

Heatwave implications for the future of longleaf pine savanna understory restoration

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Keywords: bunchgrass | climate extreme | fuel load | grass plug | ground layer | productivity

Article:

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Bunchgrass · Grass plug · Climate extreme · Fuel load

Introduction

Restoration of ecosystems is a key priority in biodiversity conservation globally. However, restoration success is threatened by climate change (Lavendel 2003). Worldwide, anthropogenic climate change has resulted in global warming and increased variability in the hydrological cycle (Hayhoe et al. 2018). As a

result, many regions around the world are experiencing higher occurrences of extreme weather events, such as heatwaves (Overpeck 2013); (Mazdiyasi and AghaKouchak 2015); (Ades et al. 2020), here defined as increased temperature accompanied by decreased precipitation and humidity. Therefore, to properly restore the biodiversity in degraded ecosystems, climate change must be factored into current and future restoration plans (Harris et al. 2006); (Wilsey 2020). When climate change is accounted for in restoration planning, practitioners will be better equipped to work within an adaptive management framework to more successfully restore ecosystems and, therefore, conserve biodiversity (Buckley et al. 2011).

Within the USA, the longleaf pine (LLP) savanna ecosystem in the Southeast is of particular importance when considering the intersection of restoration and climate change (Noss et al. 2015); (Kirkman and Jack 2017). Currently, there are large efforts underway to restore the LLP savanna ecosystem (Oswalt et al. 2012); (Holland et al. 2019). Prior to the European settlement of North America, the fire-dependent LLP savanna ecosystem covered an estimated 92 million acres of the Southeast USA. However, anthropogenic disturbances, including fire suppression, led to the degradation and loss of the ecosystem and, therefore, much of its biodiversity (Frost et al. 2006). Today, the LLP savanna ecosystem covers only 3% of its historic range (Oswalt et al. 2012). While the overstory of LLP savannas are dominated by a single tree species, the longleaf pine tree (*Pinus palustris*), the understories of LLP savannas are rich in graminoid and forb species, with some sites having > 40 vascular plant species in a 1m² area (Walker and Peet 1984); (Brudvig et al. 2013). Therefore, restoration that focuses on the understory plant community is needed (Veldman et al. 2015). However, the Southeast USA is also experiencing increased heatwaves that are expected to worsen as the climate continues to change (Hopkinson et al. 2013); (Hayhoe et al. 2018); (Hoegh-Guldberg et al. 2018). The practical tools for LLP understory restoration are underdeveloped, particularly in the face of climate change.

While the understory of LLP savannas is important from a biodiversity perspective, it is also critical to the sustainability of restoration projects due to its role in the vegetation-fire feedback loop. LLP savanna is a fire-dependent ecosystem, requiring burning to reduce

litter on the understory floor and eliminate the competitive advantage of woody species (Brockway et al. 2006); (Walker et al. 2006); (Gagnon et al. 2015). Frequent burning in LLP savannas increases grass dominance and biodiversity, while maintaining an open canopy (Barnett 1999); (Brockway et al. 2006); (Veldman et al. 2014). The productivity of the grass layer interacts with fire in a positive feedback loop—a productive understory leads to a high fuel load, the high fuel load leads to frequent fire, and frequent fire leads to a productive understory (Brockway et al. 2006); (Barlow et al. 2012); (Fill et al. 2016). This vegetation-fire feedback loop is a critical target for restoration efforts of this savanna ecosystem; without a productive grass layer to fuel fires, the system cannot persist long term without intensive, costly, and continuous management in place.

Unfortunately, the understory grasses and forbs are also sensitive to climate change impacts, in part due to more shallow roots than their longleaf pine tree counterparts (Clewell 1989); (Beckage et al. 2006); (Brockway et al. 2006). Numerous studies have shown grassland communities to be resilient to heatwaves, with decreased production initially, followed by a quick recovery (e.g., (Weaver 1954); (Kreyling et al. 2008); (Hoover et al. 2014); (Isbell et al. 2015)). However, in a restoration context, newly planted grass plugs may be less resilient (Stromberg and Kephart 1996); (Huddleston and Young 2004). Additionally, heatwave interactions with disturbance could lead to a decrease in grass dominance (Ratajczak et al. 2019), impacting fuel load. Thus, climate change, particularly in fire prone ecosystems, has the potential to make the restoration of the vegetation-fire feedback loop unsuccessful and must be studied in more depth. To understand the impact that climate change in fire prone ecosystems has on the vegetation-fire feedback loop, we must first assess how different understory grass species, important in the vegetation-fire feedback loop in the LLP savanna, react to heatwaves in their first year after planting.

Here, we conducted a series of three separate greenhouse experiments (Exps) to understand how heatwaves influence the growth and development of native grass plugs commonly used in LLP savanna restoration. One heatwave event was simulated during each experiment by increasing heat and decreasing humidity and precipitation for half of the grass plugs. Heatwave severity and grass species differed slightly

between each experiment, giving each an independent experimental approach. However, the unifying goal is to understand how the occurrence of a heatwave influences the restoration of understory grass species and, therefore, the vegetation-fire feedback loop. Utilizing three independent experiments allowed us to explore the effects of heatwaves within three separate contexts, increasing the robustness of the shared findings. Across all three experiments, we measured weekly plant growth metrics (maximum leaf length, maximum plant height, and stem number) and at the end of each experiment, we measured leaf area. Using this information, we determined the heatwave-sensitive morphological traits that lead to biomass changes; biomass was measured at the end of each experiment, with aboveground biomass measurements for all three experiments and belowground biomass measurements for Exp 2 only. While we hypothesized that growth would be negatively impacted by the occurrence of a heatwave, our study aimed to explore the relative sensitivities of morphological traits that lead to reduced growth within and across species.

Methods

We conducted a series of three consecutive greenhouse experiments (Table 1) exploring the effects of heatwaves on native grass plug growth. We performed all three experiments in the Biology Department's Teaching Greenhouse at the University of North Carolina at Greensboro (UNCG), USA. All three experiments were part of a Course-based Undergraduate Research Experience (CURE) in the Ecology and Evolution Lab required for all UNCG Biology

undergraduates. We conducted one experiment per semester, with approximately 125 undergraduate researchers per experiment participating in experimental set up, data collection, and preliminary data analyses.

We obtained grass plugs of four native species common in LLP understories from the North Carolina (NC) Forest Service Claridge Nursery, a nursery that sells grass plugs specifically for LLP savanna restoration across the state of NC. Across our three experiments, we used *Andropogon gerardii*, *Aristida stricta*, *Schizachyrium scoparium*, and *Sorghastrum nutans*. All four are highly productive, C4, perennial grasses which contribute substantially to the vegetation-fire feedback necessary for healthy LLP savanna. We trimmed the bottom ~ 2.5 cm of all grass plugs and gently loosened the roots before potting using SunGro 3B Potting Mix in plastic pots (12.7 cm × 8.3 cm × 8.3 cm). Undergraduate researchers planted all of the grass plugs into separate pots (i.e., one grass plug per pot), and grasses were then placed in trays located on benches in the greenhouse, where temperature, humidity, and light availability were monitored throughout the experiment (Fig. 1). We then assigned each pot to one of two treatments: control or heatwave. We watered plugs to maintain soil moisture above the wilting point, except for the heatwave grass plugs during the simulated heatwave. All plugs were always in identical conditions, except during the heatwave. To account for minor microclimatic differences in the greenhouse, we alternated control and heatwave grasses across the bench when the heatwave was not being imposed. To simulate the heatwave, we transferred half of the grass plugs to a different bay of the greenhouse where humidity was substantially lower

Table 1 Experimental details for the three independent greenhouse experiments, including grass species, number of replicates per treatment, and timing of experiment and heatwave

Experiment	Species	n	Experiment			Heatwave		
			Start	End	Length (days)	Start	End	Length (days)
Exp 1	<i>A. gerardii</i>	24	1/4/2019	3/22/2019	68	2/11/2019	2/25/2018	15
	<i>A. stricta</i>	24						
	<i>S. scoparium</i>	24						
	<i>S. nutans</i>	24						
Exp 2	<i>S. nutans</i>	96	8/26/2019	11/1/2019	68	10/11/2019	10/21/2019	11
Exp 3	<i>A. stricta</i>	96	1/13/2020	3/18/2020	66	3/9/2020	3/17/2020	9

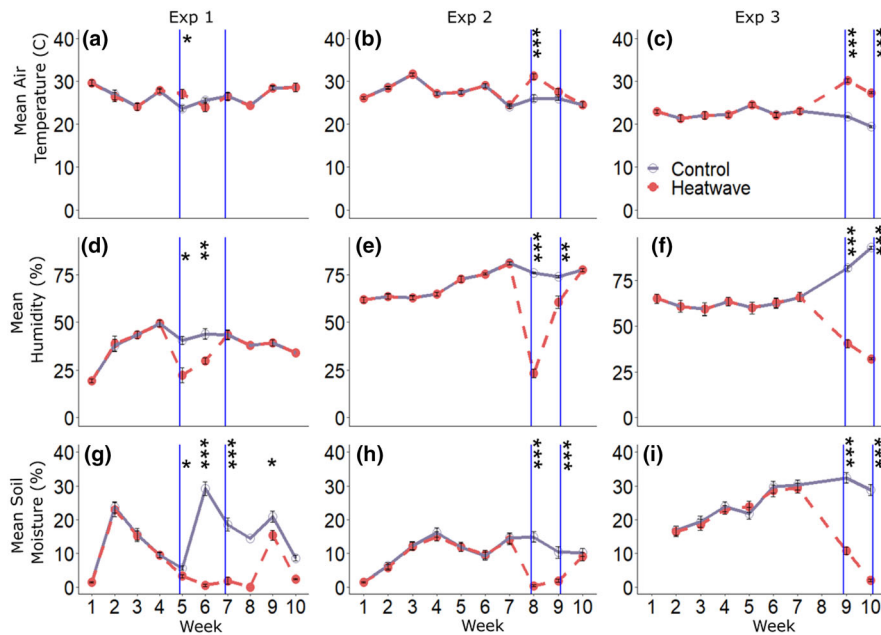


Fig. 1 Mean and standard error of weekly **a–c** temperature, **d–f** humidity, and **g–i** soil moisture for each of the three independent experiments for control (purple solid line) and heatwave (red dashed line) plants. Blue vertical lines denote the start and end of the heatwave. Significant differences between treatments using a Wilcoxon rank sum test for each experiment,

measurement, and week are denoted with * and represent $p < 0.05$, $p < 0.01$, and $p < 0.001$ for one, two, and three asterisks, respectively, from paired t-tests. Importantly, p-values were adjusted for multiple comparisons using the Benjamini–Hochberg method before determining significance. Bars represent means \pm standard error

(45% in Exp 1, 69% in Exp 2, and 51% in Exp 3; Fig. 1), temperature was higher (14% in Exp 1, 20% in Exp 2, and 39% in Exp 3; Fig. 1), and the plugs received no water resulting in reduced soil moisture (42% in Exp 1, 97% in Exp 2, and 67% in Exp 3; Fig. 1). The duration of the heatwave treatment for each experiment differed, with heatwave plugs experiencing a 15-, 11-, and 9-day heatwave for Exps 1, 2, and 3, respectively (Table 1). At the end of the heatwave, we moved heatwave plugs back to the bench with the control plugs, returning them to equivalent conditions. We determined the length of the heatwaves for each experiment based on several factors. Single heatwave events in the Southeastern United States are predicted to last from 5 to 20 days under predicted global climate temperature changes (Perkins-Kirkpatrick and Gibson 2017), so we chose heatwave lengths in the greenhouse to reflect this variability, with a target of 10 days. Additionally, altering the temperature in the greenhouse partially depends on outside air temperature. Thus, the heatwave in Exp 1 was longer than 10 days due to low outside temperatures and Exp 3 was shorter than

10 days due to warm outside temperatures. Finally, as these experiments were conducted as part of an undergraduate course, we were confined to each semester’s schedule and adjusted the heatwave accordingly to maximize student’s measurements while allowing time to properly analyze and report their results.

Undergraduate researchers measured maximum leaf length, plant height, and stem number weekly throughout the experiment over 68, 68, and 66 days during Exps 1, 2, and 3, respectively (Table 1), with primary production and leaf area measured upon completion of the experiment, which was 25, 11, and 1 day after the end of the heatwave treatment for Exps 1, 2, and 3, respectively (Table 1). For maximum leaf length, undergraduate researchers measured the longest green leaf by placing the ruler gently on the soil surface at a 90° angle to the soil and extending the longest green leaf up along the ruler to its full length. Researchers measured plant height as the height of the tallest green part of the plant without manipulating the grass leaves. Undergraduate researchers counted stem number as the number of green stems sprouting from

the base of the plant. We measured aboveground primary productivity by harvesting all aboveground biomass at the end of the experiment and separating it into alive and dead components. Then, we calculated leaf area (cm^2) using a leaf area meter (Li-Cor) directly after harvest of aboveground biomass by randomly selecting one fully emerged, live, leaf blade from the alive biomass of each sample and running it through the meter. Then, we dried both the alive and dead biomass for each sample separately in a forced air oven at 60°C for 48 h before weighing. We report aboveground production as the sum of all living and dead aboveground biomass, an indicator of fuel load, created per plug. In Exp 2 we collected belowground productivity for each pot by first sieving the soil and then gently washing the roots. We placed roots into a forced air oven at 60°C for 48 h before weighing. While planned for Exp 3, COVID-19 prevented the ability to gather belowground productivity data, as the experiment ended earlier than planned when UNCG announced research shutdown in March 2020. Undergraduate researchers recorded humidity, temperature, light availability, and soil moisture multiple times per week near mid-day. Researchers monitored humidity and temperature using digital sensors placed among the grasses on each half of the bench. Researchers measured light availability (lux) over each tray of pots using small, handheld light meters (Fisher Scientific). Undergraduate researchers collected soil moisture using a probe (6 inch, Campbell Scientific) which was inserted into “reference” pots which contained a grass plug, but these plugs were not monitored for growth due to probe disturbance. Researchers measured all four abiotic variables each time they collected data throughout the semester.

Since undergraduate researchers were mostly new to plant research, and to ensure accuracy and effective experimental manipulations, we put several quality control measures into place. First, a full-time graduate teaching assistant was in the greenhouse at all times with the undergraduate researchers to answer questions and monitor data collection techniques. Second, undergraduate researchers worked in pairs. And finally, two separate groups measured each plant. This allowed us to check the data post collection; we determined the percent difference between the two pseudo-replicated measurements. If measurements were similar, we took the mean. If measurements were very different, further exploration occurred (i.e.,

original data sheet checked for data entry errors, compared previous and following weeks measures) to determine which record was correct. If no obvious solution could be determined, we dropped measurements for that plant in that week. In addition, at times, data were not submitted at the end of the semester, and was essentially lost, thus replication throughout the experiment varied. This was particularly true for Exp 2. Here we present all data that we were able to obtain and that passed our quality control checks.

We conducted all data manipulation and statistical analyses in R (R Core Team 2020). All variables (both abiotic and biotic) were measured weekly throughout the experiments. However, only the measurements from the last week of the heatwave treatment were used in analyses for biotic variables that were measured weekly. This single week was chosen for the biotic variables for the sake of clarity in assessing multiple experiments across time and so that the same timepoint in each experiment could be assessed, as Exp 3 ended two weeks early due to COVID shutdowns. Importantly, the same timepoint was used for the paired control and treatment plots; therefore, they are directly comparable. Conversely, for the abiotic variables, we assessed data from all weekly timepoints, as this weekly information is important to show the effectiveness of the heatwave treatments and to show that when not in the heatwave, the two treatments were exposed to identical conditions. As our data were not normal and sample sizes were low, we determined differences between control and heatwave grass plugs and abiotic conditions by using a Wilcoxon rank sum test with separate tests run for each experiment, variable, and species. *P* values were adjusted for multiple comparisons using the Benjamini–Hochberg method (Benjamini and Hochberg 1995). In Exp 1, *p*-values were adjusted for the five biotic variables tested within a species, and for the abiotic variables, *p*-values were adjusted for the ten weekly measurements tested. As a note, there was not enough data to run a Wilcoxon rank sum test on week 8 of the humidity and air temperature data and week 10 of the air temperature data. Therefore adjustments were made based off the total number of weekly measurements where a Wilcoxon rank sum test was performed. In Exp 2, *p*-values were adjusted for the six biotic variables tested, and for the abiotic variables, *p*-values were adjusted for the 10 weekly measurements tested. In Exp 3, *p*-values were adjusted for the six

biotic variables tested, and for the abiotic variables, p -values were adjusted for nine weekly measurements tested (no data were collected on week 8 of the experiment).

The simulated heatwaves increased temperature and reduced humidity and soil moisture during the treatment, with a lagged recovery following the end of the heatwave (Fig. 1). Specifically, in Exp 1, we simulated the heatwave from the start of week 5 through week 7 of the experiment. In week 5, the average air temperature was significantly higher in the heatwave (Fig. 1a). In weeks 5 and 6 the average humidity was significantly lower in the heatwave (Fig. 1d), and in weeks 5, 6, 7, and 9, soil moisture was significantly lower in the heatwave (Fig. 1g). In Exp 2, we simulated the heatwave from the end of week 7 through week 9. In week 8, the average air temperature was significantly higher in the heatwave (Fig. 1b), and in weeks 8 and 9, the humidity and soil moisture was significantly lower in the heatwave (Fig. 1e, h). In Exp 3, we simulated the heatwave from the end of week 8 through week 10. In week 9 and 10, the average air temperature was significantly higher, while humidity and soil moisture were significantly lower in the heatwave (Fig. 1c, f, i). Across all three experiments, only two of 29 weeks (Exp 3—weeks 9 and 10) showed significant differences in light availability (lux) between heatwave and control plants (data not shown).

Results

Overall, the fifteen-day heatwave of Exp 1 (Table 1; Fig. 1) infrequently caused plant death (Table S2), but tended to decrease measures of plant growth; however, significant differences between treatment and control growth metrics were not common (Fig. 2 & S5; Table S3). In fact, for three of the four species (*A. gerardii*, *S. scoparium*, and *S. nutans*), no variable measured was significantly different between the two treatments (Fig. 2 & S5; Table S3), even though aboveground biomass in Week 9 was 20%, 35%, and 21% lower (not significant) for *A. gerardii*, *S. scoparium*, and *S. nutans*, respectively (Fig. 2; Table S3). *A. stricta* had the lowest aboveground biomass change of only 12% in Week 9 due to the heatwave, which was not significant (Fig. 2; Table S3); however, maximum plant height was

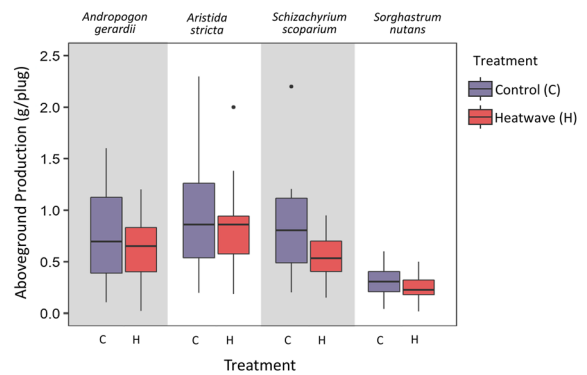


Fig. 2 Aboveground production (sum of all living and dead aboveground biomass) from Experiment 1 was not significantly reduced under heatwave conditions for any of the four grasses (*Andropogon gerardii*, *Aristida stricta*, *Schizachyrium scoparium*, *Sorghastrum nutans*). Aboveground production was collected from Control (C; purple) and Heatwave (H; red)-exposed grass plugs at the end of the experiment, 9 weeks after initial planting and 3 weeks after the heatwave ended. Significant differences between treatments were determined by using a Wilcoxon rank sum test for each species. Significance at $p < 0.05$, after correcting for multiple comparisons using the Benjamini–Hochberg method, is denoted with an *. Bars represent means \pm standard error

significantly decreased in Week 7 by the heatwave by 8% (Figure S5; Table S3). We also conducted analyses for the first week post heatwave (Week 8) and saw the same significance trends as mentioned previously (data not shown).

Similarly, the eleven-day heatwave of Exp 2 (Table 1; Fig. 1) did not cause plant death (Table S2) but significantly decreased measures of plant growth for *S. nutans* (Fig. 3 & S5; Table S4). In Week 9, at the end of the heatwave, we saw significantly lower maximum plant height (22%) and stem number (24%). In the last week of the experiment (Week 11), leaf area (Figure S5; Table S4) was 58% lower in heatwave grasses compared to control, and production was significantly lower for the heatwave plants compared to the control plants (Fig. 3; Table S4). Aboveground production was 16% lower in the heatwave treatment compared to the control (Fig. 3a; Table S4), while belowground production was 25% lower (Fig. 3b; Table S4).

Finally, the nine-day heatwave of Exp 3 (Table 1; Fig. 1) did not cause plant death (Table S2) but significantly decreased measures of plant growth for *A. stricta* (Fig. 4 & S5; Table S5). We took all

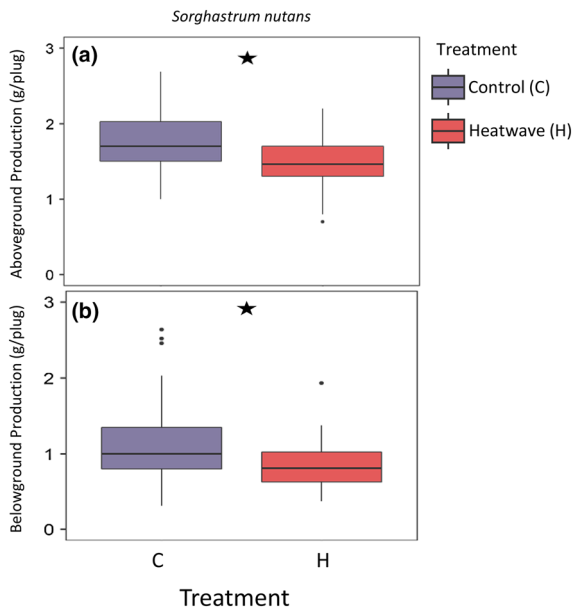


Fig. 3 **a** Aboveground and **b** belowground production (sum of all living and dead biomass) from Experiment 2 were both significantly reduced in *Sorghastrum nutans*, Indian grass, under heatwave conditions. Production was collected from Control (C; purple) and Heatwave (H; red)-exposed grass plugs at the end of the experiment, 11 weeks after initial planting and 3 weeks after the heatwave ended. Significant differences between treatments were determined by using a Wilcoxon rank sum test. Significance at $p < 0.05$, after correcting for multiple comparisons using the Benjamini–Hochberg method, is denoted with an *. Bars represent means \pm standard error

measurements the week after the heatwave ended (Week 10), as the UNCG shutdown caused by COVID-19 required us to end our experiment 2 weeks earlier than planned. Aboveground production was 13% lower in the heatwave plants compared to the control plants (Fig. 4; Table S5). Similarly, we saw significant reductions in maximum plant height (7%) and leaf area (25%), while maximum leaf length and stem number were not significantly different (Figure S5; Table S5).

Discussion

This series of greenhouse experiments shows that an increase in heatwave occurrence, predicted for much of the LLP range (Hayhoe et al. 2018); (Hoegh-Guldberg et al. 2018), will likely have consequences for the restoration of biomass production, with implications for the vegetation–fire feedback loop in LLP

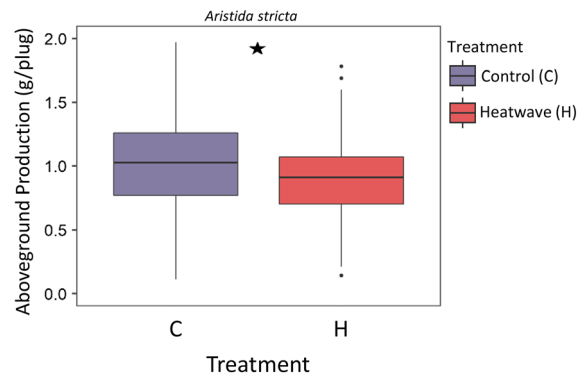


Fig. 4 Aboveground production (sum of all living and dead aboveground biomass) from Experiment 3 was significantly reduced in *Aristida stricta*, Wiregrass, under heatwave conditions. Production was collected from Control (C; purple) and Heatwave (H; red)-exposed grass at the end of the experiment, 10 weeks after initial planting and the week after the heatwave ended. Significant differences between treatments were determined by using a Wilcoxon rank sum test. Significance at $p < 0.05$, after correcting for multiple comparisons using the Benjamini–Hochberg method, is denoted with an *. Bars represent means \pm standard error

savanna restoration efforts. While nearly all individuals survived the heatwave, generally, the heatwave plugs had lower aboveground biomass compared to the control plugs at the end of each experiment. The decrease in aboveground biomass will correspond to less fuel available to carry fire, which is essential to maintaining plant biodiversity. Without a productive understory grass layer, restoration efforts aimed at high understory diversity could be more likely to fail. However, this can be overcome by considering the effects that heatwaves will have on grass plug growth when forming restoration plans.

Overall, we show that the occurrence of a single heatwave decreased growth of commonly found native understory grass species of LLP savannas in some experimental contexts. Across all three experiments and all grass species studied, we found that the occurrence of a heatwave negatively impacted measures of plant growth, though this was most obvious when looking at aboveground biomass. *S. scoparium* appears to be the most sensitive to heatwaves as seen in Exp 1, with a 35% decrease in aboveground biomass due to the heatwave. While no other species showed significant decreases in biomass in Exp 1, this may have been due to the lower magnitude of response. While variability of response among the grass species was equivalent, the lower magnitude of response of

some grasses was not significantly detectable with an $n = 24$. In Exp 2 and 3 where replication was 4 times higher ($n = 96$ per treatment) than Exp 1, *S. nutans* and *A. stricta* both showed similar magnitudes of biomass decrease as in Exp 1, but in Exp 2 and 3, the decrease was significant. *A. stricta* appears to be more resilient than the other three species, as we found only a ~ 12 – 13% decrease in aboveground biomass in both Exp 1 (not statistically significant) and Exp 3 (statistically significant). The shared findings across these different experimental contexts help to strengthen our results and suggest that while several grass species are negatively impacted by heatwaves, strategically choosing the least sensitive species in restoration could help lessen the impact of the heatwave on the vegetation–fire feedback loop.

Interestingly, in Exp 2, we also found that the occurrence of a heatwave decreased belowground biomass in *S. nutans* (25% reduction), in addition to the observed decrease in aboveground production (16% reduction). While this decrease belowground would not directly impact the vegetation–fire feedback loop, it has an indirect impact by decreasing the ability of grasses to regrow following fire the following summer. In fire prone ecosystems that experience low-severity fires, dominant grass species consistently lose aboveground biomass through burning, while belowground root systems remain intact (Blair et al. 2014). These belowground roots and storage organs (e.g., rhizomes and tubers), which carry over from year to year, serve as a regenerative source of carbon for these dominant grasses to utilize in aboveground biomass production following fire (Bowen and Pate 1993); (Bellingham and Sparrow 2000). When belowground reserves are depleted, growth the following year can be dampened, again leading to low fuel production, and hindering the successful establishment of the vegetation–fire feedback loop in subsequent year. Additionally, the decrease in belowground production has consequences for carbon sequestration. In general, terrestrial plant productivity is a major carbon sink, capturing carbon from the atmosphere and sequestering it in plant tissues, both above- and belowground (Knapp et al. 2014). Grasslands and savannas store much of their carbon belowground, especially those that experience frequent fire events (Johnson and Matchett 2001); (Kitchen et al. 2009). Thus, grass-dominated systems are important for global carbon sequestration (Scurlock and Hall 1998). As such,

carbon sequestration is an important ecosystem service provided by LLP savannas and is frequently a target of restoration efforts. Our work with Exp 2 further reinforces the need to understand the impact of heatwaves both above and belowground and suggests that this might be a particularly sensitive consequence of increased heatwave occurrence.

Our findings generally align with the results of previous work from other grass-dominated ecosystems. At a tallgrass prairie site, aboveground production of dominant species significantly decreased due to increased heat (infrared heat lamps) and decreased precipitation (drought-simulating rain-out shelters) in situ (Hoover et al. 2014). Further, belowground production in grasses under heatwaves in a Mongolian grassland decreased, which affects grass resilience (Li et al. 2020). Interestingly though, when isolating the effects of heat and water stress in a tallgrass prairie, drought (reduced precipitation) significantly reduced photosynthesis and productivity in *A. gerardii* and *S. nutans*, but the combination of heat and water loss (what our study calls a heatwave) did not add to any additional negative responses. This suggests drought alone dictates plant responses to heatwave stress (Hoover et al. 2014). While the experiments presented here cannot tease apart the interactive effects of drought and heat, we plan to explore this idea in the future through further greenhouse studies.

In this study, we saw that a single heatwave event caused a significant decrease in biomass. Practically, this means that there will be less forage and cover for animals, as well as less fuel for the even spread of fire, thereby lessening the potential for successful restoration. The structure of these species-rich LLP savannas is maintained by frequent fire that is carried across the understory, primarily by bunchgrass species. These greenhouse studies indicate that future climate change may disrupt ecosystem processes in newly restored LLP savannas because the spread of fire is greatly impacted by a decrease in grass productivity (Brockway and Lewis 1997). From these studies, we have seen that with an increased frequency of heatwaves, in field situations, it is likely that each grass plug, regardless of species, will be smaller and contribute less biomass to the system. With this information, land managers can be prepared to restore the understory plant community with greater efficacy. This loss of aboveground biomass can be overcome by planting resilient grass species, as well as a greater density of

grass plugs, to maintain the desired amount of productivity post heatwave events. However, too much grass biomass can lead to a decrease in plant biodiversity, as large, abundant grasses assume dominance in the understory. It is therefore important to determine precisely how many more grass plugs to plant. In these studies, we found *A. stricta* to be more resilient than other species, with the smallest biomass reduction (12%) after a heatwave. Restoration plans could therefore for example potentially incorporate a 12% increase in the number of *A. stricta* grass plugs that are planted to overcome losses from heatwaves without reducing plant biodiversity.

While the findings of this study have important implications for the management of LLP savannas in a changing environment, it is important to note a key limitation of this study. Primarily, all three experiments were conducted under greenhouse conditions and therefore do not necessarily represent the effects of natural heatwaves on understory grass species in their native environment. In our experiment, grass plugs were planted in their own, individual pots, free from belowground competition; in the field, however, there would be competition between understory and the overstory species for shared resources, such as soil water and light availability (Pecot et al. 2007). Light availability, as a result of LLP tree density, greatly affects the composition and abundance of herbaceous understory species (Harrington et al. 2003); (Harrington et al. 2006). However, while competition between understory and overstory species may be of importance, in this species-rich community, herbaceous understory competition is relatively low (Roth et al. 2008). Grass species native to LLP savannas have extensive root systems, though not as deep as their longleaf pine tree counterparts (Clewell 1989); (Nippert et al. 2012), that grow well in sandy soils. Understory grass species in the field could develop deeper roots, accessing deeper resources, and therefore may show muted impacts of heatwaves compared to grasses grown in more restrictive pots. However, in the first year of growth from a plug in the field, it is unlikely the grass plugs would be able to develop the substantial rooting system seen in these perennial grasses in native LLP savanna; therefore, our greenhouse experiment is informative of first year restoration efforts (Tony et al. 2014); (Wonkka et al. 2017). While field confirmation of our findings is still needed, these results assess the sensitivities of morphological

traits that are behind potential decreases in above-ground biomass during a heatwave in the first year.

Additionally, the effects of a single heatwave event in the first year of restoration could be compounded by subsequent heatwave events. Further, understory grass biomass accumulation is essential for even fire spread, and, even if the grass plugs used in restoration are only temporarily impacted by a single heatwave, but decrease fuel load (biomass), fire effectiveness can be hindered (Addington et al. 2015); (Gonzalez-Benecke et al. 2015). Without efficient and even fire, woody species can encroach, outcompete the herbaceous understory, and change the composition of the savanna (Kush et al. 1999, 2000). Thus, even if the impacts of a single heatwave only seem temporary, the ramifications for the trajectory of the restoration process could be longer term, especially since multiple heatwave events in a single growing season are increasing in frequency (Ades et al. 2020). Therefore, in future greenhouse studies, we plan to address the legacy effects of heatwaves on these dominant understory grasses for experiencing a subsequent heatwave event.

Overall, this study will help to ensure the successful restoration of the LLP savanna ecosystem in the face of a rapidly changing world in two key ways. First, these results provide valuable information to restoration practitioners. Heatwaves are already more prevalent and longer lasting than they historically were, and this trend is predicted to intensify (Overpeck 2013); (Mazdiyasni and AghaKouchak 2015); (Ades et al. 2020). Our findings highlight the need for restoration practitioners to consider the added stress of heatwaves when making restoration plans, potentially selecting for more heatwave tolerant species, and increasing plug numbers. Restoring the vegetation-fire feedback loop may require different restoration methods in the future than historically implemented and may require that land managers quickly change restoration plans with the most up to date research and climate models informing plans (Clark et al. 2018). Second, the use of undergraduate research in the classroom setting promises to aid in restoration efforts. Not only does the CURE expose students to research and science (Russell et al. 2007); (Thiry and Laursen 2011), ensuring a diverse and scientifically literate workforce (Barlow and Villarejo 2004); (Eagan et al. 2011), it also creates an emotional tie and a sense of pride and stewardship in ~ 250 students per year for this local

and endangered ecosystem. These undergraduates conducted the experiments, collected and analyzed data for a final report, and gave group presentations to the class on their findings. Importantly, each semester the students also virtually attend a conference where this work is presented, and watch presentations of previous semesters work ensuring that they understand these data are needed and valued by the longleaf pine restoration community. Continuation of this CURE will allow us to educate and expose potentially thousands of scientists to this imperiled ecosystem and to the need to prioritize LLP savanna restoration.

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Authors' contributions ALY, CEG, and SEK conceived and designed the experiments. ALY, KJB, MDF, and SEK analyzed data and wrote the manuscript. All authors edited the manuscript.

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Data availability All data and R code used in this manuscript can be found on GitHub (<https://tinyurl.com/e9pypphy>).

Declarations

Conflicts of interest The authors have no conflicts of interest to declare.

Ethical approval Not applicable.

Consent to participate All authors give their consent to participate.

Consent for publication All authors consent to publication.

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