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Grass functional trait responses to experimental warming and fire in Afromontane grasslands

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Climate change is one of the main challenges facing humanity in the coming century. To understand the impact of climate change on biodiversity and ecosystem functioning, we urgently require a better understanding of plant responses to climate change. To address this knowledge gap we established a full-factorial warming experiment using open-top chambers (OTCs) inside a long-term fire-manipulation experiment in Afromontane fire-climax grasslands. Fire is an essential ecosystem driver in these grasslands, but has rarely been included in experimental climate change research. To assess growth responses to elevated temperatures and fire frequency, we measured four functional traits: vegetative height, leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC). Grasses responded to fire exclusion with increased height, and lower LA, SLA, and LDMC. Grasses responded to warming with lower height and LA, and higher LDMC, suggesting that plant growth was negatively affected by warming. This response was mostly attributed to intra-specific trait variability, highlighting an important role for trait plasticity in community-level processes to mediate the response of montane grassland communities to elevated temperatures and associated drought effects. These results are a first step towards establishing a more mechanistic basis for understanding future climatic changes in Afromontane grasslands.

Keywords: climate change, montane, plant functional traits

Introduction

As the effects of climate change are becoming increasingly evident, being able to predict ecosystem responses to increased temperatures is of utmost importance (Buhrmann et al. 2016; Björkman et al. 2018). Already, global surface temperatures have increased by approximately 0.8 °C in the last century and are expected to rise another 1.4–5.8 °C during the 21st century (IPCC 2013). Temperature increases affect plant communities worldwide and are predicted to result in longer growing periods, higher plant fecundity, higher biomass allocation towards roots, and in the African context, a possible shift from grass-dominated towards tree-dominated biomes (Scheiter and Higgins 2009; Midgley and Bond 2015). Such changes are likely to affect the important services delivered by grassland ecosystems, such as water provisioning and carbon sequestration (Lamarque et al. 2014). Therefore, predicting these ecosystem responses to a warming climate using knowledge gained in climate-manipulation experiments is becoming increasingly important. Climate-manipulation experiments provide a powerful way of testing how plant communities respond to increasing temperatures associated with climate change. However, recent literature

highlights the strong geographical bias towards performing warming experiments in temperate, boreal and arctic systems where temperature effects are likely to be more pronounced. There is currently a lack of reliable data and insight regarding the impact of climate warming on plant communities in tropical and subtropical systems (Laurance et al. 2011, Cavaleri et al. 2015), particularly from Africa.

Forty to fifty percent of Africa is dominated by grassy biomes, i.e. grasslands and savannas with varying degrees of tree cover (White 1983; Parr et al. 2014). Grasslands play a critical role in nutrient cycling, water retention and the global carbon cycle (Fynn et al. 2005; Parr et al. 2014). Southern African grasslands hold multiple biodiversity hotspots, and are largely dominated by highly productive C4 grasses that provide fuel for frequent fires (Forrestel et al. 2014; Gordijn et al. 2018). However, there is a large knowledge gap regarding climate change impacts in these grasslands. In Africa, a major part of the human population directly depends on grassy biomes for their subsistence (Thomas et al. 2007), which makes the African continent very vulnerable to climate change impacts and increased climatic variability (Engelbrecht et al. 2015). The montane

grasslands of Africa are particularly vulnerable to the effects of increasing temperatures, having evolved to exist at the cooler end of Africa's temperature gradient and being characterised by high elevations and relatively cool climates (Meadows and Linder; 1993; Finch and Marchant 2011). Two regions in Africa support montane grasslands: the higher altitudes of the east African Rift Valley system and the Great Escarpment in southern Africa. These Afromontane grasslands are host to a unique, fire-dependent ecology, which supports high levels of endemism and biodiversity (Meadows and Linder 1993; Finch and Marchant 2011; Gordijn et al. 2018). In addition to their sensitivity to temperature-induced habitat shifts, Afromontane grasslands are at risk from changes in fire regimes, a predicted indirect effect of climate change (Midgley and Bond 2015).

Many African grasslands are fire-climax ecosystems, i.e. climax communities that are maintained by periodic fires (White 1983; Mucina & Rutherford 2006). For this reason, burning is a common grassland management practice (Behling and Pillar 2007; Archibald 2016), and is therefore important to take into account in climate change manipulation experiments. In mesic grasslands, burning results in increased biomass production, an extended growing season, and positively affects biodiversity and basal cover (Ojima et al 1994; Boakye et al. 2013; Gordijn et al. 2018). Fire also affects soil chemical, physical and biological properties (Michelsen et al. 2004; Manson et al. 2007; Granged et al. 2011), as well as soil organic carbon (Fynn et al. 2003), although processes are complex and poorly understood (Archibald et al. 2018). The future of Africa and that of other tropical grassy ecosystems involves a hotter and drier climate (Engelbrecht et al. 2015), which is expected to severely affect global fire regimes. Fire seasons are expected to increase in intensity and duration over the coming decades, paired with longer periods of extreme droughts (Jolly et al. 2015). Temperature increases and related water deficits may change the properties of the fuel load by affecting plant growth and mortality (Osborne et al. 2018), but also result in a higher probability of more intense wildfires that may increase the effects on plant communities (Werf et al. 2010) and restrict the post-fire recovery of plants (Prieto et al. 2009). A better understanding of how grasslands will respond to increased temperatures and altered fire regimes can help contribute to their future conservation and management.

Plant traits, i.e. morphological, structural or physiological characteristics that influence overall fitness of individual organisms, are powerful predictors of ecosystem response and can be used to define the ecological roles of species in an environment (Diaz and Cabido 2001). At the ecosystem level plant traits determine primary productivity, litter decomposability, carbon and nutrient cycling and hydrology (Björkman et al. 2018). The most commonly measured functional traits in plant ecology are leaf traits, such as leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC). These traits have been shown to strongly correlate to size and resource economics (Wright et al. 2004). The current study will focus on two traits related to the leaf economic spectrum (Wright et al. 2004), SLA and LDMC, and two size-related traits, leaf area and plant height.

Size-related traits reflect the competitive ability with respect to light capture (Hudson et al. 2011), whereas traits related to the leaf economics spectrum affect plant resource acquisition and resource-use strategies at leaf, plant and community level and, hence, reflect plant community functioning (Lavorel and Garnier 2002; Wright et al. 2004). The SLA is positively correlated to the relative growth rate (RGR) (Poorter and Remkes 1990), the photosynthetic rate and leaf nitrogen (N) content of a plant and negatively correlated with leaf longevity (Pérez-Harguindeguy et al. 2013). Therefore, a high SLA allows an early successional plant to efficiently produce leaf area at a low cost for construction and support (Poorter and Remkes 1990, Garnier et al. 2001). Opposite to SLA, LDMC is often negatively correlated with the relative growth rate of a plant and positively with leaf lifespan (Garnier et al. 2001; Hudson et al. 2011). The LDMC is a good predictor of resource capture, usage and availability and is related to a plant's water-use strategy (Wright et al. 2001; Chaves et al. 2002). Leaves with high LDMC tend to be relatively tough and decompose slower, compared with leaves with a low LDMC content (Pérez-Harguindeguy et al. 2013). Therefore, SLA and LDMC often represent a trade off in plant functioning between a fast growth strategy (high SLA, low LDMC) versus an efficient nutrient-conservation strategy (low SLA, high LDMC), although this relationship seems to be less straightforward in disturbance-driven systems that are controlled by fire or herbivory (Forrestel et al. 2014; Wigley et al. 2016).

To study how Afromontane grassland communities respond to global warming in interaction with fire, we established a full-factorial warming experiment in January 2017 using transparent hexagonal open-top chambers (OTCs) inside a unique long-term fire-manipulation experiment, the Brotherton trial. Despite some clear disadvantages, such as changes in wind, soil moisture and humidity (Harte et al. 1995; Marion et al 1997), OTCs are an effective and widely used method to passively elevate air temperature by 1–2 °C and soil temperatures by 0.5–1 °C above ambient. We measured four key functional traits of the dominant grass species (vegetative height, LA, SLA and LDMC) to assess changes in growth in response to elevated temperatures and fire frequency. Two alternative hypotheses regarding plant responses to warming were tested. The first hypothesis is based on the plant response to warming in Northern temperate, boreal and Arctic ecosystems (Hudson et al. 2011; Björkman et al. 2018), where plants respond to warming with enhanced growth. Here, we expect the size-related traits vegetative height and leaf area, to increase with elevated temperatures. For the traits related to resource economics, we expect a fast growth strategy, i.e. SLA to increase and LDMC to decrease with warming. The alternative hypothesis is based on the plant response to warming in dryland ecosystems (Musil et al. 2005, 2009), where an increase in temperature could exceed the optimal for photosynthesis and result in increased evaporative stress. Here, size-related traits (height and LA) would be expected to decrease with elevated temperatures. Similarly, for the traits related to resource economics, SLA would be expected to decrease to reduce transpiration, whereas LDMC would be expected to increase, because the leaf water content would decrease

under heat stress. For the fire treatments, we expect a shift in the grassland community towards tall and slow-growing species with lower fire frequency (Fynn et al. 2005, 2011), i.e. grasses with higher vegetative height, lower LA and SLA, and higher LDMC.

Methods

Study area

The experiment is situated on the Brotherton plateau near Cathedral Peak (29°00' S, 29°15' E), uKahlamba Drakensberg Park, South Africa (Figure 1) at an altitude of 1 890 m (Manson et al. 2007). The geology underlying the plateau consists of basalt on top of cave sandstone. Soils over the experimental area are humic and oxidic (Manson et al. 2007). This area has a temperate humid climate, with mean monthly temperatures ranging between 17.1 °C during the hottest month (January) and 10.0 °C in the coldest month (June) (Manson et al. 2007). The mean annual precipitation is 1 380 mm (Gordijn et al. 2018), of which the largest part falls in the summer months (October to March) and some occasional snow during winter (May to August). Weather data were collected at several elevations in the study area from 2012 onwards. We used data from a fully automated weather station (Mike's Pass) located at the same elevation, approximately 1.5 km from the Brotherton plateau. The native vegetation in this study area is classified as uKahlamba Basalt Grassland, dominated by the grass *Themeda triandra* Forssk (Mucina and Rutherford 2006).

Experimental design

In January 2017, hexagonal Open-Top Chambers (OTCs) were set-up within the Brotherton trial, a long-term fire-manipulation experiment that has been ongoing since 1980 to examine the effects of different fire regimes on plant community dynamics in montane grasslands (Figures 1 and 2). Each OTC was paired with a 1 × 1 m control plot, placed 2 m from the OTC. The dimensions of the OTCs were modeled after the International Tundra Experiment (ITEX) and OTCs had an inside diameter of 1.6 m, with a height of 58 cm (Molau and Mølgaard 1996; Marion et al. 1997). The Brotherton trial consists of 25 × 25 m plots with different fire frequencies (annual, biennial, quinquennial, fire exclusion) and burning season (spring, autumn, alternating) in a randomised block design (Manson et al. 2007). In the winters of 2000, 2007 and 2016 unplanned arson fires burned through the experiment. The 2016 arson fire removed all the standing biomass on all fire treatments just four months prior to the initiation of the warming treatment. However, the long-term soil legacy effect of the different fire treatments should still be present and biomass quickly recovered (Mvelase, in prep). OTCs and control plots were placed in the periphery of the fire plots across all fire frequencies (annual, biennial, quinquennial and fire exclusion), for only the spring burns. This resulted in a full-factorial randomised-block experiment with two main treatments: warming and fire frequency, with a replication of four (Figure 1). OTCs are only taken off during the application of the fire treatment in October. The plots receiving the annual fire treatment were burned in October

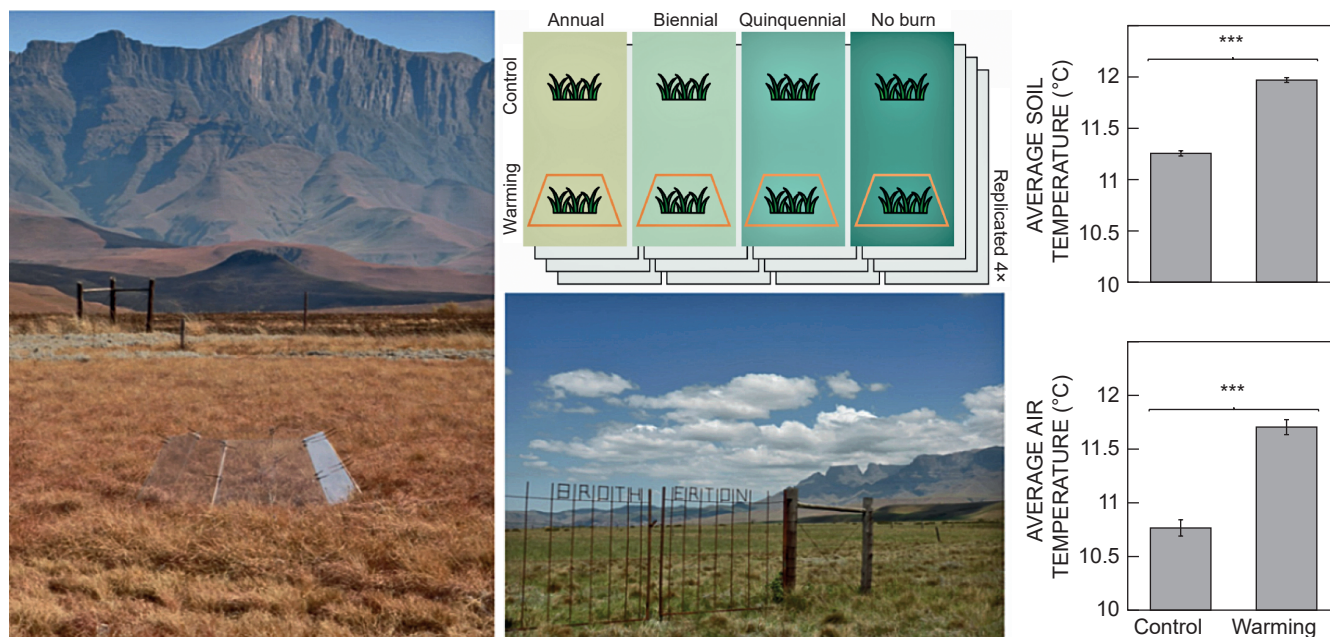


Figure 1: Experimental lay-out of the warming × fire experiment in the uKahlamba-Drakensberg Mountains, South Africa. The experiment is set up in a full-factorial randomised block design (Mariska te Beest, $n = 4$). Fire treatments include annual, biennial and quinquennial burns and a no-burn control, each with an OTC paired with a 1 × 1 m control plot. Experimental burning takes place in October. The OTCs are then removed for 1–2 weeks. Temperature measurements for 2017–2018 show that OTCs increased average daily air temperatures by 1 °C and soil temperature by 0.7 °C. Asterisks denote significant differences ($. < 0.1$, $* < 0.5$, $** < 0.1$, $*** < 0.001$) between control plots and OTCs after repeated measures ANOVA. Images by M te Beest

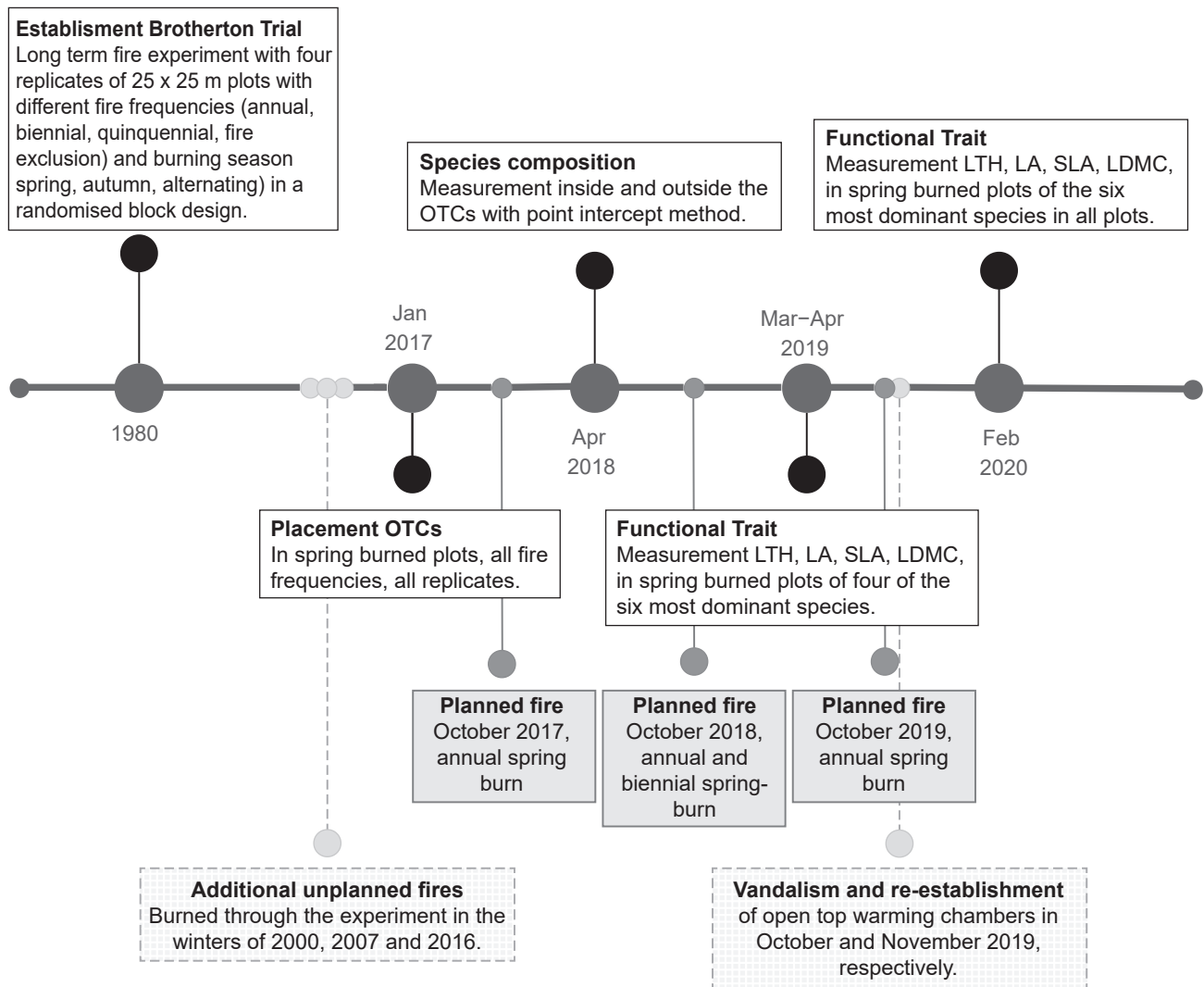


Figure 2: A timeline of the experimental treatments and sampling dates. OTC: open-top chambers, LTH: leaf table height, LA: leaf area, SLA: specific leaf area, LDMC: leaf dry matter content

2017, 2018 and 2019. The plots receiving the biennial fire treatment were burned in October 2018. The quinquennial and fire exclusion plots did not receive a fire treatment since the arson fire of 2016. In October 2019 the OTCs were unfortunately subject to vandalism. They were re-erected a month later in November 2019, just before the growing season. Air and soil temperature were monitored at hourly intervals between January 2017 and November 2017, and at 4-hour intervals from November 2017 to April 2019 using Thermochron DS1921G iButtons (Maxim Integrated).

Data collection

In April 2018 (15 months after OTC set-up), we measured species composition inside and outside the OTCs using a point-intercept method with a levy bridge, a standing frame that holds seven pins vertically aligned, with a distance of 10 cm between pins. The bridge was placed across the sample plot seven times to create seven equidistant rows of sampling points ($n = 49$). We recorded one hit

per pin recording the nearest plant basal stem of tuft at ground level, including bare soil. We measured species composition in 30 of the 32 plots. Data were excluded from one no-burn plot and its adjacent control that has been invaded with non-native brambles (*Rubus cuneifolius*). Relative abundances per species were calculated as the percentage of hits relative to the total amount of sampled points per plot (Mariska te Beest, $n = 49$). The plant community consisted on average of 67% grasses, 11% bare soil and 22% forbs and dwarf shrubs, notably *Bulbostylis humilis*, *Commelina africana*, *Oxalis obliquifolia* and several *Helichrysum* species. The six dominant grass species included in this study (see below) represented on average 64% of the total number of hits per plot, which represented on average 96% of the total grass community. Plant functional traits were measured in the OTCs and control plots in March-April 2019 and February 2020. Figure 2 presents a timeline of the experimental treatments and data collection.

Trait measurements

We measured four leaf traits (vegetative height, LA, SLA and LDMC) for the six most dominant grass species present in the OTCs and control plots: *Themeda triandra*, *Tristachya leucothrix*, *Heteropogon contortus*, *Harpochloa falx*, *Stiburus alopecuroides* and *Koeleria capensis*. These species were selected *a priori*, based on their relative abundances derived from the 2018 species composition data (Mvelase, in prep). For the 2019 trait data, we randomly selected a maximum of ten grass tufts per species in the OTCs and control plots spread across the fire treatments where they occurred (see Table 1 for sample sizes). Two species (*Stiburus alopecuroides* and *Koeleria capensis*) were not collected inside the OTCs in 2019, because of low abundances and time constraints. For the 2020 trait data, we used a similar approach, albeit with larger sample sizes and inclusion of the two missing species (see Table 1). We randomly selected a maximum of six grass tufts per species from the OTCs for each of the four fire treatments and the same for the control plots for the spring burn plots only. For both years, the measurements of individual traits were conducted in the same way, albeit by different observers, following the protocols described in Perez-Harguindeguy (2013). Per tuft, the vegetative height was measured as leaf table height (LTH), i.e. the distance from the ground to the height where 80% of the leaves are subjectively judged to occur (Eskelinen et al. 2012). Five leaves per tuft were collected to measure: (i) LA, to determine fresh and dry weight to calculate (ii) SLA, the ratio of leaf area to dry mass ($\text{cm}^2 \text{g}^{-1}$), and (iii) LDMC, the leaf dry matter per unit leaf fresh mass (mg g^{-1} , Perez-Harguindeguy 2013). Data were averaged per tuft. We only selected relatively young, but fully expanded and hardened leaves from adult plants. To avoid dehydration in the field, the leaves were wrapped into moist paper and sealed in a plastic bag. The collected samples were stored in a cool box or fridge, until further processing in the laboratory. Fresh weight and leaf area were measured as soon as possible after collection. The leaves were cut from the stem (just above the ligule) and gently patted dry with tissue paper to remove any surface water. Leaf area was determined using a LI-3000C Leaf Area Meter (LI-COR, Lincoln, USA). Leaves were oven-dried at 50 °C for at least

48h, after which dry mass was determined. Leaves were weighed directly after being taken from the oven to avoid absorption of moisture from the air.

Community-weighted trait means

We calculated community-weighted trait means (CWM) using the relative abundance per plot for the six dominant species as weights. Community-weighted trait means are used to describe the trait composition of the whole community and are based on the assumption that each plant species is predicted to contribute to community functioning in proportion to its relative abundance (Eskelinen et al. 2012; Björkman et al. 2018). We calculated the CWM per species for the warming and ambient treatments separately (Table 1), but had to average across the different fire treatments, because of low sample sizes for the treatment combinations. For the two missing species in the 2019 data we used a fixed trait value, i.e. the average value for the species, for both the warmed and ambient plots. Trait values were multiplied by the relative abundance of each species measured in 2018 and afterwards summed across species to gain a single value for each trait per plot, CWM_{war} (Eskelinen et al. 2012; Björkman et al. 2018). Because the same relative abundance data were used to calculate the CWM for both the 2019 and 2020 trait data, they could not be regarded as independent and therefore both sampling periods were tested separately.

Intraspecific trait variability

We assessed the relative contribution of intraspecific trait variability (ITV) on the response of community-weighted mean traits. For this we calculated CWM with a single mean trait per species, averaged across all treatments ($\text{CWM}_{\text{fixed}}$), following de Bello et al. (2011). Their method is based on the comparison of CWM calculations where the trait variability per species is kept constant (i.e. one average value per trait per species used for the entire experiment, so that only species turn-over is taken into account [$\text{CWM}_{\text{fixed}}$]), to CWM calculations where the trait variability per species is allowed to vary across the experimental treatments to reflect both species turn-over and intraspecific trait variability. As explained in the previous paragraph, because of low sample size, we

Table 1: Trait means \pm standard deviation and the number of individuals sampled for the six study species per warming treatment. These trait values were used for the calculation of the CWM_{war}

Species	Treatment	Leaf table height		Leaf area (cm^2)		SLA ($\text{cm}^2 \text{g}^{-1}$)		LDMC (mg g^{-1})		Sample size	
		2019	2020	2019	2020	2019	2020	2019	2020	2019	2020
<i>Harpochloa falx</i>	Ambient	34.2 \pm 8.9	28.9 \pm 9.7	4.5 \pm 0.8	3.0 \pm 0.8	69.0 \pm 4.0	48.9 \pm 5.8	580.0 \pm 57.6	347.2 \pm 20.1	10	13
	Warming	27.5 \pm 12.0	35.8 \pm 8.5	3.3 \pm 1.8	3.3 \pm 0.7	73.3 \pm 10.5	46.8 \pm 5.5	611.5 \pm 71.5	346.8 \pm 15.9	14	12
<i>Heteropogon contortus</i>	Ambient	15.2 \pm 1.8	15.4 \pm 3.1	3.2 \pm 0.4	3.0 \pm 0.7	137.4 \pm 11.1	129.5 \pm 21.8	586.5 \pm 54.9	428.1 \pm 27.6	10	18
	Warming	14.2 \pm 1.7	13.3 \pm 2.7	2.8 \pm 0.6	2.6 \pm 0.7	131.0 \pm 6.7	140.8 \pm 43.0	567.0 \pm 37.8	448.8 \pm 41.4	7	18
<i>Koeleria capensis</i>	Ambient	20.6 \pm 5.0	12.5 \pm 2.6	1.9 \pm 0.5	1.3 \pm 0.6	68.9 \pm 19.3	56.4 \pm 13.7	742.4 \pm 87.2	438.8 \pm 60.1	10	6
	Warming	No data	12.8 \pm 6.2	No data	1.2 \pm 0.7	No data	54.6 \pm 8.7	No data	401.4 \pm 84.2	0	5
<i>Stiburus alopecuroides</i>	Ambient	23.5 \pm 4.3	19.3 \pm 6.1	1.9 \pm 0.3	3.1 \pm 0.8	74.7 \pm 15.6	123.6 \pm 33.9	656.4 \pm 55.0	438.7 \pm 102.8	10	25
	Warming	No data	19.5 \pm 6.1	No data	3.0 \pm 1.0	No data	125.4 \pm 26.6	No data	426.0 \pm 82.5	0	21
<i>Themeda triandra</i>	Ambient	32.1 \pm 5.2	26.6 \pm 5.9	5.4 \pm 2.7	6.4 \pm 2.0	121.2 \pm 13.1	171.0 \pm 45.6	710.5 \pm 74.0	447.4 \pm 45.8	10	24
	Warming	26.7 \pm 7.7	25.8 \pm 6.9	4.1 \pm 1.2	6.6 \pm 2.6	120.9 \pm 18.9	177.0 \pm 53.7	713.4 \pm 104.5	458.8 \pm 91.0	15	24
<i>Tristachya leucothrix</i>	Ambient	25.5 \pm 8.0	25.6 \pm 6.1	3.5 \pm 1.0	5.0 \pm 1.5	79.6 \pm 6.4	94.6 \pm 17.2	533.8 \pm 37.3	409.6 \pm 35.7	10	24
	Warming	23.9 \pm 7.0	24.3 \pm 8.7	3.7 \pm 1.0	4.4 \pm 1.2	83.5 \pm 11.2	98.2 \pm 21.8	571.8 \pm 112.6	416.5 \pm 61.5	14	24

calculated a different trait value per species only across the warming treatments (CWM_{war}). We calculated intraspecific trait variability (ITV) as $ITV = CWM_{war} - CWM_{fixed}$ for the 2019 data only. Then, to calculate the portion of the total variability that is determined by intraspecific trait variability we ran separate one-way ANOVA models of each of the three variables: ITV, CWM_{war} , and CWM_{fixed} with warming treatment as the fixed predictor variable and extracted the corresponding sums of squares (SS_{intra} , SS_{war} and SS_{fixed}). The total sum of squares (SS) within each ANOVA corresponds to the total variability explained by each of these three components, whereas the SS of the individual effects correspond to the amount of variability explained by the individual terms of the model and are additive (de Bello et al. 2011). Finally, we calculated the effect of covariation between species turn-over and intraspecific trait variability as $CovSS = SS_{war} - SS_{fixed} - SS_{intra}$ (de Bello et al. 2011). A positive covariation indicates a positive correlation between species turn-over (SS_{fixed}) and intraspecific trait variability (SS_{intra}), whereas a negative covariation indicates a negative correlation. To compare between the four traits the total variation in CWM_{war} (SS_{war}) was set as 100%.

Statistics and data analyses

We first tested for the actual differences in temperature between the OTC and control plots using a linear mixed-effects model, where we included plot ID and year as random variables to account for the repeated measurements. To assess fluctuations in ambient temperatures between the different sampling years, we used the Mike's Pass weather station data to test for differences between years in average and maximum temperatures of the first quarter (January to March). We used a linear mixed-effect model, including year as fixed predictor variable and 'month' nested within 'year' as random variable to account for repeated measurements.

To test for differences in the leaf trait response to the warming and fire treatment, we used linear models, with the CWM of LTH, LA, SLA and LDMC as response variables and warming and fire treatment as fixed predictor variables. In the initial models we included block as a random effect and tested for the interaction between the fire and warming treatments. Because the block effect did not test significant and neither did any of the interactions, models were simplified to only include the main effects of fire and warming. Sampling year could not be included in the model, because of dependency of the 2019 and 2020 CWM data (see section on CWM calculations). Tukey-HSD tests were used to test for contrasts between the fire treatments. All data were tested for assumptions of normality and homogeneity of variance. Analyses were conducted in R version 4.0.1 (R Core Team 2020) using the packages nlme (Pineiro et al. 2020), car (Fox and Weisberg 2019), ggplot2 (Wickham 2016), sjplot (Lüdtke 2020), and rstatix (Kassambara 2020).

Results

Temperature and rainfall

The warming treatment increased average air temperature by 1 °C and average soil temperature by 0.7 °C (Figure 1; Air temperature $F = 40.3$, $p < 0.001$; Soil temperature $F =$

102, $p < 0.001$). Maximum air temperatures at midday were up to 4 °C higher in the OTCs, compared with the control plots, soil temperatures at midday were up to 1 °C higher in the OTCs (data not shown). Ambient rainfall and temperature conditions differed between years (Figure 3). The first quarter of 2019 was dry, with monthly rainfall anomalies of 50–100 mm below average, whereas the first quarter of 2020 was much more average (Figure 3a). Temperature anomalies show above-average temperatures towards the end of each year, notably in 2018, where above-average temperatures extend into December (Figure 3b). Average and maximum daily temperatures were highest in the first quarter of 2019 (Figures 3c and 3d; Average temperature: $F = 4.1$, $p = 0.068$; Maximum daily temperature: $F = 4.3$, $p = 0.061$).

Trait response to warming

While there was relative consistency in the community trait responses to the fire and warming treatments over time, there was a high intraspecific variation in individual traits over time (Table 1). Some species, notably *Koeleria capensis*, showed an increase in height, leaf area and SLA between the 2019 and 2020 measurements, whereas other species showed an increase in height, but a decrease in leaf area and SLA, e.g. *Stiburus alopecuroides* and *Themeda triandra*. The LDMC measurements differed most between both sampling years and values for 2019 were on average 200 mg g⁻¹ higher, compared with 2020.

The direction of the community trait responses to the warming treatment were consistent between both years, with one major exception in the leaf table height. In 2019, community LTH was significantly lower in the OTCs (Table 2a), but this result was not found in 2020 (Table 3). In general, trait responses were stronger in 2019, compared with 2020. Whereas community LA was 0.69 cm² smaller in the OTCs in 2019 (Table 2a), in 2020 this was only 0.29 cm² (Table 3). The same was found for community LDMC, which was 24.1 mg g⁻¹ higher in the OTCs, compared with the control plots in 2019 (Table 2a), but only 8.47 mg g⁻¹ higher in the OTCs in 2020 (Table 3). Community SLA did not respond to the warming treatment (Tables 2a and 3).

Trait response to fire

Community trait responses to the fire treatment were consistent for both years. For the 2019 data, community LTH was significantly higher in the fire exclusion treatment, compared with the other treatments (Table 2a, Figure 4). The 2020 data show the same result; higher community LTH in the fire exclusion treatment (Table 3, Figure 5). Community LA did not respond to the fire treatments in 2019 (Table 2a, Figure 4) and was higher in the annual, compared with the fire exclusion treatment in 2020 (Table 3), although a p -value adjustment accounting for multiple comparisons during *post hoc* tests showed no significant contrasts (Figure 5). Community SLA is consistently lower in the fire exclusion treatment for both years and the patterns are roughly the same between years across fire treatments. For 2019, community SLA was lower in the quinquennial and fire exclusion treatments,

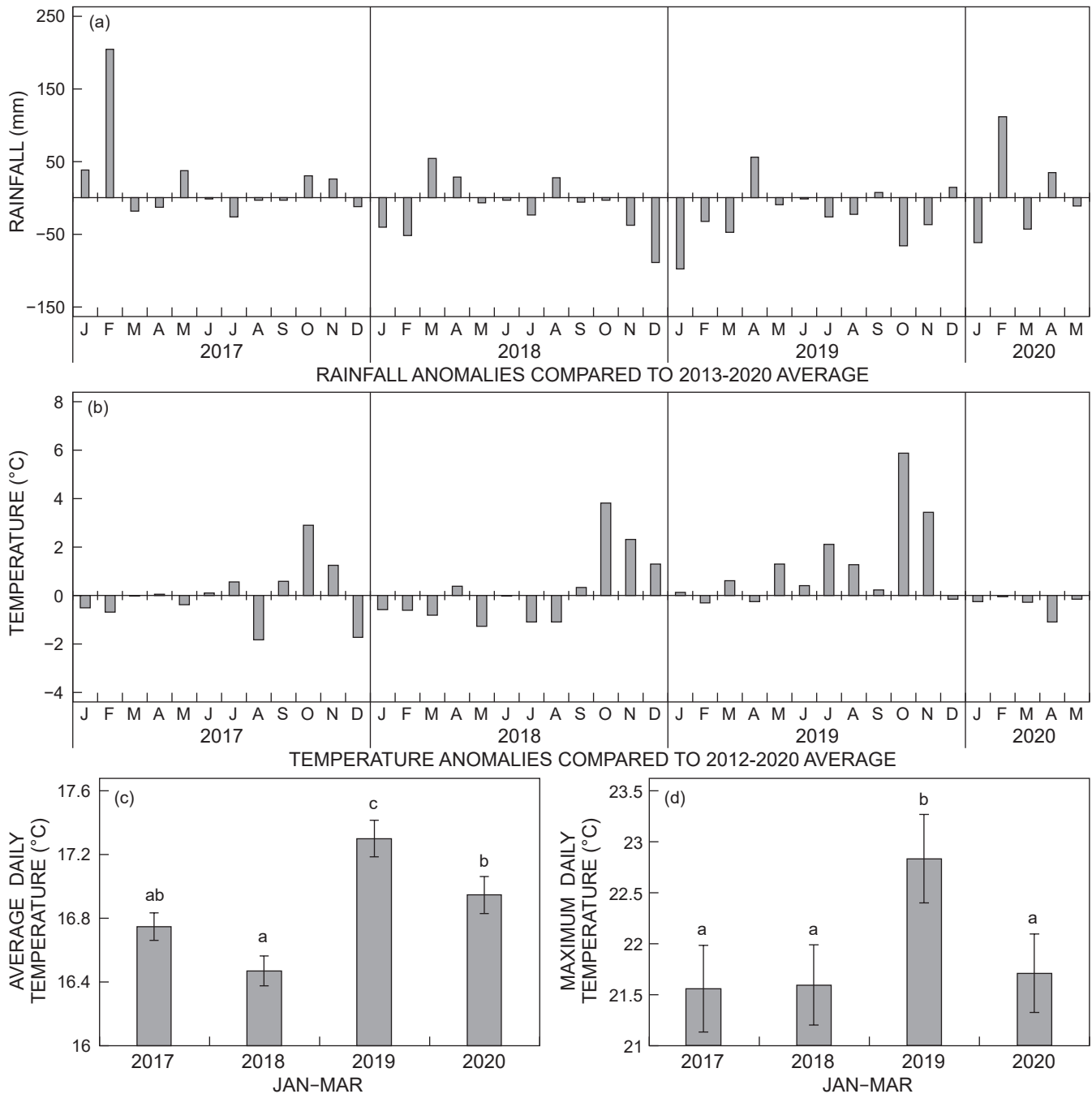


Figure 3: Rainfall (a) and temperature (b) anomalies for the Cathedral Peak region in the uKhahlamba-Drakensberg Mountains, South Africa. Also shown are (c) average daily temperature and (d) maximum daily temperature (means \pm SE). Different letters denote significant differences after *post hoc* testing. Data are derived from the weather station at Mike's Pass, located at the same elevation, approximately 1.5 km from the Brotherton experiment. All data shown are for the duration of the warming \times fire experiment, i.e. 2017–2019

compared with the annual fire treatment (Table 2a) and in the fire exclusion, compared with the biennial fire treatment (Figure 4). For 2020, community SLA was lower in the fire exclusion treatment, compared with the other treatments (Table 3, Figure 5). Community LDMC was highest in the biennial fire treatments and lowest in the fire exclusion treatments for both 2019 (Table 2a, Figure 4) and 2020 (Table 3, Figure 5).

Intraspecific trait variability

The warming treatment induced high ITV that can be seen from the difference in the direct comparison between the CWM_{war} and CWM_{fixed} data in Figure 4, as well as from the variation partitioning in Figure 6. Size-related traits (height and leaf area) showed greater ITV than resource economics-related traits (SLA and LDMC). Community SLA showed a low level of intraspecific trait variability,

Table 2: Summary tables of the linear models for the 2019 data. A: Model results for CWM_{war} where community-weighted trait means were calculated using mean traits per species per warming treatment. B: Model results for CWM_{fixed} where community-weighted means were calculated using a fixed mean trait per species. Significant effects with $p < 0.5$ are shown in bold and with $p < 0.1$ in italics

Predictors	LTH			LA			SLA			LDMC		
	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>
Intercept	26.42	42.82	< 0.001	4.11	36.91	< 0.001	102.48	31.05	< 0.001	609.76	115.14	< 0.001
Fire (Biennial)	0.44	0.56	0.580	-0.16	-1.15	0.263	-4.55	-1.10	0.283	14.98	2.25	0.033
Fire (Quinquennial)	1.06	1.36	0.185	-0.23	-1.63	0.115	-13.89	-3.35	0.003	-11.96	-1.80	0.084
Fire (No burn)	4.17	4.98	< 0.001	-0.02	-0.14	0.889	-24.18	-5.40	< 0.001	-12.87	-1.79	0.086
Treatment (warming)	-4.05	-7.15	< 0.001	-0.69	-6.74	< 0.001	3.69	1.22	0.235	24.10	4.96	< 0.001
Observations		30			30			30			30	
<i>R</i> ² / <i>R</i> ² adjusted		0.762/0.724			0.662/0.608			0.589/0.523			0.649/0.593	

Predictors	LTH fixed			LA fixed			SLA fixed			LDMC fixed		
	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>
Intercept	24.39	42.73	< 0.001	3.77	37.98	< 0.001	103.36	31.18	< 0.001	619.91	119.28	< 0.001
Fire (Biennial)	0.35	0.49	0.625	-0.16	-1.30	0.206	-4.29	-1.03	0.312	16.42	2.51	0.019
Fire (Quinquennial)	1.22	1.70	0.102	-0.17	-1.35	0.190	-13.75	-3.30	0.003	-10.67	-1.63	0.115
Fire (No burn)	3.95	5.10	< 0.001	-0.08	-0.56	0.580	-24.26	-5.39	< 0.001	-13.24	-1.88	0.072
Treatment (warming)	-0.60	-1.14	0.265	-0.10	-1.14	0.266	2.59	0.85	0.402	8.37	1.75	0.092
Observations		30			30			30			30	
<i>R</i> ² / <i>R</i> ² adjusted		0.559/0.489			0.129/-0.010			0.584/0.518			0.519/0.442	

Table 3: Summary tables of the linear models for the 2020 data. Model results are for CWM_{war} where community-weighted trait means were calculated using mean traits per species per warming treatment. Significant effects with $p < 0.5$ are shown in bold and with $p < 0.1$ in italics

Predictors	LTH fixed			LA fixed			SLA fixed			LDMC fixed		
	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>	Estimates	<i>t</i>	<i>p</i>
Intercept	23.36	26.78	< 0.001	4.51	26.25	< 0.001	116.58	19.67	< 0.001	416.82	81.55	< 0.001
Fire (Biennial)	-0.61	-0.55	0.586	-0.06	-0.29	0.772	0.55	0.07	0.941	3.90	0.61	0.549
Fire (Quinquennial)	1.44	1.31	0.201	-0.13	-0.58	0.566	-14.64	-1.97	0.060	-9.37	-1.46	0.157
Fire (No burn)	5.02	4.24	< 0.001	-0.51	-2.20	0.038	-37.27	-4.63	< 0.001	-36.22	-522.00	< 0.001
Treatment (warming)	-0.19	-0.23	0.818	-0.29	-1.81	0.083	7.58	1.39	0.175	8.47	1.81	0.083
Observations		30			30			30			30	
<i>R</i> ² / <i>R</i> ² adjusted		0.511/0.433			0.260/0.142			0.548/0.475			0.628/0.568	

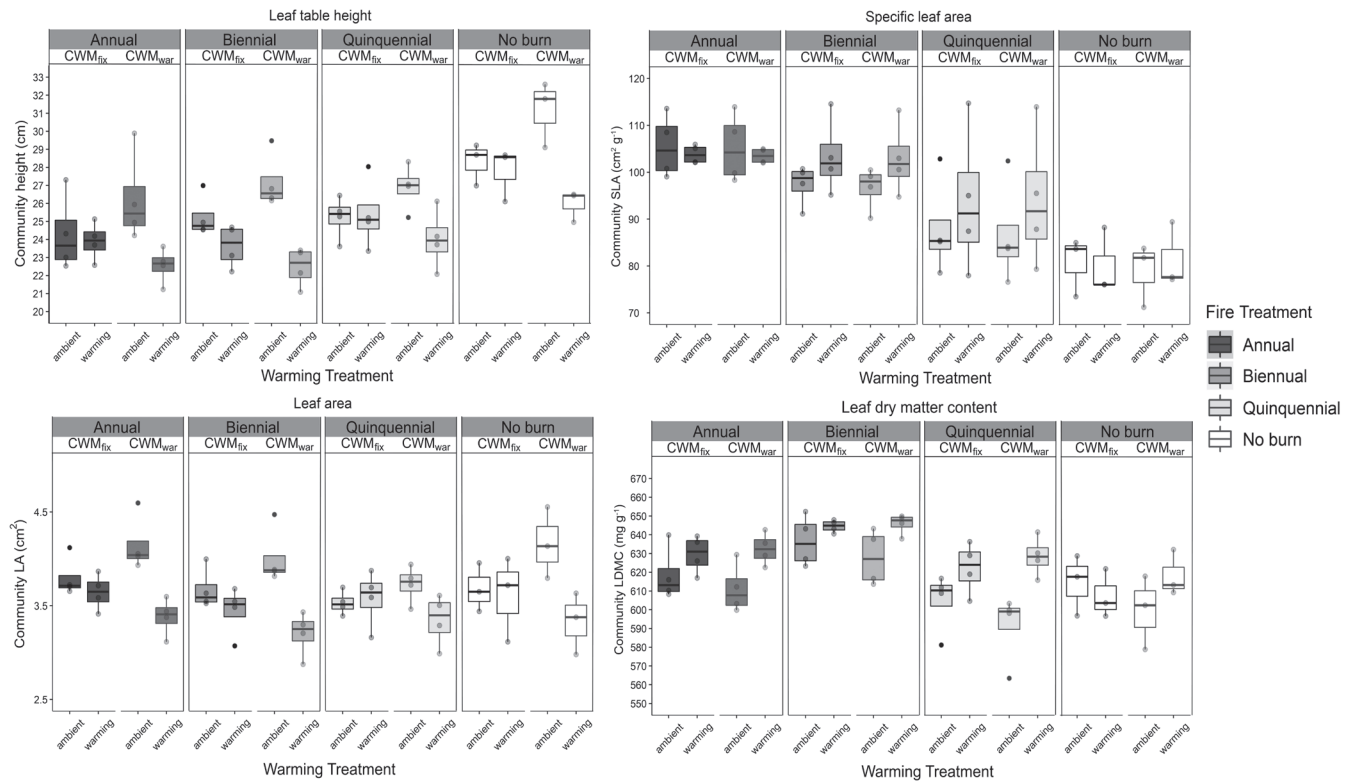


Figure 4: Community-weighted mean traits for 2019 for leaf table height, leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) on the y-axis, for the warming treatment on the x-axis and the fire treatments (annual, biennial, quinquennial and no-burn) represented by a colour gradient from dark to light. For each trait the CWM_{fixed} is displayed with an uncoloured background and the CWM_{war} with a shaded background. Mean traits with confidence intervals are shown. Different letters denote significant differences between the fire treatments after *post hoc* testing. Capital letters show the *post hoc* results for CWM_{fixed} , small letters show the *post hoc* results for CWM_{war} .

suggesting that species turn-over was the largest contributor to variation in community SLA. Community LDMC showed a higher level of intraspecific trait variability than community SLA, but lower than community LTH and LA. The observed trait response for community LTH and LA to the warming treatment (CWM_{war}) can be almost completely attributed to intraspecific trait variability, which is confirmed by the lack of significant effects of the warming treatment for CWM_{fixed} (Table 2b).

Discussion

We studied the effect of fire and temperature on four key functional traits of six dominant grass species in South African montane grassland communities. Both fire and warming affected plant traits, but no interactive effects were found (Tables 2 and 3, Figures 4 and 5). The warming treatment affected plant height, leaf area and LDMC, but not SLA. Plant height and leaf area were lower, whereas LDMC was higher in the warmed treatments, compared with the controls. These findings reject the first hypothesis that plants respond to warming with enhanced growth and accept the alternative hypothesis that an increase in temperature can induce heat stress and result in a reduction in growth. This effect was, however, only found for the 2019 data and could be attributed mostly to intraspecific trait variability, suggesting that this is a plastic

response to elevated temperature. The ambient weather data show that the first quarter of 2019 was exceptionally warm and dry, compared with 2020 (Figure 3). This likely added to the effect of the warming treatment, resulting in the observed trait response. The response to the fire treatment is partly consistent with our hypothesis that lower fire frequencies induce a shift towards taller and slow-growing grass species. We found higher LTH, lower LA and SLA, but also lower LDMC in the fire exclusion treatments, where we expected to find a higher LDMC. This result was most pronounced in the 2020 data, again suggesting possible confounding effects of the ambient weather conditions.

Trait response to warming

We suggested two alternative hypotheses regarding plant responses to warming. The first hypothesis is based on studies from temperate, boreal and Arctic climates where elevated temperatures would increase plant performance, as shown by increased height, LA, SLA and decreased LDMC (Hudson et al. 2011; Zhang et al. 2015; Björkman et al. 2018). The alternative hypothesis is based on studies of plant responses to warming in dryland ecosystems (Musil et al. 2005, 2009), where an increase in temperature could exceed the optimal for photosynthesis and lead to increased evaporative stress. Under this scenario height, LA and SLA would be expected to decrease with elevated

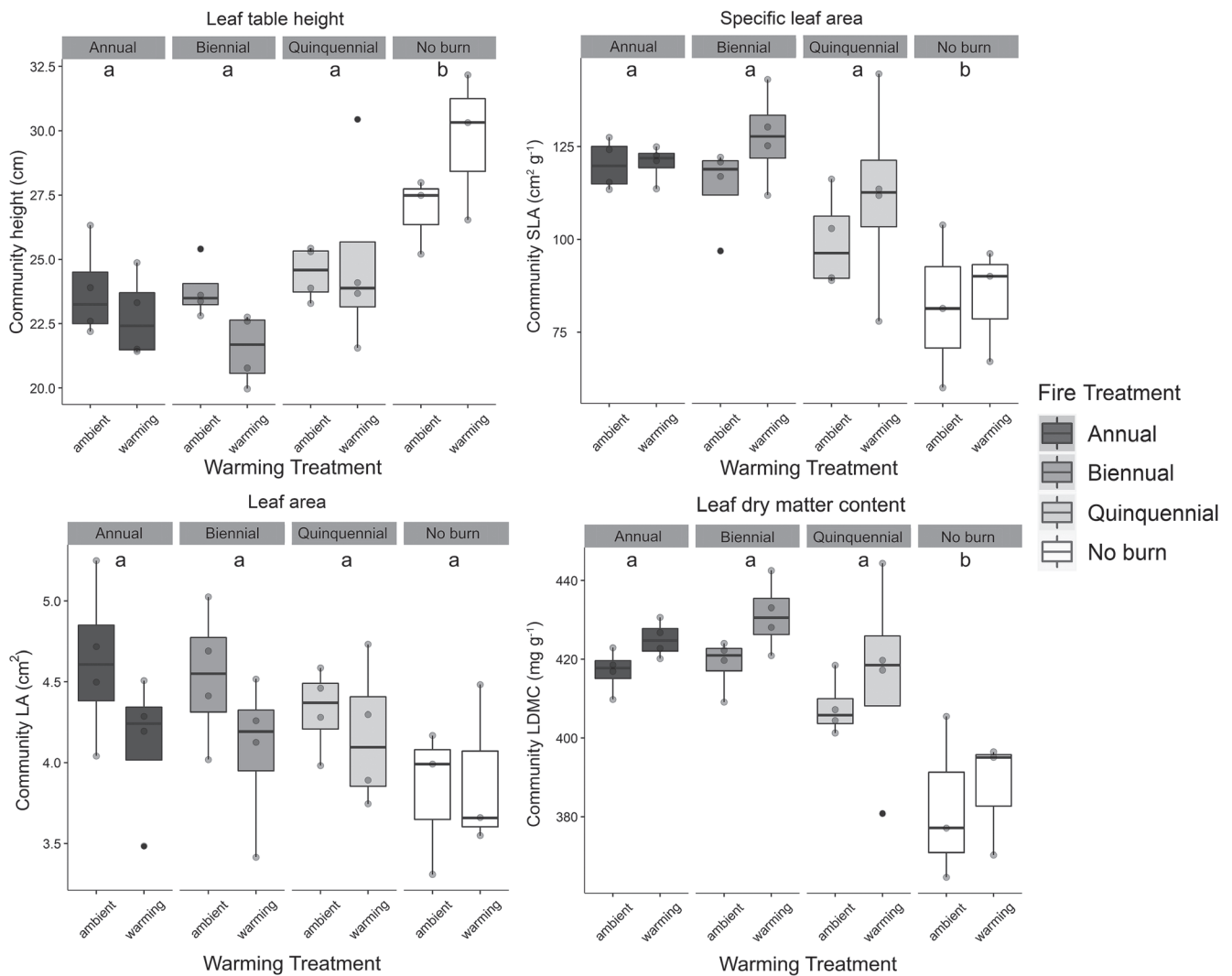


Figure 5: Community-weighted mean traits for 2020 for leaf table height, leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) on the y-axis, for the warming treatment on the x-axis and the fire treatments (annual, biennial, quinquennial and no-burn) represented by a colour gradient from dark to light. Mean traits with confidence intervals are shown. Different letters denote significant differences between the fire treatments after *post hoc* testing

temperatures, whereas LDMC would be expected to increase, because the leaf water content would decrease under heat stress. Because our study was conducted in montane grasslands with a temperate climate, we expected the first hypothesis of enhanced plant performance to be the more logical one. Yet, in the 2019 data we found clear evidence pointing towards the alternative hypothesis. The 2019 data show lower plant height and LA and a higher LDMC in the OTCs, compared with the controls. This indicates that the rainfall deficits from October 2018 to March 2019, coupled with elevated temperatures in the OTCs, led to enhanced reduction in growth traits and elevated LDMC. This response is strongly driven by intraspecific trait variability, because no significant effects are observed when the variability as a result of ITV is taken out of the community response, except for LDMC (CWM_{fixed}, Table 2b). The 2020 data show much less of a response to experimental warming. Height and SLA do not respond

to warming, whereas LA decreases and LDMC increases, similarly to the 2019 data. Combined our results suggest that in the montane grasslands of the Drakensberg, there is a delicate balance between the positive and negative effects of drought and elevated temperatures, inducing heat stress. The regional temperature data for 2019 and 2020 show that 2019 was significantly warmer than 2020 (Figure 3). This makes it plausible that in 2019 the grassland community was tipped beyond its thermal niche and experienced heat stress, whereas in 2020 there was a dampened response.

Differences in the seasonal timing of data collection might also have affected the trait response. The 2019 trait data were collected in February (summer), whereas the 2020 trait data were collected in March/April (late summer/early autumn). A study by Römermann et al. (2016) conducted in Germany showed that LDMC can increase throughout the growing season with as much as 150–200 mg g⁻¹. Together

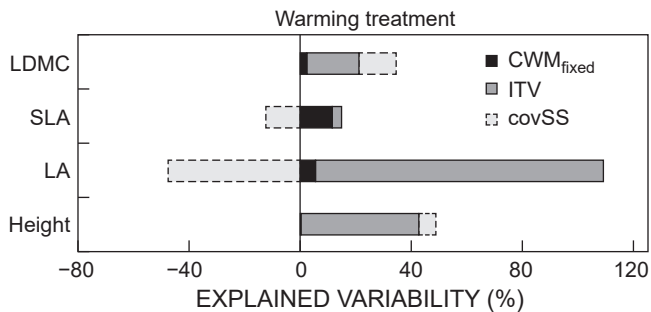


Figure 6: Variation partitioning for the 2019 trait data. For each trait (height, LA, SLA and LDMC) the relative contribution of species turn-over (CWM_{fixed} , black bars), intraspecific trait variability (ITV_{fixed} , grey bars) and their covariation ($covSS$, white dashed bars) is shown. The x-axis shows the % explained variability of CWM_{war} , where $CWM_{war} = CWM_{fixed} + ITV + covSS$

with the differences in ambient weather conditions between 2019 and 2020, this seasonal difference could explain the large differences in LDMC values observed between both years. These responses could have been further exacerbated by the fact that soil moisture changes often confound the temperature change in warming experiments. Experimental warming often increases vapour pressure deficit and reduces soil water content (Harte et al. 1995). Indeed, in Tasmanian grassland communities, seasonal rainfall has been shown to be more important than annual rainfall for grass biomass responses to elevated CO_2 (Hovenden et al. 2014). Drier conditions would increase LDMC, because of lower leaf water content, which is consistent with our results. This delicate balance between warming and water availability has also been found in other studies. For example, a study on post-fire succession in a Mediterranean shrubland showed that warming slowed down post-fire succession under drought conditions (Prieto et al. 2009). Other studies did not find a relation between LDMC and warming without taking into account other environmental variables, such as water availability (Hudson et al. 2011; Lamarque et al. 2014). This is also illustrated in a study by Björkman et al. (2018) where LDMC decreases with increasing temperatures under wet conditions, but shows no effect under dry conditions.

Trait response to fire

In line with earlier studies (Fynn et al. 2005, 2011; Kirkman et al. 2014), we hypothesised that less frequent fires would result in a shift in the grassland community towards tall and slow-growing species, i.e. grasses with higher vegetative height, lower LA and SLA, and higher LDMC. Invariably, species that dominate frequently-burned environments are mostly short species possessing traits associated with rapid post-fire regeneration (Kirkman et al. 2014). We found that in the fire exclusion treatment, grass communities were indeed taller, with lower LA and SLA, compared with the annually-burned treatments, supporting the hypothesis. Lower SLA is indicative of lower relative growth rates, photosynthetic rates and leaf nitrogen (N) content and higher leaf longevity, a strategy often found in late-successional species that have a higher

shade tolerance (Poorter and Remkes 1990; Garnier et al. 2001; Wright et al. 2004; Kirkman 2014). Hempson et al. (2019) showed that grasses in fire-prone environments outcompete other grasses by pre-empting the light environment, resulting in upright and tall species. When burning frequencies are low, dead biomass accumulates and obstructs light at ground level so that species need to grow taller to maintain photosynthetic ability. Tall and erect tufts require high C:N ratios, indicating high LDMC values, to provide structural support. This in turn leads to slower decomposition and further contributes to accumulation of dead biomass in infrequently burned communities (Hempson et al. 2019). However, contrary to our hypothesis, we found a lower LDMC in the fire exclusion treatment in 2020 and no strong response in 2019. Although this result seems counter-intuitive, a study comparing grass community responses to different fire frequencies in mesic grasslands in South Africa and North America, found similar results, i.e. lower LDMC values in less frequently burned plots in North America and no trend in community LDMC with fire frequency in South Africa (Forrestel et al. 2014). Because 2019 was a considerably drier year than 2020, the different LDMC response between 2019 and 2020 may suggest possible confounding influences of water availability, as was also shown in other studies (Hudson et al. 2011; Lamarque et al. 2014; Björkman et al. 2018).

Intraspecific trait variability

Intraspecific trait variability describes the trait variation of individuals within species and provides one of the key prerequisites for natural selection (Bolnick et al. 2011). Quantification of intraspecific trait variation helps to understand to what extent plant functional traits change as a response to e.g. climate manipulations (de Bello et al. 2011). In our study we quantified the contribution of ITV in montane grasslands as a response to experimental warming, which showed that intraspecific trait variability was very important. The majority of trait variation in response to warming for height, LA and LDMC could be explained by intraspecific trait variability, whereas differences in SLA were to a large extent determined by species-turnover. This suggests an important role of trait plasticity allowing species to respond to changes in climatic conditions (Read et al. 2014). Higher trait plasticity decreases the vulnerability of species to changing climatic conditions (Liancourt et al. 2015). In general, species tend to be shorter with increased altitude and related increase in weather extremes (Moles et al. 2009). Such abiotic conditions related to altitudinal gradients can act as filters for trait variability in plant communities. De Bello et al. (2013) show lower trait variability at high elevations in the French Alps, whereas Pescador et al. (2015) find the opposite in a Spanish montane grassland. Stronger environmental filters in montane grasslands, resulting in lower trait variability at community scales would increase their vulnerability to climate change and lower their capacity to survive heat waves, compared with low-elevational plants (Laurance et al. 2011). Similarly, intraspecific trait variability has been shown to mediate the response of montane grassland communities to drought events (Jung et al. 2014). This

indicates the importance of intraspecific trait variability in montane grassland communities and the existence of complex plastic responses of plants to environmental changes should not be underestimated (Kichenin et al. 2013; Liancourt et al. 2015; Pescador et al. 2015).

Understanding how montane grassland communities will respond to climate change and associated changes in fire regime is essential to protect the unique biodiversity and functional properties of these ecosystems. Climate change manipulation experiments provide a powerful way of testing how communities respond to climate-change drivers. Open-top warming chambers are widely used to mimic global warming (Marion et al. 1997; Hudson et al. 2011; Wolkovich et al. 2012; Zhang et al. 2015). Despite their disadvantages, such as changes in wind, space limitation or altered soil moisture and relative humidity (Harte et al. 1995; Marion et al. 1997), they are very effective to elevate ambient temperatures with 1–2 °C in inaccessible montane ecosystems. We have shown that plants in Afrotropical ecosystems responded differently to warming than those in Northern temperate, boreal and Arctic ecosystems where the majority of warming experiments are being performed. Interactive effects of warming with drought may result in plants being closer to a heat-stress tipping point, compared with cooler systems. Our study highlights the need to widen our efforts and include disparate ecosystems to gain a better understanding of global responses to climate variability. Our results suggest an important role for intraspecific trait variability to mediate the response of montane grassland communities to elevated temperatures and associated drought effects. However, although the plasticity in plant traits observed in this study demonstrate an ability to adapt to climatic variability, the boundaries of this plasticity will be pushed under global climate change. Continued observation, building on the identified responses of plant communities and species to simulated climate change, will provide valuable insight for conservation management into the future.

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