbivory in Africa are studied in exclosures with fire excluded or with a variable and often uncontrolled fire regime (McNaughton *et al.* 1982, Young *et al.* 1998, Jacobs & Naiman 2008). Alternatively, fire is manipulated without controlling herbivory (Tainton *et al.* 1978, Biggs & Potgieter 1999, Morris & Fynn 2001, but see Augustine & McNaughton 2006). Thus, rigorous comparisons with NA systems were only initiated with our studies three years ago.

4. Conceptual Framework, Research Approach, Questions and Predictions

To address whether differences in the effects of fire and grazing on ecosystem processes and community dynamics between NA and SA arise from contingent factors (Fig. 2) or reflect research bias or disparate methodology, we are conducting concurrent experiments in which fire, grazing, and herbivore diversity are manipulated independently and in tandem on both continents with responses measured using identical methodology. Three unique, long-term (20-50+ yr) experiments in SA and NA (see below) serve as a platform for a suite of core studies to assess the impacts of 1) **fire alone**, 2) **grazing and fire/grazing interactions**, and 3) **differences in megaherbivore diversity**. Our research focuses on key *herbaceous* community (species richness, diversity and turnover) and ecosystem (ANPP and nutrient cycling) 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 (e.g., Hector *et al.* 1999, Smith & Knapp 2003, Tilman *et al.* 2006).

In general, our expectation is that the impacts of fire and grazing on ecosystem processes (e.g., ANPP, N and C cycling) will be qualitatively similar in NA and SA sites, although the magnitude of responses may differ due to differences in soil fertility (Fig. 2). In contrast, we expect divergent effects of fire and grazing on plant communities (diversity, compositional dynamics), both in direction and magnitude (Fig. 2). Impacts of differences in megaherbivore diversity are predicted to follow similar paths. With moderate grazing intensities, we predict that reductions in megaherbivore diversity to a single grazer species or no megaherbivores will have little effect on ecosystem processes but will cause substantial changes in plant community structure in SA.

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. *C₄* grasses are the most abundant herbaceous species in both SA and NA, and as a consequence, these dominant species contribute most to ecosystem function and community structure. In both NA and SA, changes in abundance of *C₄* grasses can have important consequences for community structure (diversity), dynamics (turnover) and species interactions in response to fire and grazing (McNaughton 1983, 1985, Milchunas *et al.* 1988, Collins *et al.* 1998, Collins & Smith 2006). A long evolutionary history in SA has allowed for extensive diversification of *C₄* grasses (Scholes *et al.* 2003a). By contrast, only a few, broadly distributed *C₄* grasses dominate in the younger communities in NA. We expect these differences in the diversity and evolutionary history of the dominant *C₄* grasses to lead to divergent community responses to fire and grazing in NA and SA. New phylogenetic community structure and trait-based studies proposed below are designed to assess the importance of evolutionary history and trait variation in determining community pattern and ecosystem processes.

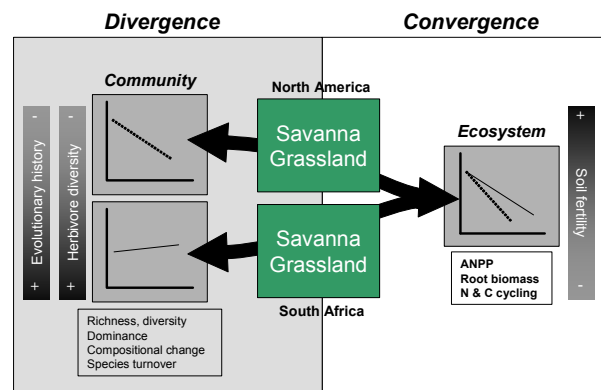


Fig. 2. Conceptual illustration of divergence (left) and convergence (right) at the community and ecosystem levels in response to long-term manipulation of fire and grazing in NA and SA savanna grasslands. Contingent factors (evolutionary histories, herbivore diversity) will result in species with different traits and life histories in SA vs. NA, fundamentally altering plant community responses to fire and grazing. In contrast, we predict that contingent factors will only modify (due to differences in soil fertility, for example) the extent, but not the direction of key ecosystem responses.

Differences in megaherbivore diversity between NA and SA also are important. Bison in NA have been shown to preferentially consume C₄ grasses, reducing their competitive impacts and increasing species diversity (Vinton & Hartnett 1992, Collins *et al.* 1998). Community structure and dynamics may 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. However, because C₄ grasses are always dominant in the herbaceous community on both continents 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. This is a central and we believe fundamentally important idea that our research is testing - *that divergence in community structure and dynamics does not preclude convergence in ecosystem function.*

Research Questions and Predictions

A. Long-term fire regimes

a. Are ecosystem responses to long-term fire regimes (without megaherbivores), such as herbaceous ANPP, root biomass, tissue N, and pools and dynamics of soil C and N, convergent in NA and SA?

With annual fire in the absence of megaherbivores in NA, ANPP and root biomass are increased, and root tissue N concentration and N availability are reduced (resulting in greater C:N ratio) compared to unburned sites (Hobbs *et al.* 1991, Blair 1997, Knapp *et al.* 1998b). We predict similar responses in SA, but the magnitude of responses may be muted due to greater nutrient limitations such that ANPP and root biomass 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 in the absence of fire (Knapp & Seastedt 1986), and soils will be drier in burned sites reducing N availability (Blair 1997). In infrequently burned sites, burning increases ANPP above that in annually burned sites in NA (Knapp *et al.* 1998b). 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 are lowest with annual fire, intermediate in the absence of fire and highest with intermediate fire frequency for savanna grasslands in NA (Collins *et al.* 1998), whereas community change over time exhibits more complex patterns (Collins 2000, Collins & Smith 2006). We predict divergence from these NA patterns in SA; plant community richness and diversity will not be affected by fire regime in SA (Uys *et al.* 2004). We posit that trait diversity in the species rich pool of SA C₄ grasses will maintain strong grass dominance and result in competitive suppression of the high N-requiring C₃ forbs regardless of fire regime in SA. This contrasts with NA where only a few C₄ grasses are available to dominate, and in the absence of fire, reduced grass dominance and increased N availability allow forb abundance to increase (Collins & Steinauer 1998). Consequently, we expect forb species to play a much larger role in influencing community diversity and dynamics in response to fire regime in NA than SA.

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 contrary to conclusions in a recent metaanalysis (Elser *et al.* 2007) 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). We expect similar N limitation to ANPP in annually burned sites in NA and SA. In contrast, we predict more rapid species turnover in SA due to the greater trait diversity and larger species pool capable of responding to increased N availability.

B. The importance of grazing and fire-grazing interactions

a. Does grazing by megaherbivores affect key ecosystem processes similarly in NA and SA?

In NA savanna grasslands, grazing by native megaherbivores consistently increases N cycling and availability (Frank & Evans 1997, Johnson & Matchett 2001). We predict similar responses in SA. With comparable, moderate grazing intensity, ANPP will be stimulated, soil N availability will be increased, and root biomass decreased in both annually burned and unburned sites (McNaughton *et al.* 1998,

Johnson & Matchett 2001) relative to sites (exclosures) without grazers.

b. Do plant communities respond differently to megaherbivore grazing in SA vs. NA?

Native megaherbivores in NA savanna grassland strongly influence plant community structure and dynamics because the primary herbivore (*Bos bison*) consumes the dominant C₄ grasses, 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). In contrast to this NA response, 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 consumption of the less abundant forbs by the large number of browsers (du Toit 2003, Jacobs & Naiman 2008). We expect, however, that composition will change significantly (compared to the grazing exclosures) due to turnover of the dominant grasses with grazing (Martens *et al.* 1996). Despite decreases in cover, there is little turnover of grass dominance in NA with moderate grazing (Collins *et al.* 1998), and thus compositional changes will be driven by forb responses.

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

Consistent with the logic above, we predict convergence in fire-grazing interactions at the ecosystem level. A reduction in N cycling (*in situ* N availability) due to annual fire is not evident 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 (Holdo *et al.* 2007). In NA, fire and grazing strongly 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. In SA, we predict that interactions will not have strong effects on plant diversity, as fire and grazing are predicted to have little effect separately, and browsers will likely reduce forb abundances in all burn treatments. 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. The role of megaherbivore diversity

a. How does megaherbivore diversity – a single megaherbivore vs. a full suite of megaherbivores - affect ecosystem processes and plant community structure?

At moderate grazing intensity, we predict little measurable effect of variation in megaherbivore diversity (one vs. many) on ecosystem processes in annual or infrequently burned SA savanna grassland, as long as herbivores are present that feed primarily on the dominant grasses (true grazers *sensu* du Toit 2003). In contrast, if specialist forb browsers (McNaughton & Georadiis 1986) are absent from the megaherbivore guild (i.e., in the Cape buffalo enclosure), then plant species diversity will increase in response to grazing by a single megaherbivore that consumes mainly grasses (i.e., Cape buffalo). Higher diversity will result from an increase in forb abundance, similar to that in NA ecosystems (Collins *et al.* 1998). When comparing NA and SA, grazing by bison and Cape buffalo (both primarily graminoid consumers, Knapp *et al.* 1999, du Toit 2003) will have similar ecosystem effects (increased N availability, reduced root biomass) regardless of fire regime. Community responses will be divergent however with greater turnover of the dominant grasses in SA vs. NA.

b. 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 is expected to recover. We also predict that the magnitude of effects of megaherbivore loss on C and N cycling will be similar regardless of megaherbivore diversity. Plant communities in NA and SA are expected to respond to megaherbivore removal as described above in Section B.b.

5. The Long-term Research Platform

We have invested considerable resources and time enhancing the research infrastructure in place at the three long-term experimental sites described below. The NA site is one of the most intensively studied mesic tallgrass prairies in the world (Knapp *et al.* 1998a), and the two SA sites, located ca. 400 km apart, are 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).

Konza Prairie Biological Station (KPBS). The KPBS is a 3,487 ha savanna grassland ecosystem composed primarily of native (>90%) perennial C₄ grasses such as *Andropogon gerardii* and *Sorghastrum nutans* that account for the majority of ANPP (Knapp *et al.* 1998b). Scattered shrub and tree species include *Cornus drummondii*, *Gleditsia triacanthos*, and *Prunus spp.* Numerous sub-dominant grasses and forbs contribute to the floristic diversity of the site (Towne 2002). The climate is continental (Fig. 2), with mean July air temperature of 27°C. Annual precipitation is ca. 820 mm/year, with 75% falling as rain during the Apr-Oct growing season (Fig. 1). Soils are fine textured, silty clay loams (Ransom *et al.* 1998).

KPBS includes fully replicated watershed-level fire and fire/grazing treatments, 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 April, 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).

Kruger National Park (KNP) - Experimental Burn Plots and Cape buffalo enclosure. The KNP is a 2 million ha protected area of savanna grassland that includes many of the large herbivores common to southern Africa (du Toit *et al.* 2003). The extant abundance and grazing intensity of herbivores in KNP is considered moderate for regional savanna grasslands (Trollope, pers. comm.). In the south-central region of KNP where our research takes place, average rainfall is 537 mm (Higgins *et al.* 2007) with most falling during the growing season (Fig. 5; Oct-Apr). The dormant season is mild, dry and frost free, and summers are warm with mean monthly maximum air temperature of 28.9°C in January (Fig. 1).

Because of the importance of fire in this savanna grassland ecosystem (Trollope 1982, Biggs & Potgieter 1999), the Experimental Burn Plot (EBP) study 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 treatments), each ~7 ha (370 x 180 m) in size, were established in four of the primary vegetation types covering the two major soil types (granites and basalts) and spanning the precipitation gradient in the park. Megaherbivores (12-14+ species) have had unrestricted access to the plots (Burns *et al.* in prep), and thus fire and grazing effects are combined.

For our research, we have focused on three blocks of EBPs located near Satara. Vegetation on the blocks is co-dominated by C₄ grasses, such as *Bothriochloa radicans*, *Panicum coloratum* and *Digitaria eriantha*, and woody plants, such as *Acacia nigrescens* and *Sclerocarya birrea*. Soils are fine-textured and derived from basalts. The Satara EBPs were selected because precipitation, soil type, and the mix of herbaceous and woody plants are most similar to KPBS (see Photo 1), and because of their proximity to the Cape buffalo enclosure. This 900-ha permanent enclosure, which is divided into blocks burned at different frequencies, was erected in 2000 for veterinary purposes and contains ~90 Cape buffalo. Due to the large body size of Cape buffalo, the grazing intensity inside is comparable to the moderate levels imposed in the park and at KPBS.

Ukulinga Research Farm (URF) - Long-term fire and mowing plots. The URF of the University of KwaZulu-Natal is located in Pietermaritzburg, SA. The site is dominated by C₄ grasses, such as *Themeda triandra* and *Heteropogon contortus*, with scattered shrubs and trees (Fynn *et al.* 2004). Mean annual precipitation is 790 mm, mostly as convective storms during summer (Oct-Apr, Fig. 1). Summers are warm with a mean monthly maximum of 26.4°C in February, and winters are mild with occasional frost. Soils are fine-textured and derived from shales. There has been no grazing at this site for >60 years.

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 haying treatments and 11 subplot fire or mowing treatments (Morris & Fynn 2001). Subplot sizes are 13.7 x 18.3 m.

6. Core Studies

Our research program is based on the long-term research platform and consists of a suite of core studies that experimentally address the questions and specific hypotheses related to a) the role of long-term fire regimes (without megaherbivores), b) the importance of grazing and grazing/fire interactions, and c) the impacts of reductions in megaherbivore diversity on key ecosystem processes and herbaceous plant community structure and dynamics. For all of these studies, we have established identical experiments in NA and SA, and we have collected data using identical sampling protocols (see *Detailed Methods*). This allows us to directly compare measured responses between the study sites and to rigorously test whether there is convergence or divergence in community and ecosystem processes of savanna grasslands in NA vs. SA in response to fire and grazing.

A. The role of long-term fire regimes. To address the long-term effects of fire frequency in the absence of megaherbivores on community dynamics and ecosystem processes, we began a study in the long-term experiments at KPBS and URF in which fire frequency has been manipulated for >25 yrs without megaherbivores. At URF, we used replicate plots (not hayed or mowed) burned every 1 and 3 yr in the spring, and those left unburned (Fig. 3; N=9 plots).

At KPBS, we established identically-sized permanent plots in ungrazed watersheds that are unburned (20-yr interval) or burned every 1 and 4 yr in the spring (Fig. 3; N=9 plots). To assess the role of N limitation in community and ecosystem responses to fire, we initiated identical N addition experiments at URF and KPBS in YR 1 by adding 10 gN/m²/yr as NH₄⁺/NO₃⁻ to replicate subplots within each of the 1-yr, 3-4 yr burned, and unburned plots (Fig. 3). For both studies, we have collected data on herbaceous ANPP, soil N availability, light availability (to assess canopy structure), and plant community composition over the past

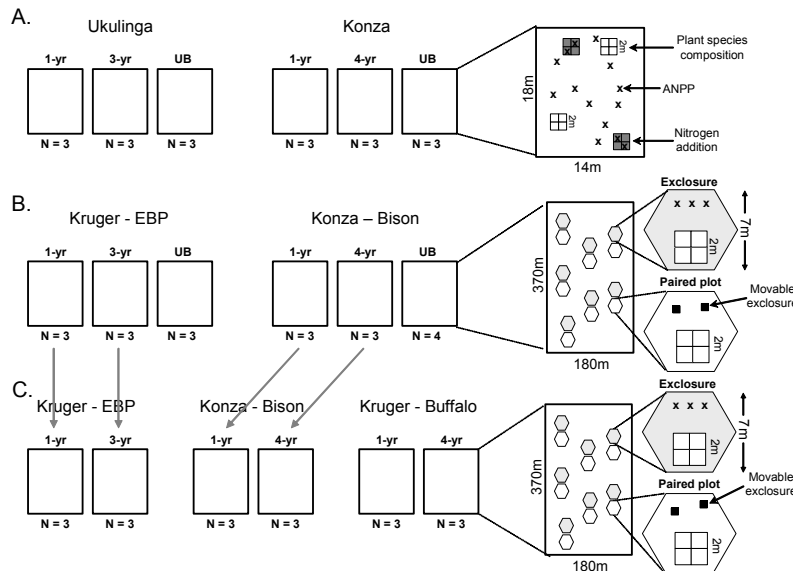


Fig. 3. Experimental design and sampling for the core studies: A) the role of long-term fire regimes (without megaherbivores), B) the importance of grazing and grazing/fire interactions, and C) the role of megaherbivore diversity. Permanent exclosures (grey plots, N=7 per plot) exclude all large herbivores. Moveable exclosures (N=2) are used to estimate ANPP in the grazed plots. N addition subplots (2 x 2 m) are divided into 4 1 x 1 plots, with two designated for plant species composition sampling and the other two for destructive sampling. Soil samples are collected from areas not designated for ANPP or plant composition sampling. Note that the same 1-yr and 3-4 yr burned plots at KNP and KPBS will be used in (B) and (C), and similar plots were established in the 1-yr and 4-yr burned blocks of the Buffalo enclosure for (C).

At URF, we used replicate plots (not hayed or mowed) burned every 1 and 3 yr in the spring, and those left unburned (Fig. 3; N=9 plots). At KPBS, we established identically-sized permanent plots in ungrazed watersheds that are unburned (20-yr interval) or burned every 1 and 4 yr in the spring (Fig. 3; N=9 plots). To assess the role of N limitation in community and ecosystem responses to fire, we initiated identical N addition experiments at URF and KPBS in YR 1 by adding 10 gN/m²/yr as NH₄⁺/NO₃⁻ to replicate subplots within each of the 1-yr, 3-4 yr burned, and unburned plots (Fig. 3). For both studies, we have collected data on herbaceous ANPP, soil N availability, light availability (to assess canopy structure), and plant community composition over the past



Photo 1. Examples of the megaherbivore exclosures (7 m diam. x 2.2 m tall; 38.5 m²) established at KNP (left) and KPBS (right). Each exclosure consists of chain-link fencing to a height of 1.8 m and two strands of wire located above the fencing to a height of 2.2 m. This design effectively excludes all megaherbivore species (>5 kg; rhino and elephant avoid these structures rather than being excluded).

three growing seasons.

B. The importance of grazing and fire-grazing interactions. For this study, we are utilizing the long-term experiments at KPBS and KNP in which native megaherbivore grazers are present and fire frequency is manipulated. To assess the effects of grazing and fire-grazing interactions, we have constructed permanent exclosures at both sites (Photo 1). The exclosures and matching paired open plots were established in YR 1 of the project in the Satara EBPs burned every 1 and 3 yr in the spring or left unburned and at KPBS in the 1-, 4-yr and unburned watersheds (N=63 exclosures/site; Fig. 3). Within each exclosure and paired open plot, we have sampled plant community composition and light availability in permanent subplots over the past three growing seasons. We also collected ANPP at the end of each growing season from each exclosure, and throughout the growing season in grazed areas adjacent to the unexclosed plots using 1x1 m moveable exclosures (Fig. 3). In addition, differential responses of megaherbivores to fire frequency may mediate fire-grazing interactions, thus we surveyed their abundances on the fire treatments in SA and NA throughout each growing season.

C. The role of megaherbivore diversity. We are assessing the role of megaherbivore diversity by comparing community and ecosystem responses to multiple megaherbivore species (12-14+ species in the EBPs) vs. a single megaherbivore grazer (Cape buffalo in SA and bison in NA). This study focuses on the 1-yr and 3-4 yr fire regimes (Fig. 3). In the Cape buffalo enclosure, we established three replicate plots (same size as the EBPs) in the 1- and 4-yr burned blocks and constructed identical permanent exclosures (Photo 1) with matching paired open plots (N=42 exclosures; Fig. 3). We have collected three years of ANPP (both inside and outside the exclosures), plant species composition, and light availability data in all exclosures and paired open plots. As noted above, we also have been assessing the abundances of megaherbivores on the fire treatments.

7. Results from Prior Support¹ and Progress to Date

We have made significant progress with our core studies. As indicated above, three years of community and ecosystem-level responses have been collected for each study with current funding. In most cases, two years of data have been analyzed (the third yr of data collection was recently completed in SA and is now being collected in NA) and these results are summarized below. Manuscripts to date are highlighted in the *References Cited* section.

Overall, the most progress to date has been made in assessing the impacts of fire alone. This was expected given that fire experiments have been in place >25 yr and all that was required was to consistently sample the study plots at KPBS and URF. For the N, grazing and megaherbivore diversity manipulations, additional time is needed to comprehensively assess these, as community and ecosystem responses are still in a state of flux.

Ecosystem and community responses to fire.

We have found that annual burning stimulates ANPP on both continents but only in sites with deep soils (Fig. 4). These results support our hypothesis that fire will have qualitatively similar effects on ANPP in both NA and SA; however, over the first two years the magnitude of response to fire was greater in SA despite the potential contingent factor of lower soil fertility (Fig. 4). These results contrast with previous studies reporting neutral or even negative effects of fire on ANPP in SA savanna grasslands (Tainton *et al.* 1978, Morris & Fynn 2001, Morris & Tainton 2002), demonstrating the value of measurements made in directly comparable ways.

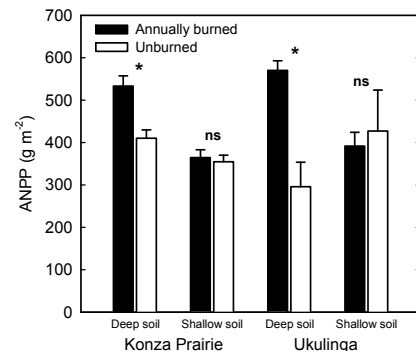


Fig. 4. Consistent responses in aboveground net primary productivity (ANPP) to fire in NA (Konza) and SA (Ukulinga) mesic savanna grasslands. In both sites, fire stimulates ANPP only in sites with deep soils (Buis *et al.* in prep.)

¹ Knapp, A.K., M.D. Smith, J.M. Blair, & S.L. Collins. *Collaborative Research: Convergence and Contingencies in Savanna Grasslands*. DEB 0516145, \$800,000, 2005-2008.

In NA savanna grasslands, frequent fire reduces soil N availability and increase N limitation to ANPP (Seastedt *et al.* 1991, Blair 1997, Blair *et al.* 1998). As with ANPP responses to fire, our first two years of results indicate convergence in N response to fire, with N availability declining with frequent fire at both sites (Fig. 5). Similarly, we found convergence in limitation of ANPP by N. At both sites, N addition resulted in an increase in ANPP in annually burned but not in unburned sites (Fig. 5). Thus, for the ecosystem responses we have measured to date, there is broad convergence in fire response and N limitation between NA and SA in the absence of megaherbivores.

Preliminary analysis of herbaceous plant community responses to fire provide support for divergence between the two sites (continent*fire treatment interaction was significant for plant community diversity, richness, evenness, relative abundance of grasses and forbs, etc.); however, the patterns of divergence were not as we expected. For example, total richness in NA tended to be highest with intermediate fire frequency, intermediate in the absence of fire, and lowest with annual burning in NA (Fig. 6). Decreased richness with annual fire was related to an increase in dominance (but not richness) by mainly C₄ grasses, as evidenced by two-fold higher ratios of grass/forb abundance. These responses are consistent with those of Collins (2000). In contrast, total richness was highest with annual burning in SA and lower but similar between the infrequently burned and unburned treatments (Fig. 6). In SA, the increase in richness with annual burning was driven by an increase in the number (and change in identity) of C₄ grass species present in the community (Fig. 6), but not an increase in their relative abundance. Thus, our results provide support for divergence at the community level between NA and SA, but the role of C₄ grasses in determining divergence was not as expected. New phylogenetic and trait-based studies (described below) will allow us to examine in detail how evolutionary history and variation in traits among the C₄ grasses contribute to divergence of community responses to fire in NA vs. SA.

Ecosystem and community responses to grazing, fire-grazing interactions, and differences in megaherbivore diversity.

Although the initial two years of data from these core studies are intriguing, both community and ecosystem responses to megaherbivore removal are still on a rapid trajectory of change, making it difficult to conclude whether there is convergence or divergence in these responses between NA and SA without additional years of data. Results from a separate, complementary study (Burns *et al.*, in review) in which we assessed plant community composition differences between infrequently burned (3-4 yr burn) sites in NA and SA with or without single herbivores (bison or Cape buffalo) provides support for convergence in community structure (diversity, richness) and divergence in plant composition to a reduction in herbivore richness from one to no species. At both sites, herbivore removal reduced plant species richness and diversity and increased C₄ grass dominance. Compositional differences between the no herbivore and single herbivore sites were driven primarily by changes in abundance and identity of C₄ grasses in SA, whereas

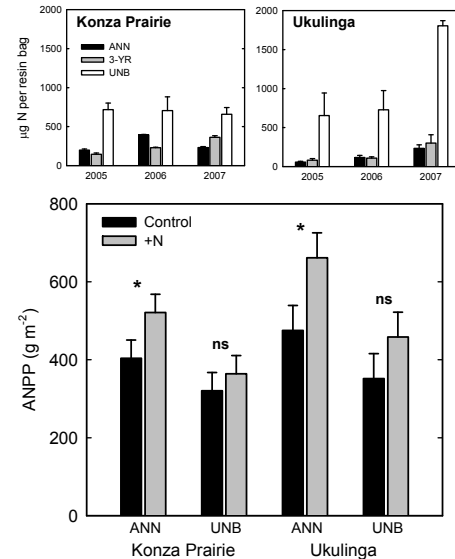


Fig. 5 Top - Similar patterns of reduction in soil N (measured with resin bags) with increasing fire frequency in ungrazed NA (Konza) and SA (Ukulinga) sites (data not yet analyzed for 2007 from Konza). Bottom - ANPP responds positively to N addition (10 g/m²/yr) only in annually burned sites where soil N is reduced. ANN = annual burn; 3-YR = burned every 3-4 yrs; UNB = unburned.

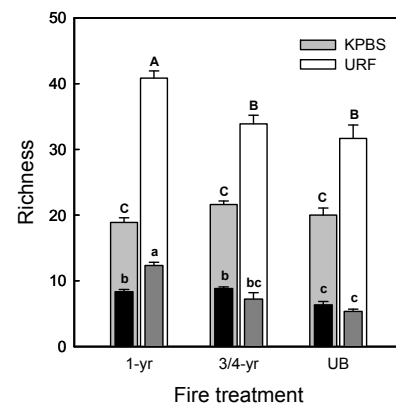


Fig. 6 Total (light grey and white bars) and grass (black and dark grey bars) richness each respond differently to increasing fire frequency in ungrazed NA (KPBS) and SA (URF) sites. Continent*fire interactions were significant (P<0.05) for total and grass richness. Different letters denote significant (P<0.05) differences among the fire treatments.

in NA, compositional differences were driven by a large suite of forbs and subdominant grasses. These responses are consistent with our expectation that turnover of the dominant grass species drives changes in composition and diversity in SA, whereas changes in forb richness and abundance drive those in NA.

8. Proposed Renewal Activities

Continuation of the core studies of our research program will allow us to assess whether purported differences in responses of key ecosystem processes and plant community structure and dynamics to fire and grazing are due to contingent factors (age, evolutionary history, megaherbivore diversity). This is because we can control for ecological context and sampling bias by using directly comparable experimental designs and identical sampling methods. Further, our manipulations of megaherbivore presence/absence, coupled with the megaherbivore surveys, will allow us to assess the role of megaherbivore diversity (i.e., many vs. one species) in determining divergence or convergence in responses. Although the other contingent factors, ecosystem age and evolutionary history, are impossible to manipulate as ultimate causal factors, our comparative approach does enable us to broadly distinguish between evolutionary and ecological mechanisms. Because we are measuring community and ecosystem-level responses in the same way on the two continents and across the different fire and grazing treatments, we can determine to what extent ‘treatment’ vs. ‘continent’ or ‘continent x treatment’ interaction explains the most variation. If ‘treatment’ explains the most variation, then convergence in a response is supported. This approach, though powerful (Losos 1996), is still somewhat descriptive, and we propose to complement this with phylogenetic and trait-based analyses focused on the dominant C₄ grasses. Given our original hypotheses and preliminary evidence for differential plant community responses to fire and grazing as a consequence of differences in species pools and traits of the dominant C₄ grasses between NA and SA, these analyses can be used to identify underlying mechanisms based on evolutionary history and trait diversity (Webb et al. 2002). Thus, the proposed phylogenetic and trait-based studies will provide a more comprehensive assessment of the factors contributing to convergence or divergence in community and ecosystem responses to fire and grazing in NA vs. SA.

We request renewal funding to complete our ongoing core studies and initiate and complete these new phylogenetic and trait-based studies. This will allow us to maintain the substantial investment in infrastructure in place at KPBS and KNP (168 permanent megaherbivore exclosures and 224 moveable exclosures), to accomplish the considerable data collection activities associated with the core studies (i.e., 1560 1 m² species composition plots sampled twice per year, 720 ANPP quadrats and ~2240 moveable exclosure plots harvested per year, etc.), and to conduct the new mechanistic studies. Below we describe in detail the continuing data collection activities and the new studies to be supported by the renewal.

Ongoing core studies

Long-term fire regimes. We will continue to sample over the next three growing seasons the fire treatments and N addition experiments at KPBS and URF to further assess ANPP, plant community composition, and N availability responses to the N addition treatments. This sampling also will allow us to capture the post-burn recovery period of the 3-4 yr burn treatments, permitting us to compare the fire history response between NA and SA. In the final year of the study, we will measure root biomass and tissue C/N content and soil C and N content in all plots.

Grazing, fire-grazing interactions, and megaherbivore diversity. Because community and ecosystem processes are still on a steep trajectory of change in response to megaherbivore removal, we will continue to collect data over the next three growing seasons in all of the exclosures and paired plots at KPBS and KNP. This includes plant community composition, ANPP (inside and outside exclosures), light availability, and soil N. We also will continue the megaherbivore surveys during each growing season to assess the distributional responses of megaherbivores to the fire treatments. In the final year of the study, we will assess soil C/N, root biomass and tissue C and N content in all of the exclosures and paired plots.

New mechanistic studies

We propose to use phylogenetic relatedness and functional traits to test mechanisms underlying divergence in community structure and dynamics and feedbacks between community and ecosystem processes in response to fire and grazing in NA and SA. Phylogenetic approaches allow us to statistically test for over- or under-representation of trait-relatedness in communities (Webb *et al.* 2002, Cavender-Bares *et al.* 2003). Functional traits reflect the evolutionarily-derived strategies of resource capture and

interactions among species (Diaz & Cabido 2001, Lavorel & Garnier 2002, Suding *et al.* 2003), providing a mechanistic link between community structure and ecosystem processes (Suding *et al.* 2008). For these new studies, we will quantify phylogenetic relatedness among all species found in a given treatment combination, and conduct a more detailed analysis of both response and effect traits (*sensu* Diaz & Cabido 2001) among the dominant C₄ grasses and other key species in NA and SA. We will then relate this trait variation to the different evolutionary histories of these plant species. If differences in evolutionary history and resultant species pools and traits give rise to differences in community responses to fire and grazing, then these studies should enable us to assess the underlying mechanisms that determine differences in plant community responses in NA and SA.

A. Phylogenetic community structure. We will 1) compare phylogenetic community structure across continents and among treatments and 2) interpret the dynamics of community structure from a phylogenetic perspective in response to megaherbivore exclusion and N addition. We predict that when comparing the species pools of each of the three sites (i.e., all species encountered across all plots sampled) to the entire Angiosperm phylogeny, that phylogenetic diversity (phylodiversity, Webb *et al.* 2006) will be greater (i.e., greater phylogenetic divergence among species) for the SA sites than NA, reflecting the greater age of these SA communities. For within-site comparisons of phylogenetic structure, our interest is in whether all species in the community or just the C₄ grasses are distributed non-random among the fire/grazing treatments with respect to phylogeny of the total species pool for a particular site. Similar comparisons will be made for the dynamics of phylogenetic community structure over time. For these comparisons, the expectation is that the distribution of species, either for the entire species pool or C₄ grasses only, could be either phylogenetically clustered or overdispersed depending on whether environmental filtering or competition is more important in determining community membership and whether traits are conserved or convergent. On the one hand, competitive exclusion and other negative density-dependent interactions (i.e., herbivory) can give rise to phylogenetic overdispersion due to negative effects on phylogenetically close relatives, resulting in species within a community being more distantly related than expected by chance (Webb *et al.* 2002). In contrast, environmental filters can restrict community membership to those species with traits suited to particular environmental conditions, causing species to be clustered phylogenetically and more closely related to each other than by chance (Cavender-Bares *et al.* 2006). However, knowledge of the distribution of traits, as well as relatedness, also is important (see below), because if traits important for environmental filtering are convergent, then closely related species might not co-occur (Cavender-Bares *et al.* 2006).

To assess phylogenetic community structure, we will use methods described by Webb *et al.* (2002) and Kembel & Hubbell (2006). For each comparison, community phylogenies for the species pools will be based on the most maximally resolved Angiosperm supertree and constructed using Phylomatic online software (<http://www.phylodiversity.net/phyloomatic>). We will work with M. Donoghue at Yale University (see letter of support) to construct these trees. Analysis of community phylogenetic structure will be conducted using Phylocom v4.0.1 (Webb *et al.* 2008). For each comparison, we will 1) calculate the mean pair-wise phylogenetic distances among species within a site or a plot (e.g., net relatedness index, nearest taxon index, Webb *et al.* 2002), 2) randomly generate null communities at the site or plot level and estimate mean pair-wise phylogenetic distances for each null community, and 3) compare observed pair-wise distances to the null distribution. This will allow us to quantify overall clustering of species within a community. To distinguish among mechanisms causing phylogenetic overdispersion, we will calculate trait conservatism for measured species traits (see below) using the “Analysis of Trait” module of Phylocom (Swenson *et al.* 2007). If traits are phylogenetically conserved, species that are closer to one another phylogenetically have traits that are more similar than expected. Overall, these analyses will provide a test of under- or overrepresentation of community trait relatedness, and help elucidate the role of evolutionary history and the relative strength of environmental filtering vs. competition in determining community membership in response to fire and grazing.

B. Functional trait analyses. There has been extensive diversification of C₄ grasses in SA, whereas the pool of C₄ grasses is smaller in NA (e.g., 31 vs. 11 C₄ grass species in the URF and KPBS fire treatments, respectively). It is differences in trait diversity between the pools of C₄ grasses (and other common species) in SA and NA that we hypothesize will give rise to divergence in community responses to fire, grazing and megaherbivore diversity. A hypothesized mechanism for divergence is greater turnover of C₄

grasses and variation of traits among the treatments in SA when compared to NA. To evaluate this mechanism, we will combine new measurements and data from the literature to assemble a suite of traits thought to be important in response to fire and grazing ('response traits'), as well as those traits that could impact ecosystem processes via changes in their representation in the community ('effect traits', Diaz & Cabido 2001, Suding *et al.* 2008). We will focus primarily on the dominant C₄ grasses; however, traits of other species may also be measured, based on their importance in community responses to the treatments. Focus on the dominant C₄ grasses is particularly relevant as these species have been shown to contribute most to community structure and ecosystem processes in both systems (McNaughton 1983, 1985, Milchunas *et al.* 1988, Collins *et al.* 1998, Smith & Knapp 2003, Collins & Smith 2006). Thus, linkages between response and effect traits and community and ecosystem responses should be strong.

Potential response and effect traits that will be measured include: maximum photosynthetic rate, specific leaf area (SLA), leaf dry matter content (LDMC), height, leaf size, growth form (bunchgrass vs. rhizomatous), seed mass, leaf carbon content (LCC), leaf nitrogen content (LNC), leaf lignin content (LLC), individual biomass (aboveground and root), relative growth rate, and grazing (clipping) tolerance. Several of these (e.g., individual biomass, photosynthesis, grazing tolerance) have already been quantified for the NA and SA dominant C₄ grasses (Swemmer 2007). Some of these traits (e.g., higher SLA, higher LNC, lower LDMC) may favor species under increased N availability, whereas others may favor species (lower height, growth form, higher LDMC, higher LLC, grazing tolerance) with grazing (Diaz *et al.* 2004, Garnier *et al.* 2004). Other traits were chosen because they have been shown to affect ecosystem processes (e.g., SLA, LDMC and LNC are known to affect components of C and N cycles, Garnier *et al.* 2004). For each species, we will collect trait data from at least 15 individuals at peak growth, and leaf-level traits will be measured on the youngest fully expanded leaf of each individual. We will use the effect-and-response framework described by Suding *et al.* (2008) to assess relationships between 'community aggregated' traits (*sensu* Garnier *et al.* 2004), species abundances and ecosystem processes. We will also measure trait similarity in the different treatments by comparing absolute pairwise differences in trait values to the degree of co-occurrence between species pairs (Cavender-Bares *et al.* 2006). This will allow us to assess the extent of "phenotypic clustering" vs. "phenotypic overdispersion" among the dominant C₄ grasses and other species within a community with respect to fire or grazing treatment (Cavender-Bares *et al.* 2006). Finally, functional traits will be linked to phylogenetic community structure via the trait conservatism analyses described above.

9 Detailed Methods

Statistical analyses and specific sample sizes for each response variable listed below are denoted based on the three core studies of our research: A) the role of long-term fire regimes, B) the effects of grazing and fire/grazing interactions, and C) the effects of megaherbivore diversity.

Statistical analyses:

To assess A and C, we will use repeated measures mixed-model ANOVA with continent, fire and/or megaherbivore diversity as fixed effects and year as a repeated measure. To assess A (N limitation with long-term fire), B and C, we will use split-plot, repeated measures mixed-model ANOVAs with continent and fire as whole plot treatments, grazing as a subplot treatment, and year as a repeated measure. In all cases, convergence in ecosystem or community responses will be based on whether there is a significant interaction between continent and treatment (fire, grazing or megaherbivore diversity), which would be indicative of responses diverging between NA and SA. In addition to these more general analytic procedures, additional question-specific analyses will be conducted. For example, we will use relative abundance data to compute pairwise Euclidean distances (ED) between the set of plots at each site. Based on these ED matrices, we will use non-metric multi-dimensional scaling (NMDS) and Analysis of Similarity (ANOSIM) analyses to determine if plant community composition differed significantly among the treatments at each site. We also will use the relative abundance data to calculate similarity percentages (SIMPER), to compute average similarity and dissimilarity among the treatments at a site, and to identify the plant species that most strongly contributed to the similarities *within* treatments and to the differences *among* treatments. In addition, time-lag analysis based on the ED matrices will be used to quantify rates of species compositional change over time (Collins 2000, Collins *et al.* 2000). From these spatial and temporal measures of compositional change, we can infer other community level mechanisms, such as

competition. Regression analyses will be used to assess relationships among changes in soil N availability, productivity, plant species diversity, and other response variables, such as light availability. In addition, correlations between the abundance of herbivores (for all herbivore species combined and for each species individually) and plant community structure, productivity, and tissue C/N content will be used to assess top-down effects on community and ecosystem responses. Primer v.5 will be used to compute each ED matrix and the ANOSIM, NMDS and SIMPER analyses (Clarke & Gorley 2001). SAS statistical software (v 9.1) will be used to conduct ANOVA, regression and correlation analyses.

Response variables:

Aboveground NPP: Herbaceous ANPP has been estimated from end-of-season harvests of 0.1 m² quadrats in ungrazed treatments (A: N=10/plot, N addition plots: N=2/subplot; B & C: N=3/exclosure; 720 quadrats total harvested each year). In grazed treatments, we are using 1x1 m moveable exclosures and paired plots (McNaughton *et al.* 1996), which are sampled at 3-4-wk intervals throughout the growing season (N=2 MEs/open plot; ~2240 plots total each year). Biomass is sorted into grass, 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 from the dominant grasses has been collected monthly during the growing season and ground for analysis for C/N content (Carlo-Erba NA 1500 C/N analyzer). All ground samples will be archived for potential future analyses (i.e., lignin content).

Belowground biomass: Soil cores (5 cm diam. x 20 cm deep; A: 10/plot; B & C: 2/subplot; 852 samples total) collected at the end of the growing season are used to quantify root biomass. The cores are washed and the roots collected for biomass and C and N determinations. Root in-growth bags (5 cm diam x 20 cm deep; B only: 672 total) are used to estimate belowground production over the growing season.

Soil C and N pools and fluxes: Resin bags (A: N=10/plot; B & C: N=2/subplot; 852 resin bags) are buried and incubated *in situ* over a growing season to provide an integrated index of NO₃ and NH₄ availability (Baer *et al.* 2003). Resin bags are made from nylon stockings filled with equal amounts of strong cation/anion exchange beads (5 g each) and inserted through narrow slits in the soil to a depth of 10 cm. Our initial focus was on ungrazed fire treatments, and currently we also have resin bags in grazed and exclosure sites. Soil samples (2 cm diam. x 10 cm deep cores, A: N=10/plot or exclosure, B & C: N=2/subplot; 852 samples total) will be collected at the end of each growing season. Samples will be split, and a portion dried, ground, and analyzed for total C and N content. Soil samples will be archived for assessment of any additional long-term changes in soil properties.

Plant species composition and light availability: Permanent 2x2 m subplots (A: N=3/plot; 54 total), B & C: N=1/exclosure plus paired open plot; 336 total) have been established and each divided into four 1x1m plots in which canopy cover of each species will continue to be visually estimated as in Knapp *et al.* (2002). These measures are 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. Light availability is measured at the end of the growing season above and below the canopy at the ground surface in each subplot (N=4/subplot) using a Decagon ceptometer.

Megaherbivore surveys: The abundance of megaherbivores (body mass >5 kg) on each plot in NA and SA will be visually surveyed from a vehicle at fixed observation points (every 60m) along plot perimeters twice weekly throughout each growing season (Burns *et al.* in prep). At each point, the plot is scanned for 60 sec and the species, age (juvenile vs. adult), and sex of each sighted individual is recorded. The precise location of each individual/group is recorded by noting the compass bearing and distance from the fixed observation point using a laser rangefinder. Separately, behavior classifications, including resting, moving and consumption, for a subset of individuals are collected (N=>20 surveys/plot/growing season) for 15-min per individual at 15-sec intervals.

10. Project management and South African collaborators

Overall project management will continue to be shared by Smith (community responses) and Knapp (ecosystem responses). The logistics of working in SA are challenging in many ways, particularly with the SA growing season occurring during the academic year in the US. Thus, we have relied on post-doctoral associates based in SA to accomplish our research goals. One of the keys to our success and

progress has been our collaboration with Dr. Richard Fynn who is based at URF but lives during the field season in KNP. Dr. Fynn provides invaluable oversight of studies related to plant community and belowground responses, and megaherbivore diversity at both KNP and KPBS, and for providing critical logistical support for the PIs, graduate students and technicians. Therefore, we are requesting continued support for his position. Collins and his graduate student will focus on fire/grazing interactions and temporal community dynamics. Blair will continue to provide logistical assistance at KPBS and oversee processing of resin bags and samples for soil and tissue analyses. In addition to Dr. Fynn, other SA colleagues that have agreed to continue to collaborate include Dr. Kevin Kirkman (Chair, Grassland Science) at the University of Kwa-Zulu Natal and Ms. Navashni Govender (Fire Ecologist & Manager of the EBPs) at KNP. Their CVs are included as supplemental documents.

11. 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 opportunities afforded by the three long-term experiments that form the centerpiece of our research is truly unprecedented. The comparative research approach based on identical experimental designs and sampling protocols in both NA and SA 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 herbivore diversity, for a suite of important ecosystem and community properties. The congruence in ecological attributes (i.e., climate, productivity, growth form dominance and structure) of these NA and SA savanna grasslands provide the backdrop from which we can discern the importance of contingencies, such as biome age, evolutionary history, and herbivore diversity. This will allow us to resolve claims that NA and SA savanna grasslands respond to fire and grazing in fundamentally different ways, as well as assess the trait-based mechanisms behind these differences, and to ascertain the kinds of inferences that can be made from one region to another. The identification of divergent and convergent ecological processes across systems despite contingencies will provide a basis for more focused comparative studies in other ecosystems – our long-term goal. 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, Holdo *et al.* 2007). Such an assessment will advance our general understanding of the structural and functional determinants of savanna grasslands far beyond that of most biomes.

II. Broader Impacts

Our research program provides unique educational, cultural and research experiences for both SA and NA undergraduates, graduate students and post-docs, as well as providing employment and educational opportunities to underprivileged South African citizens living adjacent to KNP. During the last 2.5 yrs, we have involved multiple graduate students (4 from UNM, 1 from CSU, 1 from Yale; 5 female) and undergraduates/recent graduates from SA (1) and NA (8) in the research on both continents (5 female). We also have employed seven different SA nationals from areas near KNP with an unemployment rate of 50-80%. We have been able to further their education by financially supporting them (with non-NSF funds) to take courses necessary for obtaining a driver's license and to become proficient at tracking animals, both of which are crucial for gaining permanent, higher paying jobs in SA. Although we can only directly support US students, we will actively recruit SA students through our SA colleagues for graduate assistantships supported by a new Mellon Foundation grant (see Smith C&P). PI's have already incorporated results from these studies into course content, and we plan to develop online TIEE course material based on data from this project. Moreover, signs are posted at the research plots in KNP to increase public awareness and outreach, and the project has received very positive local SA media attention. In addition, research plots at KPBS are highly visible and are incorporated into K-12 (as part of Schoolyard LTER) and public education tours. Data and results will be available on-line via the PIs webpages and the KNP website to scientists, educators and the general public. They are of particular 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.

References Cited

Manuscripts published, in press or in review that have resulted from this project (* indicates graduate students supported by this project, + indicates South African co-authors)

Burns, C.E., S.L. Collins, & M.D. Smith. Plant community response to loss of large herbivores: Comparing consequences in a South African and a North American grassland. *Biodiversity and Conservation*, in review(a).

Knapp, A.K., C.E. Burns, R.W. S. Fynn⁺, K.P. Kirkman⁺, C.D. Morris⁺ & M.D. Smith. 2006. Convergence and contingency in production–precipitation relationships in North American and South African C₄ grasslands. *Oecologia* 149: 456-464.

Smith, M.D., B.W. van Wilgen⁺, C. Burns, S.J. Andelman, H. Biggs⁺, N. Govender⁺, J. Kruger⁺, A.L.F. Potgieter⁺, and W.S. Trollope⁺. Long-term effects of fire on South African savanna grassland community structure. *Journal of Ecology*, submitted.

Swemmer*, A.M., A.K. Knapp & H.A. Snyman⁺. 2008. Intra-seasonal precipitation patterns and aboveground productivity in three perennial grasslands. *Journal of Ecology*, in press.

Zeglin*, L.H., M. Stursova, R.L. Sinsabaugh & S.L. Collins. 2007. Microbial responses to nitrogen addition in three grassland ecosystems. *Oecologia* 154:349–359.

Allen-Diaz, B. 1996. Rangeland in a changing climate: Impacts, adaptations and mitigation, pp. 131-158, in *Climate Change 1995, Impacts, adaptations and mitigation of climate change: Scientific-Technical Analyses*, (R.T. Watson, M.C. Zinyowera, R.H. Moss and D.J. Dokken, eds.), Cambridge Press, Cambridge, England.

Amthor, J.S. et al. 1998. *Terrestrial Ecosystem Responses to Global Change: A Research Strategy*, ORNL/TM-1998/27, Oak Ridge National Laboratory, Oak Ridge, TN.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134: 545-561.

Archer, S. 1995. The role of herbivores in mediating grass-woody plant interactions. *Tropical Grasslands* 29:218-235.

Archer, S, C. J. Scifres, C. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: rates, dynamics and processes in the conversion of grassland to thorn woodland. *Ecological Monographs* 58:111-127.

Augustine, D.J. and S.J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* 9: 1242-1256.

Austin, A.T. and O.E. Sala. 2002. Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. *Journal of Vegetation Science* 13: 351-360.

Axelrod, D.I. 1985. Rise of the grassland biome, Central North America. *The Botanical Review* 51: 163-201.

- Baer, S.G., J.M. Blair, A.K. Knapp, and S.L. Collins. 2003. Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology* 84:724-735.
- Beringer, J., L.B. Hutley, N.J. Tapper, and L.A. Cernusak. 2007. Savanna fires and their impacts on net ecosystem productivity in North Australia. *Global Change Biology* 13:990-1004.
- Biggs, H.C. and A.L.F. Potgieter. 1999. Overview of the fire management policy of the Kruger National Park. *Koedoe*. 42:101-110.
- Biggs R., H.C. Biggs, T. Dunne, N. Govender, and A.L.F. Potgieter. 2003. What is the design of the Experimental Burning Plot (EBP) trial in the Kruger National Park? *Koedoe* 46: 1 - 15.
- Blair, J.M. 1997. Fire, N availability and plant response in grasslands: A test of the transient maxima hypothesis. *Ecology*. 78:2539-2368.
- Blair, J.M., T.R. Seastedt, C.W. Rice and R.A. Ramundo. 1998. Terrestrial nutrient cycling in tallgrass prairie. pp. 222-243, in *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A.K. Knapp, J.M. Briggs, D.C. Hartnett and S.C. Collins, eds.), Oxford University Press, New York.
- Brooks, T, A. Balmford, N. Burgess, J. Fjeldsa, L.A. Hansen, J. Moore, C. Rahbek and P. Williams. 2001. Toward a blueprint for conservation in Africa. *BioScience* 51: 613-624.
- Brown, J.H., and E.J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- Brown, J.H., T.G. Whitam, S.K. Morgan Ernest, and C.A. Gerhing. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments, *Science* 293: 643-650.
- Bond, W.J., and G.F. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16: 45-51.
- Bond, W.J., G.F. Midgley and F.I. Woodward. 2003. What controls South African vegetation – climate or fire? *South African Journal of Botany* 69: 79-91.
- Booyesen, P. de V., and N.M. Tainton (eds.). 1984. *Ecological Effects of Fire in South African Ecosystems*. Springer-Verlag, NY.
- Briggs, J.M., and A.K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. *American Journal of Botany* 82: 1024-1030.
- Briggs, J.M., A.K. Knapp and B.L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a 15 year study of fire and fire-grazing interactions. *American Midland Naturalist* 147:287-294.
- Cavender-Bares, J., and A. Wilczek. 2003. Integrating micro- and macroevolutionary processes in community ecology. *Ecology* 84: 592-597.
- Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87: S109-S122.
- Cody, M.L. and H.A. Mooney. 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* 9: 265-321.

- Cole, M.M. 1986. *The savannas: biogeography and geobotany*. Academic Press, New York, NY.
- Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *The American Naturalist*. 155:311-325.
- Collins, S.L., F. Micheli, L. Hartt. 2000. A method to determine rates and patterns of variability in ecological communities. *Oikos* 91: 285-293.
- Collins, S.L., and L.L. Wallace. 1990. *Fire in North American Tallgrass Prairies*. Univ. Oklahoma Press, Norman, 175 pp.
- Collins, S.L., and S.M. Glenn. 1991. Importance of spatial and temporal dynamics in species regional abundance and distribution. *Ecology* 72:654-664.
- Collins, S.L., and M.D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87:2058-2067.
- Collins, S.L., and E.M. Steinauer. 1998. Disturbance, diversity, and species interactions in tallgrass prairie. pp. 140-156, in *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A.K. Knapp, J.M. Briggs, D.C. Hartnett and S.C. Collins, eds.), Oxford University Press, New York.
- Collins, S.L., A.K. Knapp, J.M. Briggs, J.M. Blair, and E.M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*. 280:745-747.
- Coughenour, M.B. 1993. *The SAVANNA Landscape Model - Documentation and Users Guide*. Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins CO.
- Cowling, R.M., D.M. Richardson and S.M. Pierce. 1997. *Vegetation of southern Africa*. Cambridge University Press, Cambridge, UK.
- Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16: 646-655.
- Diaz, S., J.G. Hodgson, K. Thompson, et al. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295-304.
- du Toit, J.T., K.H. Rogers, and H.C. Biggs. 2003. *The Kruger Experience, Ecology and Management of Savanna Heterogeneity*. Island Press, Washington, DC.
- du Toit, J.T. 2003. Large herbivores and savanna heterogeneity. pp. 292-309, in *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (J.T. duToit, K.H. Rogers and H.C. Biggs, eds.), Island Press, Washington.
- Eckhardt, H.C., B.W. van Wilgen and H.C. Biggs. 2000. Trends in woody vegetation cover in Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology* 38: 108-115.
- Elser, J.J., and 9 other authors. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Letts.* 10:1135-1142.

- Enslin, B.W., A.L.F. Potgieter, H.C. Biggs and R. Biggs. 2000. Long term effects of fire frequency and season on the woody vegetation dynamics of the *Sclerocarya birrea*/*Acacia nigrescens* savanna of the Kruger National Park. *Koedoe* 43: 1-11.
- Frank, D.A., and R.D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* 78:2238-2248.
- Frank, D. A., S. J. McNaughton, and B. Tracy. 1998. The ecology of the earth's grazing ecosystems. *Bioscience* 48: 513-521.
- Fuhlendorf, S.D. and D.M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625-632.
- Fynn, R.W.S., C.D. Morris, and T.J. Edwards. 2004. Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Applied Vegetation Science*. 7:1-10.
- Fynn, R.W.S., and T.G. O'Connor. 2005. Determinants of community organization of a South African mesic grassland. *Journal of Vegetation Science* 16:93-102.
- Fuhlendorf, S.D., and D.M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51: 625-632.
- Garnier, E., J. Cortez, G. Billes, et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630-2637.
- Hartnett, D.C., K.R. Hickman, and L.E.F. Walter. 1996. Effects of bison grazing, fire and topography on floristic diversity in tallgrass prairie. *Journal of Range Management*. 49:413-420.
- Hayden, B.P. 1998. Regional climate and the distribution of tallgrass prairie. pp. 19-34, in *Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie* (A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, eds.), Oxford University Press, New York, NY.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286:1123-1127.
- Higgins, S.I., W.J. Bond, and W.S.W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213-229.
- Higgins, S.I. and 13 other authors. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88:1119-1125.
- Hobbie, J.E., S.R. Carpenter, N.B. Grimm, J.R. Gosz, and T.R. Seastedt. 2003. The US Long Term Ecological Research Program. *BioScience* 53: 21-32.
- Hobbs, N.T., D.S. Schimel, C.E. Owensby, and D.S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72: 1374-1382.
- Hoch, G.A., J.M. Briggs, and L.C. Johnson. 2002. Assessing the rate, mechanism and consequences of conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 6:578-586.
- Holdo, R.M., R.D. Holt, M.B. Coughenour and M.E. Ritchie. 2007. Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. *Journal of Ecology* 95: 115-128.

- Johnson, L.C., and J.R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology* 82:3377–3389.
- Kaufman, D.W., P.A. Fay, G.A. Kaufman, and J.L. Zimmerman. 1998. Diversity of terrestrial macrofauna. pp. 101-112, in *Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie* (A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, eds.), Oxford University Press, New York, NY.
- Kembel, S.W., and S.P. Hubbell. 2006. The phylogenetic structure of a neotropical forest tree community. *Ecology* 87: S86-S99.
- Knapp, A.K., and T.R. Seastedt. 1986. Detritus accumulation limits productivity in tallgrass prairie. *BioScience* 36:662-668.
- Knapp, A.K., J.M. Briggs, D.C. Hartnett, and S.L. Collins. 1998a. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, NY.
- Knapp, A.K., J.M. Briggs, J.M. Blair, and C.L. Turner. 1998b. Patterns and controls of aboveground net primary production in tallgrass prairie. pp. 193-221, in *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A.K. Knapp, J.M. Briggs, D.C. Hartnett and S.C. Collins, eds.), Oxford University Press, New York.
- Knapp, A.K., J.M. Blair, J.M. Briggs, S.L. Collins, D.C. Hartnett, L.C. Johnson, and E.G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49:39-50.
- Knapp, A.K., P.A. Fay, J.M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M.S. Lett and J. K. McCarron. 2002. Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. *Science* 298: 2202-2205.
- Knapp, A.K. M.D. Smith, S.L. Collins, N. Zambatis, M. Peel, S. Emery, J. Wojdak, M.C. Horner-Devine, H. Biggs, J. Kruger and S.J. Andelman. 2004. Searching for Generality in Ecology: Testing North American Grassland Rules in South African Savannas. *Frontiers in Ecology and the Environment* 9: 483-491.
- Knapp, A.K., C.E. Burns, R.W.S. Fynn, K.P. Kirkman, C.D. Morris, and M.D. Smith. 2006. Convergence and contingency in production-precipitation relationships in North American and South African C₄ savanna grasslands. *Oecologia* 149:456-464.
- Lauenroth, W.K., I.C. Burke, and M.P. Gutmann. 1999. Grassland ecosystems in central North America. *Great Plains Research* 9: 223-59
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545-556.
- Likens, G.E., C.T. Driscoll, and D.C. Buso. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* 272: 244-246.
- Leach M.K., and T.J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273: 1555-1561.
- Losos, J.B. 1996. Phylogenies and comparative biology. 2. Testing causal hypotheses derived from phylogenies and data from extant taxa. *Systematic Biology* 45: 259-260.

- Lusk, C., and P. Bellingham. 2004. Austral challenges to northern hemisphere orthodoxy. *New Phytologist* 162: 248-250.
- Mares, M.A. 1980. Convergent evolution among desert rodents: a global perspective. *Bulletin of Carnegie Museum of Natural History* 16: 1-51.
- Martens, J.C., J.E. Danckwerts, and P.J.K Zacharias. 1996. Species responses to grazing in the Smaldeel area of the Eastern Cape. *African Journal of Range and Forage Science* 13: 29-36.
- Martin, P.S. 1984. Prehistoric overkill: The global model. pp. 354-403, in *Quaternary Extinctions: A Prehistoric Revolution* (P.S. Martin and R.G. Klein, eds.), University of Arizona Press, Tucson, AZ.
- McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecol. Monogr.* 53: 291-320.
- McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55: 259-294.
- McNaughton, S.J., and N.J. Georiadis. 1986. Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics* 17: 39-65.
- McNaughton, S.J., M.B. Coughenour and L.L. Wallace. 1982. Interactive processes in grassland ecosystems. Pages 167-193 in Estes, JR, Tyrl, RJ, Brunken, JN (eds.) *Grasses and Grasslands: Systematics and Ecology*, Norman OK, University of Oklahoma Press.
- McNaughton, S.J., D.G. Milchunas and D.A. Frank. 1996. How can net primary productivity be measured in grazing ecosystems? *Ecology* 77: 974-977.
- McNaughton, S.J., F.F. Banyikwa, and M.M. McNaughton. 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. *Ecology* 79:587-592.
- Meserve, P.L., D.A. Kelt, W.B. Milstead and J.R. Gutierrez. 2003. Thirteen years of shifting top-down and bottom-up control. *BioScience* 53: 633-646.
- Milchunas, D.G., O.E. Sala, and W.K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132:87-106.
- Morris, C.D., N.M. Tainton, and M.B. Hardy. 1992. Plant species dynamics in the Southern Tall Grassveld under grazing, resting and fire. *Journal of the Grassland Society of Southern Africa* 9: 90-96.
- Morris, C.D., and N.M. Tainton. 1996. Long-term effects of different rotational grazing schedules on the productivity and floristic composition of Tall Grassveld in KwaZulu-Natal. *African Journal of Range and Forage Science* 13:24-28.
- Morris, C.D., and R.W.S. Fynn. 2001. The Ukulinga long-term grassland trials: reaping the fruits of meticulous, patient research. *Bulletin of the Grassland Society of South Africa* 11: 7-22.
- Morris, C., and N. Tainton. 2002. Lessons from Africa. *Rangelands* 24: 8-12.

- Oesterheld, M, J. Loreti, M. Semmartin, and J.M. Paruelo. 1999. Grazing, fire and climate effects on primary productivity of grasslands and savannas. pp. 287-306, in *Ecosystems of Disturbed Ground. Ecosystems of the World 16* (L.R. Walker, ed), Elsevier, Amsterdam.
- Ojeda, F., M.T. Simmons, J. Arroyo, T. Maranon and R.T. Cowling. 2001. Biodiversity in South African fynbos and Mediterranean heathland. *Journal of Vegetation Science* 12: 867-874.
- Overbeck, G.E. and J. Pfadenhauer. 2007. Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora* 202:27-49.
- Owen-Smith, R.N. 1988. *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge University Press. Cambridge, UK.
- Palmer, M., E. Bernhardt, E. Chornesky, S. Collins, A. Dobson, C. Duke, B. Gold, R. Jacobson, S. Kingsland, R. Kranz, M. Mappin, M.L. Martinez, F. Micheli, J. Morse, M. Pace, M. Pascual, S. Palumbi, O.J. Reichman, A. Simons, A. Townsend and M. Turner. 2004. Ecology for a crowded planet. *304*: 1251-1252.
- Price, T., I.J. Lovette, E. Bermingham, H.L. Gibbs and A.D. Richman. 2000. The imprint of history on communities of North American and Asian warblers. *American Naturalist* 156: 354-367.
- Ransom, M.D., C.W. Rice, T.C. Todd, and W.A. Wehmueller. 1998. Soils and soil biota. pp. 48-66, in *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, eds.), Oxford University Press. New York.
- Reid, R.S., and J.E. Ellis. 1995. Impacts of pastoralists on woodlands in South Turkana, Kenya: Livestock-mediated tree recruitment. *Ecological Applications*, 5(4), pp 978–992.
- Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, and J.A. Weins. 1981. *The True Prairie Ecosystem*. Hutchinson Ross Publ. Co., Stroudsburg, PA.
- Roques, K.G., T.G. O'Connor, and A.R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall, and density dependence. *Journal of Applied Ecology* 38:268-280.
- Sankaran, M, J. Ratnam and N. Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, in press.
- Sankaran, M and 29 co-authors. Determinants of woody cover in African savannas. *Nature* 438: 846-849.
- Schimel, D.S., B.H. Braswell, E.A. Holland, R. McKeown, D.S. Ojima, T.H. Painter, W.J. Parton and A.R. Townsend. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles*, 8: 279-293.
- Scheiner, S.M., S.B. Cox, M.R. Willig, G. Mittelbach, C.W. Osenberg, and M. Kaspari. 2000. Species richness, species-area curves, and Simpson's paradox. *Evolutionary Ecology Research* 2:791-802.
- Scholes, R.J. 1993. Nutrient cycling in semi-arid grasslands and savannas: its influence on pattern, productivity and stability. pp. 1331-1334 in *Proceedings of the XVII International Grasslands Congress 1993*, New Zealand Grassland Association, Palmerston North.

- Scholes, R.J., and B.H. Walker. 1993. *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge Univ. Press, 306 pp.
- Scholes, R.J., and S.R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517-544.
- Scholes, R.J., W.J. Bond, and H.C. Eckhardt. 2003a. Vegetation dynamics in the Kruger ecosystem. Pp. 242-262 In: J.T. duToit, K.H. Rogers and H.C. Biggs (eds.). *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington.
- Scholes, M.C., R.J. Scholes, L.B. Otter, and A.J. Woghiren. 2003b. Biogeochemistry: the cycling of elements. pp. 130-148, in *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (J.T. duToit, K.H. Rogers and H.C. Biggs, eds.), Island Press, Washington.
- Seastedt, T.R., J.M. Briggs, and D.J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. *Oecologia*. 87:72-79.
- Smith, M.D., and A.K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* 6:509-517.
- Suding, K.N., D.E. Goldberg, and K.M. Hartman. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84: 1-16.
- Suding, K.N., S. Lavorel, F.S. Chapin III, J.H.C. Cornelissen, S. Diaz, E. Garnier, D. Goldberg, D.U. Hooper, S.T. Jackson, and M.-L. Navas. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125-1140.
- Swemmer, A.M. 2007. The effect of intra-seasonal variation in precipitation on the productivity of grasses and grasslands. PhD Dissertation, Colorado State University. Fort Collins, CO. 173 pp
- Swenson, N.G., B.J. Enquist, J. Thompson, and J.K. Zimmerman. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88: 1770-1780.
- Tainton, N.M., P.V. Booysen, D.I. Bransby, and R.C. Nash. 1978. Long term effects of burning and mowing on tall grassveld in Natal: dry matter production. *Proc. of the Grassland Society of Southern Africa* 13: 41-44.
- Tilman, D., P.B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294: 843-845.
- Tilman, D., P.B. Reich, and J.M.H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629-632.
- Titshall, L.W., T.G. O'Conner, and C.D. Morris. 2000. Effect of long-term exclusion of fire and herbivory on the soils and vegetation of sour grassland. *African Journal of Range and Forage Science* 17: 70-80.
- Towne, E.G. 2002. Vascular plants of Konza Prairie Biological Station: An annotated checklist of species in a Kansas tallgrass prairie. *Sida*. 20:269-294.

- Trollope, W.S.W. 1982. Ecological effects of fire in South African savanna. pp. 292-306, in *Ecology of Tropical Savannas*. Ecological Studies Vol. 42 (B.J. Huntley, and B.H. Walker, eds.), Springer-Verlag, New York.
- Trollope, W.S.W., L.A. Trollope, H.C. Biggs, D. Pienaar, and A.L.F. Potgieter. 1998. Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. *Koedoe* 41: 103-112.
- Uys, R.G., W.J. Bond, and T.M. Everson. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118: 489-499.
- Van Wilgen, B.W., H.C. Biggs, S.P. O'Regan, and N. Mare. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Science* 96: 167-178.
- Vinton, M.A., and D.C. Hartnett. 1992. Effects of bison grazing on *Andropogon gerardii* and *Panicum virgatum* in burned and unburned tallgrass prairie. *Oecologia*. 90:374-382.
- Walker, B.H. 1985. Structure and function of savannas: an overview. pp. 81-91, in *Ecology and Management of the World's Savannas* (J.C. Tothill and J.J. Mott, eds.), CAB Press, Slough, UK.
- Walter, H. 1985. *Vegetation of the earth and ecological systems of the geo-biosphere*. Springer-Verlag, NY.
- Webb, C.O., D.D. Ackerly, and S.W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. URL: <http://www.phylodiversity.net/phylocom/>
- Webb, C.O., G.S. Gilbert, and M.J. Donoghue. 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* 87: S123-S131.
- Webb, C.O., D.D. Ackerly, M.A. McPeck, and M.J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475-505.
- Young, T.P., B. Okello, D. Kinyua and T. Palmer. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science* 14: 92-104.