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RESEARCH ARTICLE

Landscape heterogeneity and fire behavior: scale-dependent feedback between fire and grazing processes

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Abstract Fire and grazing are ecological processes that frequently interact to modify landscape patterns of vegetation. There is empirical and theoretical evidence that response of herbivores to heterogeneity is scale-dependent however the relationship between fire and scale of heterogeneity is not well defined. We examined the relationship between fire behavior and spatial scale (i.e., patch grain) of fuel heterogeneity. We created four heterogeneous landscapes modeled after those created by a fire–grazing interaction that differed in grain size of fuel patches. Fire spread was simulated through each model landscape from 80 independent, randomly located ignition points. Burn area, burn shape complexity and the proportion of area burnt by different fire types (headfire, backfire and flankfire) were all affected by the grain of fuel patch. The area fires burned in heterogeneous landscapes interacted with the fuel load present in the patch where ignition occurred. Burn complexity was greater in landscapes with small patch grain than in landscapes with large patch grain. The proportion of each fire type (backfire, flankfire and headfire) was similar among all landscapes regardless of patch grain but the variance of burned area within each of the three fire types differed among treatments of patch grain. Our landscape fire simulation supports the supposition that feedbacks between landscape patterns and ecological processes are scale-dependent, in this case spatial scale of fuel loading altering fire spread through the landscape.

Keywords Burning · Herbivory · Landscape pattern · Modeling · Shifting mosaics · Simulation · Vegetation biomass

Introduction

Spatial patterns of landscapes dictate organization and flow of many ecological processes (Turner 1989). In turn, ecological processes determine the spatial pattern of landscapes. Fire and grazing are ecological processes that respond to and modify landscape pattern. In ecosystems with an evolutionary history of fire and grazing, the fire–grazing interaction is critical to structuring landscape heterogeneity (Knapp et al. 1999; Fuhlendorf and Engle 2001, 2004). These disturbances interact through a series of feedbacks to establish patterns of vegetation biomass. Biomass

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accumulation is limited by preferential grazing within recently burned patches (Fuhlendorf and Engle 2004). Bison (*Bison bison*) and cattle (*Bos taurus*), like other large ungulates, selectively graze recently burned patches for the high-quality regrowth forage (Svejcar 1989; Coppedge and Shaw 1998; Coppedge et al. 1998; Archibald and Bond 2004). Patches not burned recently accumulate litter because of reduced foraging pressure when ungulates focus on more recently burned patches (Fuhlendorf and Engle 2004). Recently burned and grazed patches are unlikely to ignite and, if ignited, are unlikely to support fire spread. In contrast, patches not recently burned are very likely to support fire spread if ignited (Hobbs et al. 1991).

Vegetation heterogeneity influences grazing pattern across spatial scales (Senft et al. 1987; Etzenhouser et al. 1998; Hobbs 1999; Wallis de Vries et al. 1999). Large ungulates adjust their foraging strategy in response to heterogeneity at multiple spatial scales ranging from individual plant selection to habitat preference. Biotic factors that influence response to heterogeneity include herbivore nutritional requirements, social behavior, forage quality and vegetation structure (Senft et al. 1987; Hobbs 1999). Abiotic factors that influence herbivore foraging strategies include topography, weather and water distribution (Bailey et al. 1996). Large herbivores also are capable of creating or enhancing spatial heterogeneity (Hobbs 1999). Selectivity of feeding sites may create grazing lawns, localized areas of reduced biomass that are repeatedly grazed (McNaughton 1984; Ring et al. 1985). Preferential selection of existing patches further enhances contrast among grazing lawns and adjacent vegetative structure (Bond and Archibald 2003). Spatial scale, or grain, of vegetation patchiness can be altered further by fluctuating density of herbivores. Increased density of large herbivores can expand the extent of grazing lawns or instigate creation of additional lawns whereas decreased grazing pressure can result in grazing lawn contraction or disappearance (Ring et al. 1985; Archibald et al. 2005).

The importance of fuel heterogeneity to fire behavior has been recognized primarily from small-plot experiments that generally employ homogenous fuelbeds despite the recognized importance of fuelbed heterogeneity (Cheney et al. 1993, 1998). Because heat transfer is reduced by fuel discontinuity, fire spread can be expected to be altered by fuelbed heterogeneity in which horizontal spacing of fuel particles is discontinuous (Pyne et al. 1996). In essence, average fuel mass can be less important than spatial variation in fuel mass if fuel gaps function to reduce or eliminate heat transfer among fuel particles within the fuelbed (Rothermel 1972; Frandsen and Andrews 1979). Important ecological characteristics of fire spread such as proportions of fire types (e.g., headfire, flankfire and backfire) and spatial complexity of burned areas also may be altered by heterogeneous fuelbeds. Headfires (i.e., rapidly spreading fire fronts that advance with the prevailing wind) are more intense than backfires that spread opposite the prevailing wind (Gibson et al. 1990), which may alter post-fire vegetation community composition (Bidwell et al. 1990). Heterogeneous fuels also might increase the spatial complexity of burned areas when discontinuous fuels prevent fire spread in some locations or restrict fire spread through suitable fuels by less direct routes (Finney 2001). Habitat availability, survival of fire-sensitive plant species and spatial variation of trophic interactions can be enhanced by heterogeneous burn patterns (Price et al. 2003; Knight and Holt 2005).

Because spatial scale of fuel heterogeneity, particularly grain or patch size, can be altered by behavioral response of large herbivores to that heterogeneity, a fire–grazing interaction determines succeeding patterns of herbivory which in turn modifies the fuel distribution for future fire (Bond and Archibald 2003; Archibald and Bond 2004; Fuhlendorf and Engle 2004). For example, frequent, intense grazing can enlarge grazing lawns and enhance contrast among fuel patches (Ring et al. 1985; Cid and Brizuela 1998; Adler et al. 2001). While there is abundant empirical and theoretical research describing feedbacks between spatial scale of patchiness and large herbivore grazing patterns (Senft et al. 1987; Hobbs 1999; Wallis de Vries et al. 1999), there is a paucity of research on feedbacks between grain of fuel heterogeneity and fire behavior (Frandsen and Andrews 1979; Catchpole et al. 1989; Nahmias et al. 2000). Spatial scale (i.e., grain) of fuel patches would be expected to influence fire behavior. Moreover, where feedbacks between fire and grazing determine spatial heterogeneity (Fuhlendorf and Engle 2001, 2004), the relationship of patch size to fire spread is fundamental to understanding the relationship between ecological pattern and process.

The objective of this study was to examine the relationship between fire spread and behavior and spatial scale (i.e., patch grain) of fuel heterogeneity. To assess this relationship, we used single-point fire ignitions within model landscapes differing in grain size of fuel patches. We used cellular modeling to evaluate several ecologically important measurements of fire spread as a function of patch grain and fuel load. Simulated landscapes were representative of heterogeneous fuel patterns created by interacting disturbances of grazing and fire.

Methods

Fire simulation

To isolate the effect of patch grain on fire behavior in heterogeneous landscapes, we created four raster base maps (15,552 ha and resolution of 30 m) that had the same mean landscape fuel load (3,813 kg ha^{-1}), but each raster map had a different patch grain of fuel patches (2.25, 9, 36, or 144 ha). We intentionally chose a broad range of patch grains to test (i.e., 144 ha patch is 64 times larger than 2.25 ha patch). Although the fire–grazing interaction is our conceptual backdrop for this research, any number of ecological (soils, previous disturbance history, etc.) or anthropogenic processes (differences among management, property ownership size, etc.) could produce fuel heterogeneity across similar ranges. Patches on each fuel map (Fig. 1) were randomly assigned one of six possible fuel loads (Table 1) representing the range of spatial fuel heterogeneity of fuel load possible within tallgrass prairie subject to the fire–grazing interaction (Bidwell et al. 1990; Fuhlendorf and Engle 2004).

Table 1 Fuel loading of patches in simulated fire–grazing landscapes

Patch type	Patch fuel load (kg ha^{-1})	Time since fire (months)
1	458	< 6
2	1,793	12
3	3,138	18
4	4,483	24
5	5,838	36
6	7,173	>36

Mean fuel load on all simulated landscapes was 3,813 kg ha^{-1}

We used Fire Area Simulator (FARSITE, Finney 1998) to simulate randomly ignited fires within our heterogeneous landscapes. FARSITE is a Windows-based fire simulation program that uses the wave-elliptical model (Richards 1990) to produce spatially explicit predictions of fire spread. The wave-elliptic model assumes that each vertex along a fire front can serve as an independent source of elliptic fire expansion. FARSITE integrates input from raster GIS data and temporally referenced weather data to produce tabular predictions of burn area, polygon layers describing fire spread and raster outputs of fire behavior variables including fire spread direction. FARSITE also requires raster input layers that describe topography, specifically elevation, aspect and slope. Topography was level to remove any effect of slope or aspect from fire simulations. The resolution of all input data and simulated fire spread was 30 m.

Weather-related variables (Table 2) were held constant throughout each simulation of 4 h.

Table 2 Assumptions and settings for fire simulations testing the effect of spatial fuel variations on fire behavior

Variable	Assumption	Setting
Wind speed	Constant	8 km h^{-1}
Wind direction	Constant	South
Temperature	Constant	32°C
Relative humidity	Constant	30%
Elevation	Constant	305 m
Slope	Constant	0%
Aspect	Constant	none
Dead fuel moisture	Constant	6%*

* Six percent dead fuel moisture is the equilibrium fuel moisture predicted for 1-h fuels with our temperature and relative humidity (Cheney and Sullivan 1997)

Duration of burning and weather were chosen to approximate conditions during peak heating hours of afternoon when fires are most frequent. We used 80 simulations per base map with each simulation consisting of an independent ignition located randomly within each fuel map. Data for each simulation included location of the ignition patch and its fuel load, burn area at cessation of the simulation, and spatial complexity of each fire perimeter calculated with a shape index in FragStats 3.3 (McGarigal et al. 2002). The shape index was the ratio of actual patch perimeter to the minimum possible perimeter for a patch with the same area. Shape index can range from 1 (maximally compact) to infinity.

Burn area, shape and type analyses

We used analysis of variance (ANOVA) to determine the influence of patch grain and fuel load of the ignited patch on fire spread. Differences in burn area and shape complexity of burn areas were tested using a mixed linear model (SAS Institute Inc. 2003) with patch grain, ignition patch fuel load and patch grain * fuel load as independent variables. Differences were considered significant at $P < 0.05$.

We chose fire type (i.e., headfire, flankfire and backfire) as an additional metric to evaluate the effect of patch grain on fire behavior because fire type is an important element of fire ecology (Bidwell et al. 1990; Bidwell and Engle 1992) and fire management (Rothermel 1983; Pyne et al.1996). Fire types differ due to their direction of spread relative to prevailing wind direction. Headfires that move in the same direction as the wind spread fastest and are most intense. Backfires moving opposite of the wind direction are slowest and least intense, and flankfires that move perpendicular to the wind direction are intermediate. FARSITE simulations produce data describing direction (0–359°) of fire movement in each simulated cell. These data were imported and reclassified into the three fire types (direction 0–45 and 315–359° = headfire; 45–135 and 225–315° = flankfire; 135–225° = backfire).

Fire spread maps were classified by fire type using FragStats 3.3 (McGarigal et al. 2002) by calculating the proportion of the burned area occupied by each fire type. It has been suggested that excluding patches from analysis that are small (i.e., single cell patches that may occur frequently at edge boundaries) will prevent skewed results of data (Hunsaker et al. 1994). We chose to retain all patches for our analysis despite the presence of small patches around edges. Visual inspection of our maps revealed that small patches also occurred frequently within large fire patches, perhaps the result of converging or diverging fire fronts causing small, localized areas of distinct fire type (i.e., a single-cell patch of backfire between converging headfires).

Data on proportion of burn area in each of the three fire types were arc-sine transformed before statistical analysis because untransformed proportion data frequently form a binomial rather than normal distribution (Zar 1999). Examination of data histograms indicated that variance in proportion of area burned varied among fire types and patch size so we performed Levene's Test for Homogeneity of Variance for each fire type to confirm heterogeneity of variance (Levene 1960). We also performed ANOVA and used Tukey-type multiple comparison tests to separate difference in variance for each fire type within a scale of fuel patch (Zar 1999).

Results

Burn area and shape complexity

Burn area and burn shape complexity varied with patch grain and fuel load within the ignited fuel patch. Burn area changed as a function of an interaction between patch grain and fuel load within the ignited fuel patch (Table 3). Burn area generally increased with increasing patch grain and fuel load within the ignited fuel patch load (Fig. 2).

The interaction of patch grain and fuel load within the ignited fuel patch was caused by the greater magnitude of response to increasing fuel load within the ignited fuel patch by fires in landscapes with 144-ha patches than the response by landscapes with smaller patch grain. That occurred because fire growth can be extensive in 144-ha patches whereas fire growth in landscapes

Table 3 Summary of analysis of variance for area burned in fire simulation (burn area) and complexity of the perimeter of the burn area (shape complexity) as a function of landscape patch grain (GRAIN) and fuel load at the ignition point (LOAD)

Fire spread variable	Source	df	*F*	*P*
Burn area	GRAIN	3	7.03	< 0.0001
	LOAD	5	94.61	< 0.0001
	GRAIN*LOAD	15	11.12	< 0.0001
Shape complexity	GRAIN	3	370.74	< 0.0001
	LOAD	5	48.13	< 0.0001
	GRAIN*LOAD	15	1.38	0.1540

with smaller patch grain was more likely to be impeded by a fuel gap (Fig. 1a). However, fires ignited in patches with limited fuel on landscapes with small patch grain were larger than fires starting in similar patches in landscapes with large patch grain (Fig. 1b). Spreading fire quickly encountered new patches on landscapes with small patch grain, enabling rapid growth after the fire spread outside the ignition patch that constrained its spread early in the simulation because fuel was limited.

Shape complexity of fires increased linearly as a function of both patch grain and fuel load within the ignited fuel patch (Fig. 3). Fire shape complexity was roughly 1.5 times greater in landscapes with small patch grain than in landscapes with large patch grain. Shape complexity was intermediate in 9-ha and 36-ha landscapes and least in 144-ha landscapes. There was a trend of gradually increasing shape complexity of fires in all fuel patch grain treatments with increasing ignition patch fuel load but that trend was not as strong as the shape complexity response to patch grain.

Area burned in each fire type

The mean proportion of each fire type (backfire, flankfire and headfire) was strikingly similar among all landscapes regardless of patch grain. Thirteen percent and 12% of the area burned by backfire in landscapes with 2.25-ha and 36-ha patch grain and in landscapes with 9-ha and 144-ha patch grain patches, respectively. Fifty-six to 58% of the area burned by flankfires in all landscapes. Head-

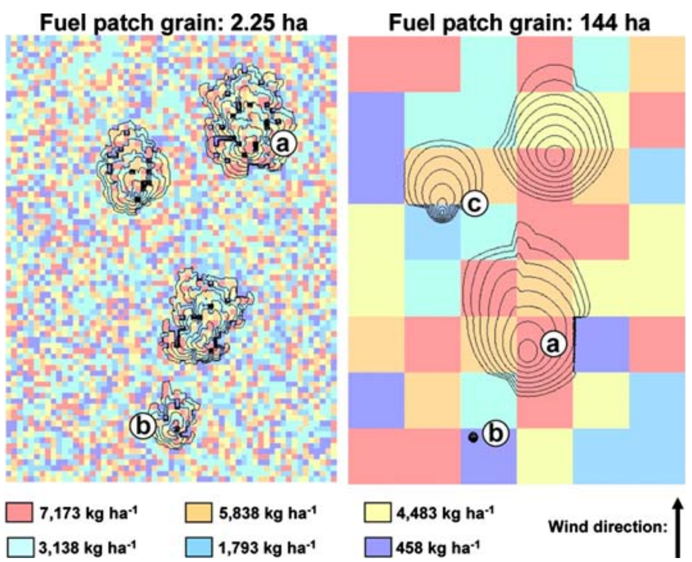

Fig. 1 Illustration of landscape fuel maps with different fuel patch grains and different fuel load within fuel patches (458–7,173 kg ha^{-1}). Concentric rings demonstrate fire perimeter at 30-min intervals for 4 h fire^{-1}. All treatments of fuel patch grain (2.25-ha and 144-ha are shown as examples here) had equal fuel loading when averaged across the entire landscape (3,813 kg ha^{-1}). Fuel patch grain and ignition point fuel load influence burn area, fire shape complexity, and proportion of headfire, backfire and flankfire. See text for explanation of causation. Note that each fire was simulated independently and that multiple fire perimeters on these maps are for demonstration only

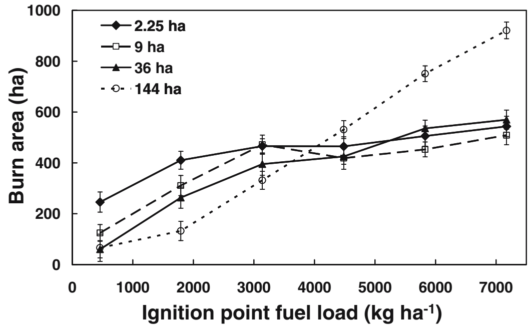

Fig. 2 Burn area across a range of fuel loads in which the ignition point is located within four landscapes differing by fuel patch grain. Error bars represent one standard error

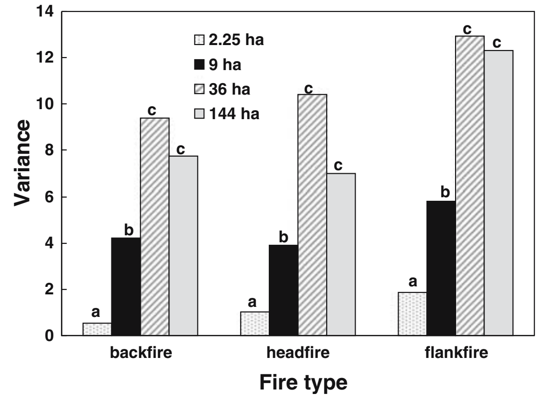

Fig. 4 Variance associated with the area burned by each of three fire types within four landscapes differing by fuel patch grain. Lower-case letters that differ within a fire type indicate the variance differs among fuel patch grains ($P \leq 0.05$)

fire burned 30–31% of the landscapes in all the treatments of patch grain. Variance of burned area within each of the three fire types differed among treatments of patch grain (backfire $F = 8.95$, $P < 0.001$; headfire $F = 12.08$, $P < 0.001$; flankfire $F = 8.30$, $P < 0.001$). For all fire types, variance associated with large patch grain was greater than variance associated with small patch grain (Fig. 4).

Discussion

Linking landscape patterns and ecological processes has been a focus of ecology for the past several decades (Turner 1989; Urban 2005) and the fire–grazing interaction clearly demonstrates the feedbacks and relationship between landscape pattern and ecological processes (Knapp et al. 1999; Fuhlendorf and Engle 2001, 2004). Our landscape fire simulation validates the fundamental principle of landscape patterns driving ecological processes, in this case spatial diversity of fuel loading driving fire spread through the landscape. These results show that patch grain (i.e., spatial scale) of fuel variation strongly affects multiple aspects of fire behavior. Studying interaction between pattern and process can identify critical feedback mechanisms (i.e., which patterns are critical to which processes and vice versa). Within a fire–grazing interaction the impact of fire behavior and fire spread processes on burning patterns likely feedback to successive patterns of grazing selectivity and vegetation biomass as well as to other ecosystem properties and processes such as species composition or woody plant invasion.

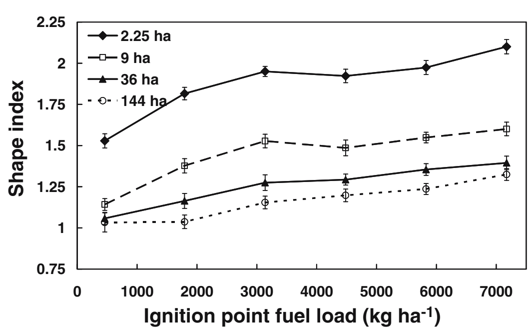

Fig. 3 Fire shape complexity (shape index) across a range of fuel loads in which the ignition point is located within four landscapes differing by fuel patch grain. Error bars represent one standard error

We found that patch grain and fuel load within the ignited fuel patch affected fire size and fire shape complexity and that patch grain produced notable differences in the variation of fire types. Our results suggest that fuel patch grain in the landscape could influence subsequent fuel patch grain across a landscape. Area burned on landscapes with large patch grain was highly variable, depending greatly on the fuel load in the ignition patch. Therefore, if multiple fires occur on landscapes with large patch grain landscape patch grain will diversify with addition of small and large burn patches relative to initial landscape patch grain. On landscapes with small patch grain fire growth is likely to result in burned patches larger than the initial patch grain. Therefore, fuel patch grain will increase with fire in landscapes composed of small patches but the diversity of burn patch grain will be low.

Visual inspection of fire simulations suggested that the difference of variance among fire types is due to the juxtaposition of ignition points and frequency with which spreading fires encounter diverse fuel patches. In landscapes with large patch grain, ignition points sometimes occurred near patch edges and fire must spread parallel to these edges for an extended period or was restricted by a patch with limited fuel downwind (Fig. 1c). Fire spreading across the edge into a markedly different fuel patch may create a disproportionate amount of flank or headfire. In contrast, all fires occurring in landscapes with small patch grain have very similar amounts of fire types. Increased diversity of fuel patches these fires encounter created multiple fire fronts that nullified any localized effect of fire spreading along edges or the location of ignition, effectively 'averaging out' differences in proportion of fire types (Fig. 1).

We showed that initial spatial scale (i.e., grain) of fuel patches within a landscape can greatly alter composition of the burned–unburned patch matrix within a landscape. In a landscape driven by a fire–grazing interaction such as tallgrass prairie, we expect that subsequent patterns of burned and unburned patches will feedback into patch selection by grazing ungulates. Bison grazing a landscape mosaic exhibit seasonal patterns of matching (patch selection that is equal to patch availability) or overmatching (patch selection that is greater than patch availability) foraging effort that varies among burn patch area (225, 900 and 3,600 m^2) within a landscape (Wallace and Crosswaithe 2005). Similar to bison in North America, grazing intensity by large ungulates on South African savanna in burned and unburned patches is dependent on the proportion of landscape burned (Archibald and Bond 2004). Cattle grazing heterogeneous grass swards also vary patch selection in response to spatial scale of patchiness (Wallis de Vries et al. 1999), even with small-scale patches (4 and 25 m^2). Because grazing ungulates modify their foraging behavior in response to spatial scale of patchiness and because different patch sizes directs selection at proportions greater than, less than, or equal to patch availability (Senft et al. 1987; Wallis de Vries and Schippers 1994), it is possible that the grazing feedback mechanism functions to strengthen or weaken the spatial scale (i.e., grain) of fuel patches. Increased grazing pressure can expand grazing lawns or create additional grazing lawns but decreased grazing pressure can result in grazing lawn contraction or disappearance (Ring et al. 1985; Archibald et al. 2005). Therefore, feedback between fire and grazing appears to be constrained by abundance and size of grazing lawns, which impede fire spread or reduce fire intensity via fuel reduction.

Peterson (2002) suggested that the degree of ''ecological memory'' that exists in a fire-dependent landscape is a function of fire frequency, rate of vegetation recovery and influence of previous fire patterns on subsequent fires. If large ungulates exhibit overmatching foraging strategy in a particular patch grain, the patch will accumulate less fuel and be less able to support spread of a future fire, effectively prolonging the ecological memory of the patch. In contrast, patch grains that experience undermatching foraging effort by herbivores will accumulate fuel quickly, enabling a future fire to effectively spread with great fire intensity, and therefore exhibit a short patch ecological memory. In a landscape in which patch size encourages matching or undermatching foraging effort in recently burned patches, landscape diversity normally promoted in fire–grazing interaction might be moderated because diversity of fuel loading would be low. In contrast, recently burned patches that experience overmatching will reinforce heterogeneity promoted in the fire–grazing interaction because preferentially grazed patches will persist as effective fire breaks while adjacent patches will accumulate fuel. The result is heightened diversity of fuel load patches, and ecological memory of the pre-existing pattern of fuel patches will be reinforced.

Variation in fire patchiness caused by landscape heterogeneity likely plays a dominant role in structuring vegetation (Price et al. 2003). Fire types differ in fire intensity and other behavior, with headfire more intense than backfire (Gibson et al. 1990). In grasslands where woody species are invading, fire intensity might determine vulnerability to invasion (Ansley et al. 1998; Briggs et al. 2002; Kupfer and Miller 2005) because fire intensity closely relates to scorch height and tree mortality (Van Wagner 1973). Our simulations showed greater variation in proportion of fire types in landscapes with larger patches, which suggests greater opportunity to manipulate patterns of fire intensity to meet objectives exists in landscapes with larger fuel patches. Primary production (Bidwell and Engle 1992) and species composition (Bidwell et al. 1990) in grasslands can vary with differences in fire intensity corresponding to different fire types.

Time, weather and topography also interact with spatial fuel variation to create patterns of fire growth (Catchpole et al. 1989; Bessie and Johnson 1995; Mermoz et al. 2005). This does not diminish the relevance of our conclusion that spatial scale of fuel variation (i.e., landscape patch grain) is critical to the feedback between landscape pattern and process. Rather, we suggest that the importance of spatial fuel patterns on fire behavior will vary with the magnitude and scale of variation of other variables that are significant to fire behavior, particularly when weather and other abiotic factors cross critical thresholds (Hargrove et al. 2000). Patch grain and fuel load within the ignited fuel patch were critical in our simulations, but temporal scale (i.e., duration of simulation), weather, and topography were held constant. Although our objective was to evaluate the importance of spatial fuel variation our findings are particularly well-suited to describe the importance of temporal variation. For example, if we examined any of our response variables after 10 min of simulation rather than 4 h we would find that patch grain is almost entirely irrelevant to fire behavior because most randomly located fires would not have spread past the boundaries of the ignition patch. Thus all variation among fires would be caused wholly by fuel load in each fire's ignition patch and variance would be equal across all fuel patch grains. Also consider if we allowed simulations to vary temporally, holding the number of patches encountered by each fire constant. This would also cause variation of fire sizes, fire types and complexity among landscape patch grains to be equal but fire simulations on large grain landscapes would have to burn much longer than fires on small grain landscapes to achieve that (i.e., days versus hours). However, in reality fires that burned for days instead of hours would encounter greater variation of topography and weather and those interactions with spatial fuel variation remain unknown. Although we suggested earlier that patch grain might alter landscape patchiness after multiple fires this conclusion depends on a suite of other factors held constant in our experiment. Thus important future avenues of fire behavior research with simulation and field observation include investigation of interactions among spatial fuel variation, fire duration and extent of fire spread, weather and topography across the full range of possible conditions. Further understanding of these interactive elements will broaden our perspective of historic fire regimes and have application for current wildland management.

Conclusions

Our simulations demonstrate the importance of the relationship between spatial scale of fuel heterogeneity and fire spread when considering potential patterns of fire and grazing processes. We also showed that the importance of spatial scale is context specific, depending on ignition point. When fire and grazing interact, scale of patchiness might either moderate or amplify the effect of patchiness on subsequent patterns of fire and grazing. Although our simulated landscapes were based on heterogeneous grasslands created by a fire–grazing interaction, the implication of feedbacks between spatial scale of fuel variation and fire behavior may broaden to include fuel types other than grasses and other fuel variation caused by other processes.

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