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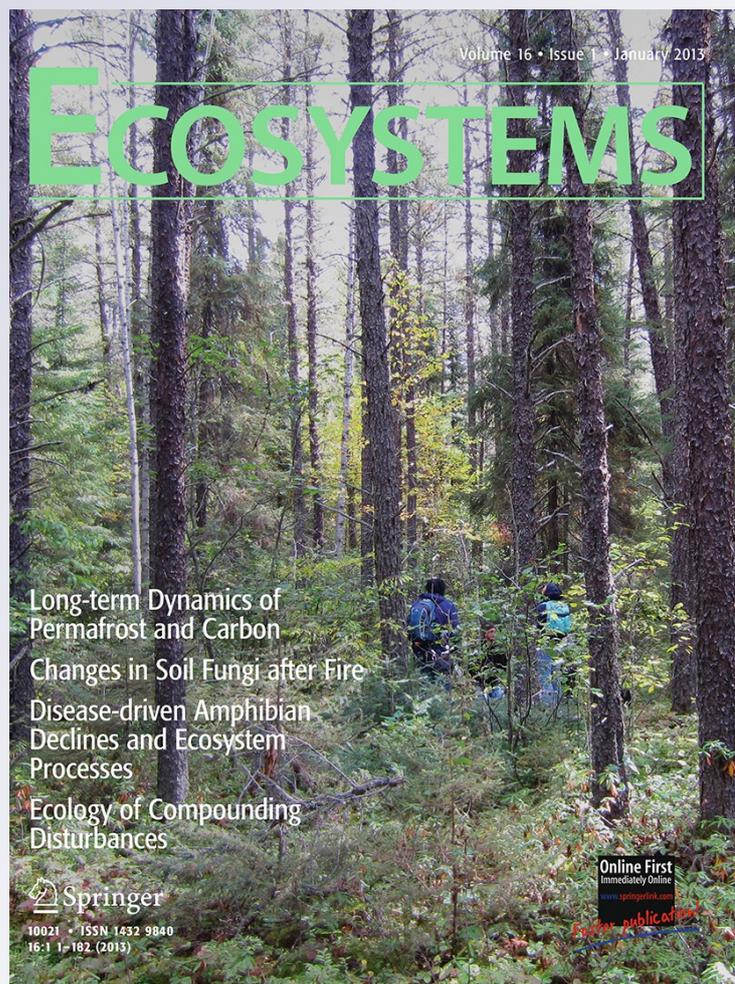
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An Invasive Grass Increases Live Fuel Proportion and Reduces Fire Spread in a Simulated Grassland

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ABSTRACT

Fire is a globally important ecosystem process, and invasive grass species generally increase fire spread by increasing the fuel load and continuity of native grassland fuelbeds. We suggest that invasive grasses that are photosynthetically active, while the native plant community is dormant reduce fire spread by introducing high-moisture, live vegetation gaps in the fuelbed. We describe the invasion pattern of a high-moisture, cool-season grass, tall fescue (*Schedonorus phoenix* (Scop.) Holub), in tallgrass prairie, and use spatially explicit fire behavior models to simulate fire spread under several combinations of fuel load, invasion, and fire weather scenarios. Reduced fuel load and increased extent of tall fescue invasion reduced fire spread, but high wind speed and low

relative humidity can partially mitigate these effects. We attribute reduced fire spread to asynchrony in the growing seasons of the exotic, cool-season grass, tall fescue, and the native, warm-season tallgrass prairie community in this model system. Reduced fire spread under low fuel load scenarios indicate that fuel load is an important factor in fire spread, especially in invaded fuel beds. These results present a novel connection between fire behavior and asynchronous phenology between invasive grasses and native plant communities in pyrogenic ecosystems.

Key words: FARSITE fire area simulator; fire regime; fuel moisture; fuel load; tall fescue; tallgrass prairie.

INTRODUCTION

Fire is an important ecological process worldwide (Bowman and others 2009). The observable

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characteristics of fire in a given ecosystem constitute its fire regime, which includes the intensity, severity, seasonality, frequency, and spatial distribution of fire, often over long time periods and broad spatial scales (Whitlock and others 2010). Fire regimes are often managed to control undesired plant species and/or promote desired species, and the effects of fire on many species and ecosystems are well documented (DiTomaso and others 2006; Pyke and others 2010). At the same time, invasive plant species that introduce fuel characteristics that are substantially different from native

vegetation can alter the fire regime of the invaded ecosystem (D'Antonio 2000). Alteration includes increased or decreased intensity, frequency, and spread of fire, depending on the native fire regime and the specific characteristics of the invasive species (Brooks and others 2004).

Generally, invasive grasses increase fire spread by increasing the amount of fine, dead fuel and homogenizing an otherwise spatially patchy fuelbed (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998; Brooks and others 2004). A classic example of an invasive grass increasing fire spread is the invasion of cheatgrass (*Bromus tectorum* L.) in western North America. Cheatgrass is an annual grass that rapidly accumulates fine dead fuel and increases the horizontal continuity of semi-arid fuelbeds, increasing fire frequency from 60–110 years to 3–5 years (Brooks 2008).

Although the ecological literature lacks an example of an invasive grass species that reduces fire spread, we hypothesize that the fire regime of ecosystems with distinct dormant seasons are susceptible to alteration by invasive species with asynchronous growing seasons. Generally, an invasive species alters the fire regime of a native ecosystem by introducing a substantially different fuel type into the native fuelbed (D'Antonio 2000). Many ecosystems with warm-season native plant communities have a winter dormant period bookended by brief cool-season growing periods. In such systems, we predict invasion by an exotic grass with a cool-season growing period that overlaps the native dormant season will increase the proportion of live vegetation in the native fuelbed. Because fire intensity decreases as the moisture content of live vegetation increases (Jolly 2007), we expect that the interspersed high-moisture, live plant tissue will effectively create a discontinuous fuelbed and reduce fire spread.

Here, we present a specific example of an invasive cool-season grass reducing fire spread in a native warm-season community. We propose the invasion of the Eurasian cool-season grass tall fescue *Schedonorus phoenix* (Scop.) Holub into North American tallgrass prairie as a model system for asynchronous growing seasons which disrupt the pattern of the native grassland fuelbed and reduce fire spread. Tallgrass prairie is a fire-adapted ecosystem with natural, dormant-season fires—historical accounts identify April and October as peak fire months in the North American Great Plains (Higgins 1986; Anderson 1990). In the modern landscape, tallgrass prairie is widely managed with prescribed fire, and most burns are conducted during the dormant season of the native community when fine fuel moistures range from 5 to 60%

(Bidwell and Engle 1992; Engle and Bidwell 2001). However, for much of the dormant season in the Great Plains—including the peak fire months, April and October—tall fescue live fuel moisture ranges from 120 to above 350% on a dry-weight basis (McGranahan and others 2012a). Although dormant periods vary annually, it is clear that fire managers can expect a period ranging from weeks to months in the spring and fall during which the native fuelbed is dormant with low fuel moisture but invasive tall fescue is photosynthetically active with high fuel moisture. Thus, tall fescue-invaded tallgrass prairie presents a suitable system for testing the hypothesis that a high-moisture, invasive grass reduces fire spread during burns applied when the native warm-season plant communities are dormant.

We use a spatially explicit fire behavior model to simulate the effect of increased invasion on fire spread, quantified as the area burned within a fixed time period. Ecologically, fire spread is a primary fire regime characteristic (Bond and Keeley 2005), and is an important fire behavior metric in the prediction and management of wildland fire (Rothermel 1983; Pyne and others 1996). To parameterize the fire spread model, we collected field data on the spatial pattern of tall fescue invasion and fuel load in tallgrass prairie. We also test the relative impact of fire weather variables (air temperature, wind speed, and relative humidity) under each herbivory and invasion scenario. Weather variables are important factors in wildfire management and prescribed fire planning not only because weather affects the safety of fire operations, but because weather varies on shorter temporal scales than plant invasion and fuel loading, especially when total fuel load is determined by the previous grazing season. Combining fuelbed parameters and weather parameters into our model allows us to compare the relative influence of biotic and abiotic variables on fire spread—fuelbed and weather variables, respectively. We predicted that reduced fuel load and invasion will reduce fire spread in the simulations. We also predicted that low humidity and high wind speed will mitigate reduced fire spread created by tall fescue invasion and reduced fuel load.

METHODS

Spatial Pattern of Fuelbed Characteristics

We collected data on the spatial pattern of tall fescue invasion in two tallgrass prairie tracts (202 and 282 ha) in Ringgold County, Iowa. We selected these tracts for their differences in productivity, which we use here to model differences between

Table 1. Fuel, Weather and Topographic Variables Used in FARSITE Fire Spread Simulations, Including the Source of Data for Each Variable

Fire environment category	Variable (units)	Assumption	Value(s)	Data source	
Fuel	Cell size of landscape matrix (m)	Constant	30	Fuel transects	
	Extent invasion of live fuel type (%)	Varied	0–70, 10% increments	Range of tall fescue invasion ¹	
	Total fuel load (kg/ha)	Varied	High fuel load: 10,378 Low fuel load: 4,646	End-of-season biomass	
	Live fuel load (kg/ha)	Invaded ²	High fuel load: 1,038 (10%)	Fuel transects	
	Fuel model:		Low fuel load: 1,211 (26%) 124 (<3%)		
	Dead fuel load (kg/ha)	Uninvaded ³	Constant	Calculated from fuel transects and end-of-season biomass	
	Fuel model:	Invaded ²	Varied	Reference fuel moisture samples	
	Live fuel moisture (%)	Uninvaded ³	High fuel load: 9,341 Low fuel load: 3,435		
	Fuel model:	Invaded	Constant	250	
	Dead fuel moisture (%)	Uninvaded	Constant	75	
Weather	Air temperature (°C)	Varied ⁴	15.5, 21.1, 26.6	Reference fuel moisture samples	
	Relative humidity (%)	Varied ⁴	20%, 30%, 40%	Range typical for prescribed fire in region ⁵	
	Wind (km/h)	Varied ⁴	8, 16, 24	Range typical for prescribed fire in region ⁵	
		Direction	South	Frequent direction in region ⁶	
	Elevation (m)	Constant	400 m	Approximate elevation of sampled grasslands	
	Slope (%)	Constant	0		
	Aspect	Constant	South		
		Speed	Varied ⁴		
		Direction	Constant	South	
			Constant	400 m	
Topography	Elevation (m)	Constant	400 m	Approximate elevation of sampled grasslands	
	Slope (%)	Constant	0		
	Aspect	Constant	South		

¹ McGranahan and others (2012a)

² Live, dead, and total fuel loads for invaded fuel models modify standard GR4 fuel model (Scott and Burgan 2005); all other fuel model parameters unchanged

³ Live, dead, and total fuel loads for Uninvaded fuel models modify standard GR7 fuel model (Scott and Burgan 2005); all other fuel model parameters unchanged

⁴ Each value remained unchanged during the 2-h burn period for each of the 20 simulations per weather and fuel scenario

⁵ See Table 1 in Bidwell and Engle (1992)

⁶ Weir (2011) Regional values refer to North American tallgrass prairie. Fuel moisture (percent) expressed on a dry-weight basis

high and low fuel load in tallgrass prairie fuelbeds. The tracts were similar in plant species assemblages (McGranahan 2008), and each tract had been stocked with cattle (*Bos taurus*) at the same stocking density in the season before data collection. However, the tracts lay on opposite ends of a local productivity gradient in soils (USDA-NRCS 2010) and aboveground net primary production (Table 1). Therefore, we classified the fuelbeds at the low-productivity and high-productivity tracts as low fuel load and high fuel load, respectively.

We used visual obstruction (VO, Robel and others 1970) to estimate the total fuel load—live and dead components—of each tract. Used frequently as a non-destructive sampling method to estimate the height and density of vegetation at the sample point (for example, Harrell and Fuhlendorf 2002), VO is correlated with total plant biomass in grassland (Robel and others 1970; Vermeire and others 2002; Limb and others 2007). These data represent the total fuel load in these grasslands. We estimated total plant biomass (total fuel load) with 30 VO measurements per tract, collected after the grazing season to represent the post-grazing fuel load available for dormant-season fire. Total plant biomass determined by clipping all vegetation within 0.25 m² quadrats and drying for 48 h at 60°C was regressed against VO data collected at each clipped sample point.

We estimated the dimension and fuel load of live fuel patches by visually scoring live fuel along a scale of live fuel load classes. We moved a 0.5 m² quadrat along each of eight, randomly located, 100-m transects to sample 100 m² per transect, four each at the high and low fuel load tracts. Within each quadrat, we visually estimated mass of tall fescue using a 0–5 scale for fuel load classes and calibrated each visually estimated fuel load class against data from clipped plots (Twidwell and others 2009). The upper bound of the scale was defined as the maximum amount of tall fescue observed across the tracts in a single quadrat located in an ungrazed, monotypic stand of tall fescue in the high-productivity tract. The lower bound of the scale was defined as zero—trace (<5 single culms, none bunched) tall fescue in the quadrat. We sampled during the dormant period of the native plant community, before and after snowfall (15 November–1 December and 1–15 March, 2010). During this period, tall fescue was green and photosynthetically active (live fuel) but all native plants and all other exotic species were dormant (dead fuel). Thus, for the purposes of the fuel data presented in this paper, photosynthetically active tall fescue and live fuel are synonymous.

To estimate the proportion of the total fuel load represented by each live fuel load class, we used the constituent differential method for determining live and dead biomass (Gillen and Tate 1993). By this method, the respective fractions of live fuel in the total fuel load can be determined if the dry matter content of both the live and dead components, as well as that of the total fuel load, are known (Gillen and Tate 1993). This method required us to determine the dry matter content of both the live and dead fuel components, thus we collected reference samples of pure live tall fescue tillers ($n = 5$) and several reference samples ($n = 5$ each) of the dead fuel component. We identified representative locations for each live fuel load class and clipped all of the vegetation from five, 0.5 m² quadrats and dried the harvested biomass for 48 h at 60°C. We input the reference live and dead fuel moisture data described above and these total fuel load samples into the equations for the constituent differential method described by Gillen and Tate (1993) to determine the live fuel load corresponding with each live fuel class. We also calculated moisture content on a dry-weight basis for each reference sample for use in fire behavior models. Fuel moisture data are presented as fire behavior model parameters in Table 1.

We compared the estimated live fuel load classes to the calculated proportion live fuel values determined by the constituent differential method with linear regression. We forced regression lines through the origin by removing the intercept term from the linear models to reflect that live fuel class 0 would constitute 0% of the fuel load. Our visual index to estimate live fuel class significantly predicted the actual proportion of live fuel in sampled plots ($t = 19.91$, $p < 0.001$, $R^2 = 0.91$) (Online Appendix Figure A). The proportion of dead biomass was greater among transects on the higher productivity tract, which increased the proportion of live vegetation in the fuelbed of the low-productivity tract (Online Appendix Figure B).

To determine the spatial extent of tall fescue patches, we calculated the range of Gaussian curves fit to semi-variograms calculated from the live fuel load transects. The range estimates the spatial extent at which the maximum semi-variance in live fuel load along the transect occurs. We calculated these spatial statistics with the geoR package for Program R (R Development Core Team 2011; Ribeiro and Diggle 2011). The range of Gaussian curves varied between 26 and 50 m, with a mean of 32 m (± 4.8 SE) (Online Appendix Figure C). Thus, we use 30 m as the cell size in hypothetical

landscape matrices describing the spatial extent of tall fescue invasion.

Fuel Models and Modeling Fire Spread to Compare Invasion and Fuel Load Scenarios

The FARSITE Fire Area Simulator

We used the FARSITE Fire Area Simulator (Finney 2004) to model fire spread within simulated landscapes to test the relative influence of the extent of invasion by plant species with high live fuel moisture, total fuel load, air temperature, relative humidity, and wind speed on fire spread. FARSITE simulates the spread of a fire front across a landscape matrix by connecting a series of vertices—spread of individual head fires using the Rothermel (1972) fire spread model—into an expanding polygon via a wave-elliptical model (Richards 1990). FARSITE allows user control over the three main categories of fire spread variables: fuel, weather, and topography (Finney and Andrews 1999). Both the Rothermel model (Sparks and others 2007) and FARSITE (Finney 2004) have been tested in a wide variety of fuel types including grasslands.

FARSITE was developed for wildfire management, including the study of past fires, predicting the spread of active fires in known fuels under forecast weather conditions, and predicting the effect of fuel treatments on future wildfires (Finney and Andrews 1999). The FARSITE platform, developed as part of a broad U.S. federal government initiative to increase the capacity to predict wildland fire behavior, built upon previous models by incorporating dynamic data on topography and weather into fire behavior calculations (Hanson and others 2000). Because it accurately predicts fire spread over a wide variety of complex fuelbeds and atmospheric conditions, FARSITE has been widely applied in wildland fire management in the United States and elsewhere (Fernandes and Botelho 2003; Arca and others 2007; Duguay and others 2007; Mutlu and others 2008).

Others have applied FARSITE to prescribed fire scenarios, to theoretical questions in fire ecology, and to ecosystems other than forests. Examples of FARSITE applications in rangelands include spatial implication of fire used to prevent woody plant encroachment (Miller and Yool 2002) and the effect of grazing on the pattern of fire spread (Kerby and others 2007). Although most FARSITE applications use a Geographical Information System (GIS) to provide actual topographical data and

weather conditions, hypothetical landscapes and constant variables are an effective means of controlling and manipulating model variables for hypothesis testing (Finney 2003; Jolly 2007; Kerby and others 2007; Parisien and others 2010).

Fuel Model Scenarios

We used our field data on total fuel load, proportion live fuel, fuel moisture content, and the spatial pattern of tall fescue invasion to parameterize eight scenarios consisting of two levels (low and high) of fuel load and four levels (10, 30, 50, and 70% of landscape cells invaded) of tall fescue within hypothetical landscapes. Landscapes were composed of 30 m² cells. Invaded cells were randomly assigned across the landscape, and all remaining cells were assigned the “uninvaded” fuel type (0% tall fescue). We selected live fuel class 1 (10% live fuel) as the proportion live fuel for the invaded, high fuel load fuel model. Live fuel constituted a greater proportion of the fuel bed in the low-load fuelbeds (Online Appendix Figure B), and to emphasize this difference in our fuel models, we selected live fuel class 4 (26% live fuel) as the proportion live fuel for the invaded, low-load fuel models. To compare the influence of weather variables on fire spread under each fuel load/invasion scenario, we also varied wind speed, relative humidity, and air temperature (Table 1).

Each 2-h FARSITE simulation occurred at 1,200–1,400 h on April 20 as appropriate for prescribed fire in tallgrass prairie, based on peak daily solar radiation and seasonality of fire in tallgrass prairie (Engle and Bidwell 2001). We used the following FARSITE settings: time steps = 20 min, perimeter and distance resolution = 30 m, post-frontal enclave preservation = true. Because time periods in the simulations are fixed, our response variable is “area burned” to quantify fire spread over a fixed period of time. The simulated landscape was approximately 25 km × 25 km to ensure sufficient space for randomly located ignitions and that fires would not exceed landscape boundaries. We performed 20 simulations, each a randomly placed ignition, for each combination of fuel load, extent of invasion, air temperature, relative humidity, and windspeed. Random ignitions controlled for variability in the arrangement of fuel types, which were assigned randomly to cells based on the proportion of landscape invaded by tall fescue each landscape was designed to model. We set canopy cover to zero, did not include crown fire or spot fire models, and set FARSITE to compute fuel moisture at the beginning of the burn period.

Statistical Analysis of Fire Spread

We used multiple linear regression to determine the influence of fuel load, extent of invasion, air temperature, relative humidity, and wind speed on burn area in simulated fires, and used regression coefficients to rank variables in order of importance to fire spread. We employed mixed-effect linear regression models using the lmer function in the nlme4 package for the R statistical environment (Pinheiro and others 2011; R Development Core Team 2011). Because raw data for each independent variable occurred on different scales, we centered and scaled independent variables to standardize variation using the scale function in the R environment. Such standardization is a common technique to compare regression coefficients in mixed-effect linear models when variation among predictor variables is heterogeneous (Enders and Tofighi 2007; Raudenbush and Bryk 2002), and has been applied elsewhere to ecological data (Diez and Pulliam 2007). The dependent variable in mixed-effect linear models, burn area, was log-transformed to meet assumptions of normal distribution.

To determine which variables were important predictors of fire spread—and eliminate non-influential variables if necessary—we selected the linear model with the most appropriate combination of variables using an information-theoretic approach (Burnham and Anderson 2002) with the stepAIC function (package MASS) in the R environment. The stepAIC function begins with an initial set of predictor variables, tests all combinations of variables by adding and subtracting terms, and returns the model with the least Akaike's An Information Criterion (AIC) value, and greatest weight (AIC_w) and likelihood ratio (logLik). We also report AIC, AIC_w , and logLik for the second-most competitive model and compare the two with ANOVA.

We also used multiple linear regression to test the effect of each weather variable on fire spread within a given fuel load and invasion scenario to determine the relative influence of wind speed and relative humidity. We determined relative influence of each independent variable on burn area by ranking regression coefficients, made possible by centering and scaling these data before regression analysis. Within each fuel load and invasion scenario, we used the stepAIC function in R to select the best-fitting model by AIC, beginning with a multiple linear regression model comparing burn area on a logarithmic scale to wind speed, relative humidity, and the statistical interaction of wind speed and relative humidity. The stepAIC function

returns the best-fit model with any combination of wind speed, relative humidity, a multiple additive model, or a multiple interactive model.

RESULTS

All fuelbed and weather parameters were significant in the model selected with AIC (Table 2). Values for the selected model: $AIC = 5570.4$, $AIC_w = 1.00$, $\logLik = 1.00$. By comparison, the second-most competitive model, which included only relative humidity and wind speed, had $AIC = 16426.2$, $AIC_w = 0.00$, $\logLik = 0.00$. The selected model with the lower AIC and greatest AIC_w was significantly different from the second-most competitive model ($F = 16,333$, $p < 0.001$).

Biotic variables relating to the fuelbed were more important contributors to fire spread than abiotic weather variables. Fuel load and the extent of tall fescue invasion were the first and second-most important factors affecting the area of modeled fires, followed by wind speed, relative humidity, and air temperature when ranked by regression coefficients (Table 2). Both reduced fuel load and greater tall fescue invasion reduced fire spread, and the extent of tall fescue invasion increased the variation in fire area for low-load fuelbeds, which was consistently greater than the variation in fire spread for high-load fuelbeds (Figure 1).

The regression coefficient for wind speed was four times greater than that of relative humidity (Table 2), which explains the greater response of both fire area and variation in fire spread (Figure 2) to changes in wind speed versus relative humidity within low-load fuelbeds. Wind speed and relative humidity were significant variables in regression models for each fuel load and invasion scenario,

Table 2. Results of a Multiple Linear Regression Model Comparing the Effect of Fuelbed and Fire Weather Variables on Burn Area on a Logarithmic Scale for Two Levels of Fuel Load and Four Levels of Tall Fescue Invasion in a Simulated Tallgrass Prairie Fuelbed

Variable	Regression coefficient	<i>t</i> Value	<i>p</i> Value
(Intercept)	-1.76	-250.8	<0.001
Fuel load	-1.16	-165.0	<0.001
Invasion	-1.03	-146.72	<0.001
Wind speed	0.84	120.3	<0.001
Relative humidity	-0.20	-27.9	<0.001
Air temperature	-0.11	-16.1	<0.001

Variables are ranked in order of size of regression coefficients

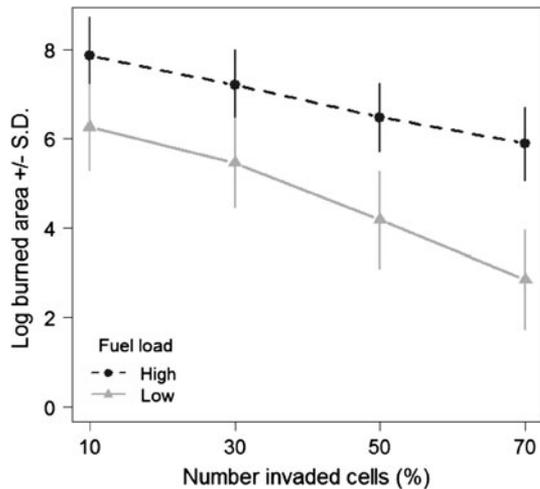


Figure 1. Burn area (± 1 standard deviation) predicted from FARSITE simulations of fire spread in a tallgrass prairie landscape for two levels of fuel load under four tall fescue invasion scenarios. Burn area is plotted on a logarithmic scale and represents fire spread as the spatial extent of fires over a 2-h period.

although an interaction between wind speed and relative humidity was only significant under the low fuel load, 70% tall fescue invasion scenario ($p < 0.05$; refer to Online Appendix Table A for complete model results).

Variation in fire area—as measured by standard deviation and shown as error bars in Figure 2—remained consistently low across all invasion and fire weather scenarios within the high-load fuelbed, but tended to increase in the low-load fuelbed at invasion levels above 10%.

30, 50, and 70% tall fescue invasion, variation in fire spread increased, especially at low (8 km/h) wind speeds (Figure 2).

DISCUSSION

In our simulated fuelbed and fire weather scenarios, invasion by a high-moisture exotic grass reduced the spatial extent of fire and increased the variability of burn area in warm-season grassland fuelbeds, and these effects were exacerbated when fuel load was reduced. That fuelbed-specific variables were more influential to fire spread than weather variables suggests that fire spread in this ecosystem is primarily controlled by biotic processes related to the fuelbed, and secondarily by abiotic weather conditions (Heyerdahl and others 2001; Parisien and others 2010). These results corroborate observations and model results that indicate increased live fuel moisture negatively impacts fire behavior (Butler and others 2004; Jolly 2007; Towne and Kemp 2008). These results present a novel link between invasive grasses and negative impacts on fire spread, and reinforce the value of research on the effect of invasive plant species on fire in addition to fire effects on invasive species in fire-prone ecosystems.

Although the high live fuel moisture of the invasive species in this ecosystem clearly reduced fire spread, there is generally a paucity of research on the effect of live fuel moisture on fire spread in both fire modeling and fire ecology. When creating the original 13 fuel models to support wildland fire suppression, Rothermel (1972) only included a live

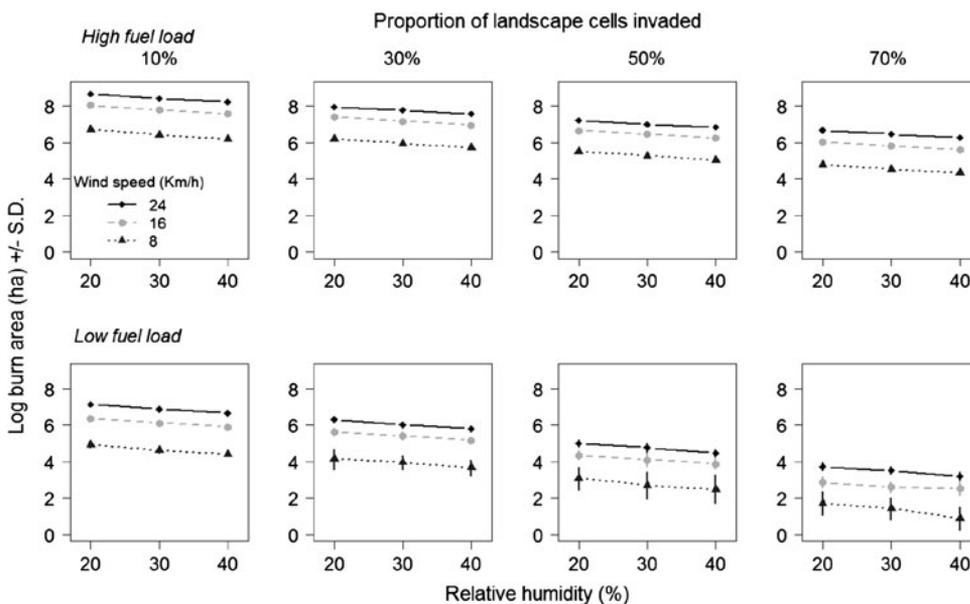


Figure 2. Burn area (± 1 standard deviation) predicted from FARSITE simulations of fire spread in a tallgrass prairie landscape at three wind speeds and three relative humidity values for two levels of fuel load (*high, top; low, bottom*) and four levels of tall fescue invasion. Burn area is plotted on a logarithmic scale and represents fire spread as the spatial extent of fires over a 2-h period.

fuel moisture parameter in five models, under a basic assumption that live fuel moisture only inhibits fire spread in specific plant communities, whereas the fuelbed in most communities is cured when wildland fire is most likely. Responding to demand for fuel models that more accurately reflect fuelbeds across a broader range of ecosystems and conditions, Scott and Burgan (2005) created 40 dynamic models in which a proportion of the live fuel load is transferred to the dead fuel load to model live fuel curing, rather than live fuel moisture creating a static barrier as in the original 13 models. Grassland fuel models are particularly sensitive to changes in live fuel moisture (Jolly 2007), but the maximum live fuel moisture to which the dynamic transition applies is 120% (Burgan 1979; Scott and Burgan 2005).

The assumption that live fuel simply transfers to the dead fuel category as heat drives out tissue moisture might not appropriately describe the heating and ignition process for live fuels. Although dead fuel moisture is controlled by physical processes (for example, atmospheric water content), live fuel moisture is controlled by plant phenology and physiology (Scott and Burgan 2005; Jolly 2007). The Rothermel fire spread model was originally developed to simulate fire behavior at peak wildfire severity (hot, dry environments, often during drought), situations in which live fuels are typically of little concern (Rothermel 1972; Scott and Burgan 2005). However, an understanding of the interactions between the physical and biological processes of live fuel combustion and their effects on fire spread remains rudimentary, and thus merits development to facilitate the application of fire behavior models in ecological management beyond the suppression of wildfire under severe environmental conditions.

Results of our simulations of fire spread address this potentially important gap in the knowledge about the effects of live fuel on fire regimes, and specifically, the effect of invasive plants on fire regime. We demonstrate that live fuel introduced by an invasive grass reduces fire spread, which is novel to both fire ecology and invasive species ecology. It is generally understood that high-moisture, live fuels reduce fire intensity and other fire effects (van Wilgren and Richardson 1985; Towne and Kemp 2008), but little attention is given to the spatial patterns that follow reduced intensity and severity, especially in grassland ecosystems. Our results link reduced fire spread to local processes that directly alter the fuelbed—*invasive species and fuel load*. Our simulations suggest that the invasion of the cool-season

grass, tall fescue, into a native warm-season community constitutes the introduction of a substantially different fuel type (D'Antonio 2000), and we demonstrate that reduced fire spread reflects an altered spatial pattern of fuel across the landscape.

Altering the spatial pattern of fire through changes to the extent or variability in fire spread has ecological and management consequences. Ecologically, changes to the spatial distribution of fire can affect the entire ecosystem, as many plant communities are characterized by two related components of fire regime: frequency and spatial distribution of fire. Without a concurrent increase in ignition frequency, less extensive or more spatially heterogeneous fires increase the fire-return interval and potentially alter plant succession in unburned patches (Bradstock and Kenny 2003; Bond and Keeley 2005). Measureable variation and contrast between patches in rangeland managed for heterogeneous vegetation structure is dependent upon fire spread, which can be inhibited by excessive herbivory and invasive plant species (McGranahan and others 2012b). Finally, fire spread is a primary component for predicting fire danger in both the U.S. National Fire Danger Rating System and the Canadian Fire Weather Index (Pyne and others 1996), and awareness of altered fire spread is important to safe and efficient wildland fire management.

The connection between live fuel and fire spread is strengthened by the novel role of the invasive grass species, which to our knowledge has not been documented elsewhere. Excluding our study, plant species that reduce fire spread appear limited to woody invaders (Brooks 2008; Mack and D'Antonio 1998; Stevens and Beckage 2009) whereas invasive grasses are categorically associated with increased intensity, frequency, and fire spread (D'Antonio and Vitousek 1992; Grace and others 2001; Mack and D'Antonio 1998). We have demonstrated that tall fescue has the opposite effect of reducing fire spread by altering the spatial arrangement of dead fuel in the native fuelbed. Together, the manipulation of the fuelbed and the altered spatial extent of fire suggest that tall fescue might be capable of altering the fire regime of the tallgrass prairie (Brooks 2008), although it remains uncertain to what extent tall fescue creates or benefits from feedback in reduced fire intensity and spread.

Although we use tall fescue invasion in tallgrass prairie as a model system, we do not suggest that tall fescue is the only invasive grass species that might reduce fire behavior or spread. On the contrary, we suggest that other such grass species exist,

and posit that a new perspective on invasive grasses and fire is required to identify them. Fire and invasive species are often discussed in terms of the effect of fire on invasive species, for example, tall fescue abundance is difficult to control with prescribed fire management (Washburn and others 1999; Madison and others 2001; Rhoades and others 2002; Barnes 2004). However, no apparent consideration is given to the intensity and spread of fire in such experimental treatments. We suggest that the more useful perspective when considering the relationship between fire and invasive species is to focus on the effect of the invasive species on the properties and pattern of the fuelbed and on fire spread. A more complete understanding of the role of live fuel moisture and other fuelbed characteristics altered by invasive species will increase our ability to predict and manage the effect of invasive species on native fire regimes in any ecosystem threatened with invasion.

In ecosystems such as the tallgrass prairie, a high proportion of potential fuel is also palatable forage for herbivores. As such, grazing reduces fuel load, and thus reduces fire intensity by removing biomass that would otherwise be fuel for fire (Leonard and others 2010). Because grazing is rarely spatially homogeneous, grazing can also alter the spatial spread of fire when biomass removal is patchy (Kerby and others 2007; Davies and others 2009, 2010). Although grazing can mitigate fuel load increases caused by cheatgrass invasion, as well as interrupt fuelbed connectivity and reduce the spatial spread of fire in cheatgrass-invaded fuelbeds (Davidson 1996; Davies and others 2009), prescribed or mismanaged grazing in tall fescue-invaded ecosystems likely exacerbates the negative effects of tall fescue invasion by reducing fuel load.

That abiotic weather variables affected fire spread less than biotic variables should not discount the relevance of weather conditions to fire spread in actual ecosystems, as weather variables change on a shorter temporal scale than fuel load and plant invasions. Weather variables relate directly to fire spread: wind speed is consistently an important determinant of fire spread in the Rothermel (1972) fire spread equation and the fire spread models that rely on it (Rothermel 1983; Finney 2004). Wind drives heat ahead of the flame front and pre-heats fuel particles with both radiative and convective heating, which decreases the time required to ignite fuel particles and accelerates the advance of the flame front (Rothermel 1972). Likewise, relative humidity and air temperature affect fire spread indirectly through their relationship with dead fuel moisture: increased dead fuel moisture reduces

reaction intensity and generally (although not directly) reduces the rate of fire spread (Rothermel 1972). Again, these relationships bear further research regarding high-moisture, live fuels, as their physical properties during heating and combustion might differ from those of dead fuel. However, we can generally state that within any combination of fuel load and tall fescue invasion, greater wind speed increased fire spread and reduced the variability in burn area.

These results are important to fire management because biotic variables—fuel load and invasion extent—are static within the dormant season, whereas abiotic weather factors vary daily and even hourly, and must be considered in prescribed fire operations or when assessing wildfire potential. In either case, these results suggest that when predicting fire behavior or characterizing the fire regime in an invaded ecosystem, one must consider the dormant season of the invasive species in addition to the dormant season of the native community. For fuelbeds invaded by a high-moisture plant species, prescribed fire managers might face a more narrow burn season than that conventionally defined by the dormant season of the native community—in this case, between November and March rather than October and May. Managers might also reduce biomass offtake (to ensure continuous dead fuel) or burn with higher wind speed or lower relative humidity (to offset live moisture content) to ensure fire spread objectives are met (McGranahan and others 2012a). As climate change continues to alter fire regimes (Flannigan and others 2009; Krawchuk and others 2009) and the distribution of species (Walther and others 2002), ecosystem researchers and managers must increase their understanding of how these changes affect the pattern of fuels and fire spread.

CONCLUSIONS

We have shown that the invasion of a high-moisture, live fuel type into a dormant, native grassland reduces the spread of fire across modeled landscapes, and that reduced fuel load exacerbates this effect. We attribute the reduced fire spread to asynchrony in the growing seasons of the exotic, cool-season grass, tall fescue, and the native, warm-season tallgrass prairie community we have used as a model system. Although these results indicate that the primary controls over fire spread in this system—fuel load and the extent of invasion—are biotic conditions of the fuelbed, abiotic weather variables—wind speed and relative humidity—account for substantial differences in

fire spread and variation in burn area within a given fuel load and invasion scenario.

These results draw connections between invasive species, live fuel moisture, and spatial patterns of fire spread that are unique within the ecological literature. Most documented cases of invasive grasses affecting any aspect of fire regime consist of increased fire intensity, frequency, and spread. Our results indicate that invasive grass species are capable of having a negative effect on fire in pyrogenic ecosystems. Although natural fire is rarely a component of modern warm-season grassland ecosystems, these results suggest that prescribed fire managers should consider the growing season of cool-season invasive grasses with reference to the dormant season of the native community. Appropriate steps might include writing total fuel load and live fuel moisture into burn plans and considering burn periods outside of the conventional fire season (Weir 2011; McGranahan and others 2012a). More generally, these results suggest that when predicting fire behavior or characterizing the fire regime in an invaded ecosystem, other invasive grasses might be recognized to have this same effect if ecologists begin to assess the fire–grass relationship from the perspective of invasive species effects on fire, rather than fire effects on invasive species.

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