12-2016

Complex Vegetation Dynamics at the Fire-Grazing-Drought Nexus

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Bielski, Christine H., "Complex Vegetation Dynamics at the Fire-Grazing-Drought Nexus" (2016). *Theses, Dissertations, and Student Research in Agronomy and Horticulture*. 115.
http://digitalcommons.unl.edu/agronhortdiss/115

COMPLEX VEGETATION DYNAMICS AT THE FIRE-GRAZING-DROUGHT NEXUS

by

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A THESIS

Presented to the Faculty of
The Graduate College at the University of Nebraska
In Partial Fulfillment of Requirements
For the Degree of Master of Science

Major: Agronomy

Under the Supervision of Professor Dirac Twidwell

Lincoln, Nebraska

December, 2016

COMPLEX VEGETATION DYNAMICS AT THE FIRE-GRAZING-DROUGHT NEXUS

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University of Nebraska, 2016

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The discipline of ecology long ago moved away from viewing systems as static entities where disturbance processes, environmental stochasticity, and spatiotemporal variability play minor roles in determining ecosystem structure and function. Ecological theory continue to develop frameworks and statistical techniques capable of describing the inherent complexity in natural systems. However, in dealing with the complexity in nature, many applied disciplines have yet to adopt such frameworks or statistical techniques. The objective of this study was bridge the gap between ecological theory and application by using complex systems theory to describe grassland vegetation dynamics at the fire-grazing-drought nexus. Chapters 2 and 3 take advantage of one of the most severe growing season droughts on modern record in the southern Great Plains and a long-term pyric herbivory experiment to investigate spatiotemporal patterns in vegetation at the fire-grazer interface. Through the application of metacommunity theory, Chapter 2 reveals scale switching in complex feedbacks between grassland productivity, fire behavior, forage quality, and grazer selection before and during extreme drought. Through the application of information-theoretic model comparison, Chapter 3 provides a

method for applied fire modeling systems to quantitatively assess the impact of favoring central tendency in the characterization of grassland fuel properties that are the basis for predicting wildfire risk and behavior. Chapter 4 identifies thresholds in the flammability of *J. virginiana* (Eastern redcedar), a commonly planted horticultural tree rapidly invading across the Great Plains, across a gradient of fuel moisture contents to improve wildland fire risk assessments and monitoring programs. The results of these case studies will become even more important during the next century, when climate models forecast an increase in frequency and severity of growing season droughts across much of the Great Plains.

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severity in the recently burned patch. Greater small-scale variability in fire intensity and severity in the recently burned patch results in greater post-fire spatial (alpha) variability in both plant quantity and quality than typically observed. Increased variability in forage quality and quantity across the burned patch (alpha variability), likely changed the scale of grazer selection, as grazers are attracted to high forage quality and are capable of changing grazing patterns to meet nutritional requirements. Consequently, we observed the negative feedback loop that typical reduces within-patch (alpha) variability switch to operating at a landscape scale and reducing among-patch (beta) variability.

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CHAPTER I

INTRODUCTION

A BRIEF HISTORY ON ECOLOGICAL THEORY

Ecological models are scientific perceptions of how nature operates (DeAngelis and Waterhouse 1987). The more we investigate and understand ecological systems, the more accurate models will become in predicting ecological system dynamics (Wu and Loucks 1995). The idea that nature has a “balance,” or “natural order,” has been the root of early ecological theory and model development (Egerton, 1973; McIntosh 1985; O’Neil et al. 1986). Continuing on this idea, an *equilibrium model* was established that stresses the importance of self-regulation, biotic feedbacks, and climax communities (Wu and Loucks 1995; DeAngelis and Waterhouse 1987; Vetter, 2005). Such a view states that, with no management input, populations, communities, and ecosystems will remain in stable equilibrium through self-regulatory processes such as biotic regulation, density dependence, and carrying capacity (Nicholson, 1933; Milne and Milne 1960; Ellis and Swift 1988). Tightly coupled relationships between herbivores and their resources further stabilize community dynamics (Ellis and Swift 1988; Vetter, 2005). Dominating in the 1960s and 1970s (Wu and Loucks 1995), equilibrium models have been well accepted in ecological theory and have served as basis for many management strategies and decisions (Fuhlendorf and Engle 2001). Modern derivatives such as *steady-state, stability,* and *homeostasis* have emerged from the equilibrium view (DeAngelis and Waterhouse, 1987; Botkin, 1990). However, since the early 20th century, ecologists have been challenging this paradigm due to lack of direct evidence that an equilibrium state is a fundamental characteristic of ecological systems (Elton, 1930; Holling, 1973; Wiens, 1977; Wu, 1992). Modern ecological perspectives recognize that spatial heterogeneity, history, variability, stochasticity, and disturbance processes have been shown to be important factors in determining ecosystem structure and function (Holling, 1973; Steele, 1978; Pickett, 1980; Fuhlendorf, 2012). Increased recognition of the importance of such factors led to the establishment of the *dynamic-equilibrium model*. Dynamic-equilibrium models stress the importance of spatiotemporal variability, environmental stochasticity, and disturbance processes in determining ecosystem structure and function (Wu and Loucks 1995). The dynamic-equilibrium paradigm has become a dominant view in many areas of ecology due to an increased awareness that patchiness occurs over a wide range of organizational, spatial, and temporal scales in both terrestrial and aquatic systems (Taylor, 1990, Wu and Loucks 1995). Unlike the equilibrium model that states equilibrium is as a fundamental property of ecological systems, a dynamic-equilibrium model states that equilibrium exists as an emergent and transient property of a system (DeAngelis and Waterhouse 1987). Few experimental landscapes, however, have conserved patterns and processes that create highly dynamic systems. This has led to a scarcity of experimental studies to genuinely improve the dynamic-equilibrium model.

Dynamic experimental grassland landscapes provide an opportunity to improve current understanding of dynamic-equilibrium ecological models and therefore should be a focus of scientific research describing ecological systems. However, very few experimental grassland landscapes have conserved historical patterns and processes that create both spatially and temporally dynamic landscapes. An example of a dynamic experimental landscape is one that uses fire and grazing to create a shifting mosaic of focal disturbances and vegetation pattern that vary both spatially and temporally (Fuhlendorf et al. 2004). Historically, heterogeneous grasslands were created through the predictable response of vegetation to time since fire and grazing (Knapp et al. 1999). In grassland landscapes, plant biomass and litter typically accumulate with greater time since fire (Allred, 2011). Correspondingly, forage quality decreases as plants senesce (Haddad et al. 2002; Sensening et al. 2010; Augustine and Derner 2014). As a result, grazers are attracted to recently burned patches due to higher forage quality (Allred et al. 2011). The strong relationship between grazer preference of recently burned patches has been termed *pyric herbivory* (Fuhlendorf et al. 2009). Over time, fire-grazer interactions create a shifting mosaic of vegetation structure, resulting in a heterogeneous distribution of plant biomass and forage quality across a landscape (Fuhlendorf et al. 2004, 2012). Experimental grassland landscapes that mimic the spatial and temporal variability of focal disturbance and vegetation pattern via pyric herbivory represent landscapes managed for dynamic-equilibrium characteristics and should serve as novel opportunities to improve current scientific understanding of ecological systems.

I aim to improve current understanding of the dynamic-equilibrium paradigm and its role in ecology by applying complex systems thinking and dynamic modeling approaches to investigate a multitude of factors in highly dynamic grassland landscapes managed for dynamic-equilibrium. Chapters 2 and 3 take advantage of an extreme drought event and a long-term pyric herbivory experiment to investigate spatiotemporal patterns in vegetation at the fire-grazer-drought interface. Chapter 2 applies metacommunity theory to investigate scales of heterogeneity and complex feedback loops between grassland productivity, fire behavior, forage quality, and grazer selection before and during drought. Chapter 3 applies complex systems thinking and information theoretic model comparison to quantify the amount of information currently lost in the characterization of wildland fuels in fire behavior fuel models. Chapter 4 identifies flammability thresholds of *J. virginiana* (Eastern redcedar) across a gradient of fuel moisture content to improve wildland fire risk assessments and monitoring programs.

CHAPTER II

DROUGHT ALTERS METACOMMUNITY DYNAMICS DRIVEN BY PYRIC HERBIVORY

INTRODUCTION

Greater precipitation variability, coupled with higher atmospheric temperatures, will have profound impacts on grassland dynamics during an era of climate change (Knapp et al. 2002). Aboveground annual net primary productivity (ANPP) in grasslands is more responsive to rainfall variability than all other biomes in North America (Knapp and Smith 2001). An increase in precipitation variability has been shown to reduce ANPP in grasslands to the same degree as a 30% reduction in total rainfall quantity (Knapp et al. 2002; Fay et al. 2003). Such climate conditions are expected to manifest in grassland-dominated regions of North America, where forecasting models project precipitation will become more variable by the end of the century, resulting in more intense rainfall events coinciding with longer, more severe, dry intervals during the growing season (Walsh et al. 2014).

The discipline of landscape ecology has long recognized the importance of spatial and temporal heterogeneity in ecological patterns and processes and how many patterns and processes are scale-dependent (Turner 1989). Attempts to identify functional relationships between pattern and process has led to the integration of metacommunity theory into landscape ecology concepts (Leibold et al. 2004; Holyoak et al. 2005). Metacommunity theory provides a framework to measure patterns and processes at multiple scales simultaneously. Further, recent advances in metacommunity theory now account for the contribution of spatial variability of local communities to the temporal stability of biomass production (Wang and Loreau 2014; McGranahan et al. 2016). Metacommunity theory predicts that greater temporal stability at landscape scales is associated with greater spatial variability across local communities, whereas variability within local communities decreases temporal stability (Wang and Loreau 2014). In grassland landscapes where grazing is driven by fire (termed pyric herbivory), local communities occur as discrete patches that differ in structure and composition with time since focal disturbance (Fuhlendorf et al. 2009). Temporal stability in biomass production should therefore increase as a result of pyric herbivory, and a recent meta-analysis confirms this expectation (McGranahan et al. 2016). However, the robustness of the relationship between spatial variability and temporal stability has not been assessed. Extreme events, like the extreme droughts that have recently occurred throughout the central and southwestern United States (Hoerling et al. 2014; Twidwell et al. 2014; Smith et al. 2015), might alter metacommunity dynamics and are important to consider with future expectations for climate change.

In this study, I use data from a long-term experimental site to quantify the robustness of metacommunity dynamics to one of the most severe droughts events on modern record in the southern Great Plains. In 2011 and 2012, soil moisture monitoring of the fraction of available water content (FAW) revealed plants were exposed to severe drought conditions (defined as FAW < 40%; Sridhar et al. 2008) for 3 and 6 months, respectively, whereas severe drought conditions usually occur for one month or less in a calendar year (Figure 2.1). Extreme plant water stress (FAW < 20%) occurred for 88% and 80% of those months, respectively (Allen et al. 1998; Sridhar et al. 2008). Growing season precipitation was 40% and 56% below historical norms in 2011 and 2012, and growing season temperatures were 4°C and 3°C warmer, respectively (Figure 2.S1). Such trends are consistent with expectations for future conditions under climate change for the southern Great Plains, and they are expected to occur more frequently by the end of the century (Walsh et al. 2014). This drought thus provides a unique opportunity to study, within long-term experimental landscapes, the potential for future climate change events to alter the spatial and temporal patterns in productivity predicted by metacommunity theory (Wang and Loreau 2014; McGranahan et al. 2016).

In terms of aboveground plant biomass production, metacommunity theory predicts that low variability within-patches (alpha variability) and high variability among-patches (beta variability) coincide with temporal stability (gamma variability) at landscape scales. I test these predictions during drought. Specifically, I test for changes in the temporal stability (gamma variability) in aboveground plant biomass production during drought. I also test for changes in the scale of heterogeneity in aboveground plant biomass and forage quality during drought. Lastly, I explore changes in the underlying feedback mechanisms that drive pyric herbivory and are responsible for promoting metacommunity stability in previous research.

METHODS

Study Site

I conducted this study on three long-term experimental grassland landscapes at the Oklahoma State University Research Range (located near Stillwater, Oklahoma, USA; lat 36°06’N; long 97°23’W). Grassland vegetation dominates the site. Grasses consists primarily of Schizachyrium scoparium (Michx.) Nash, Andropogon gerardii Vitman, Panicum virgatum L., Sorghastrum nutans (L.) Nash, and Sporobolus asper (Michx.) Knuth. Dominant forbs include Ambrosia psilostachya DC. and Gutierrezia dracunuloides (DC.) S.F. Blake. Grassland areas are separated by riparian corridors consisting primarily of Quercus stellata Wang., and Q. marilandica Münchh, and low levels of encroachment by Juniperus virginiana L. have resulted in scattered juniper trees within some grassland areas. Soils at this site consist primarily of Grainola series (fine, mixed, thermic Vertic Haplustalf), and Coyle series (fine-loamy, siliceous, thermic Udic Argiustoll), comprising approximately 60 and 35% of the area, respectively (Gillen et al. 1990). Typically, precipitation in this region is unimodal, with approximately two-thirds falling during the growing season from April to October. The average frost-free growing period is 204 d from May to October. Mean annual temperature is 15°C with normal annual extremes ranging from -4.3°C in January to 34°C in August (Fuhlendorf and Engle 2004). Average annual precipitation is 960 mm.

Experimental design and sampling

Three experimental grassland landscapes were established in 1999 at this research site to implement patch-level fire treatments in grazed landscapes (Figure 2.S2). Each landscape replicate was moderately stocked (3.0 AUM/ha) with mixed-breed yearling cattle from about 1 December to 1 September. Stocking rates were reduced in 2012 by 30% to maintain similar aboveground plant biomass production across the landscapes than before the drought. Only external fences were present on the landscapes, providing grazers the opportunity to move freely among patches within their designated landscape. Six patches of equal area (64 ha. each) were established within each landscape replicate to implement fire treatments. Historic fire intervals for this region were implemented by burning each patch once every three years. On any given year, one patch has been burned in the growing season, and one has been burned in the dormant season. As a result, each landscape replicate functions as a shifting mosaic and consists of the following patches; burned in the growing season this year, last year, and two years ago, and burned in the dormant season this year, last year, and two years ago. I focus on growing season fire treatments only.

In 2011 and 2012, extreme drought and higher than normal temperatures occurred throughout the southern Great Plains that is an example of the type of events projected to occur more frequently by the end of the century (IPCC 2013; Walsh et al. 2014). Growing season precipitation in 2011 and 2012 was 40% and 56% below historical norms, respectively. Growing season temperatures in 2011 and 2012 were 4°C and 3°C warmer than the historical average, respectively (Figure 2.S1). The proportion of the year (days) undergoing extreme plant stress at our site increased from 5% in 2009 to over 40% in 2012 (Figure 2.1). Following Krueger et al. (2015), I obtained environmental data from the Oklahoma Marena Mesonet station and calculated the degree of plant stress was calculated as:

$$FAW = \frac{PAW}{AWC}$$

where FAW is the fraction of plant available water (PAW) to available water content (AWC). PAW describes how much moisture is available in the soil for plant uptake, and AWC is the maximum PAW that the soil can store. Plants begin to experience moisture stress below FAW of about 0.5 (Allen et al. 1998), and values of 0.2 or less indicate extreme drought (Sridhar et al. 2008). AWC varies greatly across soils and is a function of soil properties such as texture and porosity (Pellizzaro et al. 2007; Qi et al. 2012). Accordingly, FAW is a preferred method for calculating plant water stress from soil moisture because it accounts for variation in soil properties over space in terms of moisture availability (Allen et al. 1998; Kruger et al. 2015). These conditions resulted in one of the most severe droughts in the southern Great Plains in modern record and caused major die-off for multiple woody plant species (Twidwell et al. 2014). This event from 2011-2012 will hereafter be referred to as a drought, while acknowledging the higher than average temperatures that also occurred during this period of lower than average precipitation.

Prior to the drought, a study was conducted in 2009 to test the strength and identify causal mechanisms of the fire-grazing interaction in tallgrass prairie. Full details of the study are available in Allred et al. (2011). The most pertinent components of the study are given here. Aboveground plant biomass was harvested biweekly from April to November in 2009 in patches burned during the growing season. Aboveground plant biomass was collected within four randomly placed 0.1-m x 0.1-m plots. Following collection, samples were dried at 70°C until a constant weight was obtained. Percent crude protein was then determined using a dry combustion analyzer (LECO Corp., St. Joseph. MI).

We conducted a complimentary, but more intensive sampling effort to Allred et al. (2011) to measure spatiotemporal patterns of plant production following the drought. Aboveground plant biomass was harvested biweekly from March 2012 to December 2013, except during winter months when snowfall or high moisture conditions made harvesting infeasible. Aboveground plant biomass was harvested from patches burned in the growing season only. A stratified random sampling technique was used to lay out parallel transects, one for each biweekly sampling period, in order to avoid repeated harvesting of biomass over the course of the study. Transects spanned the length of each burned patch. Twelve 0.5-m x 0.5-m plots were randomly located along each transect using computer-generated random numbers established *a priori.* All live and dead aboveground herbaceous biomass was collected within each plot. Following collection, samples were dried at 70°C until a constant weight was obtained. Proportion of crude protein in each sample was then derived using a dry combustion analyzer (LECO Crop., St. Joseph, MI) in the Oklahoma State University Soil, Water and Forage Analytical Laboratory (further details on forage quality analyses are provided in Allred et al. 2011).

Analysis

I measured temporal (gamma) variability in aboveground plant biomass as the mean standard deviation in aboveground plant biomass across a landscape over time. Spatial variability in aboveground plant biomass was measured as the mean standard deviation in plant biomass across (beta) and within (alpha) patches. Following McGranahan et al. (2016), I avoided measuring variability as the coefficient of variation (CV) because patch-contrast in patch-burn grazing landscapes depends on variable means, and CV scales with the mean. Consequently, using CV as a measure of variability would result in disproportionately small differences in the recently burned patch (McGranahan et al. 2016).

I used Allred et al.’s (2011) data from before the drought to develop a pre drought model describing typical spatiotemporal patterns of aboveground plant biomass as a result of pyric herbivory. To develop the pre drought model, I used standard randomization procedures (Fortin 2000; Legendre and Legendre 1998, Anderson 2001; Crowley 1992). Randomizations were restricted to biweekly sampling periods corresponding to each time-since-fire patch, following recommendations from Dutilleul et al. (1993), Fortin and Jacquez (2000), and Legendre and Legendre (1998). Restricted randomizations were used to maintain the presence of temporal autocorrelation in ecological data, which is common in most ecological studies and an *a priori* expectation for this study. A total of 999 permutations were performed.

To test for a decrease in metacommunity stability in aboveground plant biomass, I calculated the mean temporal (gamma) variability in aboveground plant biomass that would be expected in the pre drought model and compared it to temporal (gamma) variability occurring during the drought. Following Legendre and Legendre (1998), I determined significance by dividing the number of times values for temporal (gamma) variability in aboveground plant biomass were less than the pre drought model by the total number of permutations plus the original dataset, 1,000.

To test for the occurrence and strength of temporal (gamma) autocorrelation of aboveground plant biomass with time since fire, coefficients of autocorrelation were calculated as a function of temporal lags both before and during the drought (($k = n / 4$; Legendre and Legendre 1998). Temporal lags were defined by the number of days since fire that corresponded with each sampling period. Significant temporal autocorrelations were based on an α-level of 0.05 and calculated using standard approaches (Crowley 1992; Legendre and Legendre 1998; Gotelli 2000; Goslee and Urban 2007).

To test for a decrease in among-patch (beta) variability in aboveground plant biomass, I calculated the mean among-patch (beta) variability in aboveground plant biomass that would be expected in the pre drought model and compared it to among-patch (beta) variability occurring during the drought. Following Legendre and Legendre (1998), I determined significance by dividing the number of times values for spatial (beta) variability in aboveground plant biomass were less than the pre drought model by the total number of permutations plus the original dataset, 1,000. To determine the degree of dissimilarity among patches in aboveground plant biomass and forage quality, I used nonmetric multidimensional scaling (NMDS) with Bray-Curtis distances (Legendre and Gallagher 2001). The mean and standard error for each patch were determined based on the first two axis scores of NMDS.

To test for an increase in within-patch (alpha) variability in aboveground plant biomass, I calculated the mean within-patch (alpha) variability in aboveground plant biomass that would be expected in the pre drought model and compared it to within-patch (alpha) variability occurring during the drought. Following Legendre and Legendre (1998), I determined significance by dividing the number of times values for spatial within-patch (alpha) variability in aboveground plant biomass were less than the pre drought model by the total number of permutations plus the original dataset, 1,000. I repeated this process for samples collected immediately following fire (days since fire < 14) and for each time-since fire time patch type.

RESULTS

Extreme drought reduced metacommunity stability in aboveground plant biomass production in landscapes managed with pyric herbivory, as evident by increased temporal (gamma) variability in aboveground plant biomass compared to data collected at the same site before drought (Figure 2.2; $P < 0.001$). Drought also resulted in landscape-level convergence among patches (Figure 2.3). Pyric herbivory was no longer the primary driver of plant productivity patterns during drought, as evident by decreased temporal (gamma) autocorrelation in aboveground plant biomass with respect to time since fire (Figure 2.4; $P < 0.05$). Plant biomass-time since fire relationships were strongly autocorrelated before drought and aboveground plant biomass could be predicted many months following fire treatments (Figure 2.4). This relationship collapsed during drought. Significant temporal autocorrelation was reduced to from 13 time lags before drought to 4 time lags (8 weeks) during drought (Figure 2.4).

Drought significantly reduced among-patch (beta) variability in aboveground plant biomass, resulting in a uniform distribution of plant biomass and forage quality among patches (Figure 2.2; Figure 2.5; $P < 0.001$). Before drought, aboveground plant biomass increased in a logistic trend with time since fire (Figure 2.S3), resulting in a heterogeneous landscape consisting of spatially distinct patches with differing levels of plant biomass (Figure 1.5). During drought, aboveground plant biomass was less predictable and exhibited a highly oscillatory relationship with time since fire treatments (Figure 2.S3). Crude protein (%) exhibited similar patterns of change during drought. Before the drought, crude protein (%) was highest the first year following fire treatment and then rapidly declined with time since fire, resulting in a heterogeneous distribution of crude protein across the landscapes (Figure 2.5; Figure 2.S4)**.** Crude protein was less predictable during drought and was more uniformly distributed across the landscapes, regardless of time since fire (Figure 2.5; Figure 2.S4; $P < 0.001$, data not shown)**.** Correspondingly, patches became more similar in terms of both plant biomass and forage quality and spatial (beta) variability across the landscapes decreased (Figure 2.5).

Within-patch (alpha) variability in aboveground plant biomass increased during drought for the first 400 days following fire (Figure 2.2; Figure 2.6; $P < 0.001$). Biomass values within a burned patch ranged from 0 g m^{-2} to 764 g m^{-2} during the first 14 days since fire, indicating a high degree of spatial complexity in the pattern of fire spread and its severity. Many sampling locations within the burned patch had not burned at all (biomass was 764 g m^{-2} for multiple samples, similar to unburned patches), and this was more common than plots where combustion was complete (biomass < 5 g m^{-2}). Incomplete combustion of herbaceous biomass occurred in plots with intermediate biomass values. In contrast, fire completely consumed biomass in all plots before the drought. Biomass was less than 5 g m^{-2} the first 14 days since fire in 1997, indicating more uniform fire behavior and severity within the burned patch.

DISCUSSION

Drought imposed an external perturbation in this long-term experiment of fire-grazing-production patterns and provided an opportunity to test the interplay of spatial and temporal relationships predicted by metacommunity theory. Based on metacommunity theory, increased temporal (gamma) variability in ANPP should be associated with increased spatial variability within (alpha), and decreased spatial variability among (beta), local communities (Wang and Loreau 2014). Indeed, decreases in the temporal (gamma) stability of plant production during drought corresponded to increasing variability within patches (alpha) and decreasing variability among patches (beta).

An overarching hypothesis in global change research is that climate change will cause ecosystem structure and function to converge at broad scales (Huxman et al. 2004; Tjoelker et al. 2008; Choat et al. 2012). During periods of extreme drought, deserts, grasslands, and forests converge in terms of the rate of biomass production per unit rainfall, despite differences in sensitivities of ANPP to precipitation, physiognomy, climatic history, hydrology, and phylogenetic origin of characteristic flora (Huxman et al. 2004). Respiratory carbon fluxes in jack pine (*P. banksiana* Lamb.) will likely converge across North America with increasing atmospheric temperatures, despite genetic differences in respiration rates across temperate and boreal climates (Tjoelker et al. 2008). Widespread forest decline will likely result from more frequent and severe drought events associated with climate change (Choat et al. 2012). Our study adds to the mounting evidence for climate change-induced convergence. I observed landscape-level convergence in terms of plant biomass and forage quality, as discrete patches were no longer driven by the fire-grazer interaction during drought. In grasslands, structural variability among-patches (beta variability) provides crucial habitat for many small mammals (Fuhlendorf et al. 2010; Ricketts and Sandercock 2016), invertebrates (Engle et al. 2008; Doxon et al. 2011), herpetofauna (Wilgers and Horne 2006), and grassland birds (Fuhlendorf et al. 2006; Coppedge et al. 2008; Hovick et al. 2012, 2014). Within a metacommunity framework, the rescue effect states that increased spatial synchrony among patches (reduced beta variability) increases the chance of local-populations going extinct because patches are more likely to respond similarly to externalities and vice versa (Brown and Kodric-Brown 1977; Heino et al. 1997; Liebhold et al. 2004). Accordingly, convergence among patches in landscapes with pyric herbivory will likely affect grassland biodiversity that depends on structural variability at a landscape-scale. It is important to note that although drought reduced among-patch (beta) variability, it also increased within-patch (alpha) variability. However, to our knowledge, the implications of increased variability at fine scales compared to reduced variability at broad scales to grassland biodiversity have received little attention and are currently unknown.

Pyric herbivory and corresponding patterns of grassland biomass are best described as simultaneously occurring negative and positive feedback loops that manifest at different spatial scales (Figure 2.7). Negative feedbacks dampen change and stabilize process-pattern relationships, which thus reinforces uniform productivity patterns within patches following focal fire and grazing in this long-term study. Positive feedbacks amplify change and asynchrony, resulting in heterogeneity at landscape scales. (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009). Our findings strongly suggest that extreme drought triggered a switch in the scale at which negative and positive feedback loops occur in this system (Figure 2.7). The flip from negative to positive feedbacks within local communities and a corresponding switch from positive to negative feedbacks among local communities flipped the scales at which spatial variability in plant biomass manifests in this system.

The scaling switch I observed here is owed to well-understood mechanisms from case studies carried out at a single spatial scale, but which were not designed to explore the potential for a scaling switch to occur in dynamic landscape experiments. Drought slows plant maturation and plant biomass accumulation by reducing net photosynthesis in dominant tallgrass prairie species (Heisler-White et al. 2009). This leads to reductions in litter. Time lags in litter accumulation and availability of soil nutrients on plant production further increases variability in the quality and quantity of grassland biomass (Briggs and Knapp 1995; Haddad et al. 2002). Increasing variation in biomass production at local scales increases variation in fire behavior and severity (Thaxton and Platt 2006; Twidwell et al. 2009). In this study, I observed a high degree of variability in fire severity, which is usually assumed to be constant in grasslands (i.e. nearly everything always burns). Some plants completely burned, others only partially, and some did not burn at all. Incomplete combustion and unburned portions of the burned patch resulted in localized areas within the patch having higher forage quality (where combustion was complete) next to areas with low forage quality (where incomplete combustion or no combustion occurred). Because organisms make decisions at multiple scales (Senft et al. 1987; Orians and Wittenberger 1991), redistribution of forage resources is likely to have changed how grazers made decisions in this landscape during drought – i.e. changing from within patch selection of high forage quality in recently burned areas and avoidance of low forage quality in adjacent patches to selection of individual plants with high forage quality across multiple patches (as has been shown elsewhere; Coppedge and Shaw 1998; Knapp et al. 1999). Our results suggest grazers are still selecting the highest quality forage, but this high quality forage is no longer at the scale of the burned patch. Rather, the highest quality forage is at localized scales and distributed across multiple patches.

Complexity in the scales at which feedbacks operate during extreme events further reinforces the importance of scale in the study of metacommunity dynamics. Empirical assessment of metacommunity dynamics revealed important shifts that would not have been captured without an analysis that explicitly considered pattern-process relationships at multiple spatial scales. For example, if I only focused on measuring among-patch (beta) variability in aboveground plant biomass and forage quality, I would incorrectly conclude that spatial variability was lost in patch-burn grazing landscapes during extreme drought. Rather, our results show that spatial variability still persists; heterogeneity simply manifested at a different (alpha) scale. The fact that there is no single scale to correctly measure ecological phenomena (*sensu* Levin 1992) continues to be an important consideration going forward and serves as an important reminder to studies exploring pyric herbivory as a driver of heterogeneity. Such studies usually describe variation among patches only because that is where heterogeneity has typically been observed in the past (Fuhlendorf et al. 2004; Allred et al. 2011).

Understanding how extreme drought events alter metacommunity dynamics and temporal stability in aboveground plant biomass production will become increasingly important by the end of the century when climate models forecast such drought events to occur more often (IPCC 2013; Walsh et al. 2014). Under typical weather conditions, pyric herbivory creates critical ranges of variability necessary to maintain high levels of grassland biodiversity (Tanner et al. 2016). Among-patch (beta) variability created via the fire-grazer interaction has also shown to stabilize livestock productivity compared to traditionally managed rangelands (Allred et al. 2014). Our results suggest that landscapes with pyric herbivory are capable of maintaining both positive and negative feedback loops by scale-switching during periods of extreme drought and that such feedback scale-switches play a major role in determining metacommunity stability. An unexplored next step would be to identify whether the persistence of both negative and positive feedback loops in this landscape enhances temporal stability over landscapes where spatial synchrony and uniformity is promoted across all scales (which is typical of most grasslands; Fuhlendorf et al. 2012). Given projections for extreme drought to occur more frequently in the future, such information would enhance the potential for modern-day managers to adapt during periods of extreme drought.

A number of assumptions and experimental contexts need to be considered that could change the results observed in this study and provide important foundations for future research inquiry. The sampling protocol changed from before the drought (2009 data) to during the drought (2012-2013 data). Before drought, aboveground plant biomass was harvested biweekly from four randomly placed 0.1-m x 0.1-m plots in each patch. During drought, I harvested aboveground plant biomass biweekly from 12 randomly placed 0.5-m x 0.5-m plots in each patch. Typically, the amount of heterogeneity observed increases with the scale of observation in ecological studies (Levin 1992). Accordingly, one may be concerned that the amount of variability among plots might increase during drought (larger plots). However, I observed significantly less variability among plots during drought, further strengthening my results that within-patch (alpha) variability increased during drought. Another potential limitation of this study was the influence of grazing pressure on vegetation dynamics and fire behavior. If stocking rate was not reduced by 30% in 2012 to maintain similar landscape-level biomass production, we may have observed completely different results. Stocking rate determines the spatial patterning of fuels which may influence fire behavior, vegetation structure, and herbivore patch selection (McGranahan et al. 2013). The timing and application of fire also likely played a large role in determining the spatial patterning of fuels and the observed combustion efficiency. Prescribed fires like the treatments applied in this study, are typically applied under a narrow set of environmental and fuel conditions that promote safety and increased control over fire behavior (Twidwell et al. 2016). In this study, if fire treatments were applied under dryer fuel conditions (e.g. dormant season) rather than during the growing season when fuels typically have higher fuel moisture contents, combustion efficiency would have likely been higher and I may have observed more typical uniform fire severity across a patch.

ACKNOWLEDGEMENTS

I thank the following people for their field assistance and sampling: Andrew West, Bill Hiatt, Taylor Winter, and Abbey Ramirez. I thank John Weir and the OSU Fire Crew and personnel at the OSU Range Research Station for the application of treatments. This research was funded by the Joint Fire Science Program projects 11-1-2-19 and 13-1-06-8.

FIGURES

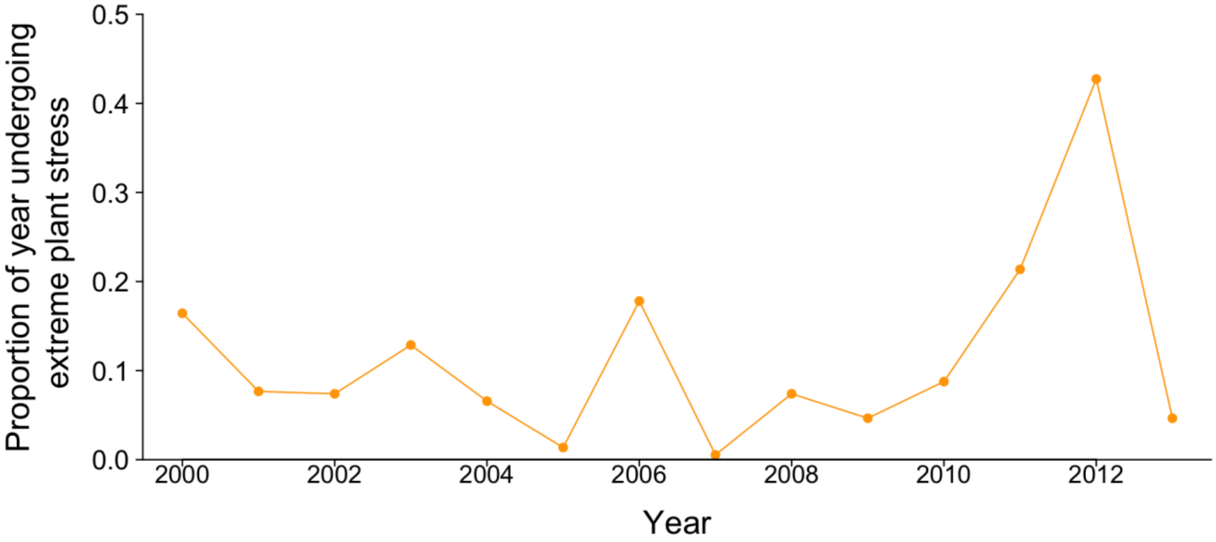

Figure 2.1 Proportion of the year plants experienced extreme moisture stress at our research site, as indicated by a fraction of available water capacity value (FAW) < 20% (Allen et al. 1998; Sridhar et al. 2008).

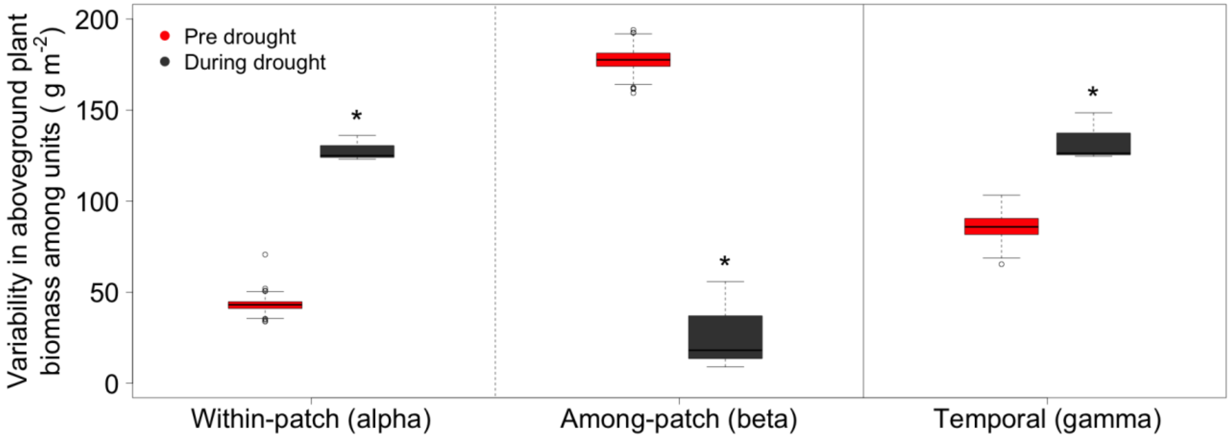

Figure 2.2 Metacommunity dynamics before and during an extreme drought event in landscapes with pyric herbivory. Asterisks (*) indicate a significant difference from pre drought values ($P < 0.001$).

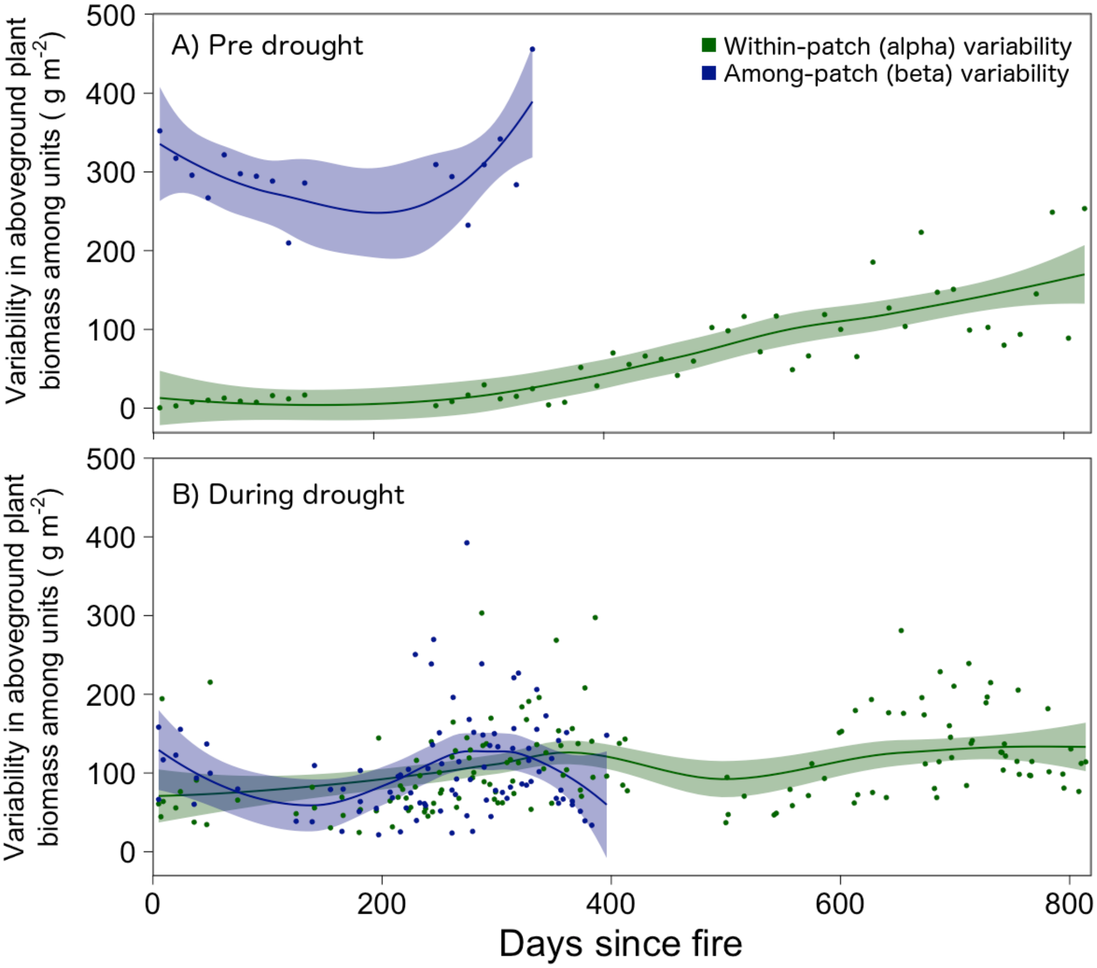

Figure 2.3 Spatiotemporal patterns of productivity within a metacommunity framework in a long-term pyric herbivory experiment. (A) Grassland biomass exhibits distinct scales of variation within (alpha) and among (beta) patches. (B) Drought triggered convergence in the variability of plant biomass within (alpha) and among (beta) patches. Lightly shaded regions represent 95% confidence intervals.

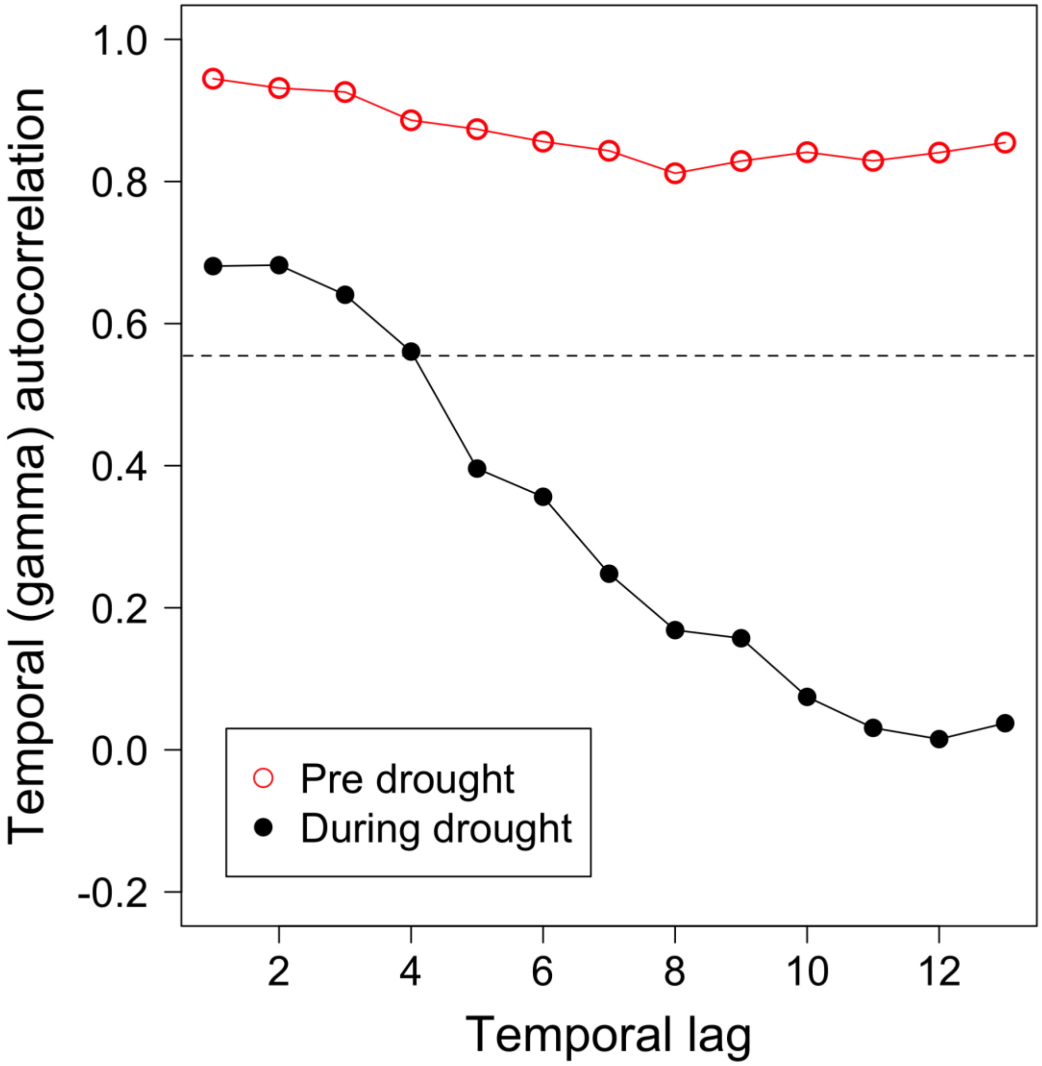

Figure 2.4 Temporal (gamma) autocorrelation of aboveground plant biomass before and during drought with time since fire treatment. One temporal lag represents a biweekly sampling period. Autocorrelation coefficients above the dotted line are significant ($P < 0.05$), indicating differences in the amount of time focal fire and grazing significantly predicts plant biomass pre-drought versus during-drought.

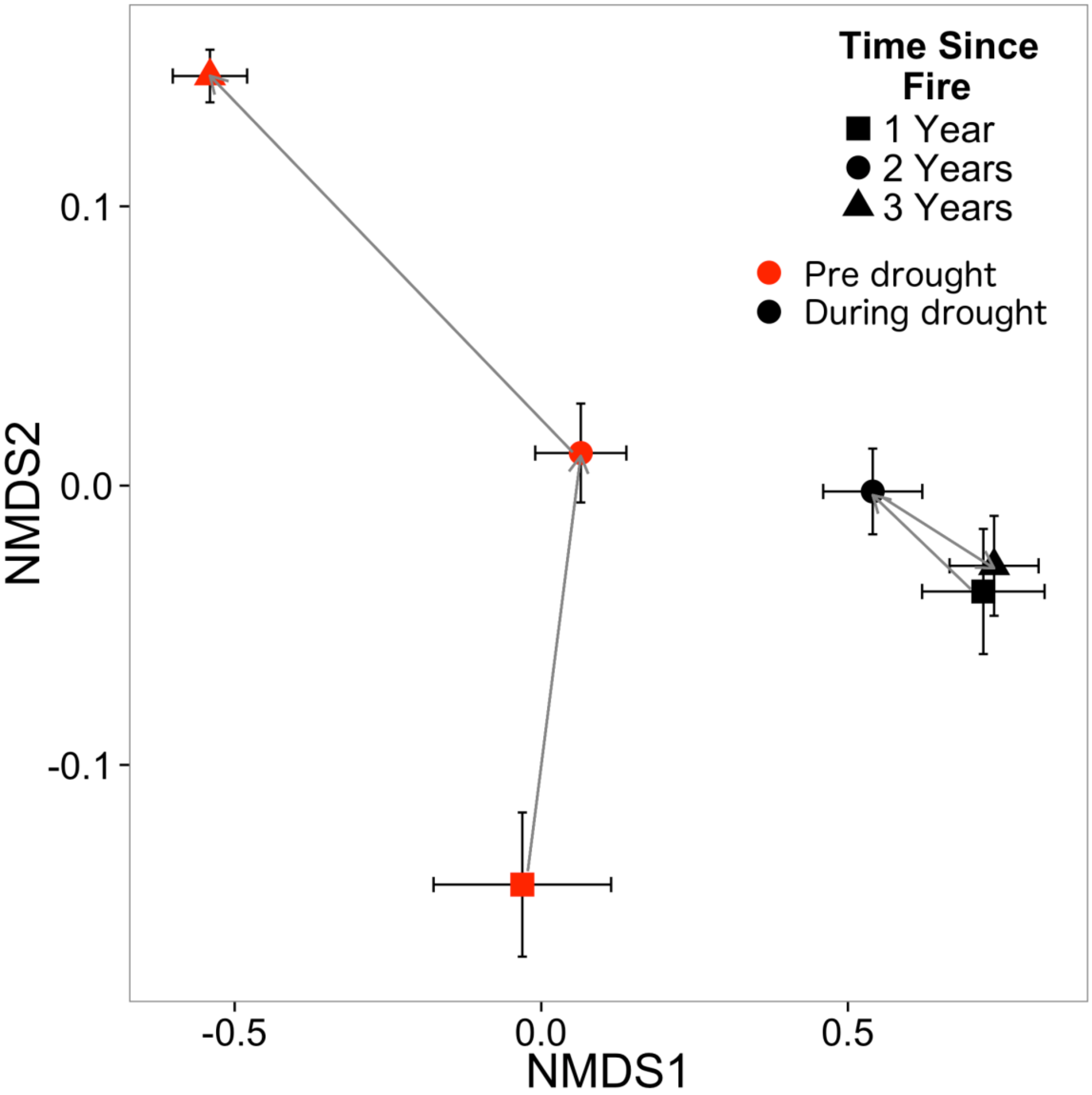

Figure 2.5 Multivariate ordination of aboveground plant biomass and crude protein production with respect to time since focal fire and grazing. The distance between points represents the degree of among-patch (beta) variability within experimental landscapes.

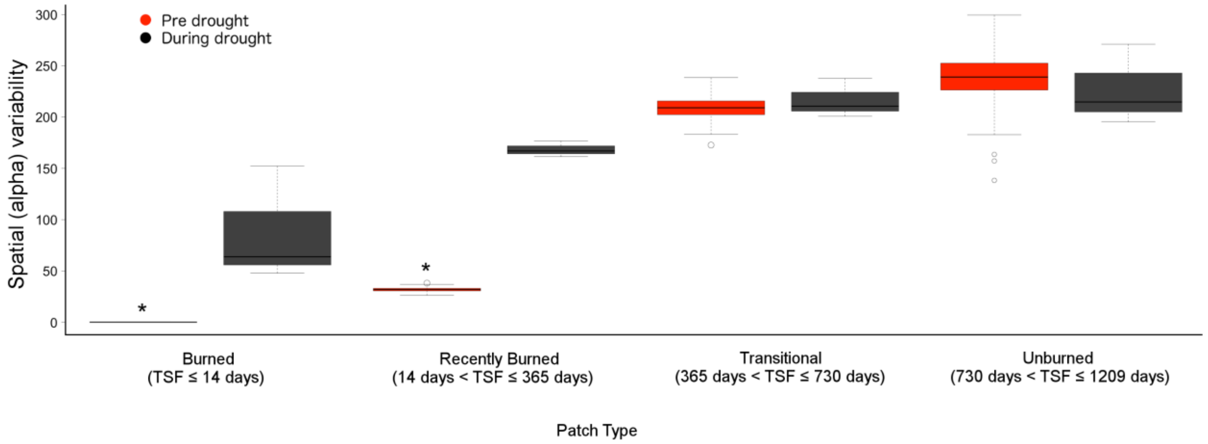

Figure 2.6 Within-patch (alpha) variability in aboveground plant biomass in experimental landscapes as a function of time since fire (TSF) before and during drought. Spatial (alpha) variability was measured as the standard deviation in aboveground plant biomass produced among plots within each patch type. Asterisks (*) indicate a significant difference from pre drought values ($P < 0.001$).

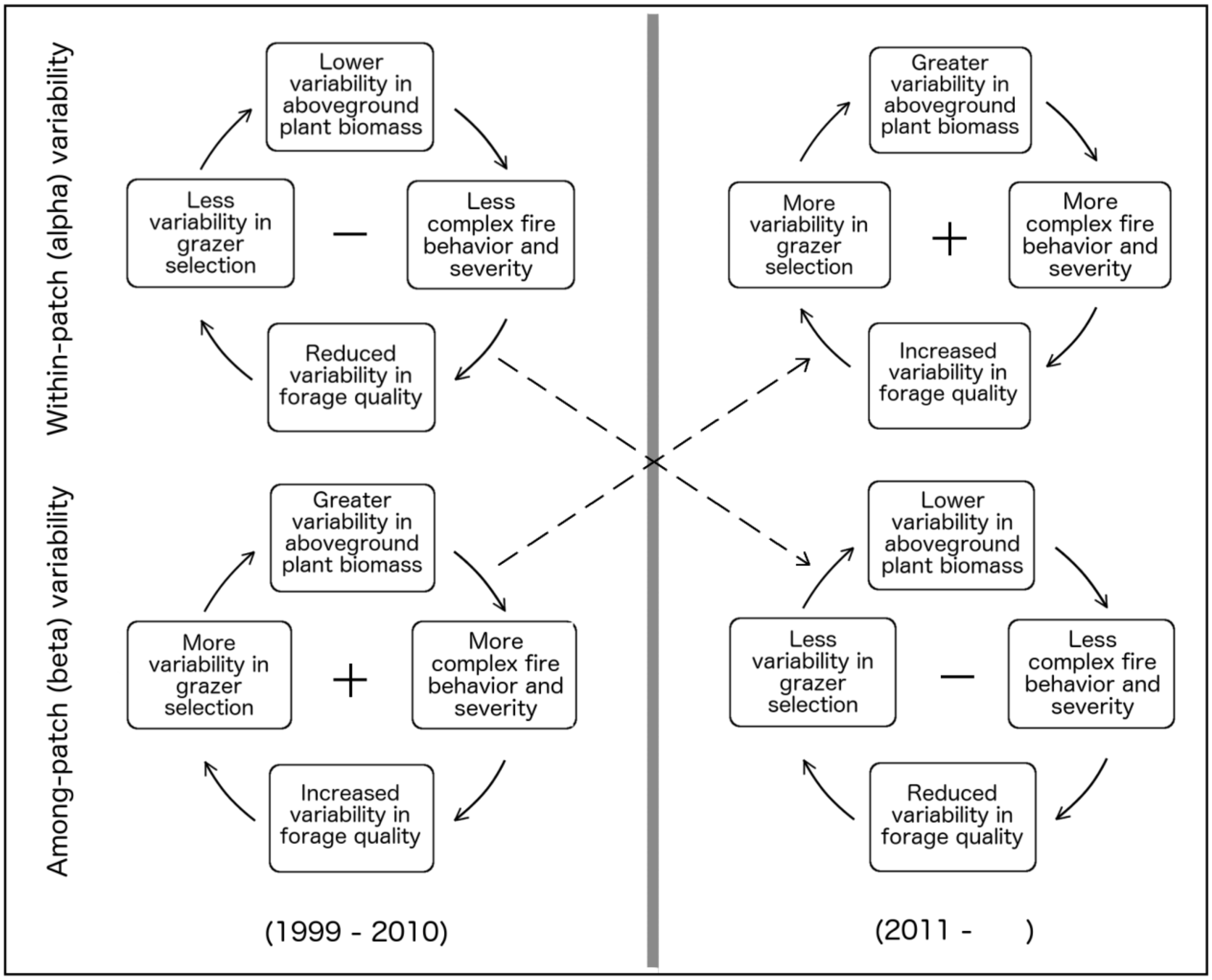

Figure. 2.7 Conceptual illustration of the hypothesized feedback loops and scale switching that occurs during periods of extreme drought in landscapes with pyric herbivory. The gray bar represents the point in time in which feedback loops switch scales. Dotted lines indicate what scale the feedback loop switches to during drought. Black arrows indicate either positive (+) or negative (-) feedbacks between productivity dynamics, fire behavior, forage quality, and grazing selection. For over a decade, low within-patch (alpha) variability and high among-patch (beta) variability were maintained via negative feedback loops operating within patches, and positive feedback loops operating at a landscape scale. During extreme drought, I observed positive feedback loops promoting within-patch (alpha) variability and negative feedback loops reducing among-patch (beta) variability. Within a patch, drought initiates a positive feedback loop by

altering typical spatiotemporal productivity patterns across the entire landscape. Greater pre-fire within-patch (alpha) variability in fuel increases small-scale variability in fire intensity and severity in the recently burned patch. Greater small-scale variability in fire intensity and severity in the recently burned patch results in greater post-fire spatial (alpha) variability in both plant quantity and quality than typically observed. Increased variability in forage quality and quantity across the burned patch (alpha variability), likely changed the scale of grazer selection, as grazers are attracted to high forage quality and are capable of changing grazing patterns to meet nutritional requirements. Consequently, I observed the negative feedback loop that typical reduces within-patch (alpha) variability switch to operating at a landscape scale and reducing among-patch (beta) variability.

SUPPORTING INFORMATION

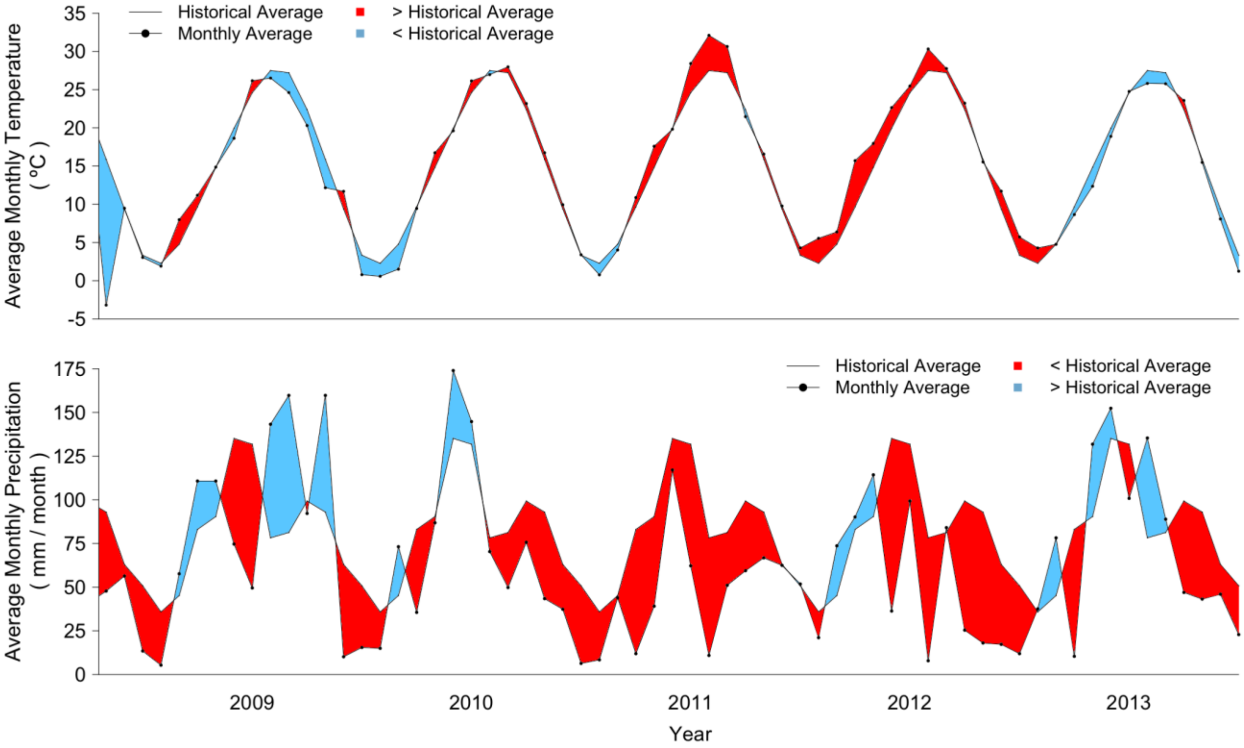

Figure 2.S1. Deviation from historical (1981-2010) average temperature and precipitation.

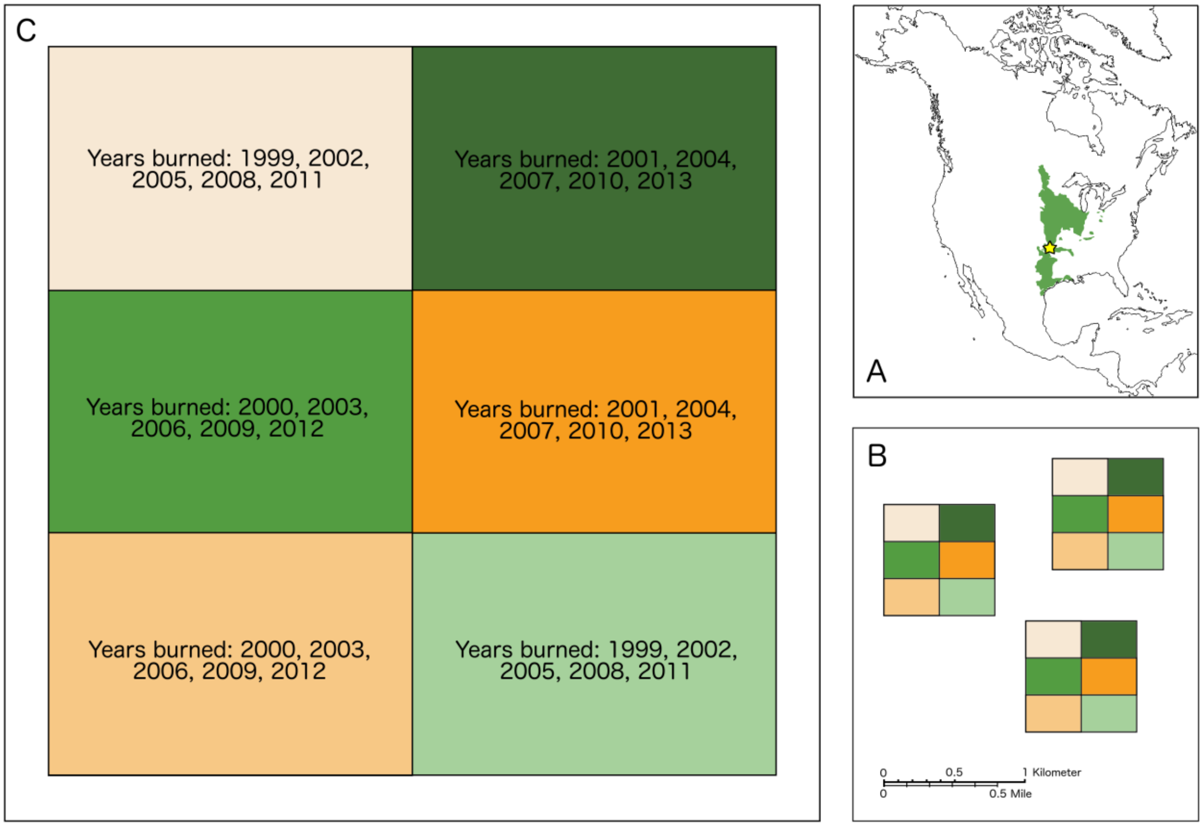

Figure 2.S2. Experimental design used to determine the influence of drought on metacommunity (gamma) stability in long-term experimental pyric herbivory landscapes during drought. Our experimental site was located in the North American Great Plains Tallgrass Prairie (A). Three experimental grassland landscapes were used as replicates, each consisting of six patches (64 ha each) at various stages of recovery from burn treatments (B). Shades of green represent growing season fire treatments and shades of orange represent dormant season fire treatments. Yearling cattle were moderately stocked (3.0 AUM/ha) from 1 December to 1 September. No internal fences were present so that livestock could graze freely across an entire landscape. Within each landscape, fire was applied to each patch once every three years either in the growing season only or dormant season only since the establishment of the site in 1999 (C).

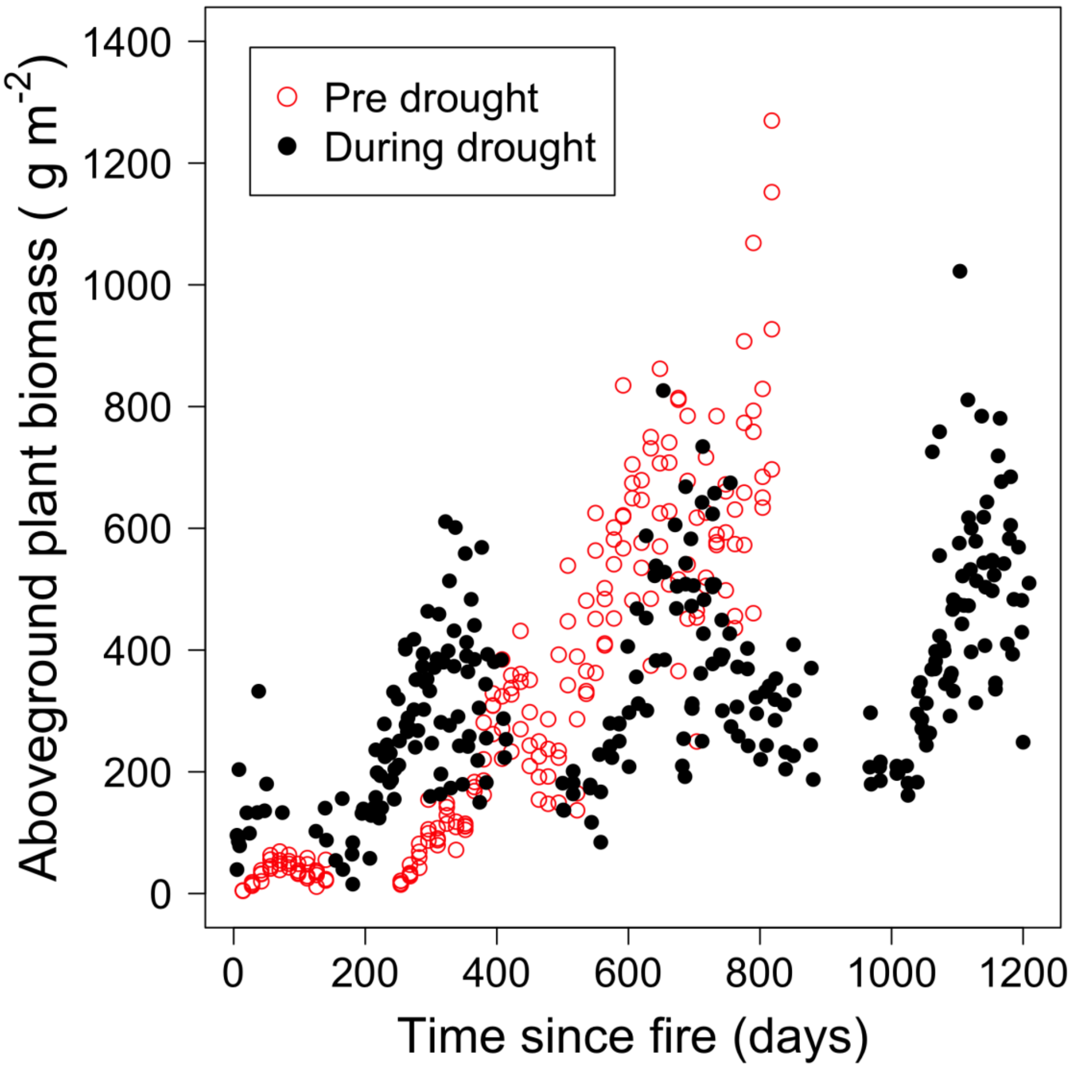

Figure 2.S3. Recovery of aboveground plant biomass across a landscape to focal fire and grazing before and during drought.

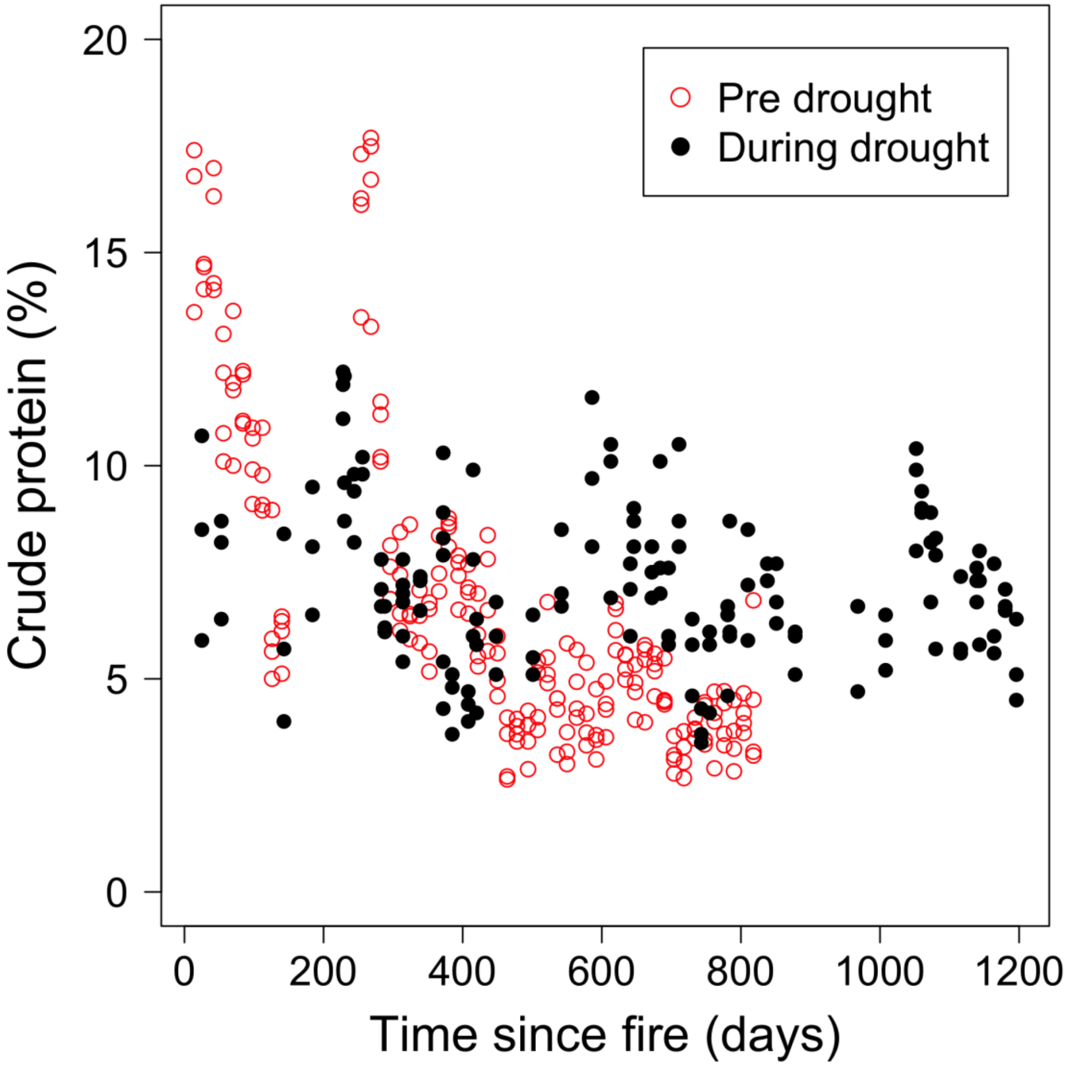

Figure 2.S4. Recovery of crude protein across a landscape to focal fire and grazing before and during drought.

CHAPTER III

MOVING BEYOND CENTRAL TENDENCY IN APPLIED FIRE MODELING

INTRODUCTION

Favoring central tendency has been identified as a major issue limiting advances in science and practice for over a century. First described by Hollingworth (1910) as the *indifference point*, or an over-reliance to default to the mean when describing complex data or patterns, favoring central tendency is the propensity for people to overestimate smaller values and underestimate larger values, resulting in a tendency for values to fall close the mean (Crawford et al. 2000; Olkkonen et al. 2014). This tendency is a well-established phenomenon documented in various contexts such as human estimates of bird population size (Estrada et al. 2005; Pérez 2011), object size (Hollingworth 1910; Weiss 1954), line length (Duffy et al. 2010; Ashourian and Loewenstein 2011), color hue (Olkkonen and Allred 2014), in school writing examinations (Engelhard 1994), and in raters scoring of national curriculum writing exams (Myford and Wolfe 2009; Lecki and Baird 2011). Further, there is a relationship between the amount of variability in the stimuli presented to the estimator and the magnitude of tendency, where more variation in stimuli increases the magnitude of central tendency and vice versa (Stocker and Simoncelli 2006; Girshick et al. 2011; Olkkonen et al. 2014).

Complex systems thinking provides a framework for disciplines to quantitatively address the impacts of favoring central tendency and start describing the inherent complexity in natural systems. In dealing with complexity in nature, the promise of complex systems modeling for society is to maximize real-world applications of science while minimizing the amount of information lost when describing reality (Goldenfield and Kadanoff 1999; Wu and David 2002; Grimm et al. 2005). With increasing demands for practical applications and adoptions of science in applied disciplines, numerous fields have benefited from complex systems modeling. The application of complex systems modeling has improved the practice of modern social networks (Goldenberg et al. 2001; Eagle and Pentland 2006), economics (Rosser 1999; Colander et al. 2004), cancer research (Schwab and Pienta 1997; Deisboeck et al. 2001), natural disaster planning and management (Gunderson 2010; Bristow et al. 2012), health care systems (Pisek and Greenhalgh 2001; Anderson et al. 2003), and organizational management (Anderson 1999; Scheider and Somers 2006). However, many applied disciplines have yet to benefit from complex systems thinking and continue to model systems as static entities.

Information theoretic model comparison (ITMC) is commonly used in tandem with complex systems thinking to develop quantitative models that account for dynamic, non-linear behavior (Anderson and Burnham 2002; Burnham and Anderson 2002). As an alternative to null hypothesis testing, an ITMC uses Kullerback-Leibler (K-L) information to quantify the strength of evidence for a given set of hypotheses (Anderson et al. 2000; Stephens et al. 2005; Burnham and Anderson 2004). ITMC has been applied in many fields of ecology, evolution, and marketing to develop practical solutions to complex problems (Johnson and Omland 2004; Rushton et al. 2004; Snipes and Taylor 2014). However, applied models in many of these disciplines continue to favor central tendency when describing ecological phenomena and have yet to benefit from ITMC and complex system thinking. In fire management, for example, despite disciplinary recognition that spatial and temporal variability are inherent in wildland fuels and are fundamental to understanding fire dynamics (Turner and Romme 1994; Twidwell 2009), the mean expected value of a give fuel parameter is currently used as the default input in many applied models of wildfire risk and fire behavior (Andrews 2006; Scott and Burgan 2005). For example, regardless of the spatial variability that might occur across a grassland landscape, if a user selects a GR2 fuel model to use in a fire behavior modeling program such as BehavePlus, fuel bed depth is assumed to be 1ft across the entire landscape (Scott and Burgan 2005). Given that the economic and social impacts of wildfire have skyrocketed over the last three decades (Westerling et al. 2006; Gill et al. 2013; NIFC, 2013), now is an important time to determine the impact of using a mean value to describe fuel properties in applied fire modeling systems (e.g. BehavePlus, NFDRS) and assess alternative approaches that embrace variability and complexity.

The objective of this paper was to quantify the amount of information lost as a result of current fuels classification approaches. I focus my efforts on grassland landscapes, which are highly dynamic ecosystems but most of which are described in fire models in terms of their mean behavior. I initiated a field study to systematically measure 14 fuel properties commonly used to predict wildlife risk and fire behavior. These fuel properties were sampled biweekly for two years, and provide the first data capable of capturing complex responses of grassland fuel properties to drought, fire and grazing. I adopt an ITMC approach to determine how much information is lost when a mean value is used to describe temporal variability in all 14 fuel properties. I then determine whether fuel properties vary significantly in space as a result of disturbance history. Further, following guidelines used to describe the relative amount of empirical support for model selection (Burnham and Anderson 2004), I discuss the impact of favoring central tendency in fire management and how an ITMC approach has the potential to identify the impact of favoring central tendency in other ecology applications.

METHODS

Study Site

The need to understand dynamic changes in wildland fuel is driven by dynamic and sudden changes in fuels that result from complex interactions among ecological drivers. In rangelands, it is well established that interactions among fire, grazing, climate and soils drive variability in vegetation structure and composition (Axelrod 1985; Oesterheld et al. 1999). I therefore selected a study site where these drivers have interacted for almost two decades.

Three experimental grassland landscapes were established in 1999 at the Oklahoma State University Research Range (located near Stillwater, Oklahoma, USA; lat 36°06’N; long 97°23’W) to implement patch-level fire treatments in grazed landscapes. Within each landscape replicate, six patches (64 ha each) were established to implement fire treatments (Figure 3.S1). Consistent with historical fire intervals for the region, each patch was burned either in the growing season or dormant season once every three years. I focus on growing season fire treatments (9 total patches, 3 patches per landscape). In any given year, each experimental landscape consisted of three patch-types: burned this year, burned last year, and burned two years ago. Landscapes were moderately stocked at 3.0 AUM/ha with mixed-breed yearling cattle from about 1 December to 1 September. No internal fences were used within the landscapes, allowing livestock to move freely among patches within their assigned landscape.

In grasslands, interactions between fire and grazing have been shown to create spatiotemporal productivity patterns at landscape scales (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009). The application of fire to discrete patches within a landscape and the preferential selection of herbivores to recently burned patches can create patch-level spatial heterogeneity (Fuhlendorf et al 2006). As fire moves across a landscape and burns discrete patches, grazers preferentially select for higher plant quality in recently burned patches allowing plant biomass in unburned patches to recover from fire (Allred et al. 2011). Over time, a shifting landscape mosaic is created that is composed of spatially distinct patches at various stages of recovery from fire and grazing at any single point in time (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006).

I monitored grassland fuel properties during and immediately following one of the worst droughts on modern record for the southern Great Plains when fuel properties play the largest role in determining fire behavior and fire effects (Rothermel 1972). Growing season precipitation was 40% and 56% below the historical average and growing season temperatures were 4°C and 3°C warmer than the historical norms, in 2011 and 2012, respectively (Figure 1.S1). In 2012, the proportion of the year (days) undergoing extreme plant stress at our site was over 40% (Figure 1.1). Environmental data were collected from the Oklahoma Marena Mesonet station. Following Krueger et al. (2015), I calculated the degree of plant stress as:

$$FAW = \frac{PAW}{AWC}$$

where FAW is the fraction of plant available water (PAW) to available water content (AWC). PAW is the amount of moisture available in the soil for plant uptake. AWC is the maximum PAW that the soil can store. Plants begin to experience moisture stress when FAW ≤0.5 (Allen et al. 1998). FAW values ≤0.2 or less indicate extreme drought (Sridhar et al. 2008). AWC is a function of soil texture and porosity and varies greatly across soils (Pellizzaro et al. 2007; Qi et al. 2012). FAW is a preferred method for calculating plant water stress from soil moisture (Allen et al. 1998; Kruger et al. 2015). Extreme plant water stress during 2011 and 2012 caused major die-off for multiple woody plant species (Twidwell et al. 2014).

Grassland vegetation dominates the site and consists primarily of *Schizachyrium scoparium* (Michx.) Nash, *Andropogon gerardii* Vitman, *Panicum virgatum* L., *Sorghastrum nutans* (L.) Nash, and *Sporobolus asper* (Michx.) Knuth. Dominant forbs include *Ambrosia psilostachya* DC. and *Gutierrezia dracunuloides* (DC.) S.F. Blake. Riparian corridors separate grassland areas and primarily consist of *Quercus stellata* Wang., and *Q. marilandica* Münchh, and low levels of encroachment by *Juniperus virginiana* L. have resulted in scattered juniper trees within some grassland areas. Soils at this site consist of approximately 60% Grainola series (fine, mixed, thermic Vertic Haplustalf), and 35% Coyle series (fine-loamy, siliceous, thermic Udic Argiustoll). Across the region, precipitation is unimodal, with approximately two-thirds falling during the growing season from April to October. Mean annual temperature is 15°C with normal annual extremes ranging from -4.3°C in January to 34°C in August (Fuhlendorf and Engle 2004). Average annual precipitation is 960 mm and the average frost-free growing period is 204 d from May to October.

Sampling

Herbaceous biomass was harvested biweekly from March 2012 to December 2013, except during winter months when snowfall or high moisture conditions made harvesting infeasible. Herbaceous biomass was harvested from patches burned in the growing season only. A stratified random sampling technique was used to lay out parallel transects, one for each biweekly sampling period (31 total), in order to avoid repeated harvesting of biomass over the course of the study. Transects spanned the length of each burned patch. Twelve 0.5-m x 0.5-m plots were randomly located along each transect using computer-generated random numbers established *a priori.* Within each 0.5 x 0.5 m plot, herbaceous fuel components were categorized into three groups to provide a more detailed examination of grassland fuels. Herbaceous fuel components were classified as either fuel bed (mixture of live and dead fuels), 1-hr fuels (dead fuel only, 0.64 cm in diameter), or live fuels (live fuel only). Fuel bed depth was measured three times in each plot for each herbaceous component (Brown, 1974). A mixture of live and dead herbaceous material was clipped from each plot, collected, and dried in a 70°C drying oven for 48 h. Fuel parameters (14 total) commonly used in fuel models were then calculated (see Table 3.1 for fuel property abbreviations and descriptions).

The percentage of live herbaceous material in each component was calculated using the constituent differential method (Gillen and Tate, 1993, McGranahan, 2013). This method uses known dry matter contents of all three herbaceous layers to estimate respective fractions of live fuel load (Gillen and Tate, 1993). To determine fine fuel load for the live and 1-hr herbaceous fuel layers, six plots were randomly selected along each transect to clip live only (n = 6) and dead only (n = 6) reference samples in accordance with Gillen and Tate (1993). Reference samples were dried in a 70°C drying oven for 48 h to determine herbaceous fuel load for the remaining two components. The following equation was used to determine the percentage of live herbaceous material (PL):

$$PL = \frac{FFL - FFLD}{FFLL - FFLD} \times \frac{FFLL}{FFL} \times 100$$

and,

$$PD = 100 - PL$$

where FFL is the total fine fuel load of the fuelbed, FFLD is the fine fuel load of 1-hr fuels, and FFLL is the fine fuel load of live herbaceous material (Gillen and Tate, 1993).

Fine fuel load (FFL) was calculated for the fuel bed using the following equation:

$$FFL\ (g\ m^{-2}) = \frac{WSW}{DSW}$$

where WSW is wet sample weight and DSW is dry sample weight.

Fuel moisture content (FMC) was calculated for each herbaceous layer using the following equation:

$$FMC = \frac{WSW - FFL}{FFL} \times 100$$

where WSW is wet sample weight and FFL is fine fuel load.

Surface area to volume ratio (SAV) was then calculated for the fuel bed. Using a digital micrometer, the diameter (d) of individual leaves and stalks were measured from the collected samples (Brown, 1970). Volumes of grass and forb stalks were measured by assuming negligible influence of fuel volume and cylindrical shaped stalks. The following equation was used to determine SAV:

$$SAV = \frac{4}{d}$$

Volume for grass and forb leaves was measured by assuming a thin parallelepiped shape and measuring thickness (t) with the following equation:

$$SAV = \frac{2}{t}$$

Bulk density was then calculated for each herbaceous component. Oven-dry bulk density (P_b) was calculated using the following equation:

$$P_b = \frac{W_o}{\delta}$$

where W_o is the oven-dry fine fuel load (kg/ m^2) and δ is fuel bed depth.

Analysis

To contrast central tendency, I used generalized additive models (GAMs; Hastie and Tibshirani 1990) to model the dynamic, non-linear nature of grassland fuel properties. GAMs are a technique used to describe complex data and are commonly applied in terrestrial systems modeling (Leathwick 1998; Yee and Mitchell 1991), marine systems modeling (Gregr and Trites 2001; Tittensor et al. 2010), and risk assessments (Brillinger et al. 2003; Preisler et al. 2004). GAMs are not limited by the assumptions of linear models and are typically thought of as data-driven models rather than model-driven models (Yee and Mitchell 1991). That is, the response curve is fitted from the data at-hand rather than a parametric class. Smoothing term (s) in GAMs use spline functions to the *j*th smoothed component to estimate nonparametric functions (Llope et al. 2012; Defeo and Gomez 2005). Accordingly, the commonality and strength of GAMs in modeling ecological data arises from their ability to account for highly non-linear and complex data with a limited number of assumptions. For a thorough review on regression techniques and GAMs see Guisan et al. (2002).

To compare how much information was lost using a mean to describe a fuel property over time compared to a GAM, I first developed a set of candidate models. To account for temporal variability in a fuel property, a smoothing term was applied to sampling period and/or years. Our set of *a priori* candidate models included:

y ~ 1

y ~ s(Period)

y ~ s(Period) + Year

y ~ s(Period, by = Year)

where y is a single fuel property, Period is biweekly sampling period (31 total) and Year is year of data collection (two total). I hereafter refer to y ~ 1 as the static model.

Once I established a list of *a priori* candidate models, I used Akaike's Information Criterion (AIC) to rank the models by relative amounts of information loss (Akaike 1973). AIC is an ITMC approach commonly applied in many aspects of ecology such as behavioral ecology (Symmonds and Moussalli 2011; Thorup et al. 2006), species distribution modeling (Rushton et al. 2004; Araújo and Luoto 2007), invasive species (Noson et al. 2006; Ficetola et al. 2007), fire propagation modeling (Drever et al. 2009; Krawchuck et al. 2006), and remote sensing (Atkinson and Curran 1995; Edwards et al. 2013). Candidate models are based on sound ecological understanding and information loss is based on Kullback-Leibler (K-L) information, where K-L information is the "distance" of each model from full reality (Kullback and Leibler 1951; Anderson and Burnham 2002; Burnham and Anderson 2004). In addition to quantifying information loss, AIC uses Fisher's likelihood theory to account for bias associated with increasing the number of parameters in a given model (Akaike 1973; Burnham and Anderson 2004). The model with the lowest AIC score represents the model with the smallest Kullback-Leibler (KL) information loss (Burnham and Anderson 2002; Anderson, 2008). Models are ranked by delta AIC (ΔAIC) values that represent the amount of information loss associated with each model compared to the "top" model. Models with ΔAIC values ≤ 2 have substantial support for describing "full reality" and ΔAIC values ranging from 4–7 have less support, but should rarely be dismissed (Burnham et al. 2011). Models with ΔAIC values ranging from 9-11 generally provide little support for describing "full reality", and models with ΔAIC values ≥20 essentially have no empirical support (Burnham et al. 2011).

I then developed a list of candidate GAM models to determine the importance of adding a parameter to account for spatial variability among patch-types (recently burned and grazed, burned one year ago, burned two years ago). GAMs including a parameter for patch were compared to GAMs without including patch as a parameter. Our set of *a priori* candidate models for detecting spatial dependencies included:

$$y \sim s(\text{Period})$$

$$y \sim s(\text{Period, by} = \text{Patch})$$

where y is a single fuel parameter, Period is biweekly sampling period (31 total) and Patch is the fire-grazing treatment. AIC was then used to rank the models by relative amounts of information loss (Akaike 1973).

RESULTS

In terms of explaining temporal variability in fuel properties, the relative amount of information lost (as indicated by ΔAIC) using the mean as the default value versus a GAM ranged from 13.41 to 1,496.07 for the 14 grassland fuel properties measured in this study (Figures 3.1-3.14; Tables 3.2-3.4). When disturbance history (patch type) was not accounted for, ΔAIC values ranged from 26.68 to 3,781.69 (data not shown). The relative amount of information lost using the mean as a default value was lowest for bulk density of 1-hr fuel, SAV, the fuel moisture content of 1-hr fuel, and bulk density of live fuel. ΔAIC values were >20 for 12/14 fuel properties, indicating essentially no empirical support for the static model. ΔAIC for 1-hr bulk density in patch C and 1-hr moisture content in patch B were 13.41 and 15.92, respectively, indicating minimal empirical support for the static model. When disturbance history was not accounted for in the GAMs, ΔAIC values were >20 for all 14 fuel properties.

Disturbance history (patch type) did not play a significant role in explaining the spatial variability in fuel properties (Table 3.5). The relative amount of information lost (as indicated by ΔAIC) resulting from adding a parameter to account for patch type ranged from 8.4 to 1432.27. Over the two growing seasons, patch type played the smallest role in determining the moisture content of the fuel bed, 1-hr fuel bed depth, and live fine fuel load. Over the two growing seasons, patch type played the greatest (although marginal) role in determining SAV, 1-hr bulk density, and 1-hr fuel moisture content. ΔAIC values were >20 for 11/14 fuel properties, indicating essentially no empirical support for the static model. ΔAIC was 8.4 for SAV, indicating minimal support for the static model and ΔAIC for 1-hr bulk density and moisture content were >16, indicating little to no empirical support for the static model.

The amount of empirical support for using the mean to describe fuel properties over time and for adding a spatial component to a GAM varied by fuel parameter. There was essentially no empirical support for using the mean to describe all but two fuel properties, as indicated by ΔAIC values ≥20. Bulk density of 1-hr fuels and 1-hr fuel moisture content were the only two static models with any (although marginal) empirical evidence for describing fuel properties over time, as indicated by ΔAIC values of 13.41 and 15.92, respectively. In terms of spatial variability, there was essentially no empirical support for adding a parameter to account for patch-type (disturbance history) in all but one fuel property, as indicated by ΔAIC values >16. For SAV, there was little to no evidence supporting a GAM with a patch-type parameter versus one with no spatial dependencies, as indicated by a ΔAIC value of 8.4.

DISCUSSION

The field of wildland fire science has used dynamic mathematical models to characterize wildland fire dynamics for decades (Rothermel 1972; Albini 1981; Anderson 1982), but favoring central tendency has emerged in application due to the complexity and computational rigor of theoretical models. The majority of fuel parameters are input into applied fire models as constants (e.g. BehavePlus, NFDRS), and scientists and professionals in wildland fire research have been calling for more dynamic models (Scott and Burgan 2005). Dynamic models are more sensitive to small changes in fuel properties that may elicit large changes in fire behavior. For example, a 10% reduction in live fuel moisture content in a GR9 fuel model has been shown to increase flame lengths to increase from 4.8 to 16.2 ft. (Jolly 2007). By developing more dynamic models that can account for small changes in fuel properties, we may improve our ability to predict large wildfires during periods of rapid transition (e.g. fuels drying out quickly, small-scale changes in fuel load over space). Our study establishes that nearly all fuel properties in grasslands are better described, and modeled, as dynamic and should not be considered constant or static. Surface area to volume ratio and 1-hr bulk density were the primary fuel parameters with sufficient empirical support to remain a constant in applied fire models.

Models of complex ecological phenomena are challenged with balancing the amount of error associated with oversimplification (large aggregations, few parameters) with uncertainty arising from overly complex (disaggregated, many parameters) models (Metcalf et al. 2008). In dealing with complex data, aggregation error commonly occurs when scaling-up nonlinear, fine-scale patterns or processes (Rastetter et al. 1992). Further, the degree of aggregation determines the applicability and amount of error associated with a model. Aggregation error associated with scaling-up complex fine-scale phenomena is evident in analyses of food chains (O’Neill and Rust 1979, Metcalf et al. 2008), primary producers (Cale and Odell 1979, 1980), and genetics (O’Neill 1979), to name a few. In moving toward more realistic and appropriate modeling of complex systems, the fine-scale behavior of a pattern or process as well as how fine-scale patterns and processes scale up must first be understood before it can be incorporated properly in coarse-scale equations (Levin 1992; Costanza et al. 1993). This study provides the first step for wildland fire science to quantitatively assess the amount of information loss resulting from favoring central tendency through exploring the full range of fine-scale temporal and spatial variability in grassland fuel properties.

Information theoretic model comparison provides a quantitative method for advancing science through constant testing and refining of *a priori* hypotheses (Burnham and Anderson 2004). Guidelines provided by Burnham et al. (2011) regarding ΔAIC values can indicate when a statistical model is implausible and should be discarded from a set of hypotheses. Our study took the first step in refining our set of *a priori* hypotheses by testing the assumption that the mean correctly characterizes grassland fuel properties. In our study, static models provided essentially no empirical support for describing temporal variability in all but two fuel properties compared to GAMs, as indicated by ΔAIC values ≥20 (Burnham et al. 2011). Static models describing bulk density of 1-hr fuels in one out of three patches and 1-hr fuel moisture content in one patch were the only two temporal models with any (although marginal) empirical support compared to GAMs, as indicated by ΔAIC values of 13.41 and 15.92, respectively (Burnham et al. 2011). I also found that adding a parameter to account for spatial variation in fuel properties with respect to time since fire and grazing was inconsequential and unnecessary for almost every fuel property, based on ΔAIC values ≥20. For every fuel parameter, except SAV, ΔAIC values were >16. For SAV, ΔAIC was 8.4, indicating that patch-type may play a significant (while likely minimal) role in describing SAV over time in our experimental landscapes. This study demonstrates that information theory can be a useful method for quantifying the impacts of favoring central tendency bias in practical applications. This is an important step toward bridging the gap between science and management in ecology and other disciplines.

Favoring central tendency may be having a major role in other ecological applications, since it has not been an explicit focus of truly applied research. Ecology long ago aimed to move away from viewing systems as static entities and moved towards a more dynamic-equilibrial view of ecological systems (DeAngelis and Waterhouse 1987; Wu and Loucks 1995). Under an equilibrium view, ecosystems are assumed to be predictable, self-regulating entities where disturbance history, stochastic factors, and environmental perturbations play a minimal role in determining ecosystem dynamics (Wu and Loucks 1995). Because of a lack of evidence supporting equilibrium systems and the inability of such a view to account for the transient behavior and patchiness of many systems, many ecologists have moved towards a more dynamic-equilibrial view of ecological systems where equilibrium is viewed as a transient property of system rather than a fundamental characteristic (Botkin and Sobel 1975; Pickett et al. 1992). Today, it is well accepted that disturbances, environmental perturbations, and climate play an important role in determining complex system dynamics. Yet, some disciplines continue to favor central tendency and assume that a mean value may describe such complex ecological phenomena. For example, in an attempt to ensure fire safety and containment, strict policies directed towards prescribed burning are implemented across much of the United States that limit the magnitude and variability in fire behavior (Twidwell et al. 2016). Further research should work towards developing more dynamic applied models and determining under what circumstances more dynamic models are more appropriate in describing ecological patterns or processes than static models.

Our results suggests a need for further investigations regarding the robustness of the dynamic models provided in this study under varying weather, topographic, and environmental conditions. For example, during extreme drought, I saw no difference in the amount of fine fuel across patches. Such results contradict what is typically observed at this study site under non-drought conditions. Typically, fine fuel load accumulates with time since fire and grazing, creating three distinct patch types with varying amounts of fine fuel (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006; Allred et al. 2011). Because only two out of the three patches were burned during the duration of our study, I expected to observe a significant spatial effect of patch type on fine fuel load. To test the validity of our statistical techniques and reasoning, I ran a *post hoc* comparison of fine fuel load across patches from samples collected at the same site and experimental landscapes under non-drought conditions in 2009 (see Allred et al. 2011). As predicted, adding a parameter in the GAM to account for spatial dependencies (patch type) in fine fuel load resulted in a lower AIC score and a ΔAIC of 37.68 (data not shown). This suggest and confirms with previous studies that patch type plays a significant role in determining fine fuel load under typical weather conditions. Our results therefore indicate that extreme drought likely altered the spatiotemporal patterns of grassland fuel properties in landscape with fire and grazing.

There are many opportunities to learn from a growing body of work that applies complex systems thinking to meet the demand for practical applications and adoptions of science (Allen and Saunders 2006; Parrott 2010; Burg et al. 2010). The problem with adhering to the central tendency in describing ecological systems is that it assumes the mean is the best way to characterize system behavior and guide natural resource management. Yet, variation is critical to understanding biological organization and functioning (Christensen 1997; Wiens 1997). Ecosystems are inherently dynamic across many spatiotemporal scales (Levin 1992; Patten & Ellis 1995; Ludwig & Tongway 1995) and failing to account for variation has weakened the potential for management frameworks to meet biodiversity and production targets (Fuhlendorf and Engle 2001; Twidwell et al. 2016). In an attempt to characterize wildland fuels, favoring central tendency results in an underestimation of the spatiotemporal variability in fuel properties, which are tightly coupled to fire behavior and effects (Rothermel 1972; Jolly 2007). The results of this study suggest that nearly all fuel properties in grasslands are better described and modeled as dynamic and that a constant or mean value should not be used to mathematically describe such fuel properties over time. Technological and analytical theory is continuing to make it easier to deal with complex data, so more opportunities are becoming available to quantitatively assess the impact of favoring central tendency and incorporate dynamic modeling approaches into ecological applications.

ACKNOWLEDGEMENTS

I thank the following people for their field assistance and sampling: Andrew West, Bill Hiatt, Taylor Winter, and Abbey Ramirez. I thank John Weir and the OSU Fire Crew and personnel at the OSU Range Research Station for the application of treatments. This research was funded by the Joint Fire Science Program projects 11-1-2-19 and 13-1-06-8.

TABLES

Table 3.1 A description of the 14 fuel properties measured in this study, abbreviations, and their definitions.

	Term	Abbreviation	Definition	Units
Fuel bed measurements	Fuel bed depth	FBD	The vertical distance from the bottom of the litter layer to the highest fuel particle	cm
	Surface area to volume ratio	SAV	The area covered by the outside of fuel per unit volume	cm^{-1}
	Fuel moisture content	FMC	The proportion of the fuel bed that is water, calculated on a dry weight basis	%
	Fine fuel load	FFL	The total mass of fuel (≤0.64 cm in diameter) per unit area of the fuel bed	$g\ m^{-2}$
	Bulk density	BD	The total amount of oven-dry fuel per unit volume of the fuel bed (fuel load/fuel bed depth)	$kg\ m^{-3}$
Dead fuel (1-hr) measurements	1-hr fuel bed depth	FBDD	The vertical distance from the bottom of the litter layer to the highest dead fuel particle	cm
	1-hr fuel moisture content	FMCD	The proportion of dead fuel that is water, calculated on a dry weight basis	%
	1-hr fine fuel load	FFLD	The mass of dead fuel (≤0.64 cm in diameter) per unit area of the fuel bed	$g\ m^{-2}$
	1-hr bulk density	BDD	The amount of oven-dry dead fuel per unit volume of the fuel bed (fuel load/fuel bed depth)	$kg\ m^{-3}$
	Percent 1-hr fuels	PD	The percentage of dead fuels in the fuel bed	%
Live fuel measurements	Live fuel bed depth	FBDL	The vertical distance from the bottom of the litter layer to the highest live fuel particle	cm
	Live fine fuel load	FFLL	The mass of live fuel (≤0.64 cm in diameter) per unit area of the fuel bed	$g\ m^{-2}$
	Live bulk density	BDL	The amount of oven-dry live fuel per unit volume of the fuel bed (fuel load/fuel bed depth)	$kg\ m^{-3}$
	Percent live fuels	PL	The percentage of live fuels in the fuel bed	%

Definitions are from the BehavePlus fire modeling system. For more information see Heinsch and Andrews (2010).

Table 3.2 (Patch A) AIC comparison of dynamic generalized additive models (GAM) to a static model (y = μ) for describing the temporal variability of 14 grassland fuel parameters. The model with the lowest AIC$_i$ score is the "top" model for describing the given parameter (Akaike 1973). The number of parameters used in each model is indicated by k_i. The relative amount of information loss compared to the top model is indicated by Δ_i. The relative strength of each model is interpreted as w_i .

Model	**AIC$_i$**	**k_i**	Δ_i	**w_i**	**Model**	**AIC$_i$**	**k_i**	Δ_i	**w_i**
FFL ~ s(Period) + Year	13,948.11	12	0.00	0.50	FBD ~ s(Period, by = Year)	8,570.51	12	0.00	0.50
FFL ~ s(Period, by = Year)	13,948.11	12	0.00	0.50	FBD ~ s(Period) + Year	8,570.51	12	0.00	0.50
FFL ~ s(Period)	13,960.92	11	12.81	0.00	FBD ~ s(Period)	8,591.25	11	20.74	0.00
FFL ~ 1	14,571.63	2	623.52	0.00	FBD ~ 1	9,329.92	2	759.42	0.00
FFLL ~ s(Period) + Year	11,586.80	12	0.00	0.86	FBDL ~ s(Period) + Year	8,568.67	12	0.00	0.66
FFLL ~ s(Period)	11,591.84	11	5.04	0.07	FBDL ~ s(Period)	8,571.41	11	2.74	0.17
FFLL ~ s(Period, by = Year)	11,591.84	12	5.05	0.07	FBDL ~ s(Period, by = Year)	8,571.42	12	2.75	0.17
FFLL ~ 1	12,230.46	2	643.66	0.00	FBDL ~ 1	9,768.24	2	1,199.57	0.00
FFLD ~ s(Period) + Year	12,438.88	12	0.00	1.00	FBDD ~ s(Period) + Year	7,423.78	12	0.00	0.47
FFLD ~ s(Period, by = Year)	12,453.81	12	14.93	0.00	FBDD ~ s(Period, by = Year)	7,423.78	12	0.00	0.47
FFLD ~ s(Period)	12,458.36	11	19.48	0.00	FBDD ~ s(Period)	7,427.85	11	4.07	0.06
FFLD ~ 1	12,834.14	2	395.26	0.00	FBDD ~ 1	7,732.53	2	308.75	0.00
FMC ~ s(Period, by = Year)	10,128.86	12	0.00	0.35	BD ~ s(Period)	7,110.45	11	0.00	0.44
FMC ~ s(Period)	10,128.86	11	0.01	0.35	BD ~ s(Period, by = Year)	7,111.32	12	0.87	0.28
FMC ~ s(Period) + Year	10,129.14	12	0.29	0.30	BD ~ s(Period) + Year	7,111.32	12	0.87	0.28
FMC ~ 1	11,606.56	2	1,477.71	0.00	BD ~ 1	7,550.06	2	439.61	0.00

FMCD ~ s(Period, by = Year)	304.85	12	0.00	0.33	BDL ~ s(Period) + Year	5,651.78	12	0.00	0.50
FMCD ~ s(Period) + Year	304.85	12	0.00	0.33	BDL ~ s(Period)	5,651.78	11	0.00	0.50
FMCD ~ s(Period)	304.85	11	0.00	0.33	BDL ~ s(Period, by = Year)	5,667.85	12	16.07	0.00
FMCD ~ 1	323.24	2	18.39	0.00	BDL ~ 1	5,841.13	2	189.35	0.00
PL ~ s(Period) + Year	8,133.01	12	0.00	1.00	BDD ~ s(Period, by = Year)	10,611.24	12	0.00	0.42
PL ~ s(Period)	8,159.80	11	26.78	0.00	BDD ~ s(Period)	10,611.25	11	0.00	0.42
PL ~ s(Period, by = Year)	8,159.82	12	26.81	0.00	BDD ~ s(Period) + Year	10,613.23	12	1.99	0.16
PL ~ 1	9,260.53	2	1,127.51	0.00	BDD ~ 1	10,670.97	2	59.73	0.00
PD ~ s(Period) + Year	8,133.01	12	0.00	1.00	SAV ~ s(Period)	4,816.63	11	0.00	1.00
PD ~ s(Period)	8,159.80	11	26.78	0.00	SAV ~ 1	4,844.05	2	27.42	0.00
PD ~ s(Period, by = Year)	8,159.95	12	26.94	0.00					
PD ~ 1	9,260.53	2	1,127.51	0.00					

Table 3.3 (Patch B) AIC comparison of dynamic generalized additive models (GAM) to a static model (y = μ) for describing the temporal variability of 14 grassland fuel parameters. The model with the lowest AIC_i score is the “top” model for describing the given parameter (Akaike 1973). The number of parameters used in each model is indicated by k_i. The relative amount of information loss compared to the top model is indicated by Δ_i. The relative strength of each model is interpreted as w_i .

Model	**AIC_i**	**k_i**	Δ_i	**w_i**	**Model**	**AIC_i**	**k_i**	Δ_i	**w_i**
FFL ~ s(Period)	14,103.80	11	0.00	0.57	FBD ~ s(Period, by = Year)	8,345.12	12	0.00	0.33
FFL ~ s(Period, by = Year)	14,105.73	12	1.93	0.22	FBD ~ s(Period) + Year	8,345.12	12	0.00	0.33
FFL ~ s(Period) + Year	14,105.73	12	1.93	0.22	FBD ~ s(Period)	8,345.13	11	0.01	0.33
FFL ~ 1	14,844.87	2	741.07	0.00	FBD ~ 1	9,090.94	2	745.82	0.00
FFLL ~ s(Period) + Year	11,036.28	12	0.00	0.33	FBDL ~ s(Period) + Year	8,779.63	12	0.00	0.98
FFLL ~ s(Period)	11,036.29	11	0.01	0.33	FBDL ~ s(Period)	8,788.43	11	8.80	0.01
FFLL ~ s(Period, by = Year)	11,036.30	12	0.01	0.33	FBDL ~ s(Period, by = Year)	8,788.43	12	8.81	0.01
FFLL ~ 1	11,494.72	2	458.43	0.00	FBDL ~ 1	9,608.91	2	829.29	0.00
FFLD ~ s(Period)	11,662.47	11	0.00	0.33	FBDD ~ s(Period)	6,450.05	11	0.00	0.42
FFLD ~ s(Period) + Year	11,662.47	12	0.00	0.33	FBDD ~ s(Period) + Year	6,450.78	12	0.73	0.29
FFLD ~ s(Period, by = Year)	11,662.47	12	0.01	0.33	FBDD ~ s(Period, by = Year)	6,450.78	12	0.73	0.29
FFLD ~ 1	12,260.48	2	598.01	0.00	FBDD ~ 1	6,728.09	2	278.04	0.00
FMC ~ s(Period) + Year	10,533.01	12	0.00	0.65	BD ~ s(Period)	7,694.41	11	0.00	0.55
FMC ~ s(Period, by = Year)	10,535.59	12	2.58	0.18	BD ~ s(Period, by = Year)	7,696.23	12	1.81	0.22
FMC ~ s(Period)	10,535.59	11	2.58	0.18	BD ~ s(Period) + Year	7,696.23	12	1.81	0.22
FMC ~ 1	11,884.08	2	1,351.07	0.00	BD ~ 1	8,340.22	2	645.81	0.00
FMCD ~ s(Period) + Year	497.38	12	0.00	0.33	BDL ~ s(Period, by = Year)	7,200.20	12	0.00	0.33
FMCD ~ s(Period)	497.38	11	0.00	0.33	BDL ~ s(Period)	7,200.21	11	0.00	0.33

FMCD ~ s(Period, by = Year)	497.39	12	0.00	0.33	BDL ~ s(Period) + Year	7,200.21	12	0.00	0.33
FMCD ~ 1	513.31	2	15.92	0.00	BDL ~ 1	7,270.71	2	70.51	0.00
PL ~ s(Period)	7,488.76	11	0.00	0.33	BDD ~ s(Period) + Year	9,042.05	12	0.00	0.88
PL ~ s(Period) + Year	7,488.76	12	0.00	0.33	BDD ~ s(Period, by = Year)	9,046.02	12	3.97	0.12
PL ~ s(Period, by = Year)	7,488.78	12	0.02	0.33	BDD ~ s(Period)	9,072.98	11	30.93	0.00
PL ~ 1	8,984.35	2	1,495.59	0.00	BDD ~ 1	9,161.58	2	119.53	0.00
PD ~ s(Period) + Year	7,488.75	12	0.00	0.33	SAV ~ s(Period)	4,845.22	11	0.00	1.00
PD ~ s(Period)	7,488.76	11	0.00	0.33	SAV ~ 1	4,873.73	2	28.52	0.00
PD ~ s(Period, by = Year)	7,488.77	12	0.01	0.33					
PD ~ 1	8,984.35	2	1,495.60	0.00					

Table 3.4 (Patch C) AIC comparison of dynamic generalized additive models (GAM) to a static model (y = μ) for describing the temporal variability of 14 grassland fuel parameters. The model with the lowest AIC_i score is the “top” model for describing the given parameter (Akaike 1973). The number of parameters used in each model is indicated by k_i. The relative amount of information loss compared to the top model is indicated by Δ_i. The relative strength of each model is interpreted as w_i .

Model	**AIC_i**	**k_i**	Δ_i	**w_i**	**Model**	**AIC_i**	**k_i**	Δ_i	**w_i**
FFL ~ s(Period)	14,312.35	11	0.00	0.57	FBD ~ s(Period, by = Year)	8,727.96	12	0.00	0.37
FFL ~ s(Period, by = Year)	14,314.30	12	1.95	0.21	FBD ~ s(Period)	8,727.97	11	0.01	0.37
FFL ~ s(Period) + Year	14,314.30	12	1.95	0.21	FBD ~ s(Period) + Year	8,728.71	12	0.75	0.26
FFL ~ 1	14,832.06	2	519.71	0.00	FBD ~ 1	9,293.64	2	565.68	0.00
FFLL ~ s(Period) + Year	12,387.96	12	0.00	0.91	FBDL ~ s(Period) + Year	8,565.79	12	0.00	0.93
FFLL ~ s(Period)	12,393.86	11	5.90	0.05	FBDL ~ s(Period)	8,572.35	11	6.56	0.03
FFLL ~ s(Period, by = Year)	12,393.87	12	5.91	0.05	FBDL ~ s(Period, by = Year)	8,572.36	12	6.58	0.03
FFLL ~ 1	13,017.57	2	629.61	0.00	FBDL ~ 1	9,614.98	2	1,049.19	0.00
FFLD ~ s(Period) + Year	13,005.15	12	0.00	0.57	FBDD ~ s(Period)	7,907.63	11	0.00	0.46
FFLD ~ s(Period)	13,007.10	11	1.95	0.22	FBDD ~ s(Period, by = Year)	7,908.69	12	1.06	0.27
FFLD ~ s(Period, by = Year)	13,007.12	12	1.97	0.21	FBDD ~ s(Period) + Year	7,908.69	12	1.06	0.27
FFLD ~ 1	13,362.56	2	357.41	0.00	FBDD ~ 1	8,114.08	2	206.45	0.00
FMC ~ s(Period, by = Year)	9,926.63	12	0.00	0.39	BD ~ s(Period)	7,379.04	11	0.00	0.35
FMC ~ s(Period)	9,926.64	11	0.01	0.39	BD ~ s(Period) + Year	7,379.16	12	0.12	0.33
FMC ~ s(Period) + Year	9,927.84	12	1.21	0.21	BD ~ s(Period, by = Year)	7,379.16	12	0.12	0.33
FMC ~ 1	11,422.70	2	1,496.07	0.00	BD ~ 1	7,583.46	2	204.42	0.00
FMCD ~ s(Period, by = Year)	475.34	12	0.00	0.33	BDL ~ s(Period) + Year	5,701.62	12	0.00	1.00

FMCD ~ s(Period) + Year	475.34	12	0.00	0.33	BDL ~ s(Period)	5,712.37	11	10.76	0.00
FMCD ~ s(Period)	475.34	11	0.00	0.33	BDL ~ s(Period, by = Year)	5,731.40	12	29.79	0.00
FMCD ~ 1	508.14	2	32.80	0.00	BDL ~ 1	5,893.58	2	191.96	0.00
PL ~ s(Period) + Year	8,320.07	12	0.00	1.00	BDD ~ s(Period, by = Year)	10,438.29	12	0.00	0.47
PL ~ s(Period)	8,346.82	11	26.75	0.00	BDD ~ s(Period) + Year	10,438.29	12	0.00	0.47
PL ~ s(Period, by = Year)	8,346.84	12	26.77	0.00	BDD ~ s(Period)	10,442.70	11	4.41	0.05
PL ~ 1	9,515.71	2	1,195.64	0.00	BDD ~ 1	10,451.69	2	13.41	0.00
PD ~ s(Period) + Year	8,320.07	12	0.00	1.00	SAV ~ s(Period)	4,864.37	11	0.00	1.00
PD ~ s(Period)	8,346.82	11	26.75	0.00	SAV ~ 1	4,901.38	2	37.01	0.00
PD ~ s(Period, by = Year)	8,346.98	12	26.91	0.00					
PD ~ 1	9,515.71	2	1,195.64	0.00					

Table 3.5 AIC comparison of dynamic generalized additive models (GAM) that describe the spatial variability of 14 grassland fuel parameters. The model with the lowest AIC_i score is the "top" model for describing the given parameter (Akaike 1973). The number of parameters used in each model is indicated by k_i. The relative amount of information loss compared to the top model is indicated by Δ_i. The relative strength of each model is interpreted as w_i .

Model	**AIC_i**	**k_i**	**Δ_i**	**w_i**
FFL ~ s(Period)	43031.95	11.00	0.00	1.00
FFL ~ s(Period, by = Patch)	43396.20	12.00	364.25	0.00
FFLL ~ s(Period)	35517.46	11.00	0.00	1.00
FFLL ~ s(Period, by = Patch)	35895.56	12.00	378.10	0.00
FFLD ~ s(Period)	38120.08	11.00	0.00	1.00
FFLD ~ s(Period, by = Patch)	38236.50	12.00	116.42	0.00
FMC ~ s(Period)	31237.91	11.00	0.00	1.00
FMC ~ s(Period, by = Patch)	32670.18	12.00	1432.27	0.00
FMCD ~ s(Period)	1265.47	11.00	0.00	1.00
FMCD ~ s(Period, by = Patch)	1285.37	12.00	19.90	0.00
PL ~ s(Period)	25040.33	11.00	0.00	1.00
PL ~ s(Period, by = Patch)	25158.04	12.00	117.71	0.00
PD ~ s(Period)	26951.84	11.00	0.00	1.00
PD ~ s(Period, by = Patch)	27482.32	12.00	530.49	0.00
FBD ~ s(Period)	26286.52	11.00	0.00	1.00
FBD ~ s(Period, by = Patch)	26878.92	12.00	592.40	0.00
FBDL ~ s(Period)	18219.97	11.00	0.00	1.00
FBDL ~ s(Period, by = Patch)	18403.35	12.00	183.38	0.00
FBDD ~ s(Period)	22144.41	11.00	0.00	1.00
FBDD ~ s(Period, by = Patch)	22345.88	12.00	201.47	0.00
BD ~ s(Period)	32381.27	11.00	0.00	1.00
BD ~ s(Period, by = Patch)	32480.88	12.00	99.61	0.00
BDL ~ s(Period)	13911.88	11.00	0.00	1.00
BDL ~ s(Period, by = Patch)	13961.61	12.00	49.73	0.00

BDD ~ s(Period)	20446.43	11.00	0.00	1.00
BDD ~ s(Period, by = Patch)	20463.16	12.00	16.73	0.00
SAV ~ s(Period)	14644.69	11.00	0.00	0.99
SAV ~ s(Period, by = Patch)	14653.08	12.00	8.40	0.01

FIGURES

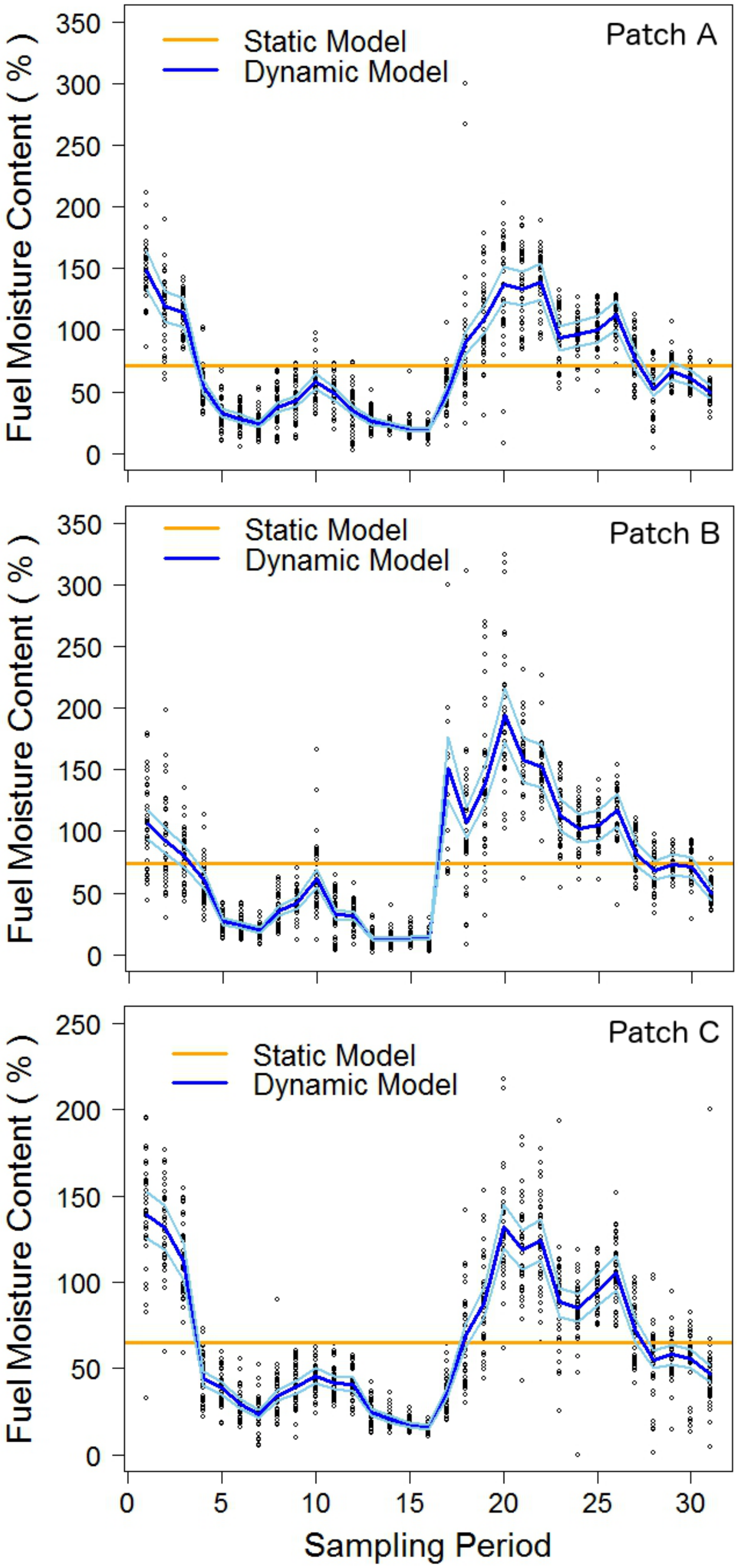
Patch A
Patch B
Patch C
Static Model
Dynamic Model
Fuel Moisture Content (%)
Sampling Period
0
50
100
150
200
250
300
350
0
5
10
15
20
25
30

Figure 3.1 Moisture content of the fuelbed over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

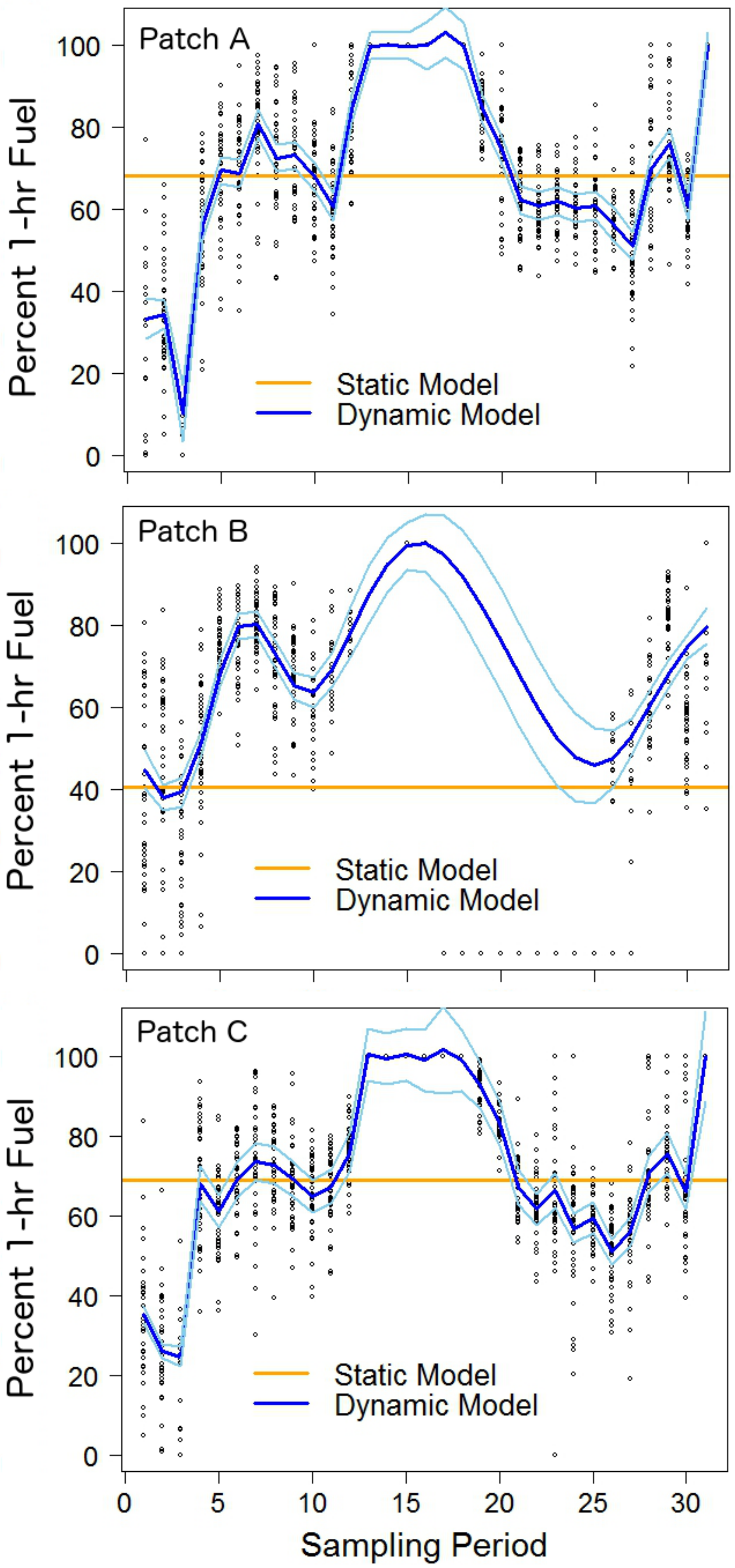
Patch A
Patch B
Patch C
Percent 1-hr Fuel
0
20
40
60
80
100
Static Model
Dynamic Model
Sampling Period
0
5
10
15
20
25
30

Figure 3.2 The percentage of 1-hr fuels in a fuelbed over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

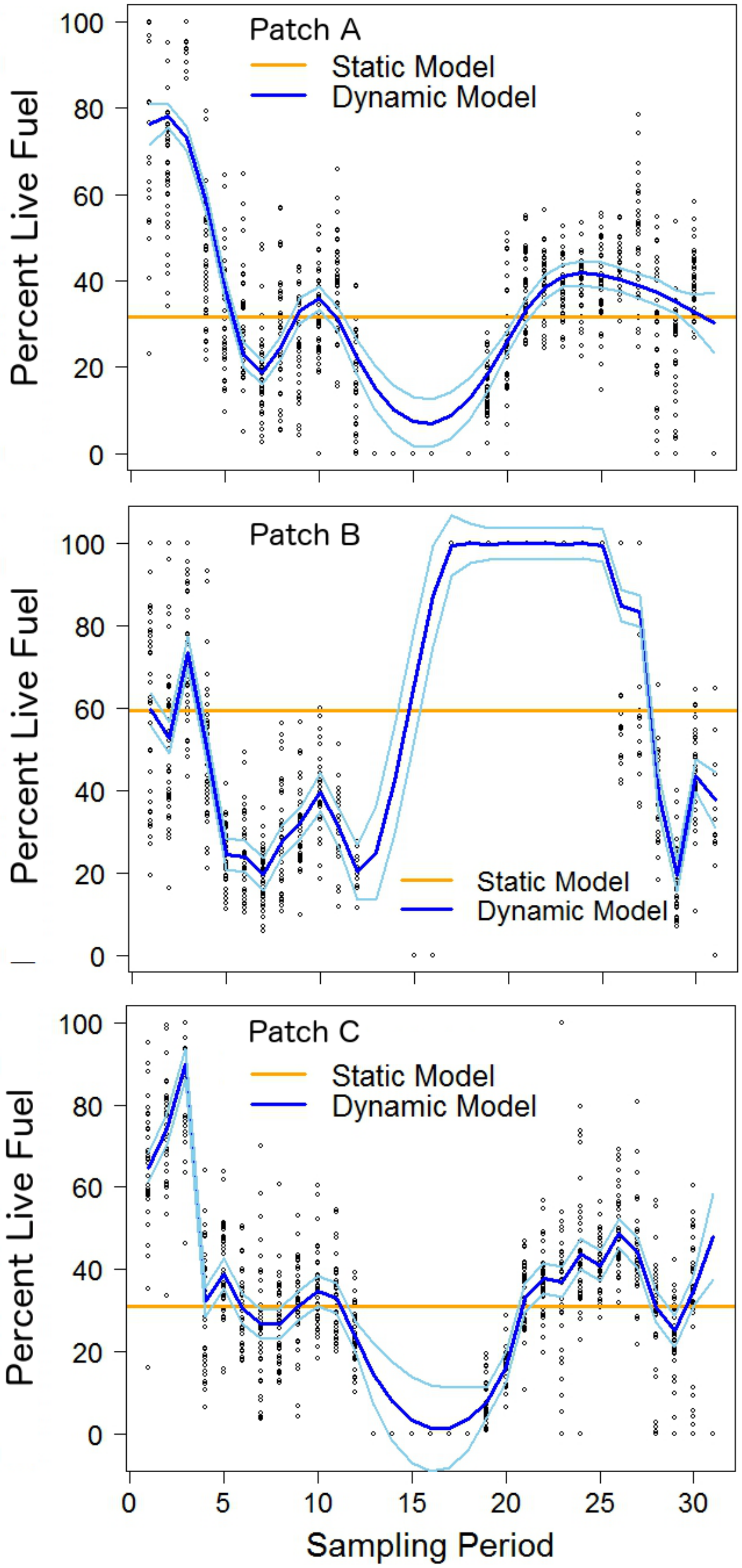
Patch A
Static Model
Dynamic Model
Patch B
Static Model
Dynamic Model
Patch C
Static Model
Dynamic Model
Percent Live Fuel
Percent Live Fuel
Percent Live Fuel
100
80
60
40
20
0
Sampling Period
0
5
10
15
20
25
30

Figure 3.3 The percentage of live fuels in a fuelbed over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

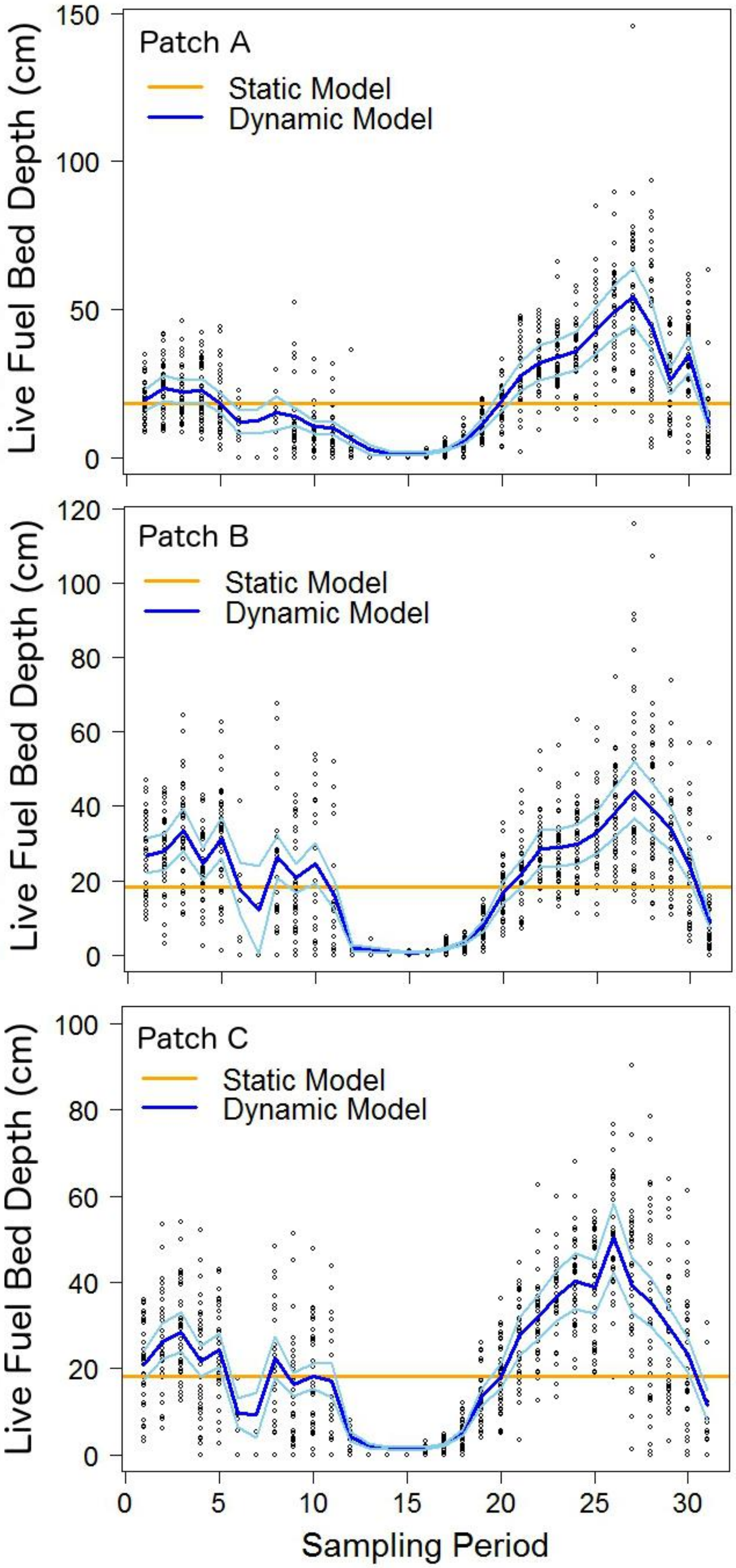
Patch A
Static Model
Dynamic Model
Live Fuel Bed Depth (cm)
0
50
100
150
Patch B
Static Model
Dynamic Model
Live Fuel Bed Depth (cm)
0
20
40
60
80
100
120
Patch C
Static Model
Dynamic Model
Live Fuel Bed Depth (cm)
0
20
40
60
80
100
0
5
10
15
20
25
30
Sampling Period

Figure 3.4 The fuel bed depth of live fuels over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property

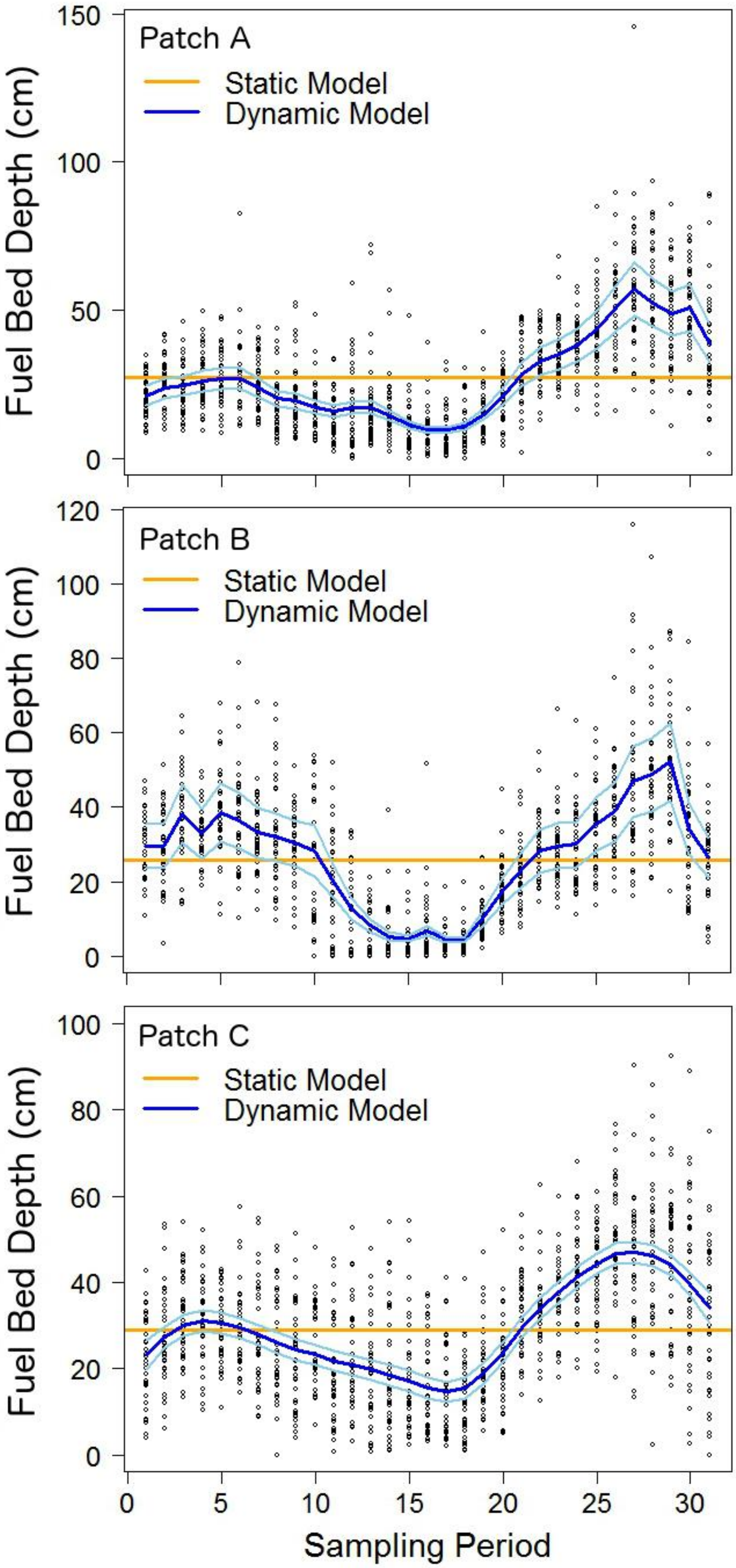
Patch A
Static Model
Dynamic Model
Patch B
Static Model
Dynamic Model
Patch C
Static Model
Dynamic Model
Fuel Bed Depth (cm)
0
50
100
150
0
20
40
60
80
100
120
0
20
40
60
80
100
0
5
10
15
20
25
30
Sampling Period

Figure 3.5 Fuel bed depth over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

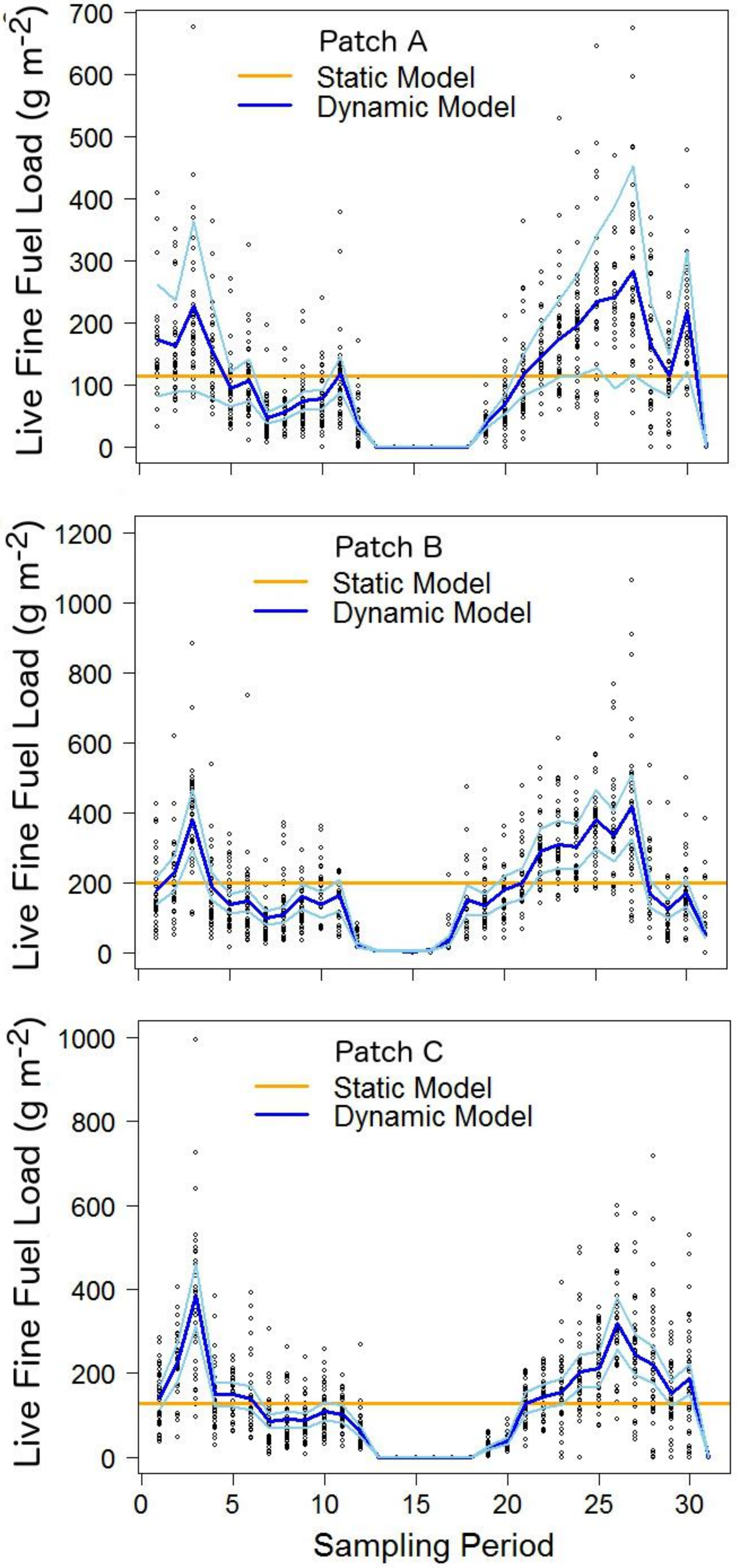
Patch A
Static Model
Dynamic Model
Live Fine Fuel Load (g m⁻²)
0
100
200
300
400
500
600
700
Patch B
Static Model
Dynamic Model
Live Fine Fuel Load (g m⁻²)
0
200
400
600
800
1000
1200
Patch C
Static Model
Dynamic Model
Live Fine Fuel Load (g m⁻²)
0
200
400
600
800
1000
0
5
10
15
20
25
30
Sampling Period

Figure 3.6 Fine fuel load of live fuels over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

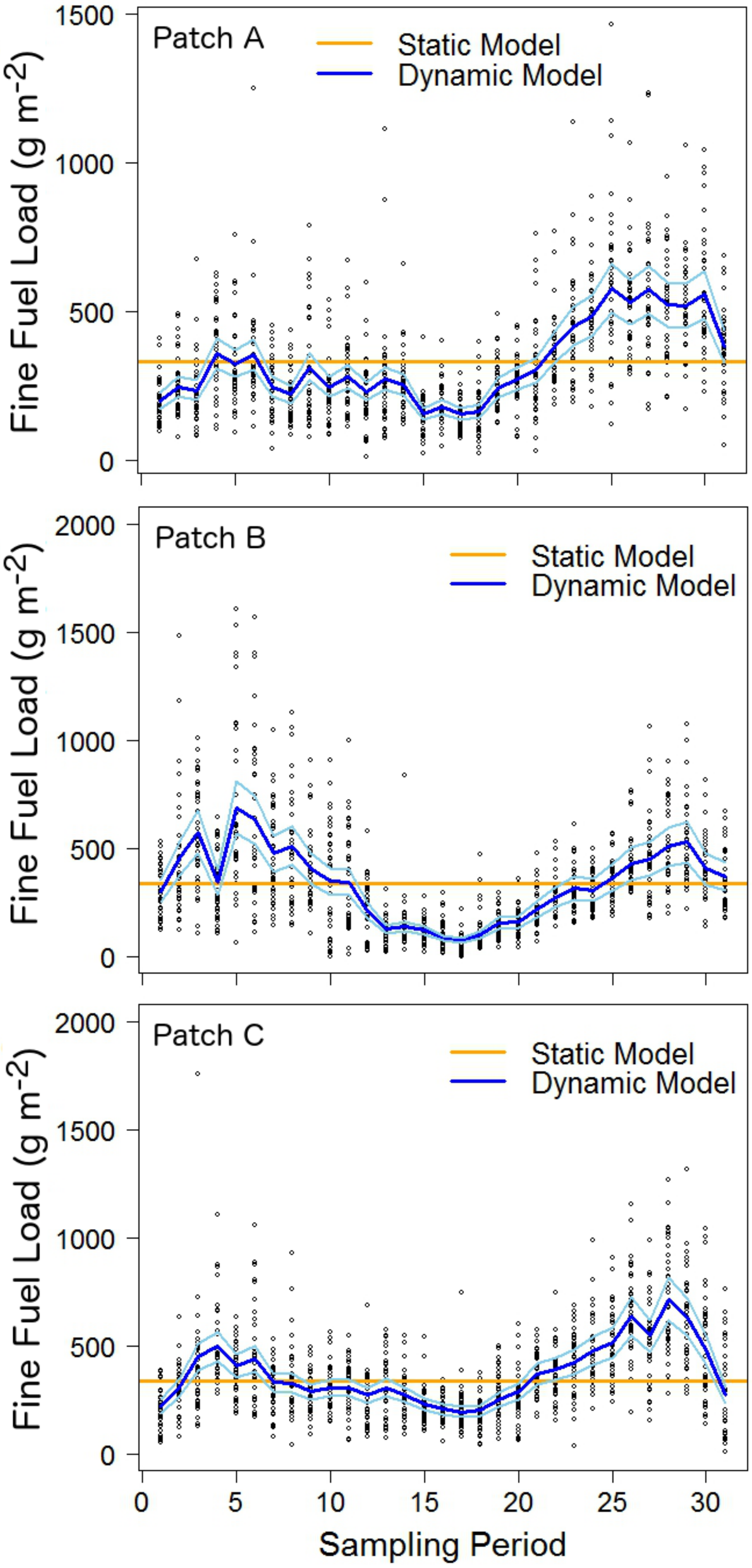
Patch A
Static Model
Dynamic Model
Patch B
Static Model
Dynamic Model
Patch C
Static Model
Dynamic Model
Fine Fuel Load (g m^{-2})
Fine Fuel Load (g m^{-2})
Fine Fuel Load (g m^{-2})
0
500
1000
1500
0
500
1000
1500
2000
0
500
1000
1500
2000
0
5
10
15
20
25
30
Sampling Period

Figure 3.7 Fine fuel load of the fuel bed over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

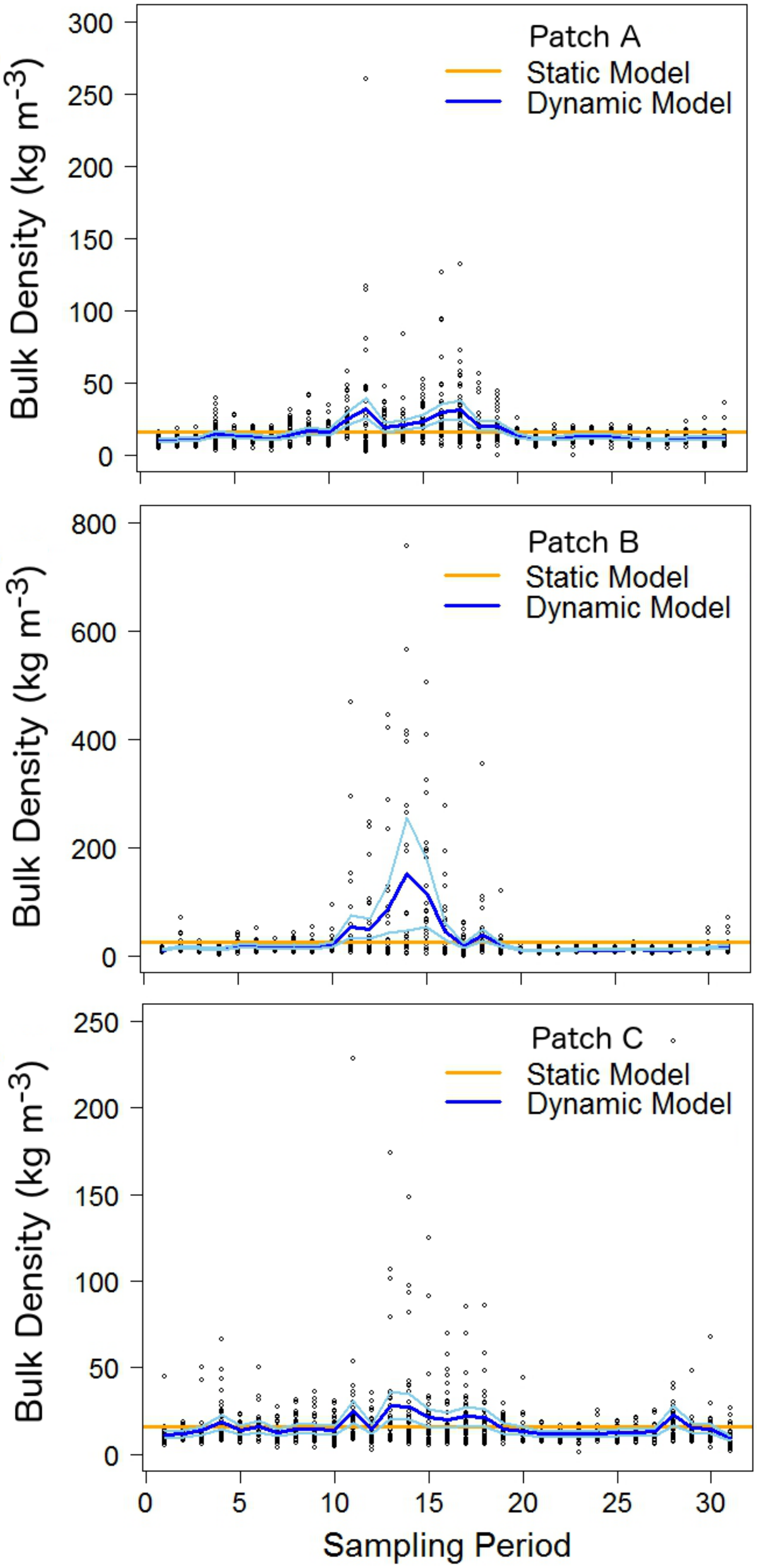
Patch A
Static Model
Dynamic Model
Patch B
Static Model
Dynamic Model
Patch C
Static Model
Dynamic Model
Bulk Density (kg m-3)
300
250
200
150
100
50
0
800
600
400
200
0
250
200
150
100
50
0
0
5
10
15
20
25
30
Sampling Period

Figure 3.8 Bulk density of the fuelbed over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

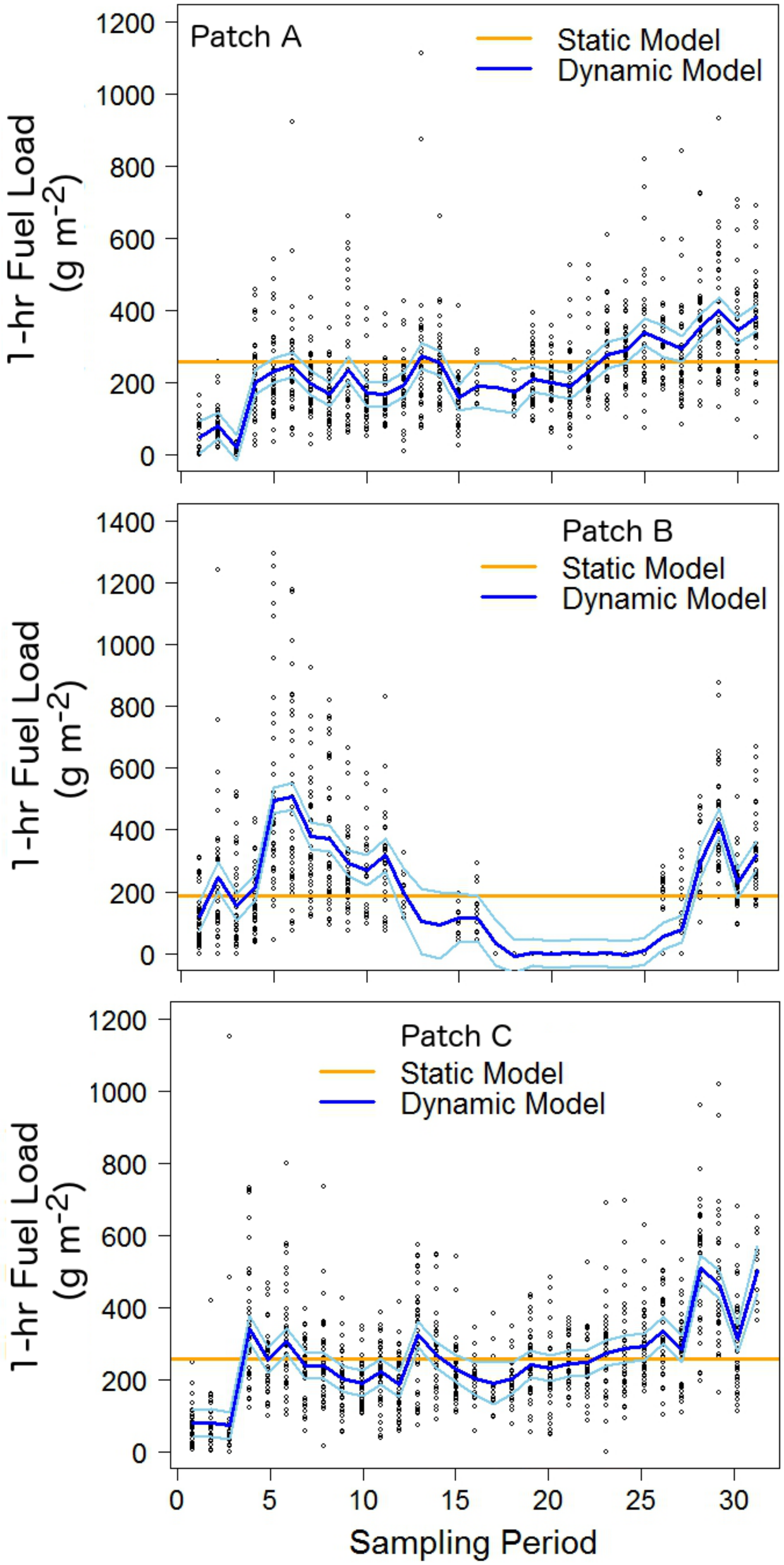
Patch A
Static Model
Dynamic Model
1-hr Fuel Load (g m^{-2})
0
200
400
600
800
1000
1200
Patch B
Static Model
Dynamic Model
1-hr Fuel Load (g m^{-2})
0
200
400
600
800
1000
1200
1400
Patch C
Static Model
Dynamic Model
1-hr Fuel Load (g m^{-2})
0
200
400
600
800
1000
1200
0
5
10
15
20
25
30
Sampling Period

Figure 3.9 Fuel load of 1-hr fuels over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

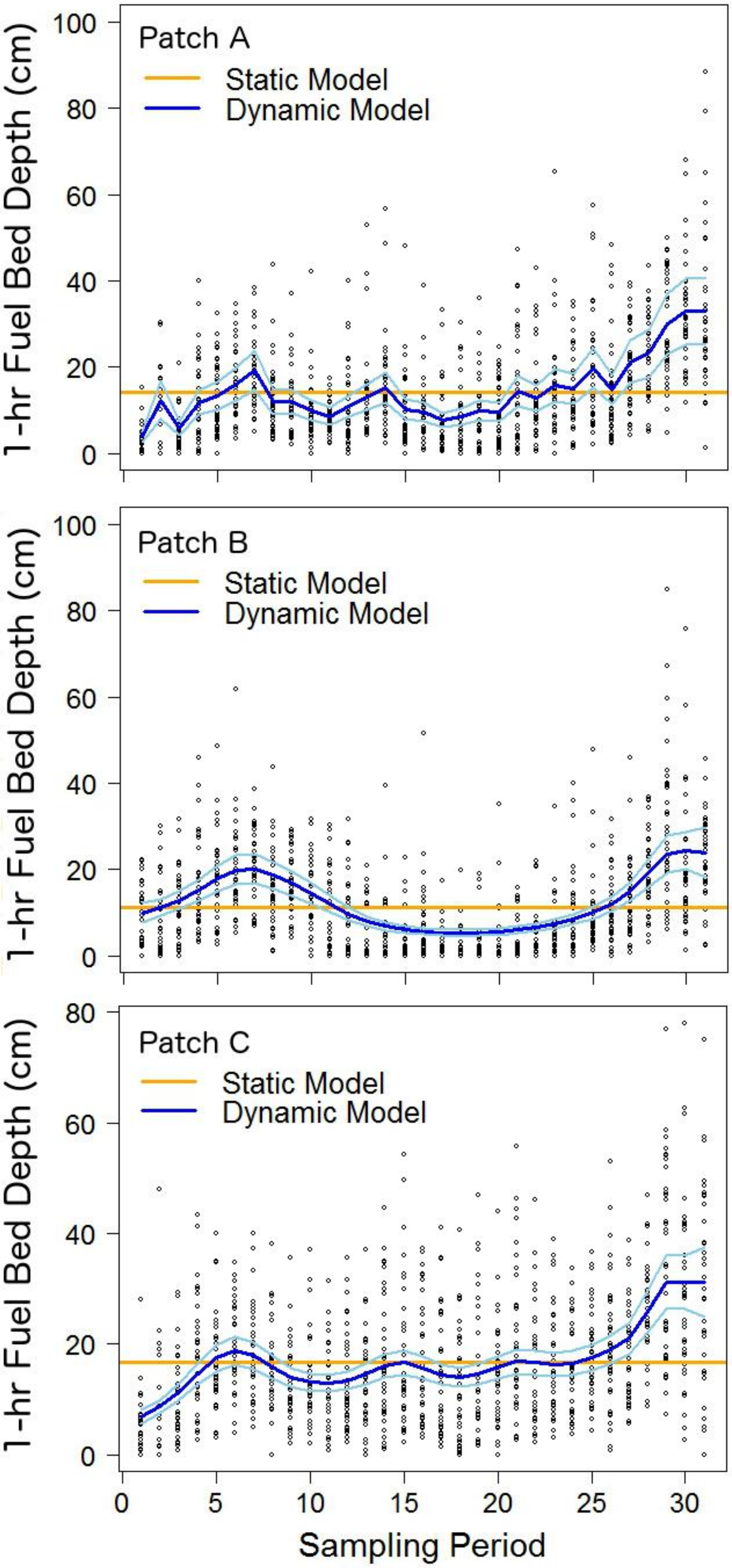
Patch A
Static Model
Dynamic Model
Patch B
Static Model
Dynamic Model
Patch C
Static Model
Dynamic Model
1-hr Fuel Bed Depth (cm)
0
20
40
60
80
100
Sampling Period
0
5
10
15
20
25
30

Figure 3.10 Fuel bed depth of 1-hr fuels over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

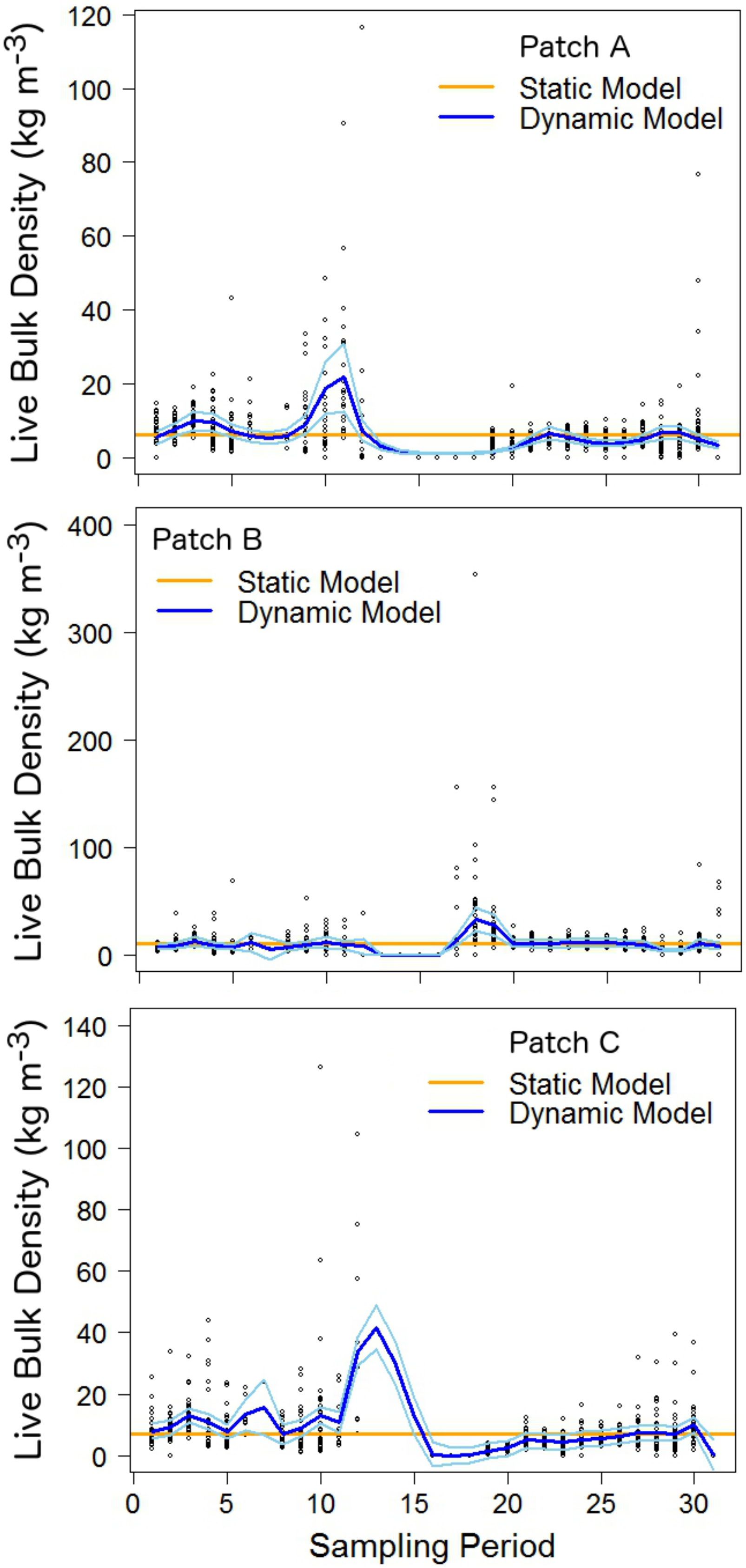
Patch A
Static Model
Dynamic Model
Patch B
Patch C
Live Bulk Density (kg m^{-3})
0
20
40
60
80
100
120
140
200
300
400
0
5
10
15
20
25
30
Sampling Period

Figure 3.11 Bulk density of live fuels over two growing (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

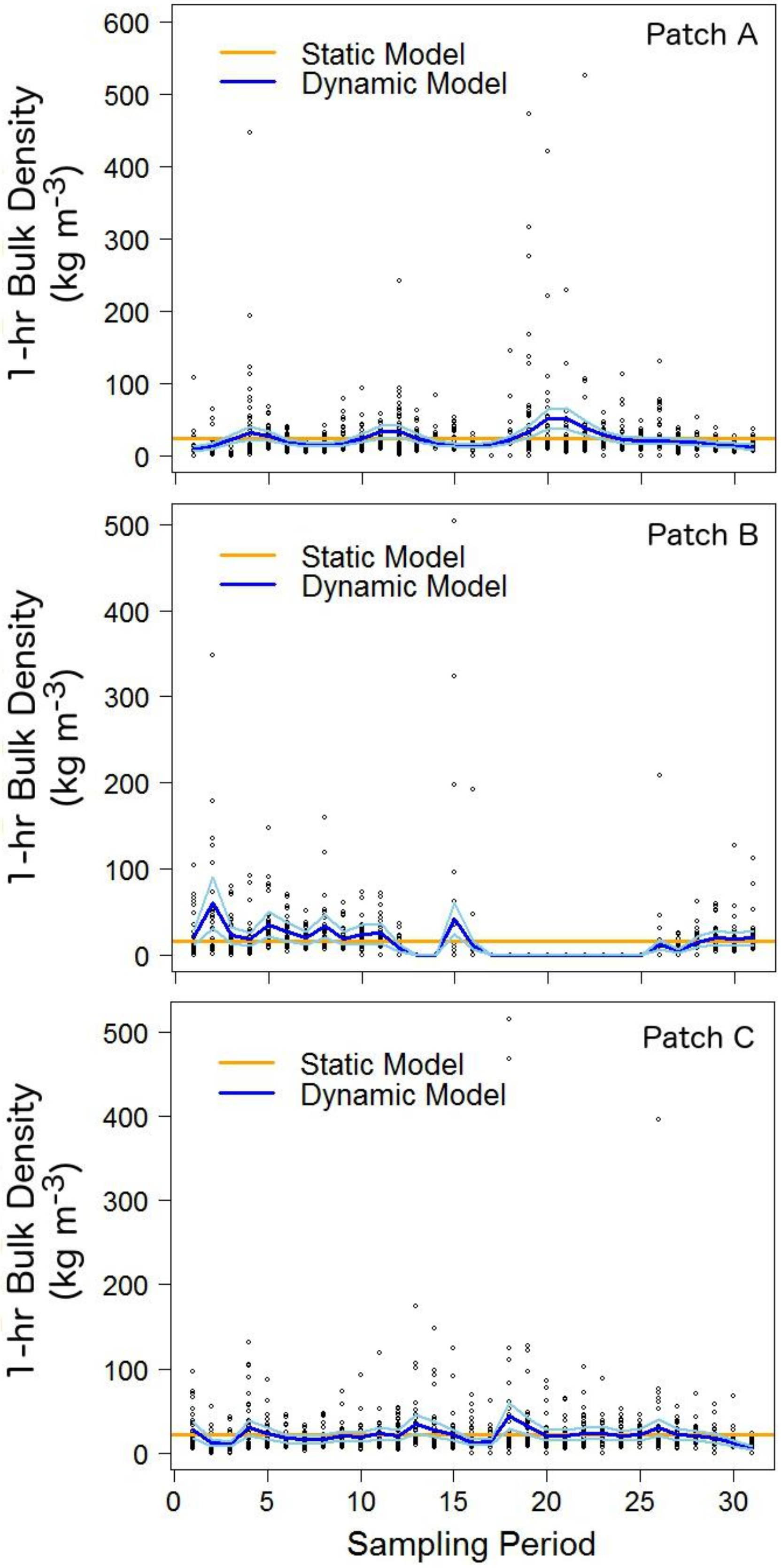
Patch A
Static Model
Dynamic Model
Patch B
Static Model
Dynamic Model
Patch C
Static Model
Dynamic Model
1-hr Bulk Density (kg m^{-3})
0
100
200
300
400
500
600
0
5
10
15
20
25
30
Sampling Period

Figure 3.12 Bulk density of 1-hr fuels over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

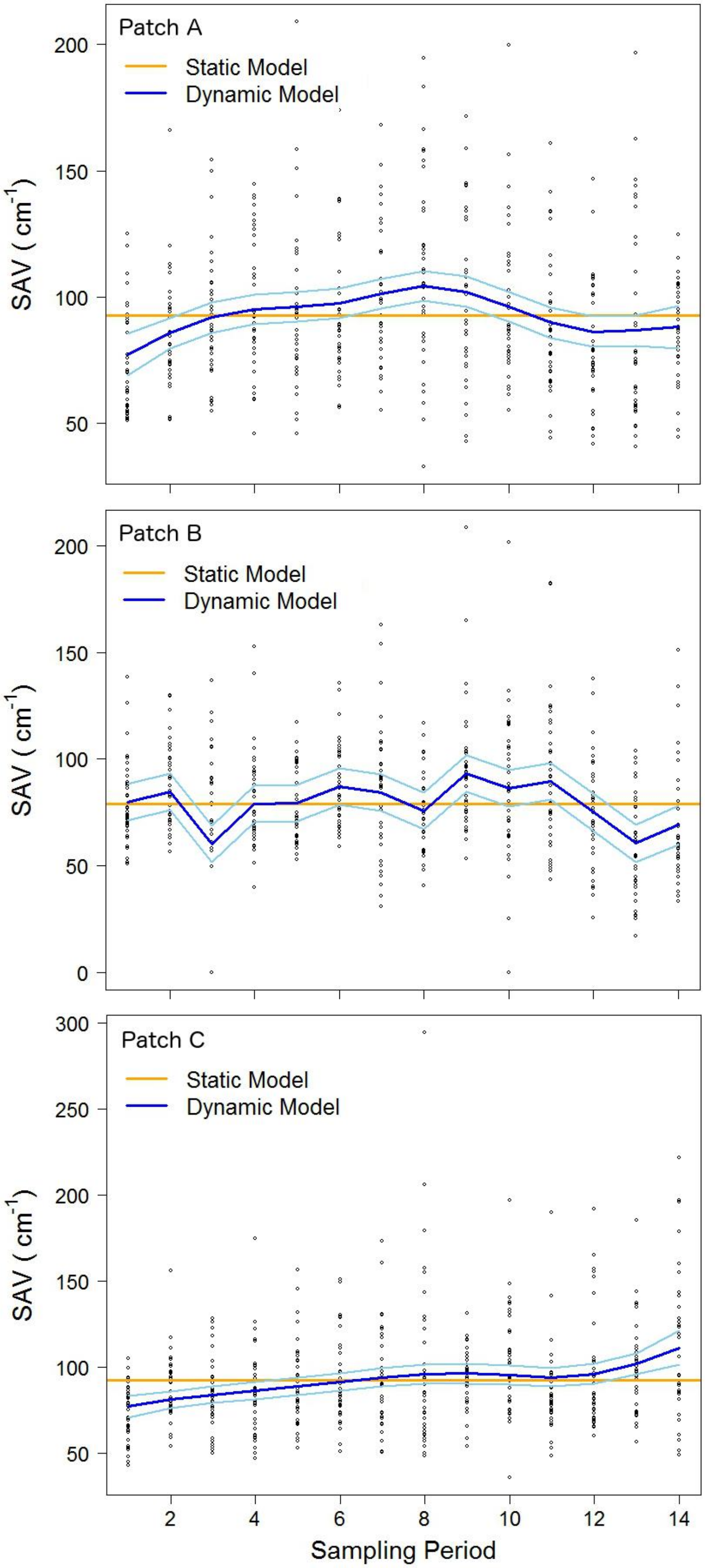
Patch A
Static Model
Dynamic Model
SAV (cm^{-1})
200
150
100
50
Patch B
Static Model
Dynamic Model
SAV (cm^{-1})
200
150
100
50
0
300
Patch C
Static Model
Dynamic Model
SAV (cm^{-1})
250
200
150
100
50
2
4
6
8
10
12
14
Sampling Period

Figure 3.13 Surface area to volume ratio of the fuelbed over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

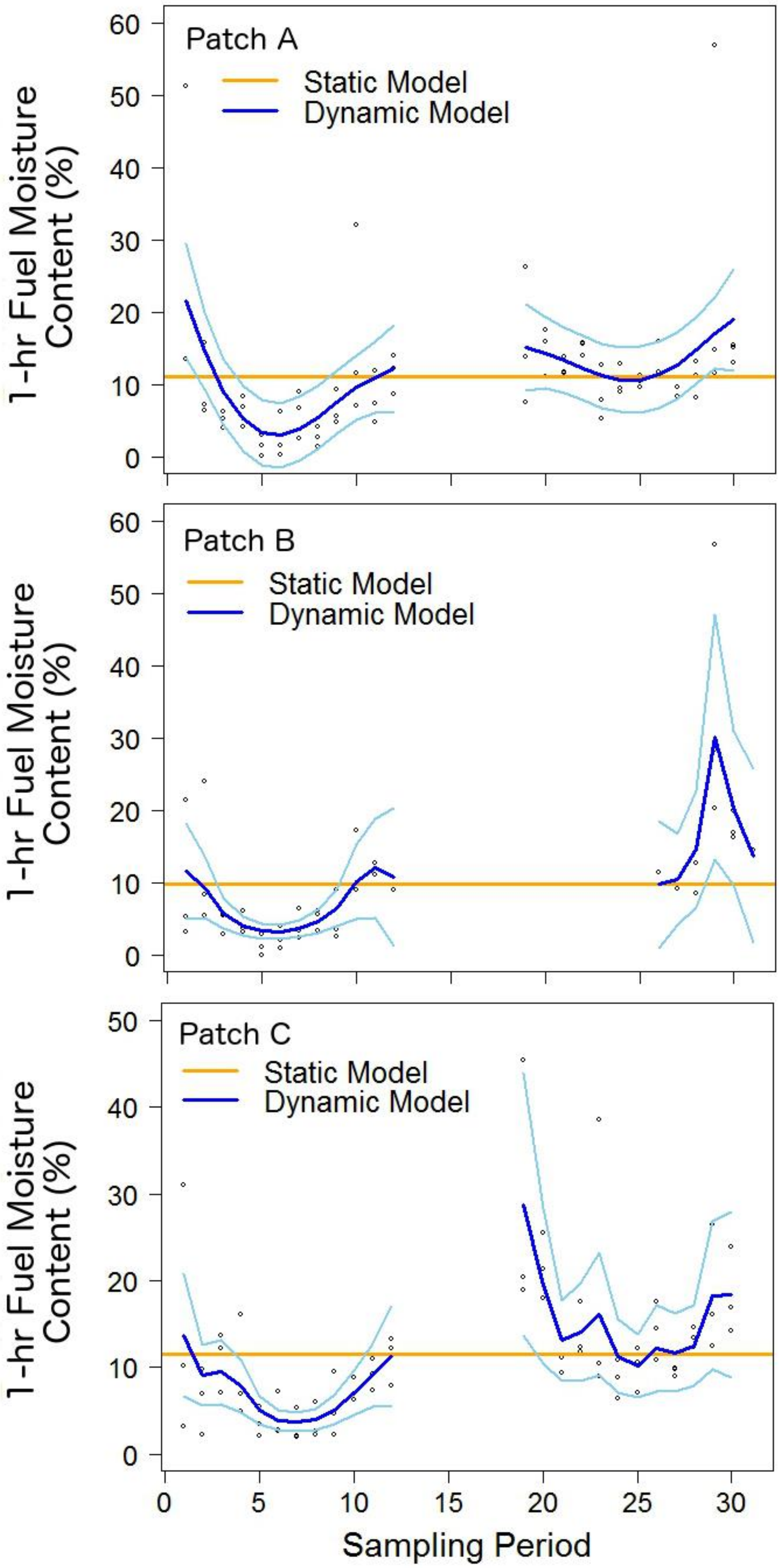
Patch A
Static Model
Dynamic Model
Patch B
Static Model
Dynamic Model
Patch C
Static Model
Dynamic Model
1-hr Fuel Moisture Content (%)
0
10
20
30
40
50
60
0
5
10
15
20
25
30
Sampling Period

Figure 3.14 Fuel moisture content of 1-hr fuels over two growing seasons (sampling periods <15 were in 2012, ≥15 were in 2013). Light blue lines are 95% confidence intervals for the top GAM model that accounted for non-linear trends in a fuel property.

SUPPORTING INFORMATION

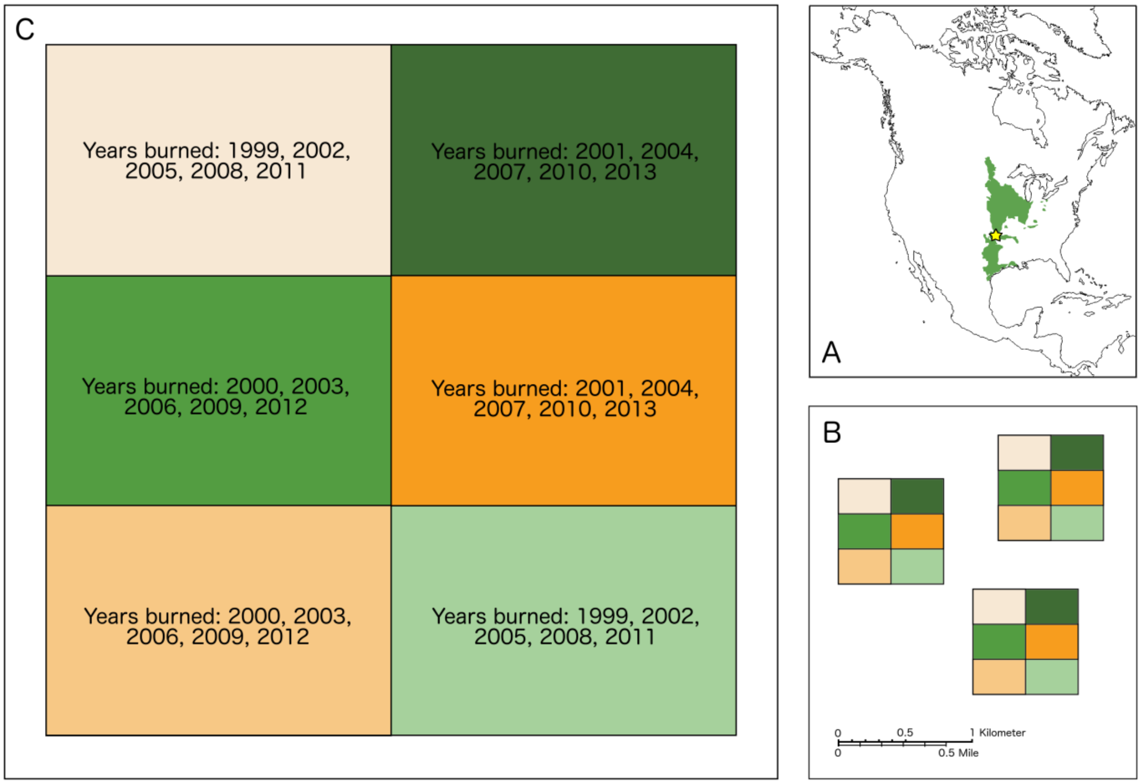

Figure 3.S5. Experimental design used to quantify temporal and spatial variability in 14 grassland fuel properties used in fire behavior fuel models. Our experimental site was located in the North American Great Plains Tallgrass Prairie (A). Three experimental grassland landscapes were used as replicates, each consisting of six patches (64 ha each) at various stages of recovery from burn treatments (B). Shades of green represent growing season fire treatments and shades of orange represent dormant season fire treatments. Yearling cattle were moderately stocked (3.0 AUM/ha) from 1 December to 1 September. No internal fences were present so that livestock could graze freely across an entire landscape. Within each landscape, fire was applied to each patch once every three

years either in the growing season only or dormant season only since the establishment of the site in 1999 (C).

CHAPTER IV

EXPERIMENTAL FLAMMABILITY THRESHOLDS OF EASTERN REDCEDAR AS A POTENTIAL INDICATOR FOR HEIGHTENED WILDFIRE DANGER

INTRODUCTION

Identifying ecological thresholds can guide managers to anticipate how a system responds to disturbance, prioritize management, prevent undesirable state changes, and promote desirable ecosystem services (Suding et al. 2004; Bestlemeyer 2006; Briggs et al. 2009; Twidwell et al. 2013). An ecological threshold is defined as the point at which a relatively small change in an environmental condition or driver leads to abrupt changes in ecosystem composition or function (Groffman et al. 2006; Suding and Hobbs 2009). Sudden changes in ecosystem composition or function are characterized as state shifts, in which a state describes a set of values or attributes typically observed in the system of interest (Suding and Hobbs 2009). The use of threshold models in ecosystem management has become increasingly popular with mounting evidence that ecosystems are highly dynamic over space and time and may respond abruptly, and oftentimes undesirably, to relatively small changes in environmental conditions (Scheffer et al. 2001).

The challenge in applying the threshold concept has been quantifying thresholds that are useful in informing management decisions, but few quantitative thresholds have been directly relevant to management actions or environmental monitoring protocols (Briske et al. 2006; Bestlemeyer 2006; Suding and Hobbs 2009). Such threshold models may result in inconsistent restoration outcomes, undesirable state shifts, or loss of desired ecosystem services. In contrast, a small number of studies have rigorously quantified ecological thresholds associated with disturbance in terrestrial systems. Petraitis et al. (2009) quantified a threshold in the amount of ice scour associated with a state change from a rockweed stand to a mussel bed marine ecosystem. Carpenter et al. (2011) quantified a threshold in the amount of top predators in a freshwater lake associated with a state change from a food web dominated by planktivorous fishes to one dominated by piscivorous fishes. Twidwell et al. (2013) coupled models from applied fire physics and fire ecology to experimental data and quantified a threshold in the fire intensity associated with Ashe juniper (*J.* ashei) mortality. However, beyond these three empirically tested threshold models, most threshold models used to guide management decisions remain largely qualitative (Standish et al. 2014).

Quantitative threshold models relating wildfire risk to horticultural plants remain an unexplored area of research that connects the discipline of applied ecology with society. Multiple horticultural tree species relate closely with wildfire occurrence and structure loss in urban communities, especially during periods of drought (Franklin 1996; Lambert et al. 2010; Syphard et al. 2014). Eastern redcedar (*Juniperus virginiana L.*) is a hardy evergreen tree commonly planted throughout the United States for its drought tolerance, rapid growth rates, and its wide native range (Engle et al. 1996; Ganguli et al. 2008). Eastern redcedar foliage becomes increasingly flammable as drought conditions worsen, meaning that it has not presented a major fire hazard in regions where wildfires have been rare in recent decades (Engle and Stritzke 1995; Weir and Scasta 2015). In the southern Great Plains, however, increases in the occurrence and severity of drought have increased awareness on the potential for Eastern redcedar to combust and heighten wildfire risks. Our current understanding of thresholds in the flammability of Eastern redcedar and its associated wildfire risk, however, remains unknown.

The objective of this study was to quantify thresholds in the flammability of Eastern redcedar and its associated wildfire risk across a gradient of fuel moisture content. Foliar fuel moisture content plays a large role in determining whether a tree will ignite, and if so, how efficient its combustion will be after ignition (Dimitrakopoulos and Papaioannou 2001). Foliage on live Eastern redcedar trees has been observed to fall below 60% moisture content during extreme drought periods, and dead foliage can approach 0% (Twidwell 2012). Foliage moisture content therefore serves as property that can be readily measured for rapid risk assessment during periods when wildfire occurrence is becoming more likely. To quantify flammability thresholds as drought worsens, I manipulated the foliage moisture content of randomly selected live cedar trees to establish a foliage moisture gradient of 0% to 180% and measured three common characteristics of flammability; ignitibility (time to ignition), sustainability (time sustained ignition), and combustibility (the intensity of combustion) (Anderson 1970; Dimitrakopoulous and Papaioannou 2001; White and Zipperer 2010).

MATERIALS AND METHODS

Foliage samples were collected at the Twin Lakes Wildlife Management Area (WMA) in Seward, County, NE (lat 40˚82N; long -96˚94W). Foliage samples were harvested from a randomly selected lush, female Eastern redcedar tree approximately 3m in height. Following standard techniques used in flammability trails in conifers, samples (6 cm in length) were harvested from the lower third of the crown and from the tips of branches only (Jolly et al. 2012; Pausas et al. 2012). This is done to limit the amount of variation in the initial moisture content of foliage samples. Immediately following harvest, all foliage samples (100 total) were placed into plastic bags to prevent moisture loss during transport to the laboratory. All samples were immediately weighed in the laboratory to obtain a field (wet) weight.

To simulate the affect of drought on foliage moisture content, I dried samples for different periods of time to establish 10 foliage moisture classes. Equidistant foliage moisture classes were established at 20% intervals and ranged from 180% (field conditions, no drying) to 0% (dead and completely dried foliage). Samples were dried in a 60°C convection oven until the desired foliage moisture content was obtained for each foliage moisture class. Each foliage moisture class consisted of 10 replicate samples. Foliage moisture content (FMC) for each class was established on a dry weight basis using the equation below:

$$FMC = \left(\frac{WW - DW}{DW}\right) \times 100$$

And where WW is the fresh (wet) weight of the sample immediately following harvest and DW is the oven dry weight of the sample after all the moisture had been removed (Norum and Miller 1984; Jolly and Hadlow 2011).

Once I established how long to keep foliage samples in the convection oven to obtain a desired fuel moisture content, I established 10 fuel moisture content classes ranging from live (wet) to 0% fuel moisture content and dried foliage samples accordingly. The fuel moisture content of fresh (wet) foliage samples was first calculated to establish the upper bound of fuel moisture content classes. Fuel moisture content classes were then established ranging from 180% (live foliage) to 0% (oven dry) in 20%

increments. Each fuel moisture content class consisted of 10 foliage samples that were individually subjected to flammability measurements.

I conducted this flammability experiment in a laboratory vent hood with no forced airflow (Pausas et al. 2012). A wide mouth Bunsen burner provided the pilot flame for ignition (Scarff and Westoby 2006). The pilot flame was placed approximately 3.3 cm below the foliage sample (Dimitrakopoulous and Papaioannou 2001; Weir and Scasta 2014). Flame height and temperatures were measured using a LumaSense MC320LHT thermal imaging camera. Flame height was held constant among samples at approximately 1.5 cm. Flame temperatures were 718 ± 3°C. Samples were securely positioned on top of a wire mesh until either (1) combustion was complete, or (2) ignition had not occurred within 120 seconds. To maintain consistency between samples and to avoid extraneous heat transfer between the wire mesh and Eastern redcedar foliage, the wire mesh was cooled and allowed to equilibrate to room temperature between ignitions.

I measured three common flammability characteristics for each sample. Ignitability is the amount of time it takes for ignition to occur once a fuel is exposed to a heat source and was measured with a stopwatch to record the amount of time it took for each sample to ignite once placed above the pilot flame (Anderson 1970; Dimitrakopoulos and Papaioannou 2001). Combustibility is the rapidity of combustion after ignition and was measured as the maximum length of the visual flame to the nearest mm (Anderson 1970; White and Zipperer 2010). Sustainability is the ability for a fuel to sustain combustion once ignited and was calculated as the amount of time that each sample maintained flaming combustion once placed above the pilot flame (Anderson 1970; White and Zipperer 2010). Measurements for combustibility and sustainability were derived *post hoc* using LumaSpec RT software. The thermal imaging camera records infrared radiation very half second for a 320 x 220 cell array. Individual cell sizes are based on the distance of the camera to the sample (406 mm in this study), resulting in 0.49 mm x 0.49 mm individual cell sizes. By replaying each video in LumaSpec RT software, I was able to derive the height of each flame to the nearest 0.49 mm (combustibility), as well as measure the duration of flaming combustion for each sample to the nearest half second (sustainability).

RESULTS

A threshold in Eastern redcedar ignitability was detected when foliage moisture content dropped below 80% (Figure 4.1), whereas thresholds in combustibility and sustainability did not occur until foliage moisture content reached 0% (Figures 4.2, 4.3). The average time to ignition between fuel moisture content classes ranged from 1.1 s (0% fuel moisture content) to 10.5 s (180% fuel moisture content). When the fuel moisture content of *J. virginiana* foliage was between 180% and 80%, the average difference between classes in time to ignition was 0.4 s. When the fuel moisture content of *J. virginiana* foliage was between 60% and 0%, however, the average difference between classes in time to ignition was 2.32 s. The average time flaming combustion was sustained between fuel moisture content classes ranged from 6.1 s (0% fuel moisture content) to 10.1 s (180% fuel moisture content). When the fuel moisture content of *J. virginiana* foliage was between 180% and 20%, the average difference between classes in the amount of time flaming combustion was sustained was 1.03 s. When the fuel moisture content of *J. virginiana* foliage was below 20%, however, the amount of time flaming combustion was sustained was reduced by 1.67 s. The average maximum flame height between fuel moisture content classes ranged from 2.2 cm (80% fuel moisture content) to 3.2 (0% fuel moisture content). When the fuel moisture content of *J. virginiana* foliage was between 180% and 20%, the average difference between classes in maximum flame height was 0.1 cm. When the fuel moisture content of *J. virginiana* foliage was below 20%, however, the maximum flame height increased by 0.7 cm.

DISCUSSION

Eastern redcedar (*J. virginiana*), a commonly planted horticultural tree, is not typically viewed as a wildfire risk because the conditions in which it becomes highly flammable seldom occur. Our study shows that there is a threshold in the flammability of Eastern redcedar once its fuel moisture content drops below 80%. Low fuel moisture content is commonly observed during extreme drought periods (Rothermel 1972, Dimitrakopoulos and Papaionnou 2001). Lower precipitation also has been shown to increase fire intensity of Eastern redcedar (Engle and Stritzke 1995). In regions where Eastern redcedar is highly abundant (e.g. the southern Great Plains), large, and oftentimes devastating wildfires occur during extreme drought years (Reid et al. 2010; Krueger et al. 2015). Further, trees planted as a part of horticultural and conservation practices might not have posed a threat to wildfire under historic climate analogues, but with increased frequency and severity of drought events projected to occur by the end of the century (Walsh et al. 2014), the traits of some species will cause them to contribute to heightened wildfire danger in coming decades.

Our results are consistent with and expand upon previous studies investigating components of Eastern redcedar flammability under varying fuel moisture contents. Weir and Scasta (2014) conducted a similar study to investigate the effects of fuel moisture content and fire temperature on the flammability of Eastern redcedar. In this study, they found that as foliar moisture content in decreased, the time it took for ignition to occur decreased and flame height increased quadratically, In contrast to our study, Weir and Scasta (2014) observed no relationship between fuel moisture content and the duration of sustained flaming combustion. I observed a threshold in the amount of time Eastern redcedar sustained flaming combustion once fuel moisture content was lower than 20%. Our study builds upon previous work by identifying thresholds in the flammability components measured rather than reporting only on directional trends. I also aim to improve the robustness of our results in practical applications by preserving the architecture of Eastern redcedar foliage during the flammability tests rather than burning a homogenous fuelbed of foliage (Schwilk 2003; Belcher 2016).

A quantitative understanding of thresholds in flammability of Eastern redcedar will become increasingly important in the upcoming decades as this commonly planted ornamental tree continues to expand into new environments in the Great Plains (Wilson and Scmidt 1990; Schmidt and Wardle 2002) and millions of new seedlings are distributed each year across Great Plains states (Ganguli et al. 2008). Recent changes in the frequency, intensity, and spatial extent of fires have been identified as one of the primary factors enabling the expansion of Eastern redcedar to open grasslands (Briggs and Gibson 1992; Twidwell et al. 2013b). Intensive grazing, landscape fragmentation, and continued planting are other primary factors enabling the expansion of Eastern redcedar to open grasslands (Schmidt and Stubbendieck 1993; Knapp and Seastedt 1998; Ganguli et al. 2008). Vast regions of open grassland have been converted to closed-canopy cedar woodland (Bragg and Hulbert 1976; Miller and Rose 1999). For example, in the matter of decades, the Grand River Grassland in Iowa observed the number of individual redcedar trees increase by over 800% (Harr et al. 2014). In the northern Flint Hills of Kansas, Eastern redcedar woodlands have increased by over 120% in just 15 years (Brigs et al. 2002). In Oklahoma, the amount of rangeland infested with Eastern redcedar more than doubled from 600,000 ha in 1950 to over 1,400,000 ha in 1985 (Snook 1985).

Moving forward, the flammability thresholds identified in this study can be used to help improve wildfire management planning, fire hazard, and risk assessments of wildland fuels. Our results show that even though the ignitibility of Eastern redcedar rapidly increases when fuel moisture content drops below 80%, if ignited, the foliage will burn for as long and have similar flame lengths until fuel moisture content reaches 0%. For a wildland firefighter, this means that the likelihood of an Eastern redcedar tree igniting as a firefront passes rapidly increases when fuel moisture content is lower than 80%. In real landscapes, both time to ignition and the amount of heat at the firefront determine the likelihood of ignition (Rothermel 1972). Accordingly, variance might be observed in real-world applications of our results. Moreover, by monitoring the fuel moisture content of Eastern redcedar, especially during drought conditions, firefighters and managers will have a better idea of when to expect rapid and sudden changes in the flammability and wildfire risk of Eastern redcedar.

ACKNOWLEDGEMENTS

This research was supported by the Joint Fire Science Program projects 11-1-2-19 and 13-1-06-8, the Nebraska Game and Parks grant W-125-R-1, and the Nebraska Environmental Trust.

FIGURES

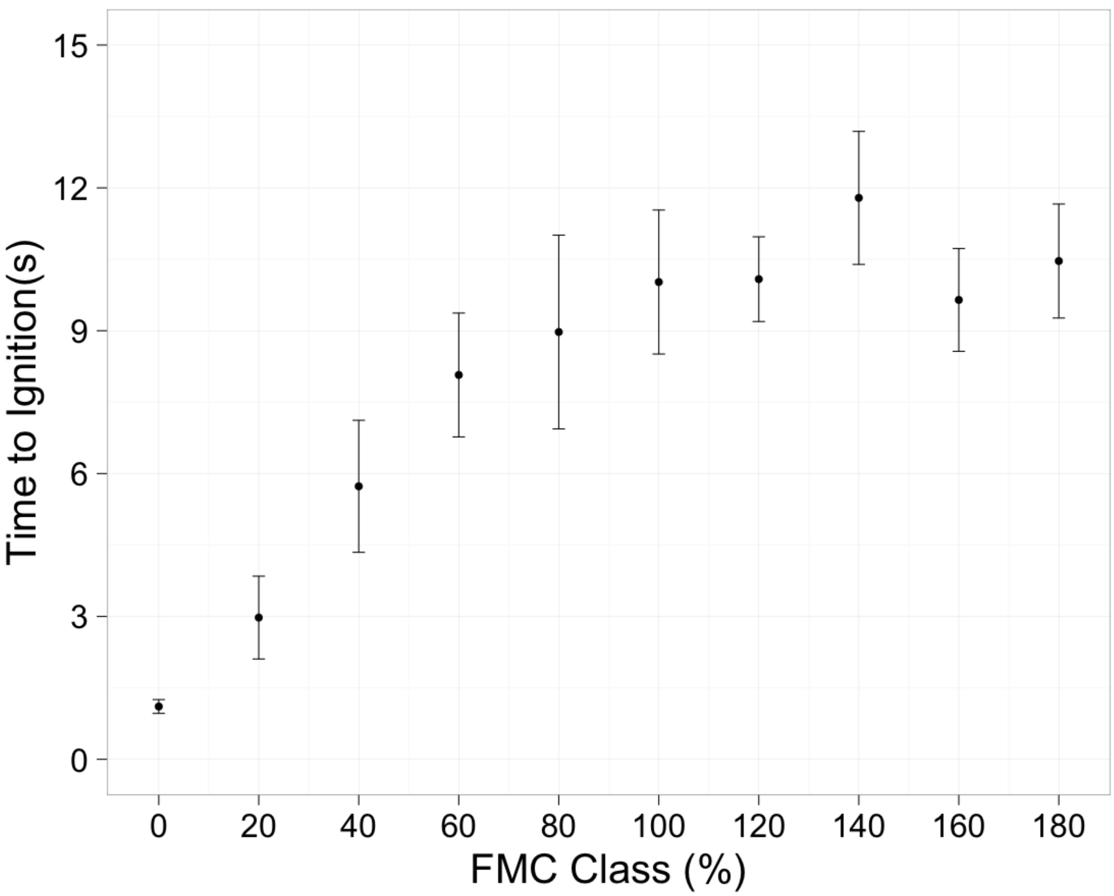

Figure 4.1. The ignitibility of Eastern redcedar (defined as the amount of time required for a given amount of heat to cause flaming combustion) across a gradient of fuel moisture contents (FMC).

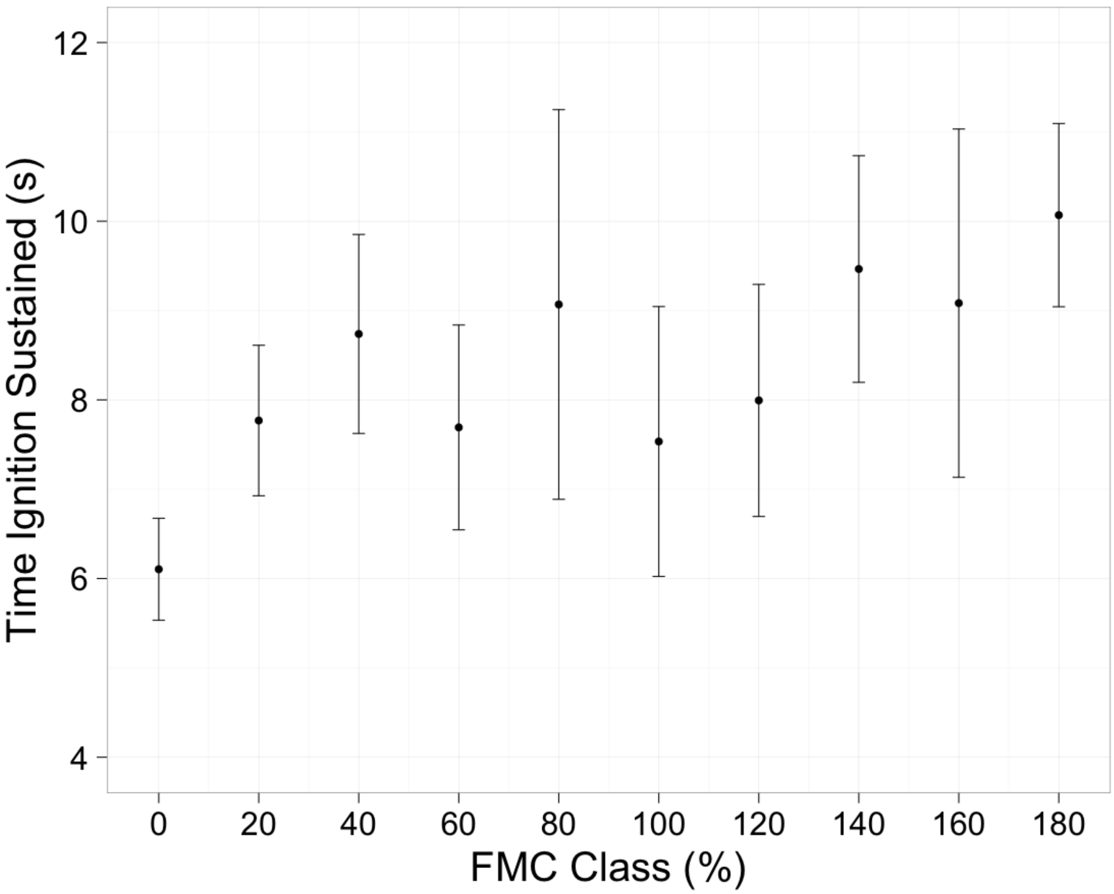

Figure 4.2. The sustainability of Eastern redcedar (defined as the amount of time flaming combustion was sustained) across a gradient of fuel moisture contents (FMC).

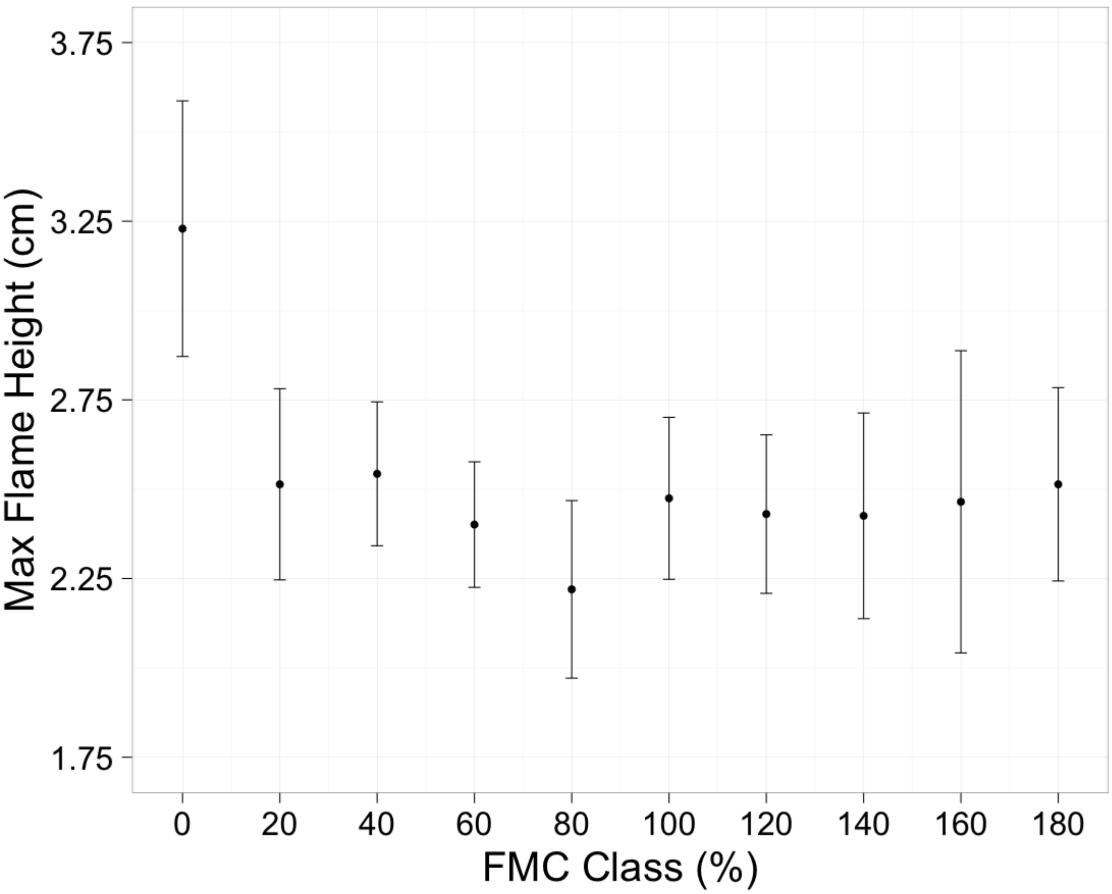

Figure 4.3. The combustibility of Eastern redcedar (measured by maximum flame height observed during combustion) across a gradient of fuel moisture contents (FMC).

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