Attracted by higher crude protein, grasshopper abundance and offtake increase after prescribed fire*

Nicholas Gregory Heimbuch[1*], Devan Allen McGranahan[2], Carissa L. Wonkka[3], Lance Vermiere[2] and David Branson[3]

[1*]University of Pittsburg, , , Pittsburg, , Pennsylvania, USA.
[2]USDA Agricultural Research Service, Livestock & Range Research Laboratory, 243 Ft. Keogh Rd., Miles City, 59301, Montana, USA.
[3]USDA Agricultural Research Service, Northern Plains Agricultural Research Laboratory, 1500 N Central Ave, Sidney, 59270, Montana, USA.

*Corresponding author(s). E-mail(s): ngh11@pitt.edu; Contributing authors: Devan.McGranahan@usda.gov; Carissa.Wonkka@usda.gov ; Lance.Vermiere@usda.gov; David.Branson@usda.gov ;

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Abstract

Little research has been done to examine the influences of fire and drought on grasshopper herbivory patterns. Climate warming is producing more frequent and more intense droughts in the Northern Great Plains region of the United States, affecting herbivore resource availability and stressing the range ecosystem. This study created three different time since fire treatments to examine how indirect fire effects (improved forage quality) affect the density and offtake of local grasshoppers. Both offtake and density were significantly higher in burned locations compared to unburned control plots. Burned plot grasshopper density increased greatly over time, while density remained constant in unburned locations. These density patterns appear to be the direct result of the high protein content found in burned locations. The results raise further questions into the mechanism that produces the magnet effect in range grasshoppers. These results also highlight the importance of understanding how fire will interact with future climate conditions to affect range herbivore interactions.

Introduction

With global climate continuing to warm, rangeland herbivores must adapt to flaring environmental disturbances. Drought and fire are among the most prevalent disturbances occurring in the American Midwest. As anthropogenic climate change continues to shift weather patterns, rainfall in the northern Great Plains is predicted to increase in the spring and fall, with annual droughts developing through summer months (Derner et al, 2018). Aboveground net primary productivity (ANPP) in grassland ecosystems is severely reduced by drought conditions (Hoover et al, 2014). Legacy effects from these droughted summers are not clearly understood on long timescales, giving range herbivores variable forage availability in the years to come (Hoover et al, 2014).

As droughts continue to worsen in summer months, fire will become even more frequent in range ecosystems (Donovan et al, 2017, 2020). In fact, mean wildfire frequency more than tripled from 2005-2014 compared to the previous 9 year mean (Donovan et al, 2017). Despite the ANPP reduction, patch burning treatments are able to buffer the drought losses through improved forage protein content (Spiess et al, 2020). Fire produces a spike in crude protein, the benchmark measurement for forage quality, which then decreases over time (Allred et al, 2011). Even in homogeneous fire regimes, fire still improves protein content and removes accumulated grass detritus, however it can also weaken the biodiversity of the region, creating inconsistent annual forage production (McGranahan et al, 2016).

The effects of these disturbances on rangeland ungulates are well understood. Drought reduces plant biomass and leads to an exodus of herbivores out of the droughted location and into wetter, more productive environments (Trisos et al, 2021). Due to lowered productivity, livestock who are unable to leave the droughted rangeland experience reduced weight gain (Allred et al, 2014). On burned rangeland, ungulate species follow a pyric herbivory feeding pattern, spending more time grazing in burned patches compared to unburned pasture (Fuhlendorf et al, 2009; Parrini and Owen-Smith, 2010).

Grasshopper response to fire and drought, on the other hand, still has many open ended questions. Drought depresses reproductive fitness of grasshoppers remaining in warm, droughted locations compared to grasshoppers in undroughted locations (Rosenblatt, 2018). Fire's relationship with herbivorous insect species is more complicated. Large fires can easily kill adult grasshoppers and destroy eggs laid in shallow soil (Branson and Vermeire, 2013). Whether grasshoppers experience the same improved growth that livestock experience from burning treatments is still the subject of ongoing research. Grasshoppers prefer high nitrogen content forage to spur growth and development and improve fecundity (Schmitz, 2010). While feeding on plants, grasshoppers are able to monitor their protein and carbohydrate intake to maintain ideal nutrient ratios (Behmer, 2009; Behmer and Joern, 2008). For instance, grasshoppers will choose to forage on plants high in carbon content to increase metabolism and respiratory function (Schmitz, 2010). More research is required to understand whether a low nutrient, droughted range ecosystem will produce the same magnet effect on grasshoppers that draws ungulates to recently burned prairie.

Our goal for this study is to examine how small-scale fall and spring burns indirectly affect grasshopper herbivory on a droughted mixed grass prairie. The primary indirect effect examined in this study is the improved forage quality produced after fire events (Allred et al, 2011). Previous research into fire's effect on grasshopper density have been conducted on relatively large burn areas (Branson, 2005; Vermeire et al, 2004). Thus, it is currently unclear how grasshoppers react to and utilize small patches of heightened resource quality within a low quality, droughted landscape. The summer of 2021 was incredibly dry in eastern Montana, producing the necessary droughted forage conditions for us to examine this research question.

Methods

Our study was conducted on a research range operated by the Fort Keogh livestock and range research laboratory in Miles City Montana. This mixed grass prairie research location is dominated by western wheatgrass (Pascopyrum smithii) and, during the summer of 2021, the migratory grasshopper (Melanoplus sanguinipes). These grasshoppers are frequently responsible for the largest outbreaks, making the migratory grasshopper especially damaging to farmers and ranchers throughout the Great Plains (Onsager and Olfert, 2000; Olfert et al, 2021). We selected nine, 375 m^2 plots to test three different time-since-fire treatments with three repetitions each: a fall burn treatment, a spring burn treatment, and an unburned control treatment. These plots were situated in a large ungrazed pasture with a two meter buffer zone between plots.

Offtake

We identified 2 exclosure and 2 control sites on each of the 9 different plots with vegetation that reflected the overall grass assemblage of the plot. We erected one, 0.25 m^2 exclosure on July 1st, and a second exclosure and two control structures of the same area on July 7th. This gap in construction was to ensure that our exclosures were successful in keeping the grasshoppers out and to gather the equipment for the other structures. Similar to previous grasshopper herbivory studies, our exclosures consisted of a PVC pipe skeleton with heavy nylon netting which kept grasshoppers out of the exclosure area (Parker and Salzman, 1985). The netting created a shading effect that reduced sunlight intensity by 400 w m^{-2} compared to the surrounding area. We designed the control structures to remain open on the north/south faces to allow grasshoppers to enter the study site while still producing shading conditions matching the exclosures during peak photosynthesis hours. Our control structures ensured that shade would not influence grass development and skew our offtake measurements.

I checked every exclosure routinely for grasshopper breaches with no more than 48 hours elapsing between examinations. The large margin of error in our spring burn offtake is likely due to an exclosure breach that occurred on July 19th, 19 days into the experiment timeline. After a 48 hour break between quality checking the exclosures I noticed a number of grasshoppers had made it into the exclosure after it sustained storm damage, so grasshoppers could have been actively foraging in the exclosure for a maximum of two days. Although this was a short period of possible contamination, this is the most likely cause for the wide margin of error. There was no statistical difference in offtake rate between spring and fall burn treatments. After 40 days, on August 9th, I clipped and bagged all aboveground biomass within the 0.25 m^2 test areas for later analysis in the Fort Keogh range sciences lab. During clipping, I counted and recorded individual grass tillers in the burn treatment plots to compare data on per tiller offtake across burn treatments. In the lab, I dried all the grass biomass samples at 60°C for two days, so that no moisture remained, and weighed them to the nearest 0.0001 gram. The difference in dry weight between exclosures and controls on the same plot provided us a measure for proportional offtake by grasshoppers between burn treatments.

Forage Quality

On the 26th day of the study period, roughly halfway through the experiment, I randomly selected 40 tillers of western wheatgrass from each plot by tossing a marker flag in the air and clipping the aboveground biomass of the tiller nearest from where it landed. This collection procedure guaranteed that my sampled tillers were representative of the plot composition without selection bias. I returned these tillers to the lab and separated leaves and stems to assess forage quality differences between the two plant organs. I dried the stems and leaves and ground them into fine powders which I then analyzed in a Carbon/Nitrogen analysis machine in the lab. Each plot produced a diagnostic graph representing the crude protein content of the analyzed forage.

Density

I assessed grasshopper density on each plot using ring count methodology (Onsager, 1977; Joern and Laws, 2013). On July 8th, I placed 5 .1 m rings on each plot in an "X" shaped pattern, with each ring approximately 1.5 m apart. Because our plots were only 375 m^2 this pattern kept our rings the correct distance from one another while also providing buffering space from the plot edges. Between July 9th and August 6th, I measured abundance on each plot a total of 19 times. For each count I walked slowly through the plot and agitated the area near each ring with a long stick and recorded the number of grasshoppers to leap out from within the ring. All counts were conducted between 1000 and 1200 for consistent solar conditions, and the temperature was recorded at the beginning of each count.

Data analysis

To determine whether accessibility to grasshoppers affected standing crop, we subtracted the dried biomass values of control frames from that of their paired grasshopper exclosure frames (n = 6 observational units per treatment) and found the mean of these two differences for each plot (n = 3 experimental units per treatment). We used a linear model with the intercept term removed to test each of the three difference values against 0 (null hypothesis: no difference in standing crop between grasshopper exclosures and control frames) using the `lm` function in the R statistical environment (R Core Team, 2020). We tested pairwise contrasts in standing crop differences across each treatment with a post-hoc Tukey test using `TukeyHSD`.

We determined whether crude protein content varied with fire treatment and plant organs (leaves vs. stems) by fitting each term and their interaction in an ANOVA. Pairwise contrasts among fire treatments were again tested with `TukeyHSD`.

To determine if there were general linear trends in grasshopper abundance patterns over the course of the study, we conducted a nonparametric test of the Kendall's tau (τ) statistic fit to the grasshopper count data within each burn treatment using the `kendallTrendTest` function in the *EnvStats* package for R (Millard, 2013). To compare the relative rates of change over the study period, we plotted the estimated slope of the trend for each burn treatment and the associated 95% confidence intervals as returned by `kendallTrendTest`.

Results

Standing crop was statistically-significantly lower outside of grasshopper exclosures in both fall and spring burns (t = -7.6, $P < 0.001$ and t = -6, $P <$ 0.001, respectively). There was no difference in offtake among spring and fall burns ($P > 0.05$), with grasshoppers removing approximately 1.0 ($\pm$ 0.2) kg ha^{-1} d^{-1} in each (Fig. 1). Standing crop was not different between grasshopper exclosures and areas accessible to grasshoppers in unburned plots (t = -0.12, $P > 0.05$). Offtake was significantly lower in unburned plots than plots burned in both the previous fall and spring ($P < 0.01$ and $P = 0.01$, respectively).

Crude protein content varied among the fire treatments (t = 57, $P <$ 0.001; (Fig. 2). Crude protein content in fall and spring burns averaged 6.4% $\pm$ 0.2 s.e. and did not differ among each other ($P > 0.05$). But crude protein content in unburned plots was lower than in both fall and spring burns plots (-2.7, $P < 0.001$ and -3.1, $P < 0.001$, respectively).

Across all samples, crude protein content did not vary among leaves and stems (t = 2.7, $P > 0.05$). Despite a trend towards higher crude protein in

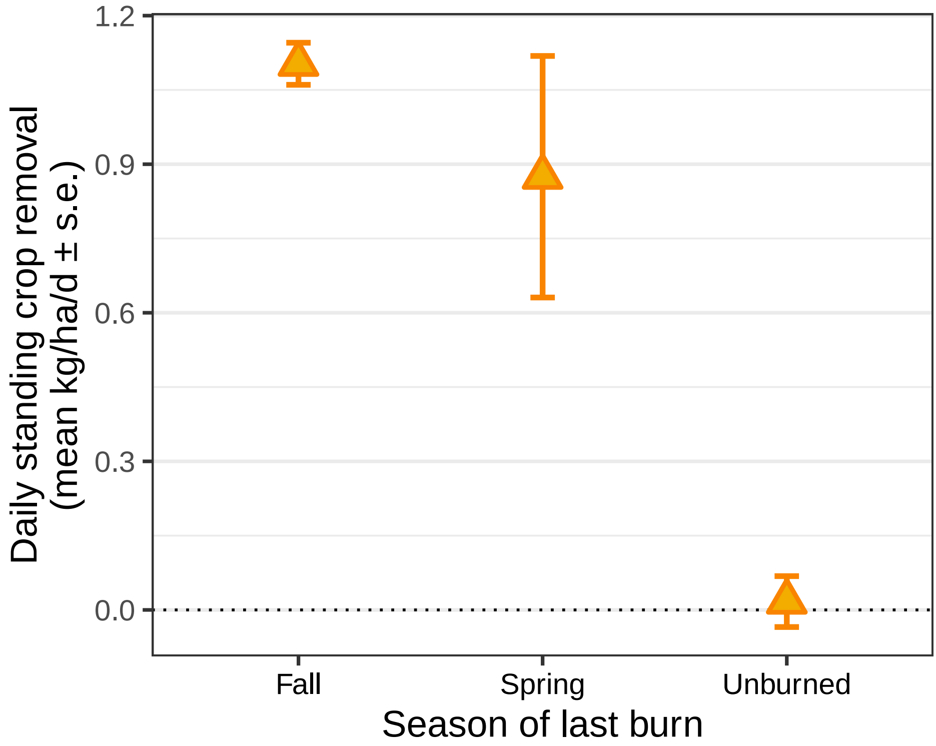

Fig. 1 Mean differences in standing crop between grasshopper exclosures and control frames in plots with three different fire treatments. Standing crop was determined by clipping at the end of the four-week study period and differences attributable to grasshopper removal are expressed as mean kg per ha per day.

leaf tissue in unburned plots (Fig. 2), the pattern was not influential enough to create a significant fire treatment × organ interaction ($t = 2.1$, $P > 0.05$).

Grasshopper abundance was similar across plots at the beginning of the study period (early July) but increased significantly over the next month in fall and spring burn plots ($\tau = 0.29$, $P < 0.01$ and $\tau = 0.62$, $P < 0.001$; Fig. 3). Grasshopper abundance remained constant over the study period in unburned plots ($\tau = 0.039$, $P > 0.05$). While grasshopper abundance increased in both burn treatments, the rate of increase was approximately three times greater in plots that had been most recently burned in the spring than those that had been burned in the previous fall (Fig. 3, *bottom*), which

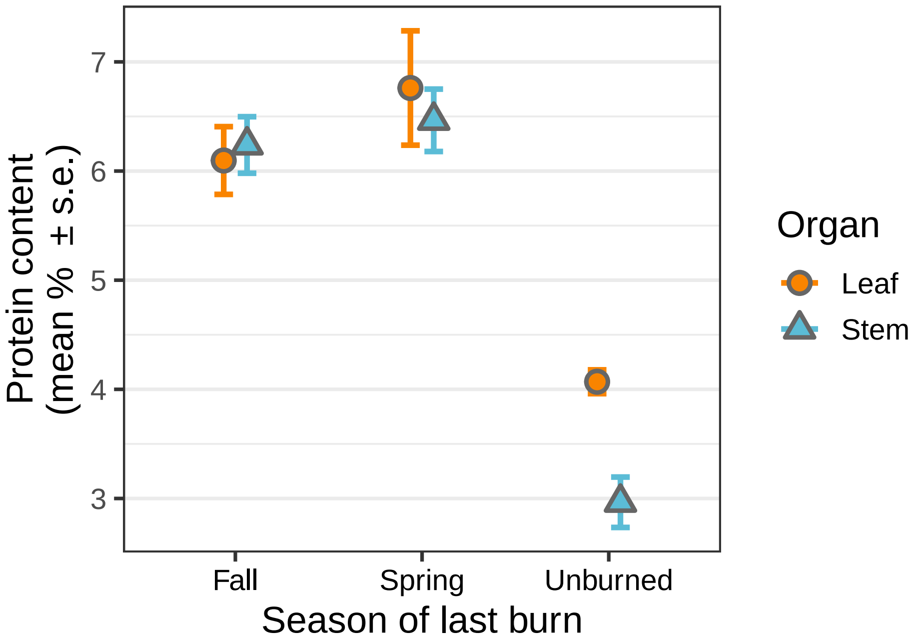

Fig. 2 Mean protein content of western wheatgrass *Pascopyrum smithii* sampled from three burn treatments as a percentage of total dry matter. Red circles indicate the protein content of leaves; blue triangles are stems.

represented more than a five-fold increase in density from approximately 10 to 55 grasshoppers m^{-2} (Fig. 3, *top*).

Discussion

Previous research indicates that prescribed fire reduces grasshopper density (Joern, 2004; Vermeire et al, 2004), our study, however, saw heightened density in small patch burning treatments which could have massive implications for predicting rangeland herbivore competition. Fire as a method of control varies greatly in effectiveness from species to species; certain species, such as Hesperotettix viridis, can be reduced by as much as 88% (Vermeire et al, 2004). Flightless species of grasshopper and species that are heavily reliant on specific plant hosts are especially susceptible to fire

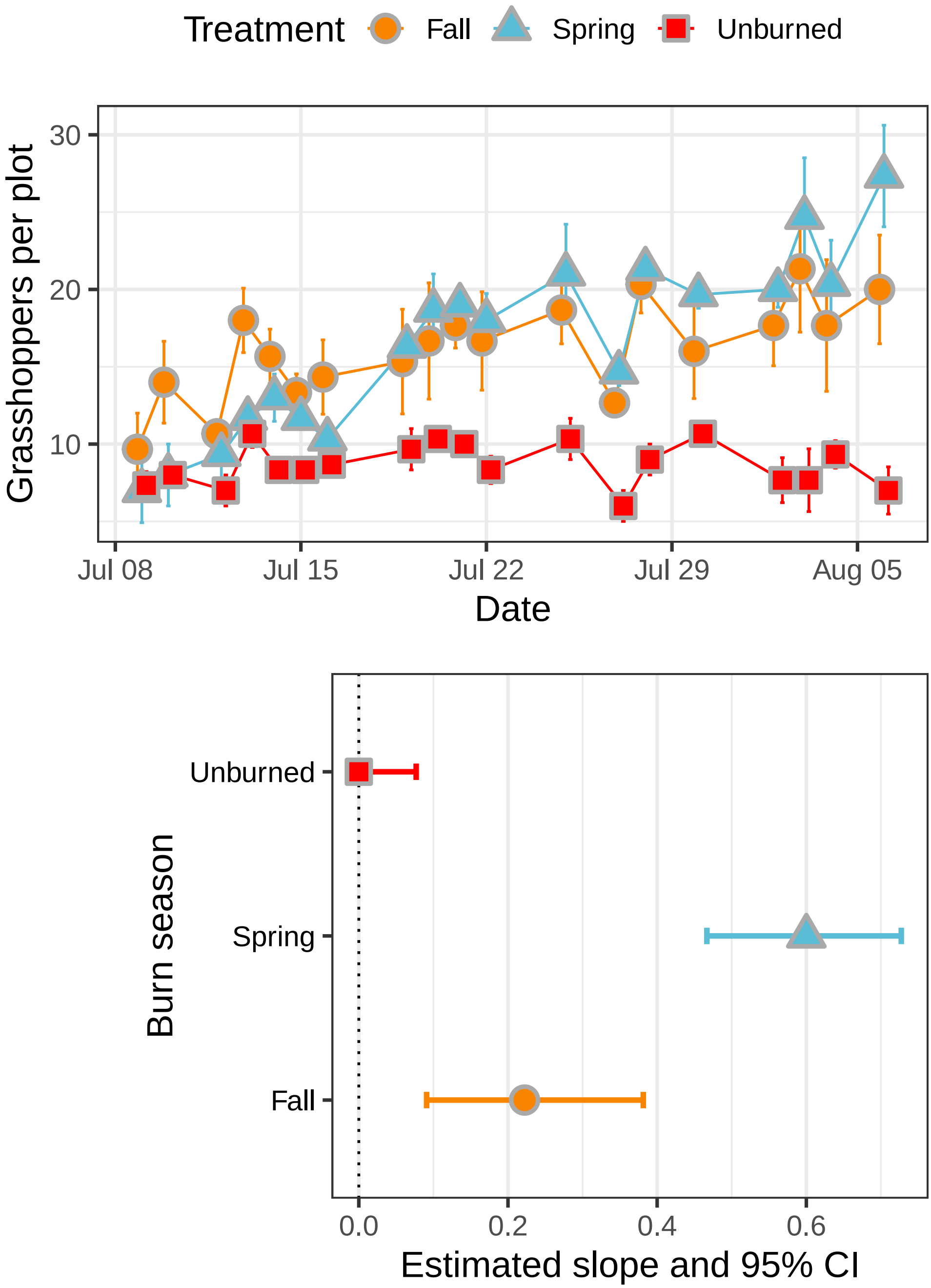

Fig. 3 Observed grasshopper counts per square meter. Red indicates data taken from fall burn treatments, green from spring burn treatments, and blue from unburned (control) plots. *Bottom* shows data from Kendall's Tau statistic which assessed the observed count trendline consistency over time. Our tau values were compared against the null hypothesis that there was no trend in our data. 95% confidence intervals were calculated to show the possible variance in slope for the data over time.

disturbances (Matenaar et al, 2014). Thanks to nutrient buffering produced by fire treatment (Spiess et al, 2020), protein availability produced a magnet effect which we believe caused the heightened density and offtake in burned plots (Meyer et al, 2002). These findings indicate fire disturbance can produce pockets of extreme competition between range herbivores, with much less forage for ungulates than what is seemingly available.

M. sanguinipes' preferred diet is a nitrogen and carbohydrate ratio of 1:1, making them especially robust and better able to adapt to nutritionally variable seasons (Behmer and Joern, 2008). Furthermore, these grasshoppers have the fastest egg production rate at intermediate dietary nitrogen levels of around 4% (Joern and Behmer, 1998) and use nitrogen to maintain their health and function (Schmitz, 2010). Due to their robust qualities, these grasshoppers were incredibly abundant on the Northern Great Plains in the summer of 2021. Although our burned plots had higher nitrogen than what is ideal for egg production, the competition between grasshoppers and the overall low nitrogen content of the landscape pushed M. sanguinipes to our plots to supplement their diets. Primary productivity in the Northern Great Plains is directly linked to rainfall (Padbury et al, 2002), therefore the steady increase in grasshopper density on our burn treatment plots is most likely attributable to an intensification of the magnet effect as the summer long drought progressed given that emergence typically peaks in late June (Belovsky and Slade, 1995; Humphreys et al, 2022). While other research suggests that grasshoppers can be attracted to heterogeneous areas for thermoregulatory microhabitats (Joern and Laws, 2013), the rapid increase in grasshopper density and the worsening of the drought over the summer points to a nutrient pull rather than a beneficial microhabitat. High temperatures, which we experienced consistently throughout the summer heat wave, weaken M. sanguinipes ability to fight infection (Srygley and Jaronski, 2022), further indicating that these grasshoppers are drawn by nitrogen content and not thermoregulation when shade was nearly completely absent in the burned plots.

Our study differs from other pyric herbivory studies because it was conducted with small, clustered areas of burn. Because density increased so greatly with burn in this study, it indicates a need for further research into small burn resource utilization by range grasshoppers. Future directions for our study can examine how grasshopper density changes with distance from a burn edge for a large burn area. This information could provide a clearer picture of recolonization effects created by burn scars combined with magnet effects. Recolonization presents an avenue for this research to be applied to larger burns in the Great Plains region, which are becoming more and more common. Grasshopper density changes could also be further examined through the offtake rate over time. Further research is needed to see if the offtake rate increased in burned plots over the duration of the drought. This would show that offtake is directly related to the quality of the surrounding forage. Because climate change is intensifying drought conditions (Derner et al, 2018), understanding how offtake will change will better inform ranching practices to ensure sustainable competition between grasshoppers and livestock.

Our study has important implications for ranch practices in the Northern Great Plains. Because prescribed fire is so often used as a forage buffer for cattle ranching (Spiess et al, 2020), it is important to know how much of the available forage will go to cattle and how much will be consumed by grasshoppers. Our research already goes against the population dynamics between grasshoppers and prescribed previously described (Joern, 2004;

Vermeire et al, 2004), so it is very likely that grasshopper abundances are being underestimated when determining how many cattle can be put out to pasture without overgrazing the landscape. Furthermore, because the density changed so much over the course of the study, ranchers must reevaluate the level of competition at the beginning of the season compared to the end of the season when resources are even more scarce in a drought.

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Conflict of Interest. The authors declare that they have no conflict of interest.

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