

RESEARCH ARTICLE

VARIATION IN GRASSLAND FUEL CURING IN SOUTH AFRICA

Devan Allen McGranahan^{1*}, Rerani Ramaano², Michelle J. Tedder²,
and Kevin P. Kirkman²

¹North Dakota State University, School of Natural Resource Sciences-Range Science Program,
201D Morrill Hall, Fargo, North Dakota 58108, USA

²University of KwaZulu-Natal, Grassland Science, School of Life Sciences,
John Bews Zoology Building-Life Science Campus,
Carbis Road, Scottsville, Pietermaritzburg 3209, South Africa

*Corresponding author: Tel.: +1-701-231-7868; e-mail: mcgranah@alumni.grinnell.edu

ABSTRACT

Fire is critical to the maintenance of ecological function in many ecosystems worldwide, especially mesic sub-Saharan rangelands. But most rangeland fire research occurs in a wildfire context, is focused on fire effects, or simply assumes that grass-dominated fuelbeds are homogeneous. In this study, we sampled fuel moisture from several species in two grassland locations in South Africa to determine (1) if grassland fuels cure differently among species or across locations, (2) whether differences in curing meaningfully affect fire behaviour, and (3) if fuel moisture is associated with soil moisture. Data were characterised by high variability among sampling sites and dates, which highlights the importance of accounting for—rather than averaging out—variation with hierarchical analysis. Variability among locations and species indicates that broad similarities among plant communities do not adequately describe fuelbed dynamics. We observed patterns in the C₃ *Festuca costata* that deviated from general patterns in C₄ grasses, particu-

RESUMEN

El fuego es crucial para el mantenimiento de las funciones ecológicas en muchos de los ecosistemas del mundo, en especial de los pastizales méxicos subsaharianos. Sin embargo, la mayoría de las investigaciones en fuego se desarrollan en el contexto de incendios naturales, se enfocan en los efectos el fuego, o simplemente asumen que las camas de combustible de pastizales son homogéneas. En este estudio, muestreamos la humedad del combustible de varias especies en dos pastizales de Sudáfrica para determinar (1) si los combustibles del pastizal se curan (secan) de manera dispar entre especies o entre distintos lugares, (2) cuándo las diferencias en el curado afectan significativamente el comportamiento del fuego, y (3) si la humedad del combustible está asociada a la humedad del suelo. Los datos fueron caracterizados por su alta variabilidad entre lugares y fechas de muestreo, lo que enfatiza la importancia de tomar en cuenta—más que promediar—las variaciones mediante un análisis jerárquico. La variación entre lugares y especies indican que una amplia similaridad entre especies no describe adecuadamente la dinámica de las camas de combustible. Nosotros observamos patrones en la especie C₃ *Festuca costata* que se desviaban de los patrones generales en gramíneas C₄, particularmente en el borde de determinadas tran-

larly in grasslands at the edge of environmentally determined transitions. These differences might have landscape-level implications under global environmental change. The temporal breadth and species-level specificity of our study constitute novel data that identify further research to improve the understanding of fuelbed ecology in grasslands worldwide, beyond the context of extreme fire weather and behaviour. Our data suggest that managers in South Africa and abroad should consider heterogeneity within grassland fuelbeds and recognize seasonal changes to ensure that objectives are obtainable ahead of burns, and to explain spatial variation in response within what might have appeared to be a homogeneous grassland fuelbed.

siciones ambientales. Esas diferencias podrían tener implicancias a nivel de paisaje en el contexto del cambio climático global. La extensión temporal y la especificidad a nivel de especies de nuestro estudio constituyen un dato novedoso que identifica futuros trabajos para mejorar el entendimiento de la ecología de las camas de combustible en pastizales alrededor del mundo, más allá del contexto de condiciones meteorológicas extremas y de comportamiento del fuego. Nuestros datos sugieren que los gestores o administradores de recursos en Sudáfrica y otros lugares deberían considerar la heterogeneidad dentro de las camas de combustible de los pastizales, y reconocer los cambios estacionales para asegurar que los objetivos sean alcanzables antes de las quemadas, y para explicar la variación espacial en respuesta a lo que parece ser una cama de combustibles de pastizales homogénea.

Keywords: Drakensberg grasslands, *Festuca costata*, fine fuel moisture, fire behaviour, KwaZulu-Natal, soil moisture, *Themeda triandra*, veld burning

Citation: McGranahan, D.A., R. Ramaano, M.J. Tedder, and K.P. Kirkman. 2016. Variation in grassland fuel curing in South Africa. *Fire Ecology* 12(3): 40–52. doi: 10.4996/fireecology.1203040

INTRODUCTION

As a major force in the evolution of many ecosystems globally, fire is often critical to the maintenance of ecological structure and function. Knowledge and application of fire science is especially important in the Anthropocene, in which many pre-historic disturbance regimes have been supplanted by human management (Bowman *et al.* 2011, Coughlan and Petty 2012). In general, mesic rangelands (savanna and grassland ecosystems) are both particularly fire prone and heavily influenced by human impact (Sauer 1950, Ellis and Ramanakutty 2008). Mesic rangeland in sub-Saharan Africa is especially fire prone and has a long history of human interactions with fire that

continues in the modern era (Shaffer 2010, Laris 2011, Trollope 2011).

While many studies report fire effects in rangeland, much of this work occurs in a wild-fire context, and little has addressed temporal and species-specific trends within fuelbeds to support proactive fire management practices and policies. A common trope throughout sub-Saharan Africa—that fire causes rangeland degradation—supports anti-burning policies (Laris and Wardell 2006, Nyamadzawo *et al.* 2013) and sets a wildfire context in which observations of fire effects are based on fully cured fuels and extreme fire weather and behaviour. The general emphasis on fire effects, positive or negative, often focuses on specific outcomes such as primary productivity, plant

community composition, or biodiversity conservation (Snyman 2004, Uys *et al.* 2004, van Wilgen *et al.* 2011) and overlooks potential effects of the plant community itself on the nature of the fire being studied.

Globally, fire ecology has begun to consider composition and structure within grassland fuelbeds, but most studies in sub-Saharan Africa regard grass-dominated fuelbeds as homogeneous. Fuelbed heterogeneity can arise from spatially explicit disturbance patterns that drive spatial patterns of fire spread and behaviour (Kerby *et al.* 2007, Davies *et al.* 2010, Leonard *et al.* 2010). Likewise, introducing substantially different fuel types can alter the spatial distribution and intensity of wildland fire (D'Antonio 2000). Similar work in sub-Saharan Africa is lacking.

In this study, we compared seasonal trends in fuel moisture of common rangeland grasses at two locations in South Africa. Sampling began prior to the conventional burning period and outside the range of conditions associated with wildfire, affording an opportunity to study species-specific differences and associations between fuel curing and soil moisture. Variation in fuel moisture can account for high variation in fire behaviour (Govender *et al.* 2006), and live fuel moisture can vary with soil moisture (Qi *et al.* 2012) but, to our knowledge, the relationship has not been tested for curing grassland fuels. It is possible that environmental data can serve as proxies for fuel moisture to support prescribed fire planning, assess wildfire risk, and predict or explain variability in fire effects. Within this context, we addressed the following questions: (1) Do grassland fuels cure differently among species or across locations? (2) Do differences in curing meaningfully affect fire behaviour? (3) Is fuel moisture associated with soil moisture?

METHODS

Study Area

The study included two locations in KwaZulu-Natal, South Africa: a mid-altitude site (840 m a.s.l.) at the University of KwaZulu-Natal Ukulinga Research Farm in Pietermaritzburg (30° 24' S, 29° 24' E; hereafter Ukulinga) and a high-altitude site (1850 m a.s.l.) at Highmoor in the central region of the uKhahlamba-Drakensberg Park (20° 32' 07" S, 29° 62' 16" E). Ukulinga is characterised by hot summers, mild winters, and 838 mm mean annual precipitation, mostly from summer rainstorms (Buis *et al.* 2009). Highmoor is characterised by cold winters, mild summers, and 1400 mm mean annual rainfall (Mentis and Bigalke 1981) occurring over a long, foggy summer rainy season. The Soil and Terrain Database for southern Africa classifies soils at Ukulinga as Dystric Regosols and soils at Highmoor as Eutric Regosols (ISRIC 2008). Regosols are a taxonomic “rest group” of soils that do not fit other major soil groups due to a general lack of diagnostic horizons characteristic of eroded land and mountainous regions (FAO 2001). In our observations, soil at Highmoor tended to have higher proportions of organic matter than soils at Ukulinga.

Despite climate and elevation differences both locations are characterised by grassland dominated by warm-season, C₄ grasses including *Themeda triandra* Forssk., *Alloteropsis semialata* (R.Br.) Hitchc., and *Aristida junciformis* Trin. & Rupr. Because of the higher elevation, Highmoor sits at a transition between sub-montane grassland dominated by warm-season species and mixed *Themeda-Festuca* montane grassland (Killick 1963). Thus, large patches of the cool-season, C₃ *Festuca costata* Nees occur among warm-season grassland at Highmoor.

Data Collection

We sampled fuel and soil moisture five times at approximately monthly intervals at both locations in 2014 (Highmoor, 8 March through 26 July; Ukulinga, 25 March through 2 August). Sampling was timed to span the end of the growing season into mid-winter when grassland fuels are typically fully cured (Everson *et al.* 1988). All three C₄ grasses (*Themeda*, *Alloteropsis*, *Aristida*) were collected at each location in addition to the C₃ *Festuca* collected only at Highmoor. We used a spatially nested design wherein two samples per sample type (three to four species plus soil) were collected at two sites per location during each sampling event ($n = 2$ true replicates per sample per event per location).

We sampled fuel and soil moisture content by clipping all aboveground biomass from a randomly located grass clump at ground level for each species, and by digging a ~6 cm³ soil core, respectively. For both biomass and soil, moisture content was determined as mass lost after drying at 60°C for 48 hr and expressed on a dry-weight basis (mass of water in sample divided by dry mass of the sample, multiplied by 100).

Data Analysis

Prior to each hypothesis test, we assessed model assumptions—specifically, independence of observations and distributions. When high variance and low sample size precluded the application of statistical models to observed data, we employed a moment-matching technique in which we simulated data based on the mean, variance, and distribution of observed data (Ricci 2005, Hobbs and Hooten 2015).

We assessed independence of observations among sample sites within locations with a variance partitioning technique that calculates the proportion of variance attributable to each sampled scale (Winter *et al.* 2012, McGranah-

an *et al.* 2015). When data were to be simulated and a substantial (>10%) proportion of variance arose from the site factor, we used site-specific moments in data simulation; otherwise, location-level mean and variance were used in simulations. When statistical models were applied to observed data without simulation, we used mixed-effect regression models that also fit site as a random variable. All analysis was performed in the R statistical environment (R Development Core Team 2013). Linear mixed-effect regression models were fit using maximum likelihood with the lmer function in the lme4 package (Bates *et al.* 2013). In addition to model comparison via analysis of deviance, which returns a P -value based on a χ^2 statistic, we estimated 95% confidence intervals from the quantiles of 1000 model simulations (Nakagawa and Cuthill 2007). When factors with more than two levels, such as species, were significant terms in the overall model ($P \leq 0.05$), we employed *post hoc* Tukey comparisons using the glht function in package multcomp (Hothorn *et al.* 2013).

Fuel curing rates. We simulated a dataset ($N = 10$) based on the mean and variance of fuel moisture for each species at each location for each sampling event based on a log-normal distribution. Moments were calculated at the location level per species per sampling event as differences among sampling sites accounted for approximately 7% of variance in fuel moisture.

To determine if fuel moisture differed across study locations, we used analysis of deviance to compare two linear mixed-effect regression models: a null, intercept-only model, and one with a location term. For each of these models, log-transformed, simulated fuel moisture values were fit as response variables. Sampling date was included as a random effect to control for the repeated measures component of the sampling design.

To determine if species differed in fuel moisture content within study locations, we

used analysis of deviance to compare two linear mixed-effect regression models: a null, intercept-only model, and one with a species term. As above, log-transformed, simulated fuel moisture values were fit as response variables, sampling date was included as a random effect, and models were fit with maximum likelihood using lmer.

Fire behaviour. To predict whether differences in fuel moisture accounted for differences in fire behaviour, we modeled fire intensity for each species at each location for each sampling event. We used a fire intensity equation based on a linear regression model developed from fuel, weather, and fire behaviour characteristics recorded from 200 fires in South African grass-dominated fuelbeds (Trollope and Trollope 2002). The Trollope equation,

$$FI = 2729 + 0.8684 \cdot x_1 - 530 \cdot \sqrt{x_2} - 0.1907 \cdot x_3^2 - 596 \cdot \frac{1}{x_4}, \quad (1)$$

returns fire intensity (FI , $\text{kJ sec}^{-1} \text{m}^{-1}$, converted for presentation here as kW m^{-1}) from fuel load (x_1), percent fuel moisture on a dry-weight basis (x_2), relative humidity (x_3), and wind speed (x_4). We used our observed fuel moisture data and set fuel load at 5000 kg ha^{-1} for both locations based on published primary production values (Everson *et al.* 1985, Buis *et al.* 2009), relative humidity at 25%, and wind speed at 3.5 m sec^{-1} . Three fuel moisture scenarios were modeled, with the following sets of inputs for x_2 : a low-moisture, species-specific scenario in which we used the second quantile of fuel moisture percentage per species per sampling event; a high-moisture, species-specific scenario in which we used the fourth quantile of fuel moisture percentage per species per sampling event; and an average fuelbed scenario in which we used the mean fuel moisture of all species combined per sampling event.

Fuel moisture and soil moisture. To test for an association between fuel curing and soil

moisture across study locations, we fit \log_{10} -transformed, observed fuel moisture against soil moisture and location in a linear mixed-effect model with site and date as nested random effects to account for spatial variation and repeated measures using the lmer function, estimated 95% confidence intervals, and ran *post hoc* pairwise comparisons on species as above.

RESULTS

Fuel Curing Rates

From the end of the growing season through mid-winter, fuel moisture varied among the Highmoor and Ukulinga study locations ($\chi^2 = 8.51$, $P = 0.004$, 95% CI = 0.11 to 0.51; Figure 1). Although fuel moisture was statistically different among species at both

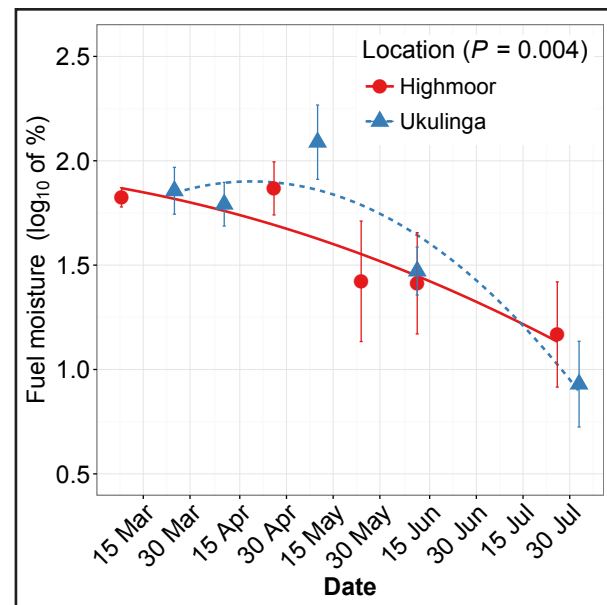


Figure 1. Second-order polynomial linear regression lines generalize the relationship between estimated fuel moisture (\log_{10} scale) and time at two grassland locations in South Africa. Analysis of deviance indicated that location was a significant term in a linear mixed-effect regression model ($\chi^2 = 8.51$, $P = 0.004$, 95% CI = 0.11 to 0.51). Sampling period spans end of the growing season into late winter.

Highmoor ($\chi^2 = 67.82$, $P < 0.001$) and Ukulinga ($\chi^2 = 7.14$, $P = 0.03$), the effect was limited to Highmoor (95% CI = 0.11 to 0.23) and did not vary from zero at Ukulinga (95% CI = -0.03 to 0.05) (Figure 2). At Highmoor, *post hoc* pairwise comparisons indicated that the C_3 *Festuca* had higher fuel moisture than all three C_4 grasses—*Alloteropsis* ($P < 0.001$), *Aristida* ($P = 0.02$), and *Themeda* ($P = 0.02$)—while among C_4 grasses, *Themeda* and *Aristida* had significantly higher fuel moisture than *Alloteropsis* ($P < 0.001$ for both). At Ukulinga,

post hoc pairwise comparisons provided marginal statistical evidence that *Aristida* had lower fuel moisture than *Alloteropsis* ($P = 0.05$) and *Themeda* ($P = 0.06$).

Fire Behaviour

Overall, predicted fire intensity increased for all species at both locations as the growing season gave way to the dormant winter season (Figure 3). At the end of the study period, when fuels were considered fully cured (<30%

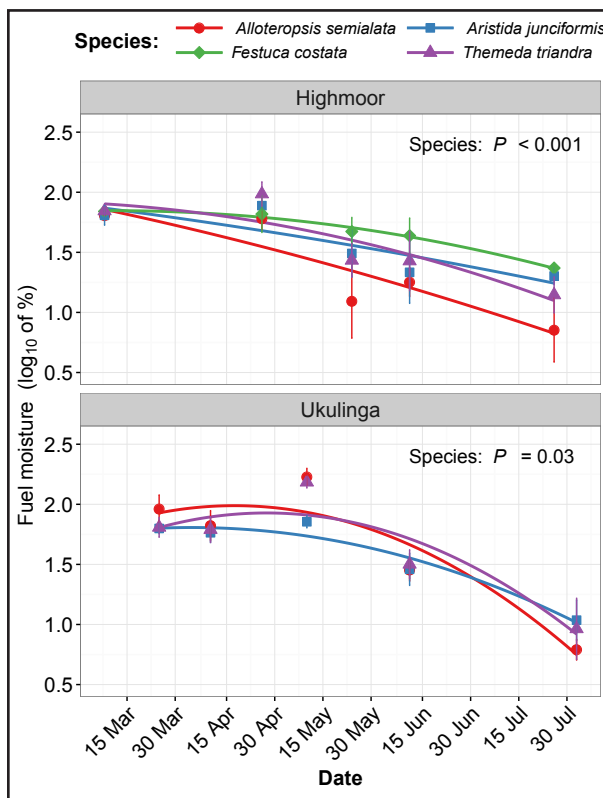


Figure 2. Second-order polynomial linear regression lines generalize the relationship between estimated fuel moisture data (log₁₀ scale) and time for four species at two grassland locations in South Africa. Analysis of deviance indicated that species was a significant term in linear mixed-effect regression models for both locations ($P < 0.05$), but estimated 95% confidence intervals suggest that the effect is limited to Highmoor (0.11 to 0.23) and not Ukulinga (-0.03 to 0.05). *Festuca costata* occurred at Highmoor only. Sampling period spans end of the growing season into late winter.

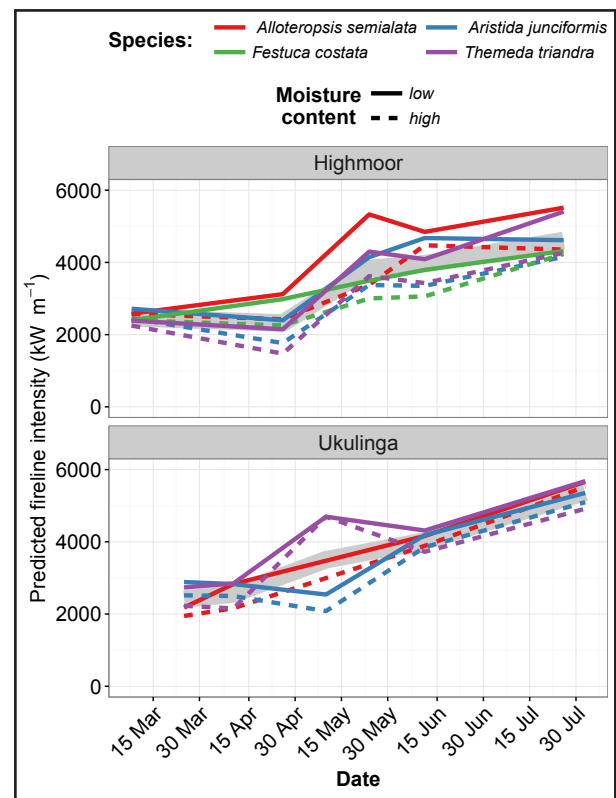


Figure 3. Trollope’s predicted fire intensity over time for three species at two grassland locations in South Africa, plus *Festuca costata* at Highmoor. Within each species for each sample date, fire intensity was predicted at two levels of fine dead fuel moisture—low and high—calculated as the second and fourth quantiles of observed moisture, respectively. Grey bar in background represents the predicted fire intensity based on the average fine dead fuel moisture of all species combined. Sampling period spans end of the growing season into late winter.

moisture), Ukulinga had consistently greater predicted fire intensity (all species >5000 kW m⁻¹) than Highmoor (all species <5000 kW m⁻¹). At Highmoor, *Festuca* had the lowest predicted fire intensity after C₄ grasses cured (Figure 3).

At Ukulinga, the increase in predicted fire intensity as fuels cured was linear and consistent across species, with the exception of a sharp divergence on the 10 May sampling event, which was likely driven by differential responses of fuel moisture to a rain event the previous day. At Highmoor, predicted fire intensity increased later and more slowly than at Ukulinga. Predicted fire intensity varied considerably within and among species at Highmoor due to differences in high and low moisture content, but within-species variation in predicted fire intensity was relatively low at Ukulinga (Figure 3). The average scenario, which predicted fire intensity using mean fuel moisture across all species, had a relatively linear increase over time at Ukulinga, but was later and slower to increase at Highmoor (Figure 3).

Fuel Moisture and Soil Moisture

Analysis of deviance indicated the significance of the regression model that fit fuel moisture against soil moisture and location ($\chi^2 = 6.95$, $P = 0.008$). Fuel moisture and soil moisture had a positive relationship (95% CI = 0.01 to 0.09), and Ukulinga generally had lower soil moisture than the wetter, more loamy Highmoor (95% CI = 0.39 to 2.60). The slope of the fuel moisture-soil moisture relationship varied substantially among sampling sites at Highmoor, with less spatial variability in slope at Ukulinga (Figure 4). Only at Highmoor was the regression model with species term significantly different from the intercept-only model ($\chi^2 = 11.76$, $P = 0.008$, 95% CI_{soil} = 0.01 to 0.08, 95% CI_{species} = 0.02 to 0.28), and only *Alloteropsis* differed from other species (*Aristida*, $P = 0.02$; *Festuca*, $P = 0.002$; *Themeda*, $P = 0.06$).

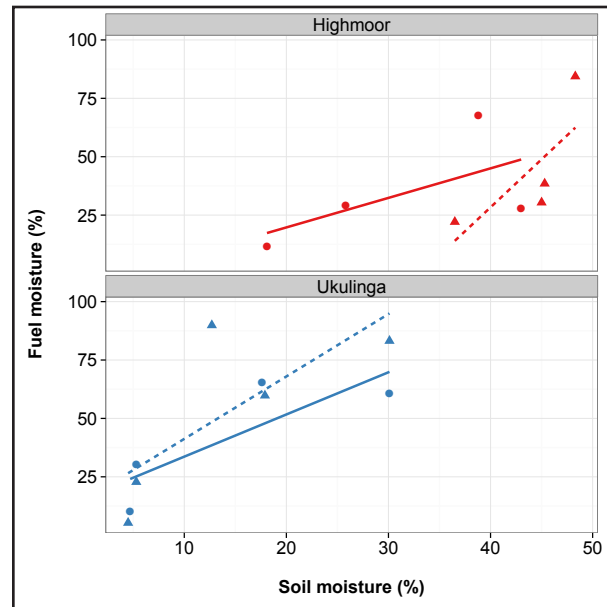


Figure 4. Linear regression lines generalize the relationship between fuel moisture and soil moisture at two sampling locations over four sampling events in two South African grasslands. Analysis of deviance indicated that, over all sites and locations, soil moisture was a significant term in a linear mixed-effect regression model ($\chi^2 = 3.97$, $P = 0.05$, 95% CI = 0.01 to 0.08). Sampling period spans end of the growing season into late winter. Each symbol represents mean of two samples per sample point, and differences in line and character shape represent spatially discrete sampling points within study locations.

DISCUSSION

Our data on fuel and soil moisture in South African grasslands were characterised by variability from several sources. First, variability among sampling sites and sampling dates within locations highlights the importance of not only replication and sample sizes, but also analytical sensitivity to this variation—accounting for it, not attempting to average it away—through hierarchical sampling and analysis (Twidwell *et al.* 2009). Secondly, variability among locations and species indicates that broad biogeographic and compositional similarities among plant communities do not adequately describe fuelbed dynamics.

Although limited to four sites across two locations in a single year, the temporal breadth and species-level specificity of our study constitute novel data that suggest areas where additional research is needed—or perhaps not needed—to gain a better understanding of fuelbed ecology in grasslands worldwide, beyond the context of extreme fire weather and behaviour.

We provide evidence that fuel moisture has a linear relationship with soil moisture, and found that the nature of the relationship (as characterised by the slope of the regression line) is spatially variable and might be soil-type dependent. While a positive association between soil moisture and live fuel moisture has been described for woody plants in a savannah-scrub type ecosystem (Qi *et al.* 2012), to our knowledge, ours is the first report on such an association in mesic grassland. The relationship is promising because sampling fuel moisture directly is labour-intensive, but soil moisture can be monitored continuously with electronic sensors and even remotely sensed (Qi *et al.* 2012). The spatial resolution and temporal replication of our data are too limited to inform accurate predictions, but they do suggest value in additional research on the relationship between fuel moisture and soil moisture, especially given the dependence of fire behaviour on fuel moisture (Govender *et al.* 2006, McGranahan *et al.* 2012).

An important ecological function of fire in mesic African rangelands is controlling the encroachment of woody plants, or “bush” (Trollope 1980). Effecting bush mortality—or at least substantial set-back of vigorous re-sprouters—requires relatively high fire intensity, which is a function of several factors including fuel load and moisture (Twidwell *et al.* 2009). We set fuel load as the average productivity for each grassland and determined that predicted fire intensity varies substantially with fuel moisture at each location. Conventional wisdom places the bush control threshold at approximately 2000 kW m⁻¹ (Trollope and Trollope 2004). While all of our estimated values technically exceeded 2000 kW m⁻¹, ob-

taining fire intensity substantially greater than the minimal threshold value required one and two and a half months curing time at Ukulinga and Highmoor, respectively.

Species-level variation in fuel moisture and predicted fire intensity at Highmoor might reflect a global syndrome of high-moisture, C₃ grasses reducing fire intensity and spread, but more focused research is required. It is difficult to distinguish whether we can attribute higher moisture and lower fire intensity of the C₃ *Festuca costata* in our data to phylogeny or physiology. Patterns in traits among South African grasses were recently attributed to phylogeny rather than different photosynthetic pathways, owing to unique responses among *Aristida* species compared to other C₄ grasses (Ripley *et al.* 2015) consistent with our data on *Aristida junciformis* (Figures 2 and 3). *Festuca costata*'s pattern of higher fuel moisture and lower predicted fire intensity than C₄ grasses is reminiscent of *Festuca* species in other rangelands: in Patagonia, *Festuca pallezens* (St.-Yves) Parodi has lower flammability than neighbouring grasses (Gonzalez *et al.* 2015); and in North American tallgrass prairie, the invasive *Festuca arundinacea* Schreb. (syn. *Lolium arundinaceum* [Schreb.] S.J. Darbyshire) reduces fire spread (McGranahan *et al.* 2013). However, the effect of *F. arundinacea* is specifically attributed to high live fuel moisture during the otherwise dormant period of native C₄ grasses (McGranahan *et al.* 2012), and Trollope's fire intensity equation does not distinguish between live and dead fuels. *F. costata* fuel moisture must be measured as live and dead components and modeled as such; the BehavePlus system does so, and although no fuel models have been specifically developed for African rangeland (Trollope and Trollope 2002), recent versions allow users to customise several fuelbed parameters (Andrews *et al.* 2008).

Ecologically meaningful differences in fire behaviour among species might create positive feedbacks in the plant community that create and increase variability among patches. Dis-

turbance that follows a spatially discrete pattern—such as heterogeneous plant community composition—can reinforce the underlying pattern by creating increasingly contrasting patches internally similar in response and increasingly variable at the landscape level (Kotliar and Wiens 1990, Adler *et al.* 2001). In these grasslands, emergence of patchiness likely depends on the fuel moisture at which these grasslands are burned: early-season fires conducted when variability in fuel moisture is high are more prone to variable fire intensities, especially at Highmoor, than later-season burns in homogeneously cured stands (Figure 3). But some areas of South Africa seek to increase the variability of burn season with more prescribed ignitions outside of the dry season (e.g., van Wilgen *et al.* 2004). In the Drakensberg grasslands, *F. costata* often occurs as discrete patches (D.A. McGranahan, North Dakota State University, Fargo, USA, unpublished data) that could benefit from lower-intensity burns and increased competitive advantage following fire relative to neighbouring C₄ species, a classic model of positive feedbacks in fire regime alteration (Brooks *et al.* 2004).

Variation in fire intensity among grass types and patches might have landscape-level implications that could be exacerbated by global environmental change, but further research into the interactions between plant biology and soil is required to determine the magnitude and direction of these changes. Drakensberg grasslands sit at an altitudinal transition between C₄-dominated montane grassland and sub-montane grassland interspersed with *Festuca costata* (Killick 1963). If the competitive advantages conferred by C₄ photosynthesis are considered, C₃ species like *F. costata* might be expected to retreat upslope as local

environments become hotter and drier (Edwards *et al.* 2010). But many Festucoid grasses are infected by fungal endophytes that can increase drought tolerance in the host (Hahn *et al.* 2008, Gibert and Hazard 2011). *F. costata* has only recently been identified as an endophyte host, and any ecological effects of the association remain to be determined (McGranahan *et al.* 2015). Understanding *F. costata* fire ecology will be enhanced by better knowledge of how *F. costata* responds to increased air temperature, altered moisture regimes, and atmospheric carbon dioxide fertilization, and how these relationships are affected by endophyte infection.

Our study suggests ways in which grassland fuelbeds might be considered both in current decision making and in plans to mitigate and manage global environmental change. We show that in compositionally similar grassland communities, both environmental factors and fuelbed dynamics can have substantial spatial variation: Ukulinga, a low-elevation location where grasses cured rapidly and consistently under hotter air temperature and a discrete rainy season, presented little variability for managers to consider; whereas the environmental context of Highmoor contributed to slower curing response, differences between species, and association between fuel and soil moisture. While the magnitude of differences in our data do not suggest radical alteration of fire practice and planning, we do hope that fire managers in South Africa and abroad consider heterogeneity within grassland fuelbeds and recognize seasonal changes to ensure that objectives are obtainable prior to burns, and to explain post-burn spatial variation in fire effects within a fuelbed that might have appeared homogeneous.

ACKNOWLEDGEMENTS

We appreciate assistance from N. Zama in the field and lab and T. Parr for statistical assistance. D.A. McGranahan appreciates support from the US State Department's Fulbright Scholarship program, the National Research Foundation of South Africa, and the North Dakota Agricultural Experiment Station.

LITERATURE CITED

- Adler, P.B., D.A. Raff, and W.K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479. doi: [10.1007/s004420100737](https://doi.org/10.1007/s004420100737)
- Andrews, P.L., C. Bevins, and R. Seli. 2008. BehavePlus fire modeling system. Version 4.0: users guide. USDA Forest Service General Technical Report RMRS-GTR-106WWW, Revised, Rocky Mountain Research Station, Ogden, Utah, USA.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. lme4: linear mixed-effects models using Eigen and S4. R package version 1.0-5. <<http://CRAN.R-project.org/package=lme4>>. Accessed 23 January 2016.
- Bowman, D.M.J.S., J. Balch, P. Artaxo, W.J. Bond, M.A. Cochrane, C.M. D'Antonio, R. DeFries, F.H. Johnston, J.E. Keeley, M.A. Krawchuk, C.A. Kull, M. Mack, M.A. Moritz, S. Pyne, C.I. Roos, A.C. Scott, N.S. Sodhi, and T.W. Swetnam. 2011. The human dimension of fire regimes on Earth. *Journal of Biogeography* 38: 2223–2236. doi: [10.1111/j.1365-2699.2011.02595.x](https://doi.org/10.1111/j.1365-2699.2011.02595.x)
- Brooks, M.L., C.M.D. Antonio, D.M. Richardson, J.B. Grace, J. Keeley, J.M. DiTomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677–688. doi: [10.1641/0006-3568\(2004\)054\[0677:EOIAP0\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAP0]2.0.CO;2)
- Buis, G.M., J.M. Blair, D.E. Burkepille, C.E. Burns, A.J. Chamberlain, P.L. Chapman, S.L. Collins, R.W.S. Fynn, N. Govender, K.P. Kirkman, M.D. Smith, and A.K. Knapp. 2009. Controls of aboveground net primary production in mesic savanna grasslands: an inter-hemispheric comparison. *Ecosystems* 12: 982–995. doi: [10.1007/s10021-009-9273-1](https://doi.org/10.1007/s10021-009-9273-1)
- Coughlan, M.R., and A.M. Petty. 2012. Linking humans and fire: a proposal for a transdisciplinary fire ecology. *International Journal of Wildland Fire* 21: 477–487. doi: [10.1071/WF11048](https://doi.org/10.1071/WF11048)
- D'Antonio, C.M. 2000. Fire, plant invasions, and global changes. Pages 65–93 in: H.A. Mooney and R.J. Hobbs, editors. *Invasive species in a changing world*. Island Press, Washington, D.C., USA.
- Davies, K.W., J.D. Bates, T.J. Svejcar, and C.S. Boyd. 2010. Effects of long-term livestock grazing on fuel characteristics in rangelands: an example from the sagebrush steppe. *Rangeland Ecology and Management* 63: 662–669. doi: [10.2111/REM-D-10-00006.1](https://doi.org/10.2111/REM-D-10-00006.1)
- Edwards, E.J., C.P. Osborne, C.A.E. Stromberg, S.A. Smith, C₄ Grasses Consortium, W.J. Bond, P.A. Christin, A.B. Cousins, M.R. Duvall, D.L. Fox, R.P. Freckleton, O. Ghannoum, J. Hartwell, Y. Huang, C.M. Janis, J.E. Keeley, E.A. Kellogg, A.K. Knapp, A.D.B. Leakey, D.M. Nelson, J.M. Saarela, R.F. Sage, O.E. Sala, N. Salamin, C.J. Still, and B. Tipple. 2010. The origins of C₄ grasslands: integrating evolutionary and ecosystem science. *Science* 328: 587–591. doi: [10.1126/science.1177216](https://doi.org/10.1126/science.1177216)
- Ellis, E.C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6: 439–447. doi: [10.1890/070062](https://doi.org/10.1890/070062)
- Everson, T.M., C.S. Everson, H.M. Dicks, and A.G. Poulter. 1988. Curing rates in the grass sward of the Highland Sourveld in the Natal Drakensberg. *South African Forestry Journal* 145: 1–8. doi: [10.1080/00382167.1988.9630327](https://doi.org/10.1080/00382167.1988.9630327)
- Everson, T.M., F.R. Smith, and C.S. Everson. 1985. Characteristics of fire behaviour in the montane grasslands of Natal. *Journal of the Grassland Society of Southern Africa* 2: 13–21. doi: [10.1080/02566702.1985.9648006](https://doi.org/10.1080/02566702.1985.9648006)

- FAO [Food and Agriculture Organisation]. 2001. Major soils of the world: world reference base for soil resources. World Soil Resources Reports. <<http://www.isric.org/projects/soter-south-africa>> Accessed 24 January 2016.
- Gibert, A., and L. Hazard. 2011. Endophyte infection of *Festuca eskia* enhances seedling survival to drought and cutting at the expense of clonal expansion. *Journal of Plant Ecology* 4: 201–208. doi: [10.1093/jpe/rtr009](https://doi.org/10.1093/jpe/rtr009)
- Gonzalez, S.L., L. Ghermandi, and D.V. Peláez. 2015. Fire temperature effects on perennial grasses from northwestern Patagonian grasslands. *Ecological Research* 30: 67–74. doi: [10.1007/s11284-014-1210-x](https://doi.org/10.1007/s11284-014-1210-x)
- Govender, N., W.S.W. Trollope, and B.W. Van Wilgen. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43: 748–758. doi: [10.1111/j.1365-2664.2006.01184.x](https://doi.org/10.1111/j.1365-2664.2006.01184.x)
- Hahn, H., M.T. McManus, K. Warnstorff, B.J. Monahan, C.A. Young, E. Davies, B.A. Tapper, and B. Scott. 2008. *Neotyphodium* fungal endophytes confer physiological protection to perennial ryegrass (*Lolium perenne* L.) subjected to a water deficit. *Environmental and Experimental Botany* 63: 183–199. doi: [10.1016/j.envexpbot.2007.10.021](https://doi.org/10.1016/j.envexpbot.2007.10.021)
- Hobbs, N.T., and M.B. Hooten. 2015. Bayesian models: a statistical primer for ecologists. Princeton University Press, New Jersey, USA. doi: [10.1515/9781400866557](https://doi.org/10.1515/9781400866557)
- Hothorn, T., F. Bretz, and P. Westfall. 2013. R package multcomp. <<http://cran.stat.sfu.ca/web/packages/multcomp/multcomp.pdf>>. Accessed 23 January 2016.
- ISRIC [International Soil Reference and Information Centre]. 2008. Soil and terrain database (SOTER) for South Africa. Version 1.0. ISRIC—World Soil Information. <<http://www.isric.org/projects/soter-south-africa>>. Accessed 24 January 2016.
- Kerby, J.D., S.D. Fuhlendorf, and D.M. Engle. 2007. Landscape heterogeneity and fire behavior: scale-dependent feedback between fire and grazing processes. *Landscape Ecology* 22: 507–516. doi: [10.1007/s10980-006-9039-5](https://doi.org/10.1007/s10980-006-9039-5)
- Killick, D.J.B. 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Botanical Survey Memoir No. 34, Republic of South Africa Department of Agricultural Technical Services, Pretoria, South Africa.
- Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253–260. doi: [10.2307/3545542](https://doi.org/10.2307/3545542)
- Laris, P. 2011. Humanizing savanna biogeography: linking human practices with ecological patterns in a frequently burned savanna of southern Mali. *Annals of the Association of American Geographers* 101: 1067–1088. doi: [10.1080/00045608.2011.560063](https://doi.org/10.1080/00045608.2011.560063)
- Laris, P., and D.A. Wardell. 2006. Good, bad or “necessary evil”? Reinterpreting the colonial burning experiments in the savanna landscapes of West Africa. *The Geographical Journal* 172: 271–290. doi: [10.1111/j.1475-4959.2006.00215.x](https://doi.org/10.1111/j.1475-4959.2006.00215.x)
- Leonard, S., J. Kirkpatrick, and J. Marsden-Smedley. 2010. Variation in the effects of vertebrate grazing on fire potential between grassland structural types. *Journal of Applied Ecology* 47: 876–883. doi: [10.1111/j.1365-2664.2010.01840.x](https://doi.org/10.1111/j.1365-2664.2010.01840.x)
- McGranahan, D.A., R. Burgdorf, and K.P. Kirkman. 2015. Epichloae infection in a native South African grass, *Festuca costata* Nees. *Plant Biology* 17: 914–921. doi: [10.1111/plb.12307](https://doi.org/10.1111/plb.12307)
- McGranahan, D.A., D.M. Engle, S.D. Fuhlendorf, J.R. Miller, and D.M. Debinski. 2012. An invasive cool-season grass complicates prescribed fire management in a native warm-season grassland. *Natural Areas Journal* 32: 208–214. doi: [10.3375/043.032.0214](https://doi.org/10.3375/043.032.0214)

- McGranahan, D.A., D.M. Engle, J.R. Miller, and D.M. Debinski. 2013. An invasive grass increases live fuel proportion and reduces fire spread in a simulated grassland. *Ecosystems* 16: 158–169. doi: [10.1007/s10021-012-9605-4](https://doi.org/10.1007/s10021-012-9605-4)
- Mentis, M.T., and R.C. Bigalke. 1981. The effect of scale of burn on the densities of grassland francolins in the Natal Drakensberg. *Biological Conservation* 21: 247–261. doi: [10.1016/0006-3207\(81\)90081-1](https://doi.org/10.1016/0006-3207(81)90081-1)
- Nakagawa, S., and I.C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* 82: 591–605. doi: [10.1111/j.1469-185X.2007.00027.x](https://doi.org/10.1111/j.1469-185X.2007.00027.x)
- Nyamadzawo, G., W. Gwenzi, A. Kanda, A. Kundhlande, and C. Masona. 2013. Understanding the causes, socio-economic and environmental impacts, and management of veld fires in tropical Zimbabwe. *Fire Science Reviews* 2: 1–13. doi: [10.1186/2193-0414-2-2](https://doi.org/10.1186/2193-0414-2-2)
- Qi, Y., P.E. Dennison, J. Spencer, and D. Riaño. 2012. Monitoring live fuel moisture using soil moisture and remote sensing proxies. *Fire Ecology* 8(3): 71–87. doi: [10.4996/fireecology.0803071](https://doi.org/10.4996/fireecology.0803071)
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricci, V. 2005. Fitting distributions with R. Contributed documentation available on CRAN. <<http://cran.r-project.org/doc/contrib/Ricci-distributions-en.pdf>>. Accessed 23 January 2016.
- Ripley, B., V. Visser, P.-A. Christin, S. Archibald, T. Martin, and C. Osborne. 2015. Fire ecology of C₃ and C₄ grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology* 96: 2679–2691. doi: [10.1890/14-1495.1](https://doi.org/10.1890/14-1495.1)
- Sauer, C.O. 1950. Grassland climax, fire, and man. *Journal of Range Management* 3: 16–21. doi: [10.2307/3894702](https://doi.org/10.2307/3894702)
- Shaffer, L.J. 2010. Indigenous fire use to manage savanna landscapes in southern Mozambique. *Fire Ecology* 6(2): 43–59. doi: [10.4996/fireecology.0602043](https://doi.org/10.4996/fireecology.0602043)
- Snyman, H.A. 2004. Estimating the short-term impact of fire on rangeland productivity in a semi-arid climate of South Africa. *Journal of Arid Environments* 59: 685–697. doi: [10.1016/j.jaridenv.2004.02.002](https://doi.org/10.1016/j.jaridenv.2004.02.002)
- Trollope, S., and L.A. Trollope. 2004. Prescribed burning in African grasslands and savannas for wildlife management. *Arid Lands Newsletter* 55: May/June 2004.
- Trollope, W. 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa* 15: 173–177. doi: [10.1080/00725560.1980.9648907](https://doi.org/10.1080/00725560.1980.9648907)
- Trollope, W. 2011. Personal perspectives on commercial versus communal African fire paradigms when using fire to manage rangelands for domestic livestock and wildlife in southern and east African ecosystems. *Fire Ecology* 7(1): 57–73. doi: [10.4996/fireecology.0701057](https://doi.org/10.4996/fireecology.0701057)
- Trollope, W.S.W., and L.A. Trollope. 2002. Fire behaviour a key factor in the fire ecology of African grasslands and savannas. Oral presentation 204 in: D.X. Viegas, editor. *Forest Fire Research & Wildland Fire Safety. Proceedings of the IV International Conference on Forest Fire Research, 2002 Wildland Fire Safety Summit*. Luso, Coimbra, Portugal, 18–23 November 2002. Millpress, Rotterdam, The Netherlands.
- Twidwell, D., S.D. Fuhlendorf, D.M. Engle, and C.A. Taylor. 2009. Surface fuel sampling strategies: linking fuel measurements and fire effects. *Rangeland Ecology and Management* 62: 223–229. doi: [10.2111/08-124R2.1](https://doi.org/10.2111/08-124R2.1)

- Uys, R.G., W.J. Bond, and T.M. Everson. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118: 489–499. doi: [10.1016/j.biocon.2003.09.024](https://doi.org/10.1016/j.biocon.2003.09.024)
- van Wilgen, B., N. Govender, H. Biggs, D. Ntsala, and X. Funda. 2004. Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conservation Biology* 18: 1533–1540. doi: [10.1111/j.1523-1739.2004.00362.x](https://doi.org/10.1111/j.1523-1739.2004.00362.x)
- van Wilgen, B.W., N. Govender, G.G. Forsyth, T. Kraaij, and B. van Wilgen. 2011. Towards adaptive fire management for biodiversity conservation: experience in South African national parks. *Koedoe* 53: 1–9. doi: [10.4102/koedoe.v53i2.982](https://doi.org/10.4102/koedoe.v53i2.982)
- Winter, S.L., S.D. Fuhlendorf, C.L. Goad, C.A. Davis, K.R. Hickman, and D.M. Leslie Jr. 2012. Restoration of the fire-grazing interaction in *Artemisia filifolia* shrubland. *Journal of Applied Ecology* 49: 242–250. doi: [10.1111/j.1365-2664.2011.02067.x](https://doi.org/10.1111/j.1365-2664.2011.02067.x)