

RESEARCH ARTICLE

FIRE RESILIENCE OF AQUATIC CRUSTACEAN RESTING STAGES IN PLAYA WETLANDS, OKLAHOMA, USA

Eric G. Bright^{1,2*}, Mohsain Gill^{1,2}, Ashtyn Barrientes^{1,2}, and Elizabeth A. Bergey^{1,2}

¹University of Oklahoma, Department of Biology,
730 Van Vleet Oval, Room 314, Norman, Oklahoma 73019, USA

²Oklahoma Biological Survey, 111 East Chesapeake Street, Norman, Oklahoma 73019, USA

*Corresponding author: Tel.: +1-405-325-7071; e-mail: brighte@ou.edu

ABSTRACT

Prescribed burns and wildfires maintain prairie vegetation by limiting tree growth and promoting prairie grasses and forb production. Previous studies have shown that fire causes mixed effects on the prairie fauna, promoting some organisms while negatively affecting other organisms. Playa wetlands are interspersed within some semi-arid prairie landscapes, and are thereby subject to fire. These temporary wetlands can remain dry for years and less mobile aquatic taxa survive dry periods as drought resilient resting stages. We experimentally examined the effect of fire on the subsequent hatching of crustacean resting stages found in playa wetlands. Soil collected from four western Oklahoma playa wetlands was mixed and left unburned or exposed to burning (at three fuel levels: 0.5 time, 1 time, and 3 times the natural vegetation biomass) to simulate different fire intensities. We rehydrated soil taken from two depths (0 cm to 1 cm and 1 cm to 2 cm) for two weeks and examined hatched invertebrates and algal biomass. We did not find any significant difference in invertebrate richness and abundance

RESUMEN

Las quemas prescriptas y los incendios naturales mantienen la vegetación de pradera limitando el crecimiento de los árboles y promoviendo la producción de gramíneas y hierbas. Estudios previos han demostrado que el fuego causa efectos mixtos en la fauna de praderas, estimulando algunos organismos y afectando negativamente a otros. Las lagunas temporarias están intercaladas entre paisajes de praderas semiáridas, y están sujetas de este modo a la ocurrencia de fuegos. Estas lagunas temporarias pueden permanecer secas por años, y los taxones acuáticos menos móviles sobreviven a períodos secos en estado de latencia, siendo resilientes a la sequía. Nosotros examinamos experimentalmente el efecto del fuego en la subsecuente eclosión de crustáceos en etapas de latencia encontrados en lagunas temporarias. Muestras de suelo recogidas en cuatro sitios de lagunas temporarias en el oeste de Oklahoma fueron mezcladas y dejadas sin quemar o expuestas al fuego (en tres niveles de combustible: 0,5 veces, 1 vez, y 3 veces la biomasa de la vegetación natural), para simular distintas intensidades del fuego. Luego rehidratamos el suelo tomado de dos profundidades (de 0 cm hasta 1 cm y de 1 cm hasta 2 cm) durante dos semanas y examinamos la eclosión de invertebrados y la biomasa de algas. No encontramos ninguna diferencia significativa en la riqueza de invertebrados

or algal biomass from treated (burned) and untreated (unburned) soil in either of the soil layers. The resting stages of invertebrates are tolerant to a wide range of environmental factors and, consequently, are apparently tolerant (as a population) to increased soil temperatures resulting from low intensity burning.

y la abundancia o la biomasa de las algas entre el suelo con tratamiento (quemado) y sin tratamiento (sin quemar) en ninguna de las capas de suelo. Las etapas de reposo de los invertebrados son tolerantes a un amplio rango de factores ambientales y, consecuentemente, son aparentemente tolerantes (como población) al incremento de la temperatura del suelo como resultado de una baja intensidad de quema.

Keywords: crustaceans, fire tolerance, grassland, invertebrate seed bank, playa wetlands

Citation: Bright, E.G., M. Gill, A. Barrientes, and E.A. Bergey. 2016. Fire resilience of aquatic crustacean resting stages in playa wetlands, Oklahoma, USA. *Fire Ecology* 12(3): 26–39. doi: 10.4996/fireecology.1203026

INTRODUCTION

Climate and fire are suspected to have been integral players in the formation of the native grasslands of North America (Vogl 1974, Wright and Bailey 1980, Higgins 1984). As such, the fauna and flora of the grasslands developed ecological and evolutionary adaptations to fire (Bond and Keeley 2005). Fire maintains the distribution and diversity of grasses and small herbaceous plants that need high light requirements; fire suppression can cause a loss of 50 % of plant species in grasslands (Leach and Givnish 1996, Uys *et al.* 2004). Some plant species in fire prone areas have developed a requirement for fire to complete their life cycle (Naveh 1975, Bond and van Wilgen 2012).

Since fires have naturally maintained the prairie ecosystem of the Great Plains, wildlife managers have used prescribed burns as a conservation tool to maintain prairies worldwide (Looman 1983, de Van Booysen and Tainton 1984). Prescribed burns and wildfires limit tree encroachment into grasslands (Briggs *et al.* 2002) and increase annual production of some native prairie grasses (Glenn-Lewin *et al.* 1990). For example, fire increases the aboveground biomass of big bluestem grass (*Andropogon gerardii* Vitman; Old 1969, Peet *et*

al. 1975, Knapp 1984, 1985, Svejcar and Browning 1988). Fire also promotes the growth of prairie plants other than grasses, such as legumes and other forbs (Howe 1999, Maret and Wilson 2000, Kaye *et al.* 2001, Brockway *et al.* 2002).

Native Americans started using fire about 5000 years ago to promote game species such as elk (*Cervus canadensis* Erxleben), moose (*Alces alces* Linnaeus), and buffalo (*Bison bison* Linnaeus) (Anderson 1990, Kimmerer and Lake 2001) and prescribed burning continues as an economical method to limit tree and scrub encroachment in prairies. Burns are a common landscape feature in the USA Southwest, with prescribed burns applied to at least 40 000 ha, with an additional 93 000 ha burned by wildfires in 2014 alone (NIFC 2015).

While the effects of wildfire and prescribed burning on the vegetative community are well studied, the effects of fire on faunal groups are less well understood and can be quite variable. Small mammals either benefit or are harmed by fire, depending on the species-specific habitat and behavior (Kaufman *et al.* 1990). Amphibians and reptiles, as a whole, may be little affected by fire (in Appalachia: Greenberg and Waldrop 2008). However, fire effects vary: in an Australian grassland, reptile diversity was influenced by successional stage of vegetation

following fire (Masters 1996); in chaparral and coastal systems, amphibians and reptiles responded negatively to large-scale wildfires (Rochester *et al.* 2010). Grassland birds may be negatively affected shortly after fire, but populations generally recover rapidly (Grant *et al.* 2010). However, continued annual burning may negatively impact some species (Powell and Stouffer 2006).

Many, but not all, terrestrial invertebrates show significant declines in response to fire (Swengel 2001, Panzer 2002). Impacts are greater for taxa with low mobility (Panzer 2002), and increase with fire severity, especially as heat penetrates the soil (Malmström 2010). In addition to direct impact from fire, the combination of a drier, warmer habitat (Sharrow and Wright 1977) and altered food resources following fire may impact some taxa (Swengel 2001, Ray and Bergey 2015). Frequently impacted groups include land snails, spiders, springtails, and mites (York 1999, Harper *et al.* 2000, Nekola 2002, Severns 2005, Gongalsky 2011)—taxa that contribute to decomposition and nutrient recycling. Highly mobile flying insects often rapidly recolonize (Harper *et al.* 2000, Panzer 2002), especially from unburned refuges (Swengel and Swengel 2007). Frequent fire may be detrimental for even presumably fire-adapted insect species, such as prairie butterflies (Swengel *et al.* 2011).

Because fires are widespread throughout the prairie landscape, dry playa wetlands embedded within the prairie matrix in the Southern Great Plains of the USA are susceptible to burns. Playas are temporary, isolated depressional wetlands that occur in semi-arid regions. Playas are most often dry and the dry phase can last several years. As a consequence, terrestrial vegetation often covers playas and can provide sufficient fuel to sustain fire.

Playa wetlands increase local biodiversity by increasing habitat heterogeneity and, during their wet phase, are a water source in a dry

landscape, providing habitat as well as feeding areas for migrating birds along the central migratory flyway in USA (Bolen *et al.* 1989, Haukos and Smith 1994). Crustaceans form an important diet component for the birds that use playa wetlands (Krapu 1974). These crustaceans cannot emigrate out of drying wetlands and survive dry periods as resting stages, either as eggs or cysts (Eriksen and Belk 1999, Anderson and Smith 2004, Hall *et al.* 2004). These resistant stages comprise the invertebrate propagule bank and can remain viable in playa soils for several years (Tronstad *et al.* 2005, Stubbington and Datry 2013).

Once the resistant stages of the invertebrate propagule bank become exposed to the correct environmental cues, a proportion of the propagules hatch or end their dormancy (Cáceres and Tessier 2003). The proportion of propagules hatching is related to the frequency of favorable conditions and the probability of survival in the dormant stage (Cohen 1966, Ellner 1985). The environmental hatching cues used by crustaceans vary among species (Brendonck 1996). Some important environmental cues for hatching include light, temperature, and aquatic oxygen levels (see review by Brendonck 1996, Gonzalez *et al.* 1996, King *et al.* 1996).

If burning of dry playas affects the viability of crustacean resting stages, burning will impact playa food webs, including food availability for migrating waterfowl. Burning may also affect algal biomass, an important food web driver, following inundation. We experimentally examined the effects of fire on crustacean resting stages and algae in soil collected from dry playas. We tested the effects of fire by burning grass fuel on top of homogenized playa soils and determined if the fire decreased the abundance of the hatching of crustacean resting stages and algal biomass following hydration of soils from the surface (more heated) and subsurface (less heated) levels. In another study of fire effects, fire did not affect the viability of fairy shrimp (Anos-

traca) eggs in vernal pools in a chaparral ecosystem (Wells *et al.* 1997), but our study experimentally examined how fire affected the entire crustacean community and whether these effects varied with fuel load. We predicted that, as fire intensity increased, the number of hatching invertebrates and algal biomass would decrease at the surface soil layer due to direct death from heat, and that organisms in subsurface soil would be little affected.

METHODS

Soil used in the experiment was combined from four different playas (Lunceford, Balzer, McKinley, and Gate playas) in the panhandle of Oklahoma. The playas were enrolled in a conservation program that ensured a grassland buffer around each wetland. Dry soil from the playas was thoroughly mixed in an attempt to homogenize the invertebrate propagule banks, which can differ among sites and soil depths (Bright 2015, Bright and Bergey 2015).

Fire Treatments

Twenty-four heavy aluminum foil baking containers, each 22 cm (length) \times 11 cm (width) \times 6 cm (depth), were filled two-thirds full with the homogenized playa soil and then a heavy foil divider was used to split each container in half (Figure 1). We randomly assigned one half of each container to the burn treatment (treated) while the other half remained unburned (untreated). We used four different burn treatments to simulate the effects of wildfire: a no burn control, and low (1.5 g of grass), medium (3.0 g of grass), and high (9.0 g of grass) burn levels, each with six replicates. These levels correspond to half of (60 g m⁻¹), equal to (120 g m⁻¹), and triple (360 g m⁻¹) the mean live grass biomass measured in playas (Farley 2000). Coarsely chopped, air-dried native prairie grass was weighed and

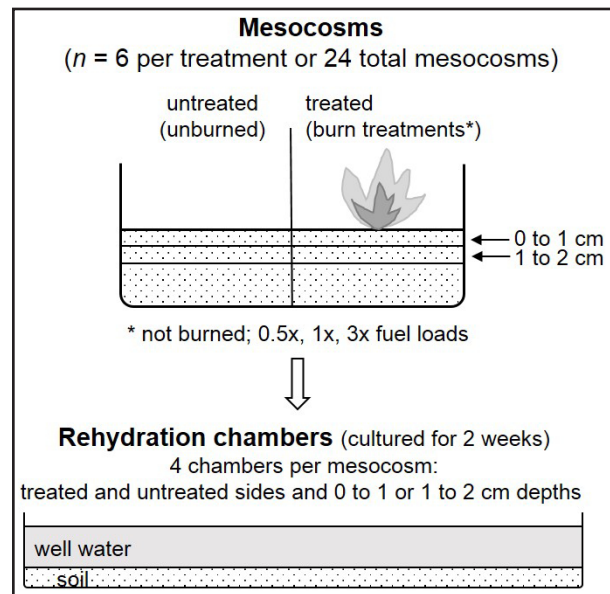


Figure 1. A schematic of the experimental design.

placed on top of the soil to be burned. A heavy foil cylinder was used to enclose the fire and the grass was ignited with a match. Surface temperatures were measured with an infrared thermometer (Model Number ST380A, Nicety Inc., Flushing, New York, USA) 10 seconds after the burn subsided. To quantify how much heat was transferred to the unburned (untreated) side, we repeated the soil burning using the same amount of fuel biomass. We measured the soil surface temperature in the center of the unburned side before and after we burned the treated side.

To test the effects of heat penetration into the soil on the viability of crustacean resting stages, soil from the treated and untreated halves of the 24 containers were each subdivided by soil depth prior to hydration. The top centimeter of soil was removed from each half of the containers, weighed, and placed into numbered translucent plastic microcosms (48 mesocosms, each 34.6 cm [length] \times 21 cm [width] \times 12.4 cm [depth]). Then the next centimeter of soil was also removed, weighed, and placed into an additional 48 plastic mesocosms. Numbering allowed tracking of the four samples from each aluminum container

(two sides \times two depths) during sample processing, but did not indicate the applied treatment.

Hydration

The 96 mesocosms were hydrated by addition of well water to a depth of approximately 5 cm and were monitored to ensure that an appropriate water level was maintained. Plastic snap-on lids with mesh insets prevented colonization by flying insects. Mesocosms were housed in a research greenhouse at the University of Oklahoma, where they were exposed to natural spring temperature and light regimes (30 March to 13 April 2015). This temperature and light regime mimicked the timing of natural playa wetlands inundation (Curtis and Beierman 1980, Bolen *et al* 1989). One of the highly burned 1 cm to 2 cm samples was spilled during collection, so one data point was missing.

Invertebrate and Algal Sampling

Following the two-week hydration period, mesocosms were sampled by pouring the water column through a 250 μm sieve. This method of sampling excludes some microcrustaceans that are less than 250 μm long (e.g., rotifers and immature microcrustaceans). However, we did collect many cladocerans and ostracods. After a visual check of the soil for any remaining macroinvertebrates, the sample retained in the sieve was collected and stored in 70% ethanol (Bright and Bergey 2015). We then counted all the invertebrates that were collected and identified them under magnification to the lowest practical taxonomic level using keys in Smith (2001).

Algal biomass (mg ml^{-1}) was estimated by using chlorophyll *a* concentration (Aloi 1990, Stevenson 1996). We collected 400 ml of water from each mesocosm prior to invertebrate sampling. Water samples were filtered through glass fiber filters and chlorophyll *a* on the filter

was extracted via an ethanol method (Sartory and Grobbelaar 1984) to quantify the algal biomass in each mesocosm.

Data Analyses

Prior to statistical analysis, we standardized invertebrate hatching by calculating the number of invertebrates and number of taxa hatching per kilogram of soil. We first analyzed invertebrate and algal metrics in the untreated (unburned) half of all mesocosms to simultaneously test for initial differences in invertebrate hatching and algal biomass, as well as any effects of varying environmental effects during the experiment. We then analyzed data from the treated (burn treatments) half on the mesocosms, which included the non-burned controls. Because the invertebrate abundance data did not meet the assumption of equal variance, we ran a Scheirer-Ray-Hare two-way non-parametric test to determine if there were any differences between soil layers and among fuel treatments. The Scheirer-Ray-Hare test requires a balanced design and, because one of the burned samples was lost during collection, one replicate from each of the other three burn treatments was randomly deleted. The invertebrate richness data and algal biomass data both met the assumptions for ANOVA and a two-way ANOVA was used to determine fuel load and soil depth effects on these metrics. We also used an ANOVA test to determine whether the fuel load affected post-burn soil surface temperature.

RESULTS

The soil surface temperature readings 10 sec after the fire ended differed across the fuel treatments ($F_{2,16} = 14.19$, $P < 0.001$). The average post-fire soil surface temperature in the high fuel treatment (174°C) was three times greater than in the low fuel treatment (49°C) and two times greater than in the medium fuel treatment (75°C) (Figure 2a). Some heat

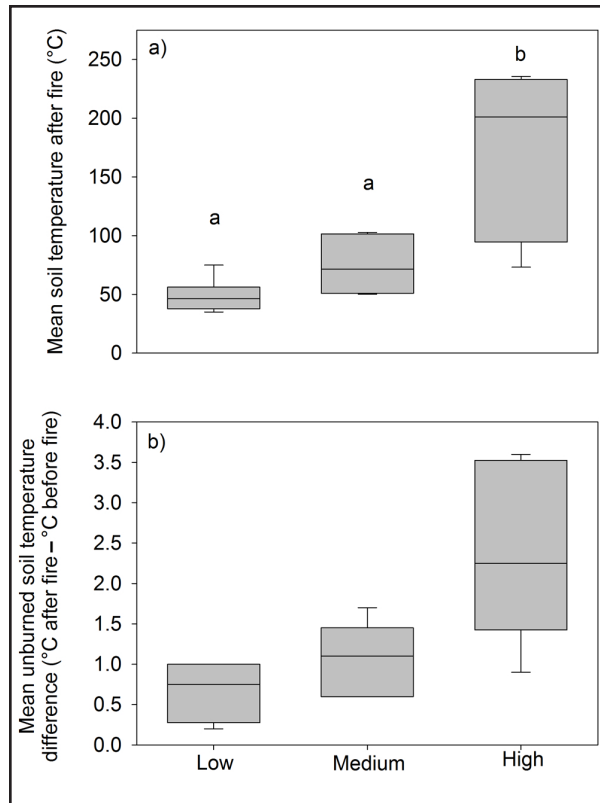


Figure 2. a) The average soil surface temperature of playa wetland soil of the treated group (burned) 10 seconds after the burn subsided. b) The average difference of the soil temperature of the center of the unburned side before and after the fire on the burned side. The line within each box is the median; each box represents the twenty-fifth and seventy-fifth quartiles; and whisker plots show the tenth and ninetieth percentiles. Different letters above plots denote significant differences.

transferred to the unburned side from the burned side, however it only raised the temperature in the center of the unburned side by a maximum of 3.6°C (0.9°C to 3.6°C) in the high fuel treatment, 1.7°C (0.6°C to 1.7°C) in the medium fuel treatment, and 1.0°C (0.2°C to 1.0°C) in the low fuel treatment ($n = 18$; Figure 2b).

Over 32 000 invertebrates from 12 taxa emerged after rehydration (Table 1). Cladocera (*Streblocerus* sp. Sars) was the most abundant invertebrate and were found in 76% of all samples. The next most abundant organisms

were ostracods and the clam shrimp *Caenestheriella setosa* Pearce, which were found in 71% and 69% of samples, respectively. Other crustaceans that hatched from the unburned and burned playa wetland soil included tadpole shrimp (*Triops longicaudatus* LeConte), Great Plains fairy shrimp (*Streptocephalus texanus* Packard), and Texas clam shrimp (*Eulimnadia texana* Packard).

In the untreated (unburned) side, there were no differences of invertebrate abundance among the associated treatments ($H_{3,47} = 2.13$, $P = 0.55$) or between the soil layers ($H_{1,47} = 0.41$, $P = 0.52$); nor was there a significant interaction effect ($H_{3,47} = 2.33$, $P = 0.51$). Invertebrate richness of the unburned sides showed the same pattern of no difference among treatment levels ($F_{3,47} = 0.17$, $P = 0.91$) or between soil layers ($F_{1,47} = 0.49$, $P = 0.49$), and a non-significant interaction effect ($F_{3,47} = 0.27$, $P = 0.85$). We saw a similar trend in the algal biomass samples of the unburned (untreated) sides.

In the treated (burned) side, the abundance of invertebrates per kilogram of soil did not differ among treatments ($H_{3,39} = 1.71$, $P = 0.63$), or between the soil layers ($H_{1,46} = 0.01$, $P = 0.91$); nor was there a significant interaction effect ($H_{3,46} = 2.73$, $P = 0.43$) (Figure 3). The richness data showed the same trend as the abundance data: no significant differences in the richness among treatments ($F_{3,46} = 0.27$, $P = 0.85$), or between soil layers ($F_{1,46} = 0.39$, $P = 0.54$), and a non-significant interaction effect ($F_{3,46} = 0.37$, $P = 0.77$) in the burned sides (Figure 4).

Finally, we did not see a difference in algal biomass among the different burn treatments ($F_{3,40} = 0.04$, $P = 0.99$) or between the soil layers ($F_{1,40} = 0.03$, $P = 0.87$), but we found a significant interaction effect ($F_{3,43} = 0.04$, $P = 0.04$). There was a greater algal biomass in the bottom soil layer from within the control group, and a greater algal biomass in the top soil layer in the high burn treatment group.

[illegible]

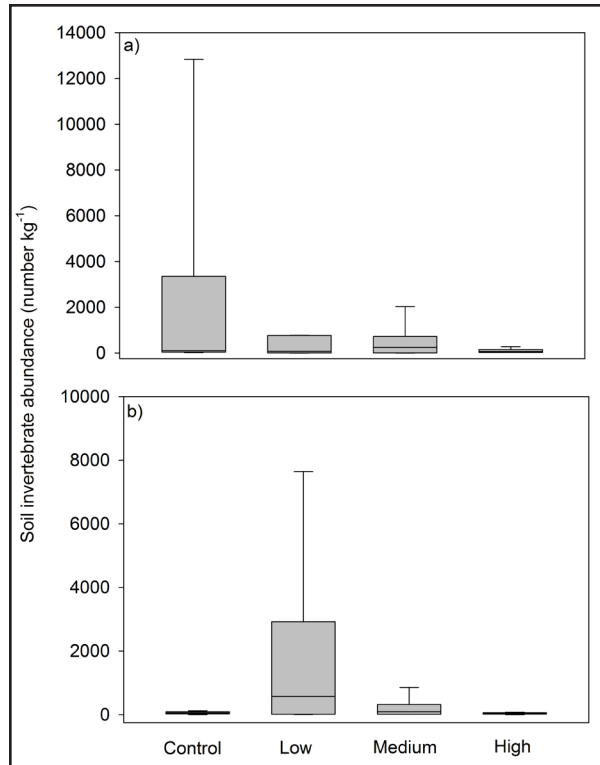


Figure 3. The average invertebrate abundance of the different treatments in the treated (burned) side in the a) top centimeter and b) the second centimeter of playa wetland soil from western Oklahoma, USA. The line within each box is the median; each box represents the twenty-fifth and seventy-fifth quartiles; and whisker plots show the tenth and ninetieth percentiles.

DISCUSSION

We hypothesized differential hatching of the crustacean resting stages among the burn treatments and that this difference would be most apparent in the top soil layer. However, we did not find any difference in the abundance nor the richness of invertebrates resulting from either the fire treatments or soil depth. The observed lack of fire effects in our study was likely a combination of two factors: heat tolerance by crustacean resting stages and low fire intensity in playa wetlands.

Crustacean resting stages in playas may tolerate relatively high temperatures through exaptation (*sensu* Gould and Vrba 1982).

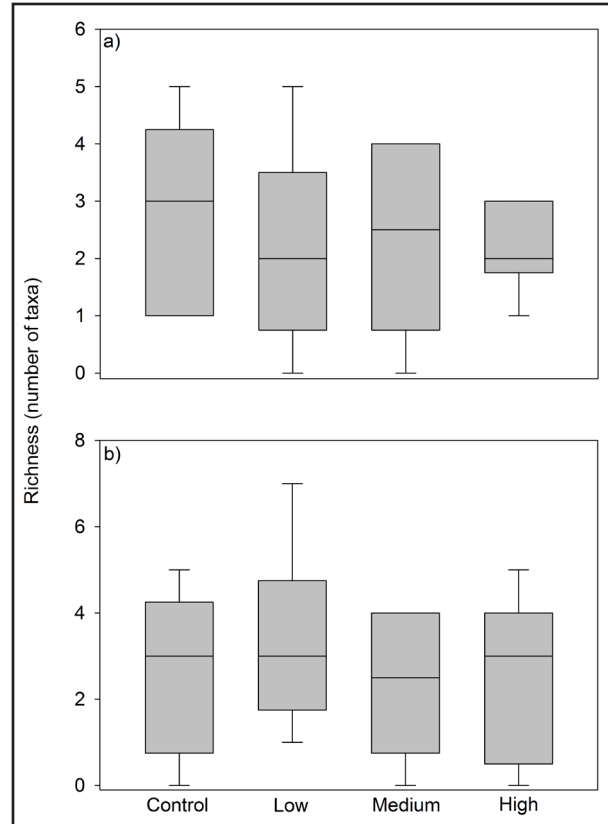


Figure 4. The average invertebrate richness of the different treatments in the treated (burned) side in the a) top centimeter and b) the second centimeter of playa wetland soil from western Oklahoma, USA. The line within each box is the median; each box represents the twenty-fifth and seventy-fifth quartiles; and whisker plots show the tenth and ninetieth percentiles.

Crustacean resting stages are crypobiotic (Lavens and Sorgeloos 1987) and resistant to a variety of environmental stresses (Lavens and Sorgeloos 1987, Brendonck 1996, Fryer 1996). In Oklahoma dry playas, these stresses include desiccation, hot summers, and cold winters. Although elevated soil temperatures associated with fires may exceed the normal range of soil temperature, adaptations associated with cryptobiosis may provide resistance to extra-normal conditions (Mattimore and Battista 1996, Jönsson 2003), including above-normal temperature. Such tolerance to extreme conditions are well known in tardi-

grades, but have also been investigated in brine shrimp (*Artemia* spp. Leach), a relative of the fairy shrimp found in playas. Brine shrimp resting eggs tolerate high temperature (Iwasaki 1973) and desiccation (Clegg *et al.* 1999). Although tolerance to excessive temperature has been little studied in playa crustaceans, fairy shrimp resting eggs in vernal pools of California are resilient to both wildfire and prescribed burns (Wells *et al.* 1997).

Fire intensity resulting from the low fuel load in dry playa wetlands may not be great enough to significantly affect crustacean resting stages. We used fuel loads based on the amount of fuel (plant biomass) in playa wetlands and the resulting soil surface temperatures (a mean of 75°C for average playa plant biomass) were lower than surface soil temperatures recorded during fire in the higher fuel load tallgrass prairie (83°C to 680°C; Wright 1974, Rice and Parenti 1978), except for our high biomass treatment that averaged 179°C using three times the average playa grass biomass. In the analogous habitat of dry vernal pools, the survivorship of fairy shrimp eggs during fire was, in part, because the low fuel load in dry vernal pools limited heat transfer to soil (Wells *et al.* 1997).

Elevated temperature from fire may not penetrate far into the soil because soil temperature declines exponentially with depth (Anderson 1990, Auld and Bradstock 1996). Therefore, the subsurface soil temperature may not have increased enough to impact subsurface invertebrate resting stages even if impacts occurred at the surface. Crustacean resting stages are not found only at the soil surface and those buried 0.25 cm beneath the surface in playas readily hatch (Bright 2015). Therefore, fire treatments would likely not affect most of the resting stages within the top two centimeters. Instead, exposure to the correct environmental cues for hatching (inundation, light, and temperature) produced similar hatching of crustaceans regardless of fire treatment.

While we had over 32000 invertebrates hatch across all samples, some species of invertebrates might not have hatched from our soil rehydration experiment. In order to survive unpredictable wetting and drying cycles, not all aquatic crustacean eggs and cysts hatch upon the first wetting but spread out their hatching over several cycles (Simovich and Hathaway 1997, Philippi *et al.* 2001, Ripley *et al.* 2004). In addition to the bet-hedging, some invertebrates might not have hatched due to the lack of the correct environmental cues for hatching. For instance, some invertebrates might need more than two weeks of inundation (Ripley and Simovich 2009) or deeper water depths to hatch (Hathaway and Simovich 1996).

The tolerance of resting eggs of crustaceans in playa wetlands to fire indicates that fire may not be of particular conservation concern for these wetlands. While not every species found in playa wetlands hatched from our rehydration, at least one species (sometimes more than one species) from the higher taxonomic groups hatched, including species from clam shrimps, fairy shrimps, tadpole shrimps, ostracods, and cladocerans, and numbers were similar across the different burn treatments. Therefore, if a fire went through a dry playa wetland, our experimental results indicate that crustacean communities would not be greatly impacted. Fires during the dry phase may not affect the immediate playa food web and will likely not impact migrating waterfowl. However, fire effects on other organisms in playa ecosystems, such as the plant seed bank, amphibians, or immigrating insects, have yet to be determined. Because playa wetlands can remain dry for several years, fire may also affect terrestrial invertebrates and vegetation in dry playa wetlands. The tolerance to fire by playa crustaceans indicates exaptation to climate change, in that playa crustaceans will likely tolerate a hotter and drier climate and the corresponding higher frequency of fire in the landscape.

ACKNOWLEDGEMENTS

We thank the private landowners and organizations for use of their playa wetlands. We thank Dr. C.L. Atkinson for her suggestions for this study. Additionally, we thank Dr. M. Kaspari's lab for the loan of field experiment. We thank two anonymous reviewers whose comments helped improve this manuscript.

LITERATURE CITED

- Aloi, J.E. 1990. A critical review of recent freshwater periphyton field methods. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 656–670. doi: [10.1139/f90-073](https://doi.org/10.1139/f90-073)
- Anderson, J.T., and L.M. Smith. 2004. Persistence and colonization strategies of playa wetland invertebrates. *Hydrobiologia* 513: 77–86. doi: [10.1023/B:hydr.0000018171.44844.20](https://doi.org/10.1023/B:hydr.0000018171.44844.20)
- Anderson, R.C. 1990. The historic role of fire in the North American grassland. Pages 8–18 in: S.L. Collins and L.L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman, USA.
- Auld, T.D., and R.A. Bradstock. 1996. Soil temperatures after the passage of a fire: do they influence the germination of buried seeds? *Australian Journal of Ecology* 21: 106–109. doi: [10.1111/j.1442-9993.1996.tb00589.x](https://doi.org/10.1111/j.1442-9993.1996.tb00589.x)
- Bolen, E.G., L.M. Smith, and H.L. Schramm. 1989. Playa lakes: prairie wetlands of the Southern High Plains. *BioScience* 39: 615–623. doi: [10.2307/1311091](https://doi.org/10.2307/1311091)
- Bond, W.J., and B.W. van Wilgen. 2012. *Fire and plants*. Springer Science and Business Media, New York, New York, USA.
- Bond, W.J., and J.E. Keeley. 2005. Fire as global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387–394. doi: [10.1016/j.tree.2005.04.025](https://doi.org/10.1016/j.tree.2005.04.025)
- Brendonck, L. 1996. Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia* 320: 85–97. doi: [10.1007/BF00016809](https://doi.org/10.1007/BF00016809)
- Briggs, J.M., A.K. Knapp, and B.L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *The American Midland Naturalist* 147: 287–294. doi: [10.1674/0003-0031\(2002\)147\[0287:EOWPIT\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2002)147[0287:EOWPIT]2.0.CO;2)
- Bright, E.G. 2015. The spatial distribution of and upland impacts on playa wetland invertebrates. Dissertation, University of Oklahoma, Norman, USA.
- Bright, E.G., and E.A. Bergey. 2015. Spatial distribution of resting stages of crustaceans and other aquatic invertebrates in playa wetlands. *Journal of Crustacean Biology* 35: 515–521. doi: [10.1163/1937240X-00002347](https://doi.org/10.1163/1937240X-00002347)
- Brockway, D.G., R.G. Gatewood, and R.B. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* 65: 135–152. doi: [10.1006/jema.2002.0540](https://doi.org/10.1006/jema.2002.0540)
- Cáceres, C.E., and A.J. Tessier. 2003. How long to rest: the ecology of optimal dormancy and environmental constraint. *Ecology* 84: 1189–1198. doi: [10.1890/0012-9658\(2003\)084\[1189:HLTRTE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1189:HLTRTE]2.0.CO;2)
- Clegg, J.S., J.K. Willsie, and S.A. Jackson. 1999. Adaptive significance of a small heat shock/ α -crystallin protein (p26) in encysted embryos of the brine shrimp, *Artemia franciscana*. *American Zoologist* 39: 836–847. doi: [10.1093/icb/39.6.836](https://doi.org/10.1093/icb/39.6.836)

- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 200: 467–475 doi: [10.1016/0022-5193\(66\)90188-3](https://doi.org/10.1016/0022-5193(66)90188-3)
- Curtis, D., and H. Beierman. 1980. Playa lakes characterization study. US Fish and Wildlife Service, Division of Ecological Service, Fort Worth, Texas, USA.
- de Van Booyesen, P., and N.M. Tainton, editors. 1984. Ecological effects of fire in South African ecosystems. Springer-Verlag, New York, New York, USA. doi: [10.1007/978-3-642-69805-7](https://doi.org/10.1007/978-3-642-69805-7)
- Ellner, S. 1985. ESS germination strategies in randomly varying environments. I. Logistcs-type models. *Theoretical Population Biology* 28: 50–79 doi: [10.1016/0040-5809\(85\)90022-X](https://doi.org/10.1016/0040-5809(85)90022-X)
- Eriksen, C.H., and D. Belk. 1999. Fairy shrimps of California's puddles, pools and playas. Mad River Press, Eureka, California, USA.
- Farley, A.L. 2000. Vegetation, soils, and surface hydrology of playa landforms in the Rio Grande Plains, Texas. Thesis, Texas A&M University, College Station, USA.
- Fryer, G. 1996. Diapause, a potent force in the evolution of freshwater crustaceans. *Hydrobiologia* 320: 1–14. doi: [10.1007/BF00016800](https://doi.org/10.1007/BF00016800)
- Glenn-Lewin, D.C., L.A. Johnson, T.W. Jurik, A. Akey, M. Leoschke, and T. Rosburg. 1990. Fire in central North American grasslands: vegetative reproduction, seed germination, and seedling establishment. Pages 28–45 in: S.L. Collins and L.L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman, USA.
- Gould, S.J., and E.S. Vrba. 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8: 4–15. doi: [10.1017/S0094837300004310](https://doi.org/10.1017/S0094837300004310)
- Gongalsky, K. 2011. The spatial distribution of large soil invertebrates on burned areas in xerophilous ecosystems of the Black Sea coast of the Caucasus. *Arid Ecosystems* 1: 260–266. doi: [10.1134/S2079096111040068](https://doi.org/10.1134/S2079096111040068)
- Gonzalez, R.J., J. Drazen, S. Hathaway, B. Bauer, and M. Simovich. 1996. Physiological correlates of water chemistry requirements in fairy shrimps (Anostraca) from southern California. *Journal of Crustacean Biology* 16: 315–322. doi: [10.2307/1548889](https://doi.org/10.2307/1548889)
- Grant, T.A., E.M. Madden, T.L. Shaffer, and J.S. Dockens. 2010. Effects of prescribed fire on vegetation and passerine birds in northern mixed-grass prairie. *The Journal of Wildlife Management* 74: 1841–1851. doi: [10.2193/2010-006](https://doi.org/10.2193/2010-006)
- Greenberg, C.H., and T.A. Waldrop. 2008. Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. *Forest Ecology and Management* 255: 2883–2893. doi: [10.1016/j.foreco.2008.01.064](https://doi.org/10.1016/j.foreco.2008.01.064)
- Hall, D.L., M.R. Willig, D.L. Moorhead, R.W. Sites, E.B. Fish, and T.R. Mollhagen. 2004. Aquatic macroinvertebrate diversity of playa wetlands: the role of landscape and island biogeographic characteristics. *Wetlands* 24: 77–91. doi: [10.1672/0277-5212\(2004\)024\[0077:AMDOPW\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2004)024[0077:AMDOPW]2.0.CO;2)
- Harper, M., C. Dietrich, R. Larimore, and P. Tessene. 2000. Effects of prescribed fire on prairie arthropods: an enclosure study. *Natural Areas Journal* 20: 325–335.
- Hathaway, S.A., and M.A. Simovich. 1996. Factors affecting the distribution and co-occurrence of two southern California anostracans (Branchiopoda), *Branchinecta sandiegonensis* and *Streptocephalus woottoni*. *Journal of Crustacean Biology* 16: 669–677. doi: [10.2307/1549187](https://doi.org/10.2307/1549187)
- Haukos, D.A., and L.M. Smith. 1994. The importance of playa wetlands to biodiversity of the Southern High Plains. *Landscape and Urban Planning* 28: 83–98. doi: [10.1016/0169-2046\(94\)90046-9](https://doi.org/10.1016/0169-2046(94)90046-9)

- Higgins, K.F. 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. *Journal of Range Management* 37: 100–103 doi: [10.2307/3898892](https://doi.org/10.2307/3898892)
- Howe, H.F. 1999. Response of *Zizia aurea* to seasonal mowing and fire in a restored prairie. *The American Midland Naturalist* 141: 373–380. doi: [10.1674/0003-0031\(1999\)141\[0373:ROZATSJ2.0.CO;2](https://doi.org/10.1674/0003-0031(1999)141[0373:ROZATSJ2.0.CO;2)
- Iwasaki, T. 1973. Tolerance of *Artemia* dry eggs for temperature, vacuum and radiation. *Annexe au Bulletin de l'Institut international du froid* 5: 79–88.
- Jönsson, K.I. 2003. Causes and consequences of excess resistance in cryptobiotic metazoans. *Physiological and Biochemical Zoology* 76: 429–435. doi: [10.1086/377743](https://doi.org/10.1086/377743)
- Kaufman, D.W., E.J. Finck, and G.A. Kaufman. 1990. Small mammals and grassland fires. Pages 46–80 in: S.L. Collins and L.L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman, USA.
- Kaye, T.N., K.L. Pendergrass, K. Finley, and J.B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. *Ecological Applications* 11: 1366–1380. doi: [10.1890/1051-0761\(2001\)011\[1366:TEOFOT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1366:TEOFOT]2.0.CO;2)
- Kimmerer, R.W., and F.K. Lake. 2001. The role of indigenous burning in land management. *Journal of Forestry* 99: 36–41.
- King, J.L., M.A. Simovich, and R.C. Brusca. 1996. Species richness, endemism and ecology of crustacean assemblages in northern California vernal pools. *Hydrobiologia* 328: 85–116. doi: [10.1007/BF00018707](https://doi.org/10.1007/BF00018707)
- Knapp, A.K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. *American Journal of Botany* 71: 220–227. doi: [10.2307/2443749](https://doi.org/10.2307/2443749)
- Knapp, A.K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66: 1309–1320. doi: [10.2307/1939184](https://doi.org/10.2307/1939184)
- Krapu, G.L. 1974. Feeding ecology of pintail hens during reproduction. *The Auk* 91: 278–290.
- Lavens, P., and P. Sorgeloos. 1987. The cryptobiotic state of *Artemia* cysts, its diapause deactivation and hatching: a review. Pages 27–63 in: P. Sorgeloos, D.A. Bengtson, W. Decleir, and E. Jaspers, editors. *Anemia research and its applications, volume 3. Ecology, culturing, use in aquaculture*. Universa Press, Wetteren, Belgium.
- Leach, M.K., and T.J. Givnish. 2006. Ecological determinants of species loss in remnant prairies. *Science* 273: 1555–1558 doi: [10.1126/science.273.5281.1555](https://doi.org/10.1126/science.273.5281.1555)
- Looman, J. 1983. Grassland as natural or semi-natural vegetation. Pages 173–184 in: W. Holzner, M.J.A. Weger, and I. Ikusima, editors. *Man's impact on vegetation*. Junk Publishing, The Hague, Netherlands. doi: [10.1007/978-94-009-7269-8_13](https://doi.org/10.1007/978-94-009-7269-8_13)
- Malmström, A. 2010. The importance of measuring fire severity—evidence from microarthropod studies. *Forest Ecology and Management* 260: 62–70. doi: [10.1016/j.foreco.2010.04.001](https://doi.org/10.1016/j.foreco.2010.04.001)
- Maret, M.P., and M.V. Wilson. 2000. Fire and seedling population dynamics in western Oregon prairies. *Journal of Vegetation Science* 11: 307–314. doi: [10.2307/3236811](https://doi.org/10.2307/3236811)
- Masters, P. 1996. The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildlife Research* 23: 39–47. doi: [10.1071/WR9960039](https://doi.org/10.1071/WR9960039)
- Mattimore, V., and J.R. Battista. 1996. Radioresistance of *Deinococcus radiodurans*: functions necessary to survive ionizing radiation are also necessary to survive prolonged desiccation. *Journal of Bacteriology* 178: 633–637.
- Naveh, Z. 1975. The evolutionary significance of fire in the Mediterranean region. *Vegetatio* 29: 199–208 doi: [10.1007/BF02390011](https://doi.org/10.1007/BF02390011)

- Nekola, J. 2002. Effects of fire management on the richness and abundance of central North American grassland land snail faunas. *Animal Biodiversity and Conservation* 25: 53–66.
- NIFC [National Interagency Fire Center]. 2015. Incident Management Situation Report. <<http://www.predictiveservices.nifc.gov/IMSR/2014/20141229IMSR.pdf>>. Assessed 9 March 2015.
- Old, S.M. 1969. Microclimate, fire, and plant production in an Illinois prairie. *Ecological Monographs* 39: 355–384. doi: [10.2307/1942353](https://doi.org/10.2307/1942353)
- Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conservation Biology* 16: 1296–1307. doi: [10.1046/j.1523-1739.2002.01077.x](https://doi.org/10.1046/j.1523-1739.2002.01077.x)
- Peet, M., R. Anderson, and M.S. Adams. 1975. Effect of fire on big bluestem production. *American Midland Naturalist* 94: 15–26. doi: [10.2307/2424534](https://doi.org/10.2307/2424534)
- Philippi, T.E., M.A. Simovich, E.T. Bauder, and J.A. Moorad. 2001. Habitat ephemerality and hatching fractions of a diapausing anostracan (Crustacea: Branchiopoda). *Israel Journal of Zoology* 47: 387–395. doi: [10.1560/LU8G-9HVP-YR80-XCL0](https://doi.org/10.1560/LU8G-9HVP-YR80-XCL0)
- Powell, A.F.L.A., and P.C. Stouffer. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. *The Auk* 123: 183–197. doi: [10.1642/0004-8038\(2006\)123\[0183:EOPBAB\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2006)123[0183:EOPBAB]2.0.CO;2)
- Ray, E.J., and E.A. Bergey. 2015. After the burn: factors affecting land snail survival in post-prescribed-burn woodlands. *Journal of Molluscan Studies* 81: 44–50. doi: [10.1093/mollus/eyu051](https://doi.org/10.1093/mollus/eyu051)
- Rice, E.L., and R.L. Parenti. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. *American Journal of Botany* 65: 1091–1097. doi: [10.2307/2442326](https://doi.org/10.2307/2442326)
- Ripley, B.J., J. Holtz, and M.A. Simovich. 2004. Cyst bank life-history model for a fairy shrimp from ephemeral ponds. *Freshwater Biology* 49: 221–231. doi: [10.1111/j.1365-2427.2004.01179.x](https://doi.org/10.1111/j.1365-2427.2004.01179.x)
- Ripley, B.J., and M.A. Simovich. 2009. Species richness on islands in time: variation in ephemeral pond crustacean communities in relation to habitat duration and size. *Hydrobiologia* 617: 181–196. doi: [10.1007/s10750-008-9548-0](https://doi.org/10.1007/s10750-008-9548-0)
- Rochester, C.J., C.S. Brehme, D.R. Clark, D.C. Stokes, S.A. Hathaway, and R.N. Fisher. 2010. Reptile and amphibian responses to large-scale wildfires in southern California. *Journal of Herpetology* 44: 333–351. doi: [10.1670/08-143.1](https://doi.org/10.1670/08-143.1)
- Sartory, D.P., and J.U. Grobbelaar. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia* 114: 177–187. doi: [10.1007/BF00031869](https://doi.org/10.1007/BF00031869)
- Severns, P.M. 2005. Response of a terrestrial mollusc community to an autumn prescribed burn in a rare wetland prairie of western Oregon, USA. *Journal of Molluscan Studies* 71: 181–187. doi: [10.1093/mollus/eyi021](https://doi.org/10.1093/mollus/eyi021)
- Sharrow, S.H., and H.A. Wright. 1977. Effects of fire, ash, and litter on soil nitrate, temperature, moisture and tobosagrass production in the rolling plains. *Journal of Range Management* 30: 266–270. doi: [10.2307/3897302](https://doi.org/10.2307/3897302)
- Simovich, M.A., and S.A. Hathaway. 1997. Diversified bet-hedging as a reproductive strategy of some ephemeral pool anostracans (Branchiopoda). *Journal of Crustacean Biology* 17: 38–44. doi: [10.2307/1549460](https://doi.org/10.2307/1549460)
- Smith, D.G. 2001. Pennak's freshwater invertebrates of the United States: Porifera to Crustacea. Wiley & Sons, New York, New York, USA.

- Stevenson, R.J. 1996. An introduction to algal ecology in freshwater benthic habitats. Pages 3–30 in: R.J. Stevenson, M.L. Bothwell, and R.L. Lowe, editors. Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, California, USA. doi: [10.1016/B978-012668450-6/50030-8](https://doi.org/10.1016/B978-012668450-6/50030-8)
- Stubbington, R., and T. Datry. 2013. The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. Freshwater Biology 58: 1202–1220. doi: [10.1111/fw.b.12121](https://doi.org/10.1111/fw.b.12121)
- Svejcar, T.J., and J.A. Browning. 1988. Growth and gas exchange of *Andropogon gerardii* as influenced by burning. Journal of Range Management 41: 239–244. doi: [10.2307/3899176](https://doi.org/10.2307/3899176)
- Swengel, A.B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodiversity & Conservation 10: 1141–1169. doi: [10.1023/A:1016683807033](https://doi.org/10.1023/A:1016683807033)
- Swengel, A.B., and S.R. Swengel. 2007. Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. Journal of Insect Conservation 11: 263–279. doi: [10.1007/s10841-006-9042-9](https://doi.org/10.1007/s10841-006-9042-9)
- Swengel, S.R., D. Schlicht, F. Olsen, and A.B. Swengel. 2011. Declines of prairie butterflies in the midwestern USA. Journal of Insect Conservation 15: 327–339. doi: [10.1007/s10841-010-9323-1](https://doi.org/10.1007/s10841-010-9323-1)
- Tronstad, L.M., B.P. Tronstad, and A.C. Benke. 2005. Invertebrate seedbanks: rehydration of soil from an unregulated river floodplain in the southeastern US. Freshwater Biology 50: 646–655. doi: [10.1111/j.1365-2427.2005.01351.x](https://doi.org/10.1111/j.1365-2427.2005.01351.x)
- Uys, R.G., W.J. Bond, and T.M. Everson. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. Biological Conservation 118: 489–499. doi: [10.1016/j.biocon.2003.09.024](https://doi.org/10.1016/j.biocon.2003.09.024)
- Vogl, R.J. 1974. Effects of fire on grasslands. Pages 139–144 in: T.T. Kozlowski and C.E. Ahlgren, editors. Fire and ecosystems. Academic Press, San Diego, California, USA. doi: [10.1016/b978-0-12-424255-5.50010-9](https://doi.org/10.1016/b978-0-12-424255-5.50010-9)
- Wells, M.L., S.A. Hathaway, and M.A. Simovich. 1997. Resilience of anostracan cysts to fire. Hydrobiologia 359: 199–202. doi: [10.1023/A:1003129929767](https://doi.org/10.1023/A:1003129929767)
- Wright, H.A. 1974. Range burning. Journal of Range Management 27: 5–11. doi: [10.2307/3896428](https://doi.org/10.2307/3896428)
- Wright, H.A., and A.W. Bailey. 1980. Fire ecology and prescribed burning in the Great Plains—a research review. USDA Forest Service General Technical Report INT-GTR- 77, Intermountain Research Station, Ogden, Utah, USA.
- York, A. 1999. Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. Journal of Insect Conservation 3: 191–199. doi: [10.1023/A:1009643627781](https://doi.org/10.1023/A:1009643627781)