Ecosystems (2016) 19: 356–368
DOI: 10.1007/s10021-015-9937-y

ECOSYSTEMS

Plant Invasions or Fire Policy: Which Has Altered Fire Behavior More in Tallgrass Prairie?

Dirac Twidwell,[1]* Andrew S. West,[2] William B. Hiatt,[2] Abbey L. Ramirez,[2]
J. Taylor Winter,[2] David M. Engle,[2] Samuel D. Fuhlendorf,[2]
and J. D. Carlson[2]

[1]*Department of Agronomy and Horticulture, University of Nebraska-Lincoln, 308 Keim Hall, Lincoln, Nebraska 68583, USA;*
[2]*Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Agricultural Hall, Stillwater, Oklahoma 74078, USA*

ABSTRACT

Human behavior has rapidly evolved from fire-promoting to aggressively attempting to minimize its magnitude and variability. This global shift in human behavior has contributed to the adoption of strict policies that govern the purposeful and planned use of fire in ecosystem science and management. However, it remains unclear the extent to which modern-day prescribed fire policies are altering the potential magnitude and variation of fire behavior in scientific investigations and ecosystem management. Here, we modeled the theoretical historical range of variability (ROV) in fire behavior for the tallgrass prairie ecosystem of North America. We then compared sensitivities in the magnitude and variation in the historical ROV in fire behavior as a result of (1) policies governing prescribed fire and (2) woody and herbaceous plant invasions. Although considerably more attention has focused on changes in fire behavior as a result of biological invasions, our model demonstrates that contemporary fire management policies can meet or surpass these effects. Policies governing prescribed fire management in tallgrass prairie reduced the magnitude and variability of surface fire behavior more than tall fescue invasion and rivaled reductions in fire behavior from decades of *Juniperus* encroachment. Consequently, fire and its potential as a driver of ecosystem dynamics has been simplified in the study and management of this system, which may be contributing to misleading conclusions on the potential responses of many highly researched environmental priorities. We emphasize the need to study changes in fire dynamics as a function of both social and ecological drivers, in an effort to advance our basic understanding of the role of fire in nature and its potential usefulness in ecosystem management.

Key words: anthropogenic change; community assembly; disturbance regime; historical range of variability (ROV); environmental policy; exotic species invasion; ecosystem management; global environmental change; social-ecological system.

Received 16 July 2015; accepted 16 September 2015;

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-015-9937-y) contains supplementary material, which is available to authorized users.
Author contributions Dirac Twidwell conceived the study, contributed to modeling and led the writing. Andrew S. West performed research and conducted modeling. William B. Hiatt, Abbey L. Ramirez, and J. Taylor Winter performed research. David M. Engle, Samuel D. Fuhlendorf, J. D. Carlson contributed to methods and models. All co-authors contributed equally to manuscript writing and revisions.
**Corresponding author; e-mail:* dirac.twidwell@unl.edu

INTRODUCTION

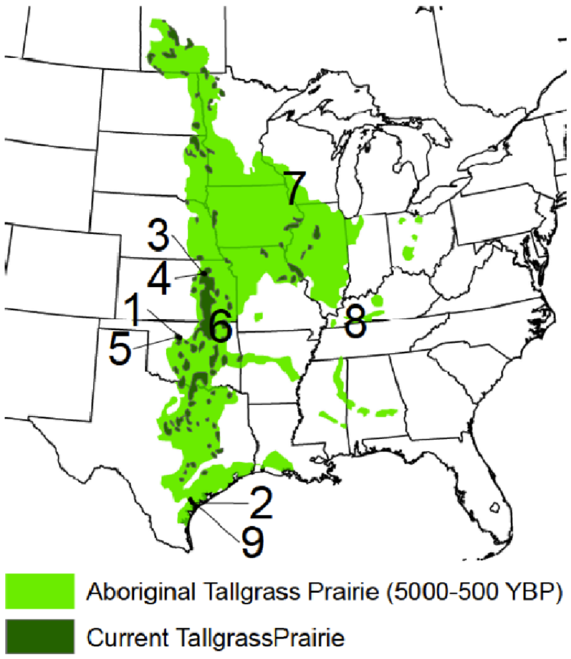
> Management should strive to retain critical types and ranges of natural variation in resource systems in order to maintain their resilience.
>
> Holling and Meffe (1996)

Variation is central to biological organization. The concept is fundamental to Darwin's (1859) *Theory of Evolution* and is the guiding principle for Holling and Meffe's (1996) *Golden Rule for Natural Resource Management.* Yet societal policies and practices often seek to limit variability in the processes driving biological organization in an effort to reduce uncertainties for human utility or well-being (Holling and Meffe 1996; Poff and others 1997). Consequently, many disturbance regimes have been greatly altered compared to their historical range of variability (ROV) (Turner 2010). Human-induced alterations of natural disturbance regimes have led to trophic cascades within food webs (Wootton and others 1996; Sanders and others 2013), threats to species and ecosystems of conservation concern (Keeley and others 1999; Chapin and others 2000; Allen and others 2002), widespread species invasions (D'Antonio and Vitousek 1992; Hobbs and Huenneke 1992) and biome-level transformations that deplete environmental services (for example, Twidwell and others 2013a). A major priority of ecologists and biogeographers is thus to characterize how recent changes in human actions and policies have altered critical disturbance processes and subsequently contributed to the degradation of natural resources in contemporary social-ecological systems around the world (Turner 2010).

The occurrence of fire in nature is at the forefront of modern humanity's attempts to minimize the magnitude and unpredictability of extreme disturbance events. However, fire is unique from other disturbances in that its historical ROV is largely coupled to human activities. For thousands of years, human inhabitants increased the incidence of fire beyond its theoretical potential for occurrence in the absence of human ignitions (Bowman and others 2011; McWethy and others 2013; Twidwell and others 2013a). This human-driven increase in fire activity has given rise to a suite of fire-dependent ecosystem services that society continues to value today (van Wilgen and others 1996; Twidwell and others 2013a). However, human fire use has changed on every vegetated continent (Bowman and others 2009, 2011). Developed countries incur incredible expenses to support formal institutions and policies designed to eliminate fires that are beyond human control (Dellasala and others 2004; Hawbaker and others 2013). Yet, fire is also recognized as an important driver of ecosystem structure and function (Bond and Keeley 2005), so many countries have developed policies that explicitly dictate when humans can ignite fires for ecosystem management. The goal of such policies is to allow prescribed fires to be conducted within a narrow range of pre-determined conditions to insure safety and containment while providing ecosystem services dependent upon fire (van Wilgen and others 2012; Hawbaker and others 2013). However, by adhering to these policies and burning under narrow prescription windows, we have also bound the conditions under which prescribed fires are used in experimental manipulations or ecosystem management. This has been referred to as the ''Failure of Safe Prescribed Burning'' (van Wilgen 2013) because tight burning windows have predominantly resulted in low intensity prescribed fires, which have failed to create differences in fire severity and corresponding spatial heterogeneity required for numerous floral and faunal specialists (Smucker and others 2005; Hutto 2008; van Wilgen 2013).

Given the importance of understanding variability in fire behavior and how ecosystem components respond to this variability, we argue that it is critical to understand how policies governing the purposeful and planned use of fire (that is, prescribed fire) have reduced the ROV in fire behavior compared to historical contexts. To date, social drivers of fire regime change have been more difficult to quantify than ecological ones, such as woody plant encroachment or exotic herbaceous invasion (D'Antonio and Vitousek 1992; Scholes and Archer 1997; Mack and D'Antonio 1998; Brooks and others 2004; Balch and others 2013; Twidwell and others 2013b). In this study, our objectives were to (1) model changes in fire behavior resulting from contemporary policies governing prescribed fire and (2) compare those changes to modeled departures in fire behavior resulting from woody and herbaceous plant invasions. We focus our efforts on the tallgrass prairie ecosystem of North America, one of the most extensively studied fire-dependent ecosystems in the world, but where fire has been primarily studied as a binary context (fire, no fire). Treating fire as a binary variable also includes experimental manipulations focused on fire frequency and time since fire when they do not consider variability in fire

The tallgrass prairie of North America is considered to be one of the most well-studied ecosystems in fire ecology, but our formal review of the scientific literature shows that only a small fraction of empirical studies have quantified any aspect of fire behavior (summary provided in table below). We propose that the degree of departure of contemporary fire management practices from the historical ROV is an unprecedented change in human behavior that needs to be accounted for in efforts to conserve biological diversity and sustain ecosystem services unique to fire-dependent ecosystems. This requires scientists and managers to consider new, core questions at the interface of disturbance ecology, invasion ecology, novel ecosystems, global environmental change, social science and governance, among others. For example, to what extent are contemporary social policies and practices changing fire as a biophysical process? How do changes in fire regimes as a result of social feedbacks compare to changes resulting from ecological feedbacks, such as those plant or animal invasions that have received the majority of attention in the ecological literature? Clearly, addressing knowledge gaps surrounding these questions has become increasingly important with prevailing human desires to completely control variability in nature, coupled with global confirmations of the decline in the distribution of fire-dependent ecosystems (as predicted by Bond and others 2005; the inset map shows losses in tallgrass prairie). Disentangling the historical ROV in fire regimes from modern social contexts will set the stage for advancing our basic understanding of the role of fire in nature and its potential usefulness in ecosystem management.



Numbers correspond to studies that have quantified fire behavior in tallgrass prairie (Table S2). Aboriginal and current tallgrass prairie remnants are based on Smith (2011) and TNC (2001).

Web of Knowledge Search	Search Results	No. of field studies conducted in tallgrass prairie	No. of field studies quantifying fire behavior*
"tallgrass prairie" fire ecology	223	149	2
"tallgrass prairie" "fire behavior"	8	2	1
“tallgrass prairie” fire intensity	75	20	6
"tallgrass prairie" fire rate of spread	8	2	1
"tallgrass prairie" fire temperature	78	29	6
"tallgrass prairie" flame	142	114	3
"tallgrass prairie" "flame length"	0	0	0
"tallgrass prairie" "flame height"	0	0	0

***Total number of independent studies quantifying fire behavior = 9**

Note: Table S2 lists the 9 studies quantifying fire behavior.

Box 1. Fire in the tallgrass prairie: an example of ecological science constrained by social influence over the ROV in fire behavior?

intensity, which represent the prevailing approaches for tallgrass prairie. A formal review of the literature supports this point—very few studies have characterized the magnitude and variation in fire behavior and its role in structuring tallgrass prairie (Box 1). This well-studied ecoregion therefore provides an outstanding model system for other areas that also impose tight constraints on prescribed burning but have yet to characterize its control over fire behavior or ecosystem response dynamics.

METHODS

We used BehavePlus ver. 5.0.5 to simulate the effect of contemporary prescribed fire policy and ecological invasions on the potential magnitude and variation in surface fire behavior in tallgrass prairie. BehavePlus is a mathematical simulation program that describes the influence of the wildland environment on fire behavior (Heinsch and Andrews 2010). The SURFACE module in BehavePlus uses Rothermel's (1972) semi-physical model of fire spread as the basis for characterizing surface fire behavior (rate of fire spread, fireline intensity, flame length). SURFACE allows users to customize the parameters driving the model and input a range of values for each input parameter. We used BehavePlus because it is widely used by fire managers in a variety of ecosystems in the USA to predict potential fire behavior, develop prescribed fire plans, assess wildland fuel hazards, and develop training programs (Andrews 2007) and it has been applied internationally (for example, Goldammer and de Ronde 2004). Because of its broad application, BehavePlus provides other researchers the opportunity to easily repeat our methodology to quantify and compare the effects of social fire policies and ecological invasions on fire behavior in other ecosystems.

MODEL PARAMETERIZATION

Modeling Historical ROV in Fire Behavior

To develop a first approximation of the historical ROV in fire behavior in tallgrass prairie, we customized a model in BehavePlus to include a reasonable range of maximum and minimum values observed for fuel properties, wind speed, and slope (the factors driving surface fire behavior in BehavePlus) in tallgrass prairie. Data values used to parameterize the model are presented in the Supplemental Materials (Table S1). Values for one-hour fuel load, fuel moisture, and fuel bed depth were available in the scientific literature. Minimum one-hour fuel moisture and maximum wind speed values were determined using the Mesonet (www.mesonet.org), a weather station network established in 1994 that has been used to parameterize regional fire danger models. Mesonet calculates 1-, 10-, 100-, and 1000-h dead fuel moisture at hourly intervals using a field-calibrated version of the Nelson dead fuel moisture model (Carlson and others 2007). Mesonet has recorded minimum 1-hr fuel moisture values of 2% multiple times for the region, and so this value served as the minimum in our model. With respect to wind speed, Mesonet measures wind speeds at 3-s intervals at 2 and 10-m elevations, the latter level being used in this study. Wind speeds of 77 km h^{-1} corresponded with the highest wind speed that was sustained for at least 5 min every year for the history of the Mesonet. We did not find any published data on surface area-to-volume ratio (SAV) for tallgrass prairie. We therefore used unpublished data from an ongoing experiment established in tallgrass prairie near Stillwater, OK (see Supplemental Materials for full details on SAV sampling). The lowest and highest mean SAV ratios from our samples were used to parameterize the range of SAV ratio values in our model (Table S1). These values fit within the range observed for other grass fuels (Brown 1970, 1971; Cheney and others 1998) as well as the values applied in grassland fuel models (Scott and Burgen 2005). Where data were not available to customize the model, we used the default parameter for a GR7 fuel model (a fuel model is a fire/fuels-based characterization of an ecosystem; see Scott and Burgen 2005); a GR7 fuel model has been used previously to characterize fuels in tallgrass prairie (McGranahan and others 2013).

Using these minimum and maximum values, independent simulations were conducted for 11 grass curing scenarios (ranging from 0 to 100% at 10% intervals, where 0 and 100% correspond to ''green'' grass fuels that are not cured and ''brown'' fully cured grasses, respectively). Curing is the process of senescence-related dehydration (Wittich 2011) and is measured as the percentage of dead grass material that is present in a grass fuel bed (Luke and McArthur 1978). The curing process results in discoloration or ''yellowing'' of the green grass material because of declines in leaf moisture and chlorophyll due to soil-water deficits, freezing, and senescence (Wittich 2011). In BehavePlus, the curing process is used to transfer a portion of the herbaceous fuel load from live to dead and is meant to represent change in surface fire behavior resulting from change in live herbaceous fuel moisture content (Scott and Burgen 2005).

Modeling Sensitivities to Contemporary Social-Ecological Change

We compared departures from the historical ROV in fire behavior by determining sensitivities of the model to changes imposed by (1) prescribed fire management policies, (2) *Juniperus* encroachment, and (3) tall fescue invasions (Table 1). In general, fire management policies and biological invasions (as well as other novel system changes; for example, climate change) either impose constraints on the historical ROV in fire behavior, thereby reducing its potential range of behavior, or push the ROV beyond historical bounds, thereby increasing its potential range. Our sensitivity analysis determines the magnitude and direction of change to the historical ROV in surface fire behavior as a result of contemporary prescribed fire policy and plant invasions.

Modeling Changes Due to Prescribed Fire Policy

Prescribed fire policies have been established to impose constraints on the upper limit of prescribed fire conditions. The most relevant policies in tallgrass prairie are associated with self-imposed guidelines used in prescribed fire management and government-imposed bans on outdoor burning practices. Based on information from the scientific literature and published reports by fire practitioners in tallgrass prairie, fire management policies in this ecosystem impose constraints on wind speed, 1-h fuel moisture, and grass curing (during the growing season) (as summarized in Table 1). We imposed these constraints on the full model to determine how prescribed fire management policies constrain the potential ROV in fire behavior when applying prescribed fires. To account for the effect of government-imposed burn bans that either limit or outlaw outdoor burning at high levels of grass curing during drought in the growing season, we imposed a conservative threshold scenario of 80% grass curing to mimic how regulatory officials enact burn bans during periods of drought in the growing season (Table 1). However, it should be recognized that, in practice, regulatory officials enact burn bans at any level of drought-induced grass curing and use various metrics to determine when to cease outdoor burning activities. Thus, our conservative estimate likely underestimates the policy effect associated with enacting burn bans in many regions within tallgrass prairie.

Modeling Changes Due to Juniperus Encroachment

Juniperus virginiana L. encroachment into tallgrass prairie decreases herbaceous fuel loading and fuel bed depth in the model. The rate of decrease in herbaceous fuel loading over time as a result of *Juniperus* encroachment was established by combining two studies: (1) Limb and others (2010) quantified the rate at which herbaceous fuel load-

Table 1. Modeling Sensitivities of the Historical ROV of Surface Fire Behavior to Contemporary Prescribed Fire Policies and Ecological Invasions in Tallgrass Prairie.

Model scenario	Description	Reference
Historical ROV	Range of potential fire conditions occurring in tallgrass prairie prior to modern social-ecological constraints	Based on range of values given in Table S1
Social		
Prescribed fire policy	Limit prescribed fires to:	
	Wind speeds <32 km h^{-1}	Wright and Bailey (1982), Weir (2009)
	1-h fuel moistures to $>7\%$	OK-FIRE (2013a, b)*
Government burn bans in growing season droughts	Eliminate prescribed fires in growing season once grass curing thresholds are crossed; thresholds are variable (0–100% grass curing levels) and specific to individual regulatory officials[†]	OK-FIRE (2013b, c)*
Ecological		
Juniperus encroachment	Reduce 1-h fuel load, live herbaceous fuel load, and fuel bed depth as Juniperus cover increases over time	Briggs and others (2002), Limb and others (2010)
Tall fescue invasion	Increase live herbaceous fuel moisture content to 250%	McGranahan and others (2013)

** Regional fire danger rating system (www.okfire.mesonet.org)*

[†] Regulatory officials actually enact burn bans at any time and for a variety of reasons, but consistently enact burn bans in this region as drought severity increases in the growing season; we used grass curing scenarios to account for such regulation since it is strongly and positively related to drought in the growing season (Wittich 2011) and the actual relationships of drought on the fuel properties used in BehavePlus are not known

ing (w) decreases as *Juniperus* cover (C_{JUVI}) increases (1), and Briggs and others (2002) characterized the rate of *Juniperus* encroachment over time (t) in tallgrass prairie when it is not burned (2). We combined the equations from these studies to give the amount of herbaceous fuel loading that has been lost over time ($w_{l,t}$) as a result of *Juniperus* encroachment (as summarized in equation, 3):

$$w = -45.6C_{JUVI} + 4727.9 \tag{1}$$

$$C_{JUVI} = \frac{0.138}{0.001 + e^{0.337t}} \tag{2}$$

$$w_{l,t} = \frac{5.0}{0.001 + e^{0.3t}} \tag{3}$$

Because no data are available that quantify reductions in herbaceous fuel bed depth (v) over time as a result of *Juniperus* encroachment, we assumed fuel bed depth (v) followed a linear rate of decrease with increasing *Juniperus* cover (C_{JUVI}), resulting in the following relationship:

$$v = -0.9144C_{JUVI} + 91.44 \tag{4}$$

Modeling Changes Due to Invasion of an Exotic Cool Season Grass

Tall fescue [*Schedonorus phoenix* (Scop.) Holub] is an introduced, cool season grass that has invaded prairies throughout North America and transformed considerable amounts of tallgrass prairie (McGranahan and others 2012). In areas with high levels of tall fescue invasion, herbaceous fuel moisture has increased the overall moisture content of the fuel bed to 250% (McGranahan and others 2013), which is well above the maximum herbaceous fuel moisture content reported in the literature for native tallgrass prairie (76%, Engle and others 1993). To simulate the effect of tall fescue invasion on potential surface fire behavior, we reparameterized herbaceous fuel moisture content from its maximum value observed in native tallgrass prairie, 76, to, 250%, the value observed in fescue-dominated tallgrass prairie, and then repeated simulations in BehavePlus. Empirical data were not available that documented changes of tall fescue invasion on other fuel bed properties, so we did not evaluate sensitivities in the model due to fescue-driven changes in other fuels components.

Statistical Analyses

Using our independent simulations of grass curing scenarios, we tested for differences in the magnitude and variation of fire behavior in historical fire regimes compared to contemporary fire management and ecological invasions. One-way analysis of variance was used to test for differences in rate of fire spread, fireline intensity, and flame length for each modeled comparison. Differences were evaluated using a Brown–Forsythe test, which accounts for nonparametric data. Multiple pair-wise comparisons were limited to comparing differences in the historical ROV in fire behavior to each scenario (1. modern fire policy; 2. *Juniperus* encroachment over time; 3. tall fescue invasion) and were evaluated using Tukey's HSD. Confidence intervals were produced for each modeled comparison to simply show the estimated historical ROV in fire behavior and the degree of departure in the ROV in fire behavior as a result of contemporary prescribed fire policies and ecological invasions.

We graphed change in rate of fire spread, fireline intensity, and flame length across the realistic ranges of variability for each BehavePlus input parameter as grass curing increased from 0 to 100% [with green representing grass fuels that are not cured (0%) and brown representing fully cured grasses (100%), respectively]. This resulted in model output characterizing the relationship between a fire behavior variable (rate of fire spread, fire intensity, flame length) and the interaction between grass curing and a given fuel, slope, or wind input. We then plotted and overlaid a prescribed fire policy envelope on each graphed output to show the range of conditions and fire behavior that could be expected after policy constraints were imposed in the model. Such an approach reveals how contemporary fire management policies influence fire behavior for the tallgrass prairie ecosystem and provides a baseline for repeating this approach to compare socio-political constraints present in other ecosystems. The difference in either the mean or variance in fire behavior across the various fuels, wind, and slope parameters was assessed between the historical model and the prescribed fire policy model using a paired samples t-test.

Model Evaluation

Congruence with Empirical Data

Empirical studies in tallgrass prairie provide a basis for evaluating the output from our model on the influence of contemporary prescribed fire policies and ecological invasions on potential fire behavior. Our primary assumption here is that empirical studies in tallgrass prairie are bound by the socially imposed constraints featured in our model. Our model accurately predicts the ROV of rate of fire spread and fireline intensity for the empirical studies that have quantified fire behavior in this ecosystem (based on our formal review; Table S2). Nearly all empirical studies recorded levels of fire behavior that fell within the range predicted for contemporary policy constraints in the model. Two studies recorded fire intensity levels above model predictions when policy constraints were imposed. Both of those studies, Crockett and Engle (1999) and Twidwell and others (2012), were specifically designed to conduct fires outside the guidelines of regional fire management policies, resulting in fireline intensities and flame lengths slightly above the maximum values output in the model (thus supporting our modeling approach). In summary, our model accurately predicted the ROV of fire behavior for the empirical studies that have quantified fire behavior and have operated both within and outside the bounds of contemporary prescribed fire policy constraints.

Potential to Replicate Wildfire Behavior

A potential concern is that our modeling approach might overestimate the maximum potential fire behavior possible in tallgrass prairie. We therefore sought to compare our model output to data from wildfires to assess the potential for the model to describe the upper range of surface fire behavior possible in tallgrass prairie. Unfortunately, almost no data have quantified fire intensity, rate of fire spread, or flame length for wildfires in the Great Plains and especially for tallgrass prairie (Fuhlendorf and others 2011). We therefore evaluated how effectively our modeling approach replicated the surface fire behavior observed for the East Amarillo Complex Wildfire, which burned more area in 24-h than any other fire in the United States in recorded history (NOAA 2010). Rate of fire spread for the 2006 East Amarillo Complex Wildfire averaged 134 m min^{-1} for a nine-hour period (Rideout-Hanzak and others 2011). Because the Amarillo Complex Wildfire did not occur in tallgrass prairie, we repeated our modeling approach for a GR2 fuel model (this fuel model better represents the semi-arid mixed grass prairie where the wildfire occurred) to approximate the fuels, slope, and wind conditions present during the wildfire. Because data are not available on the fuel conditions that occurred during the wildfire, we re-parameterized the model for the typical fuel conditions present in a GR2 fuel model (see Scott and Burgen 2005). Terrain in the region of the East Amarillo Complex wildfire is level to gently rolling, so slope was set to 5%. Wind speeds were assigned a range of 48–64 km h^{-1}, the values measured by local weather stations during the wildfire event (NOAA 2009). Using these data, our model produced rates of fire spread of 95 m min^{-1} when grass curing was 100%. Given the lack of available data on the fuel parameters occurring during the wildfire, this value is remarkably close to the rate of fire spread observed for the East Amarillo Complex Wildfire, thereby validating the broader utility of our model. In fact, using the model to reproduce the rate of spread observed in the East Amarillo Complex Wildfire (134 m min^{-1}) required only minor changes from the baseline GR2 fuel model and increasing herbaceous fuel bed depth by 14 cm.

RESULTS

Social policies governing prescribed fire management reduced fire behavior more than tall fescue invasion and rivaled reductions in fire behavior from decades of *Juniperus* encroachment. The full potential ROV in tallgrass prairie fire behavior was 2–540 m min^{-1} for rate of fire spread, 35–50,372 kW m^{-1} for fireline intensity, and 0.4–11.3 m flame length. As a result of modern policy constraints driving the use of prescribed fire, maximum rate of fire spread and fireline intensity were reduced 81 and 85%, on average, while maximum flame length was reduced 59% (Figure 1). This policy-driven reduction in fire behavior more than doubled reduction in fire behavior resulting from exotic invasion of tall fescue, and it took at least 20 years of *Juniperus* encroachment to have an effect equivalent to modern fire management policies (Figure 1).

Policy-driven reductions in the historical ROV in fire behavior were predominantly the result of how current prescribed fire policies limit the potential effect of wind speed (Figure 1). In the absence of policy constraints, simulations of surface fire behavior were based on the potential for fires to occur during sustained wind speeds of 77 km h^{-1}, which occurs at least once annually. At such high wind speeds, the effect of grass curing was considerable and resulted in rates of fire spread and fireline intensities far beyond that produced by any other factor in the absence of policy constraints (Figures 2, 3). Assuming a policy threshold in which fires could not be conducted once wind speed exceeded 32 km h^{-1} (Table 1), rates of fire spread, fireline intensities, and flame lengths were reduced 77, 75, and 48%, respectively (Figure 3). When wind speeds were below 32 km h^{-1}, the effect of grass curing on fire behavior was markedly reduced, thereby minimizing variance in all fire behavior characteristics compared to historical conditions (Figure 3; $t = 3.28$, $df = 10$, $P < 0.01$ for rate of spread; $t = 3.18$, $df = 10$, $P < 0.05$ for fire-

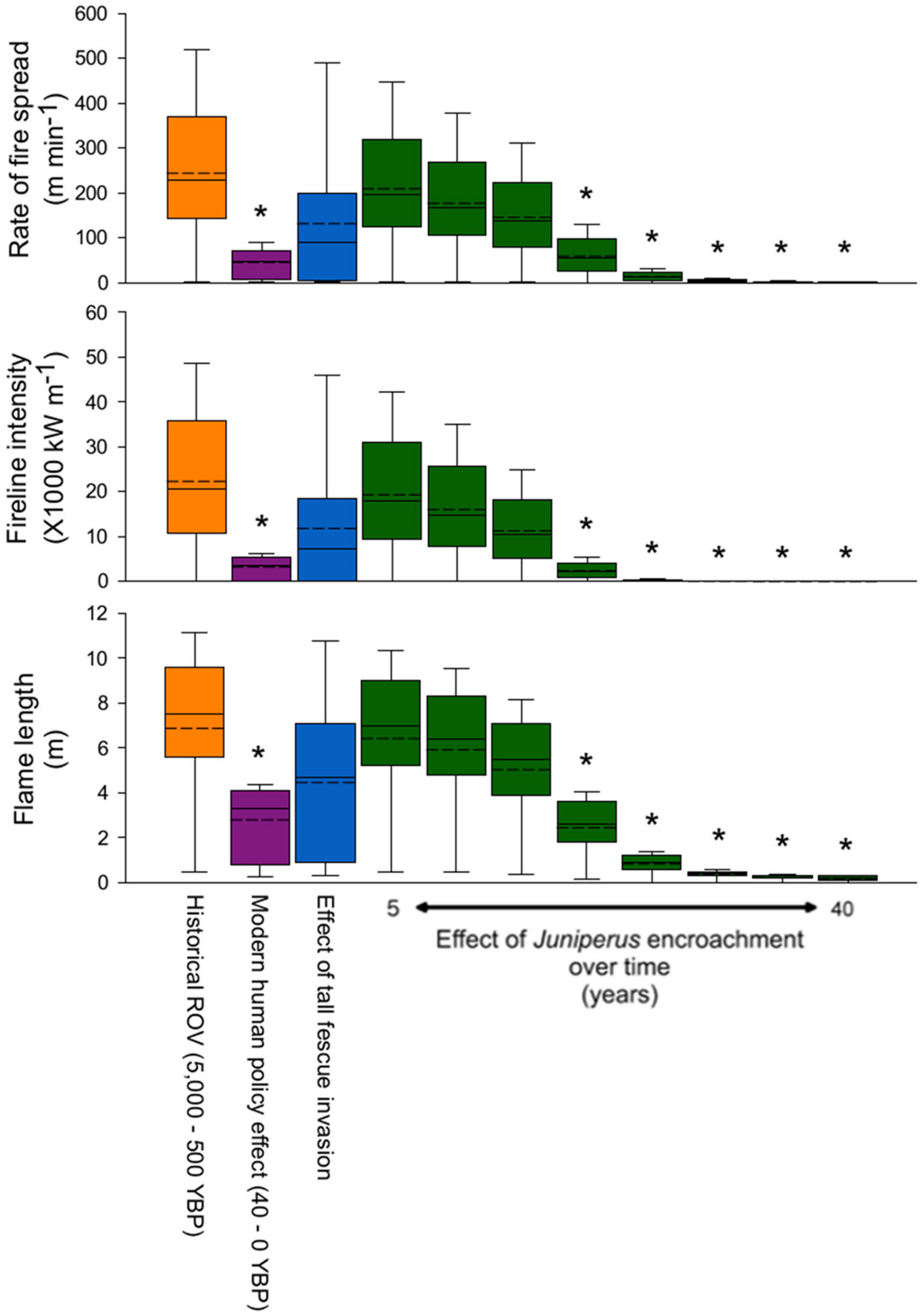


Figure 1. Departures from the historical range of variability (ROV) in surface fire behavior as a result of contemporary social prescribed fire policies and ecological invasions in tallgrass prairie. Confidence intervals represent the range of variability (ROV) across grass curing scenarios used in simulations, with *dashed lines in box plots* representing the mean value. *Asterisks* (*) indicate significant differences ($P < 0.05$) in fire behavior from historical levels as a result of isolating the effect of each modeled scenario.

line intensity; $t = 3.78$, $df = 10$, $P < 0.01$ for flame length). Yet, even beneath the policy threshold of wind speed of 32 km h^{-1}, wind continued to have a greater effect on potential surface fire behavior in tallgrass prairie vegetation than variability in any other factor. It was not until wind speeds dropped below 23 km h^{-1} that 1-h fuel moisture began to have an equivalent influence on surface fire behavior in fully cured tallgrass prairie fuels (Figure 2).

Other factors, 1-h fuel load, 1-h fuel bed depth, and 1-h surface area-to-volume ratio and slope, were constrained only by prescribed fire policies that indirectly limited fires to grass curing levels less than 80% and did not lead to differing levels of surface fire behavior in the presence or absence of policy constraints (Figures 2, 3). However, relaxing the assumption that burn bans are enacted only after grass curing levels exceed 80%, and instead considering the potential for burn bans to be

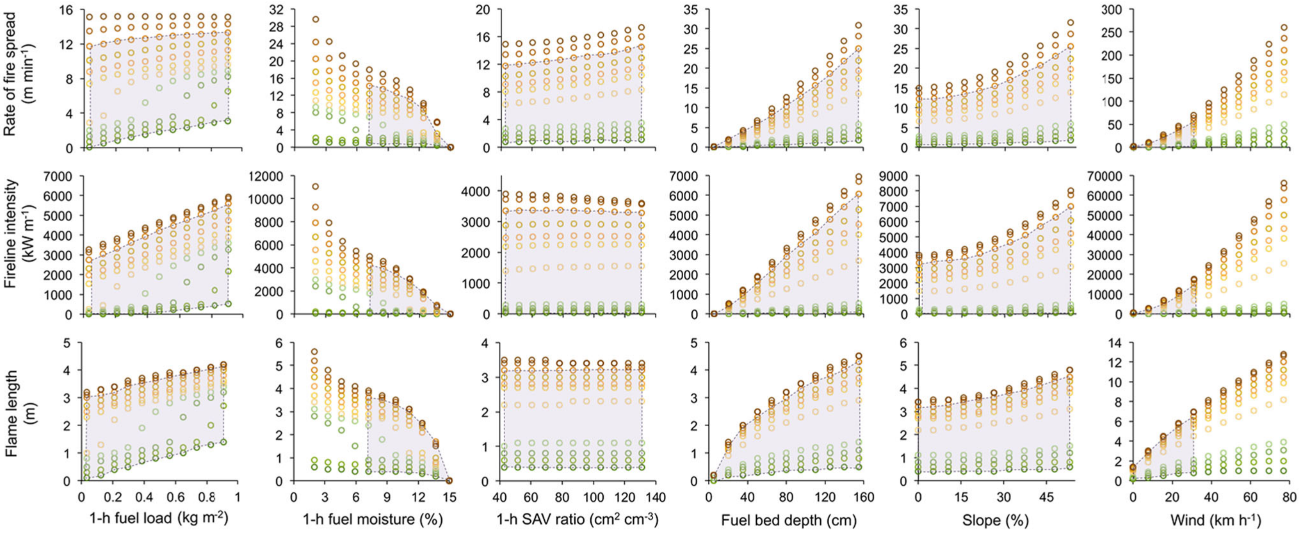


Figure 2. Policy constraints imposed on fire managers and their influence on the factors driving surface fire behavior in tallgrass prairie. The range of conditions available to modern ecosystem managers (shown as *colored envelopes*) demonstrates how policy reduces the magnitude of fire behavior for each factor across different grass curing scenarios ranging from 0% (no grass curing; shown as *dark green circles*) to 100% (fully cured grasses; shown as *brown circles*). Note the scale of the y-axis differs among panels (Color figure online).

implemented at any level of grass curing, demonstrated that surface fire behavior could be altered for every parameter input into the model when grass curing is less pronounced (Figure 2).

DISCUSSION

The effect of fire management policies on fire behavior in tallgrass prairie reveals an important modern conflict present in fire-dependent ecosystems. Ecosystem managers are tasked with using fire to enhance ecological resilience of fire-dependent ecosystems. This requires that they consider the full range of variation in fire behavior and its ecological and evolutionary role, while also weighing uncertainties of how to use fire to enhance resilience in a changing world (Bradstock and others 2005; Driscoll and others 2010). A separate mission is tasked to regulatory officials, who seek to protect society from large and destructive wildfires. In tallgrass prairie, the challenge with promoting the full ROV in fire behavior for ecosystem management is that wind speed is by far the dominant driver of rate of fire spread and fire intensity. Targeting higher wind speeds greatly increases ember transport and spotfire distance (Albini 1983), making it more difficult for fire managers to control fires using current burning systems and techniques. Moreover, high wind speeds are also the most important determinant of the occurrence of large wildfires in this system (Reid and others 2010), which greatly increases risks to firefighter personnel given the high rates of fire spread and fireline intensities produced in these conditions (Andrews and Rothermel 1982). For these reasons, it is no surprise that fire management policies aggressively select against wind speed in ecosystems around the world. For example, guidelines for when prescribed fires can be conducted limit fires to wind speeds below 32 km h^{-1} in central U.S. (Wright and Bailey 1982; Weir 2009), with wind speeds no greater than 15 km h^{-1} being recommended for most prescribed fires in sub-Saharan Africa (Goldammer and de Ronde 2004).

We contend this modern conflict is symptomatic of present-day societal norms that demand complete control over nature and the elimination of extreme disturbance events. Present-day humans have sought to eliminate ''wildfire'' from wildlands prone to burning and remove flooding from flood plains in efforts to preserve or protect certain resource values—yet these processes are often critical to biological diversity and the sustainability of many unique ecosystem services desired in contemporary society (Poff and others 1997; Bednarek 2001; Smucker and others 2005). It is becoming increasingly apparent that numerous species are dependent on high intensity and high severity disturbance regimes. The absence of high-intensity fires has been implicated in the near extinction of species (for example, *Mimetes stokoei*; van Wilgen

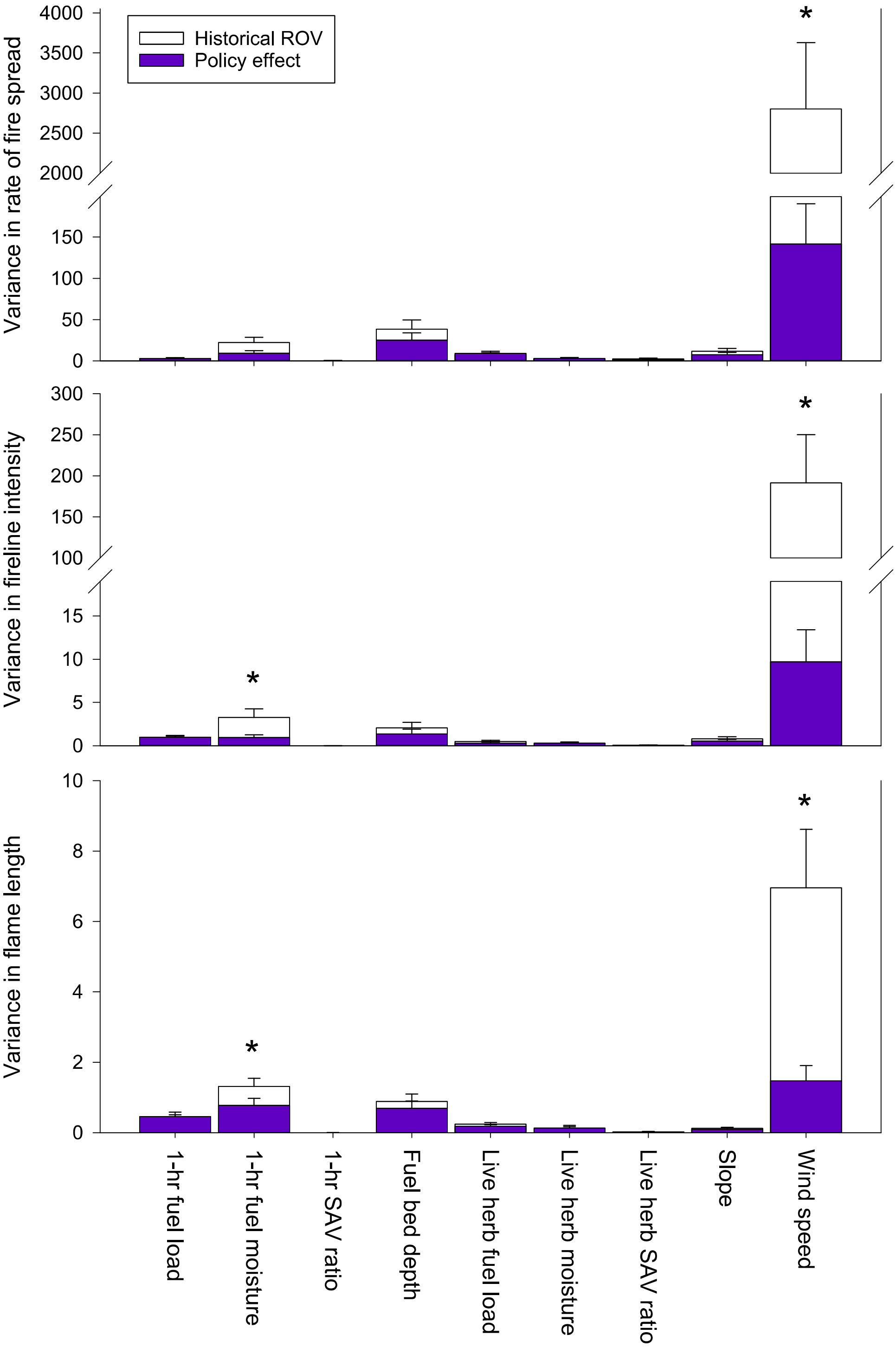


Figure 3. Reductions in the variance in surface fire behavior resulting from contemporary policies constraining variability in fuels, wind, and slope in tallgrass prairie. Asterisks (*) indicate significant differences ($P < 0.05$) when contemporary fire management policies are absent (*white columns*) or present (*purple columns*). Values are means ± SE (Color figure online).

2013), contributes to the inability of resource professionals to prevent woody encroachment in grasslands and savannas (van Langevelde and others 2003; Taylor and others 2012), constrains restoration of grasslands from woody-dominated ecosystems (for example, in the US Southern Great Plains, Twidwell and others 2013a, b), and fails to provide suitable habitat requirements for faunal specialists (for example, Hutto 2008). Similarly, the absence of infrequent extreme flood events has led to trophic cascades in riverine ecosystems (Wootton and others 1996) and the loss of top biomass species desired for human consumption (Ligon and others 1995). We highlight these examples to emphasize the point that policy-makers need to become more aware of the ecological impacts and unintended consequences of establishing broad-sweeping policies aimed at minimizing or removing extreme disturbance events.

The ecological benefits of promoting extreme events such as high-intensity fires will always be weighed against the actual and perceived risks they pose to human safety, which places very real constraints on the ability to manage for the full historical ROV in disturbance regimes. The resulting challenges forced upon ecosystem scientists and managers by society at large are to determine the extent to which the magnitude and variability of disturbance processes can be simplified while still sustaining properties of ecosystems desired by society, and to effectively communicate to society the consequences of simplifying disturbance regimes. However, the implications of simplifying disturbance have generally not been considered in the conservation of disturbance-dependent ecosystems (Parrott and Meyer 2012). As an example, the theoretical basis for fire to shape ecosystem dynamics in tallgrass prairie has been predominantly derived from socially constrained empirical studies that do not account for extreme events (for example, Box 1). Consequently, the role of fire has been simplified in the study and management of this system (for example, up to 85% of the potential magnitude of fire intensity is not being explicitly considered in empirical studies in tallgrass prairie; Table S2). The problematic assumption here is that ecosystem response dynamics observed when fires are conducted under narrow prescriptions (which is nearly always the case in the study and management of tallgrass prairie) will hold consistent across the full theoretical ROV in fire behavior. Previous studies have demonstrated that conclusions built upon this assumption do not necessarily hold when fires are conducted beyond typical fire prescriptions (for example, the irreversibility of grassland to juniper woodland regime shifts; Twidwell and others 2009, 2013b), and our model reveals that only the bottom 15–19% of the theoretical ROV in fire behavior is accounted for under this assumption. For this reason, researchers and managers alike should seriously consider the implications of reducing the magnitude and variance of disturbances when discussing potential trajectories of ecosystem responses to fire.

Many ecosystem properties and processes may respond to slight changes in management without requiring that managers restore the full historical ROV in disturbance. Simple manipulations of the spatial extent of disturbance (*sensu* patch burning or pyric herbivory, Fuhlendorf and others 2009) or intensity (*sensu* controlled flooding, Robertson and others 2001; extreme prescribed fire, Twidwell and others 2012, 2013b) have successfully reshaped disturbance regimes that sufficiently mimic the dynamics needed to support the resilience, biodiversity, and productivity of those systems. Moving forward, it would be helpful to advance beyond this study and elucidate the probabilities or frequency to which environmental conditions influenced disturbance regimes historically relative to today, and how changes in those probabilities relate to thresholds governing ecosystem responses (for example, fire-vegetation thresholds; Twidwell and others 2013b). In cases where thresholds have not been (or cannot be) quantified, management for the full range of variability in disturbance regimes provides safe operating space for managing the resilience of fire-dependent resources, given recognition that the historical ROV may not fully represent current conditions (Moritz and others 2013). Combined with models of how changes in anthropogenic fire use have altered the spatial dynamics of large fires (for example, Trauernicht and others 2015), these approaches provide the basis for understanding contemporary changes in ecological conditions as a result of departures in historical fire regimes. This information can then be used to make more informed decisions on whether the magnitude and variability of a fire regime can be simplified while still providing for ecosystem services desired by society or, in contrast, where society needs to reconsider its anthropogenic footprint in efforts to promote greater variability in fire regimes for ecosystem services.

ACKNOWLEDGMENTS

Funds for this project were provided by the Joint Fire Science Program project #11-1-2-19. We thank Trenton Franz, Erica Smithwick, and two anonymous reviewers for helpful contributions that improved this manuscript.

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