

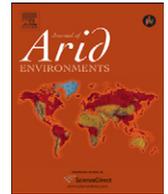


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Ecophysiological responses of Chihuahuan desert grasses to fire

B.W. Allred^{*}, K.A. Snyder¹

USDA-ARS Jornada Experimental Range, P.O. Box 30003, MSC 3JER, New Mexico State University, Las Cruces, NM 88003, USA

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ABSTRACT

To better understand the effects of fire in the Chihuahuan desert, gas exchange characteristics of two dominant grass species, *Bouteloua eriopoda* and *Aristida purpurea*, and soil nitrogen availability were studied in response to prescribed fire at the Jornada Experimental Range in southern New Mexico. Burned and unburned plant individuals were measured before and after fire. Rates of net photosynthesis and stomatal conductance were highest in burned individuals, with those of *A. purpurea* exceeding *B. eriopoda*. Soil nitrogen supply rates increased compared to unburned controls. Similar to other grasslands where fire is common, physiological characteristics of vegetation responded positively. These adaptations indicate that fire may be beneficial in the preservation and restoration of native grasses.

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1. Introduction

The semiarid grasslands of the Chihuahuan desert are declining and becoming dominated by shrubs (Gibbens et al., 2005). In attempts to both preserve remaining grasslands and restore shrub-dominated areas to grasses, prescribed fire has been suggested as a possible tool (Bahre, 1991; McGlone and Huenneke, 2004; Wright, 1974). Compared to other systems, such as the Great Plains of North America, considerably less is known concerning the effects of fire in desert grasslands (Drewa and Havstad, 2001). The few studies conducted have shown that prescribed fire can reduce cover and frequency of the dominant grass *Bouteloua eriopoda* (Torr.) Torr. (Drewa and Havstad, 2001; Valone and Kelt, 1999) and other vegetation (McGlone and Huenneke, 2004). However, responses of *B. eriopoda* to fire evaluated at the clonal scale showed a reduction in basal area and cover, but overall survivorship was dependent upon clone size, large clones having increased survivorship in comparison to small clones (Drewa et al., 2006).

The influence of fire on population and community dynamics of desert grasses can be variable. Drewa et al. (2006) suggested that the patterns of precipitation immediately following fire may be a considerable factor in regrowth and recovery. Precipitation event size and frequency in post-fire conditions may substantially alter soil water recharge (Noy-Meir, 1973; Reynolds et al., 2004), ultimately affecting aboveground vegetation and post-fire recovery. Fire induced changes in soil nutrients (e.g. N) may also be tied to grass responses. In semiarid systems, periodic fire generally has immediate increased effects on soil nitrogen (Neary et al., 1999; Rau et al., 2007). However, frequent burning in productive grasslands generally causes overall low nitrogen availability (Ojima et al., 1994). As nitrogen can be limiting in the Chihuahuan desert (Mun and Whitford, 1989) and arid grasslands worldwide (Hooper and Johnson, 1999), the immediate availability of nitrogen after fire may be critical in recovery, perhaps regulating survivorship and competitive success.

^{*} Corresponding author at: Natural Resource Ecology & Management, Oklahoma State University, 008C Ag. Hall, Stillwater, OK 74078, USA. Tel.: +1 405 744 5438; fax: +1 405 744 3530.

E-mail address: brady.allred@okstate.edu (B.W. Allred).

¹ Current address: USDA ARS Invasive and Exotic Weeds Research Unit, 920 Valley Road, Reno, NV 89512, USA.

Moreover, the ecophysiological responses of plant species to fire may play an important role in recovery. Fire may affect resource acquisition and use, which is influenced by changes in resource availability, environment, physiological, or morphological attributes. Grass responses to fire may include increased stomatal conductance and density, greater specific leaf mass, and greater leaf nitrogen content (Knapp, 1985; Knapp and Gilliam, 1985). Many plants, grasses, shrubs, and trees alike, have higher rates of net photosynthesis after fire compared to unburned individuals (Fleck et al., 1998; McCarron and Knapp, 2003; Schimel et al., 1991). These increases may be critical in enhancing the competitive success and recovery of plant individuals after fire.

Though specific studies have examined the effect of fire on production and cover of native and introduced species of the Chihuahuan desert (Drewa, 2003; Kupfer and Miller, 2005; McGlone and Huenneke, 2004), little is known concerning the ecophysiological and soil nutrient responses of these species to fire. The main objective of this study was to examine the photosynthetic responses of *B. eriopoda* and *Aristida purpurea* (Nutt.) to fire in Chihuahuan desert grasslands. These native, perennial C₄ plants are among the dominant grasses and were once abundant in the Chihuahuan and Sonoran deserts of New Mexico and Arizona. *B. eriopoda* is highly palatable and a key livestock forage. The responses of large and small clones of *B. eriopoda* were separated to investigate potential interactions and mechanisms of recovery dependant upon clone size. Soil moisture and nitrogen availability, measured as NO₃⁻-N and NH₄⁺-N supply rates, were also evaluated in response to fire. The focus on physiological, soil nutrient, and soil moisture responses may provide insight into mechanisms that regulate recovery of Chihuahuan desert grasses following fire.

2. Methods

2.1. Study site

The study was conducted during the 2005 growing season on the Jornada Experimental Range (32°37'N, 106°40'W; JER), 37 km northeast of Las Cruces, NM, USA. The JER is in the northern part of the Chihuahuan desert and is a transition between desert grasslands and shrub lands. Average annual precipitation is approximately 227 mm, with approximately 60% falling as localized thunderstorms from July through September. Average monthly temperatures range from a low of 13 °C in January to a high of 36 °C in June. The study area was located on a 410 ha pasture with deep loamy fine sands and sandy loam soils (Gibbens et al., 1986). Calcium carbonate is found at depths of 24 cm to > 1 m. Dominant grasses include *B. eriopoda*, *A. purpurea*, and *Sporobolus* spp. Dominant shrubs are *Prosopis glandulosa* Torr. and *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (Allred, 2005). Average annual stocking rates were 2.5 ha/Animal Unit Month from 1953 to 1998. Cattle have been excluded from the study area since 1998.

2.2. Experimental design and measurements

A randomized block design was used to examine the effects of fire on *B. eriopoda* and *A. purpurea*. Two sites served as blocks and were located approximately 1 km apart. Within each block, there were two contiguous 200 m × 200 m plots, which had been fenced in 1999 to exclude future cattle grazing. Treatments of fire and no fire were previously assigned to these plots in June 1999 (see Drewa et al., 2006). Three parallel (north–south oriented), 100 m transects were randomly placed in each plot. In the fire treatment plots, ten individual plants of *B. eriopoda* and five of *A. purpurea* were selected from the transects. In fire excluded plots, only five plant individuals of *B. eriopoda* and *A. purpurea* were selected along the transects. *B. eriopoda* within the fire treatment were selected at random along the transects within two predetermined basal area size classes (see below). *B. eriopoda* and *A. purpurea* in the fire excluded treatments were randomly selected along transects and varied in basal area (20–90 cm²).

Basal area for each *B. eriopoda* clone in the fire treatment was estimated using two perpendicular measurements for basal diameter and assuming an ellipsoid shape. Based upon basal area, clone size was assigned to a large (basal area >50 cm²) or small (basal area <30 cm²) category. Plants in the fire treatment were selected so that five individuals were present in each size class. All selected plants were marked before fire with a small metal stake placed nearby. Head fires were applied in early July 2005, with average relative humidity of 15–25% and average air temperature 34–39 °C. Remaining unburned vegetation was burned by hand with a drip torch. Gas exchange, water potential, and soil moisture measurements were taken in early June 2005 before fire and late September 2005 after fire, when plants had sufficiently regrown and were fully developed. The same plant was measured before and after fire.

Leaf gas exchange characteristics were determined using an LI-6400 portable photosynthesis system (LI-COR Corporation, Lincoln, NE, USA) equipped with an artificial LED light source (LI-6400-02B, LI-COR Corp., Lincoln, NE, USA). Net photosynthetic rate (A_{net}), stomatal conductance to water vapor (g_s), and leaf transpiration (E) were measured and recorded. Intrinsic water use efficiency (WUE) was calculated as the ratio between net photosynthesis and stomatal conductance (Jones, 2004). Measurements were taken on fully developed, unshaded leaves between 0930 and 1130 h local time on clear, sunny days. Light and relative humidity conditions in the measuring chamber were set to replicate full sunlight and ambient conditions, respectively. Chamber block temperature was held at 32 °C. CO₂ concentration within the chamber was maintained at +5 to 10 ppm above ambient.

Plant water stress was determined for each plant individual by measuring the predawn xylem water potential (Ψ_{pd}). Predawn water potentials were measured with a Soil Moisture 3000 (Soil Moisture Corp., Goleta, CA, USA) Scholander-type pressure chamber in the morning after gas exchange measurements. Soil gravimetric water content was determined from 10 to 15 samples per treatment. Samples were taken in close proximity to measured plant individuals (ca. 30 cm). Soil was weighed before drying, dried for 3 days at 60 °C and then weighed again.

After fire, soil nitrogen availability was measured using plant root simulator (PRS) probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada). Probes consisted of anion and cation exchange membranes. Ion exchange membranes act as a sink for collecting NO_3^- and NH_4^+ ions, showing integrated values over time. Pairs of probes were placed near *B. eriopoda*, *A. purpurea* plants, and in bare ground interspaces. When placed near plant individuals, probes were placed as to not interfere with the root system. Probes were deployed for 16 days after fire and were analyzed by Western Ag Innovations.

2.3. Statistical analysis

An analysis of variance design was used to evaluate the separate and interactive effects of species (*B. eriopoda*, *A. purpurea*) and fire on response variables related to leaf gas exchange characteristics as well as plant water stress and soil gravimetric water content. The experimental design was a randomized block, split-plot design, with fire as the whole-plot factor and species as subplot factors. The effects of species nested within treatment and location were included as random effects within the model. All analyses were performed using Proc Mixed in SAS 9.1 (SAS Institute Inc., Cary, NC, USA). Although plants were sampled on two separate time periods, we chose not to use repeated measures because the experimental question was the effect of fire. Analyses of all pre-treatment data indicated no differences between treatments or species. Only results of post-treatment analyses comparing fire and control treatments are presented. A separate analysis was used to assess the main effects of size class (large, small) of *B. eriopoda* responses to fire. Soil nitrogen availability after fire was analyzed as a randomized block, split plot design, with fire as the whole plot factor and probe placement and soil nutrient ion (NO_3^- and NH_4^+) as subplot factors. Based upon residual plots, data were log transformed as required to meet assumptions of normality. We recognize a small sample size of treatment application ($n = 2$) and therefore our inferences are to this general location only.

3. Results

Precipitation for the 2005 growing season (July–September) was 60% of the long-term average (1915–2005). May received a greater amount of rainfall than average, while no precipitation occurred in June (Fig. 1). July and August received about half of the average, while September received 71% of average. Total precipitation for 2005 was similar to the annual long-term average.

Comparisons of leaf net photosynthesis for *B. eriopoda* and *A. purpurea* showed differences between treatments. Compared to unburned plants, net photosynthesis of burned plants was 97% and 64% greater for *B. eriopoda* and

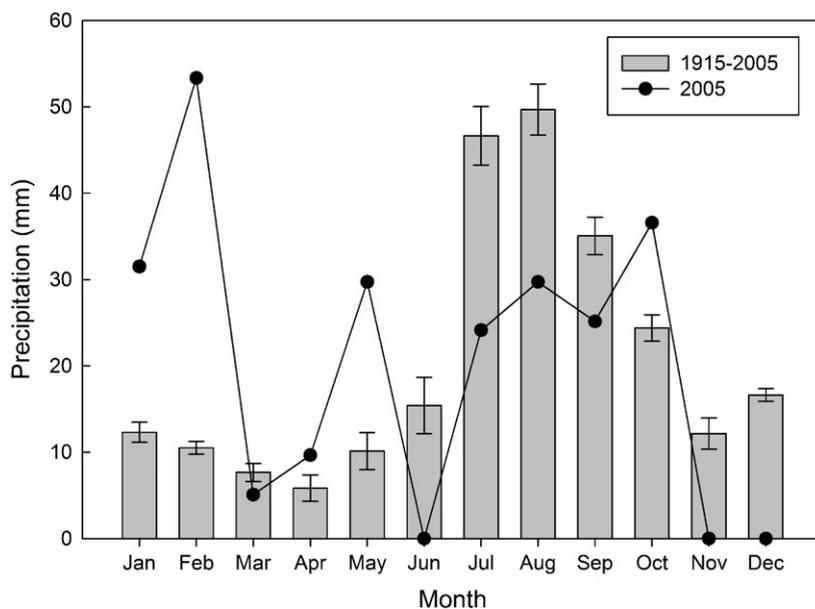


Fig. 1. Mean (\pm SE) monthly precipitation (1915–2005; bars) and monthly precipitation for 2005 (circles) on the Jornada Experimental Range. While fire was applied in early July of 2005, sampling occurred in early June and late September of that year.

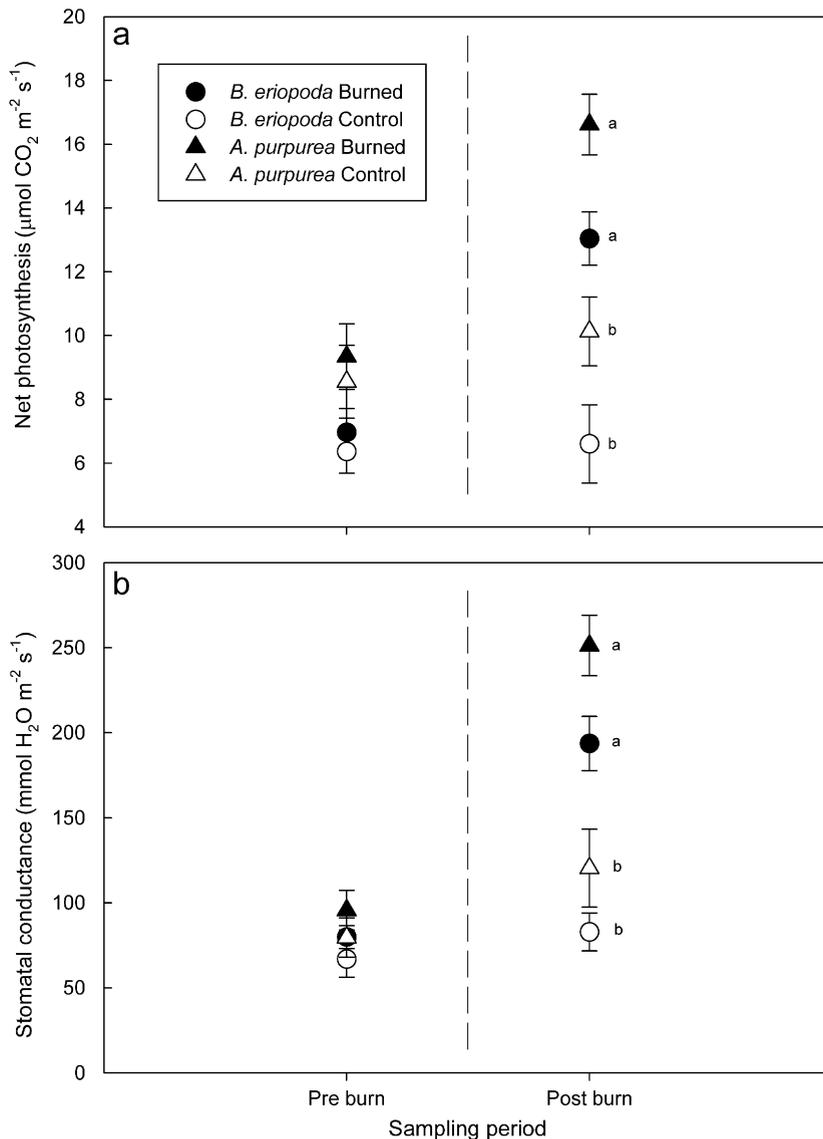


Fig. 2. Mean (\pm SE) (a) net photosynthetic and (b) stomatal conductance rates for burned and unburned *Bouteloua eriopoda* and *Aristida purpurea* plant individuals pre- and post-fire. Statistical comparisons between fire and control treatments post-fire are presented. Differing letters indicate significant differences within species, $p < 0.05$.

A. purpurea, respectively (Fig. 2). Stomatal conductance also varied between treatments, with burned plants increasing 135% and 109% for *B. eriopoda* and *A. purpurea*, respectively (Fig. 2). Intrinsic WUE did not differ between treatments (data not shown). Net photosynthesis, stomatal conductance, and WUE of burned and unburned individuals were not different between species. Clone size of *B. eriopoda* did not affect response variables related to leaf gas exchange (data not shown).

Fire had no effect on predawn xylem water potential (Ψ_{pd}) of *B. eriopoda* or *A. purpurea* (Fig. 3). Clone size of *B. eriopoda* did not affect Ψ_{pd} after fire (data not shown). Gravimetric soil moisture did not differ between treatments or associated plant species (Fig. 4).

Soil nitrogen availability varied between treatments and soil nutrient ion (NO_3^- and NH_4^+), but not installation site. Pooled across installation sites, both NO_3^- and NH_4^+ supply rates increased in burned plots compared to unburned plots. Soil NO_3^- supply rate was greater than NH_4^+ supply rate compared within treatments (Fig. 5).

4. Discussion

The ecophysiological characteristics of both *B. eriopoda* and *A. purpurea* responded positively to fire. The increased net photosynthesis and stomatal conductance of *B. eriopoda* and *A. purpurea* following fire were similar to other grassland

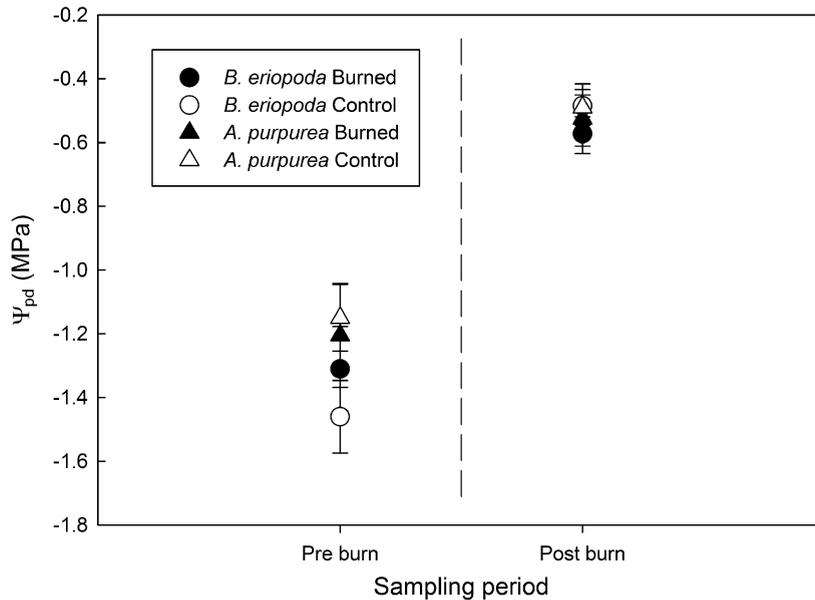


Fig. 3. Mean values (\pm SE) of predawn xylem water potentials (Ψ_{pd}) for burned and unburned *Bouteloua eriopoda* and *Aristida purpurea* plant individuals pre- and post-fire.

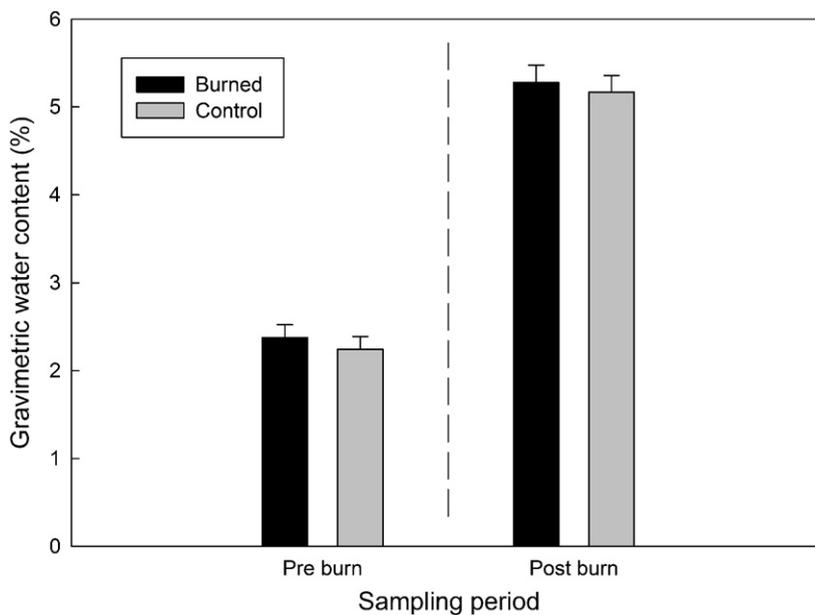


Fig. 4. Mean values (\pm SE) of soil gravimetric water content for burned and unburned plots pre- and post-fire (pooled across associated plant species).

studies (Knapp, 1985; Schimel et al., 1991). In tallgrass prairie, increased photosynthetic response of dominant C_4 grasses to fire has been attributed to the removal of detritus and leaf development in increased light environments (Knapp, 1985). In the absence of fire, standing dead biomass blocks light to sprouting plants. Subsequently, grasses develop in a more shaded environment resulting in morphological and physiological differences (Knapp and Seastedt, 1986), reducing net photosynthesis even after growing above dead plant material.

In contrast, standing dead biomass was not prevalent in our study areas. Measured plants were not shaded by dead plant material or other species and received full sunlight. Due to the growth structure of *B. eriopoda* and *A. purpurea*, it is possible that some leaves originate and develop in a lower light environment, analogous to unburned tallgrass prairie. However, pigment analyses of *B. eriopoda* by Senock et al. (1994) did not suggest that leaves were shade adapted. Consequently, it is unclear if leaves developed in a shaded environment with reduced net photosynthesis. Regardless of

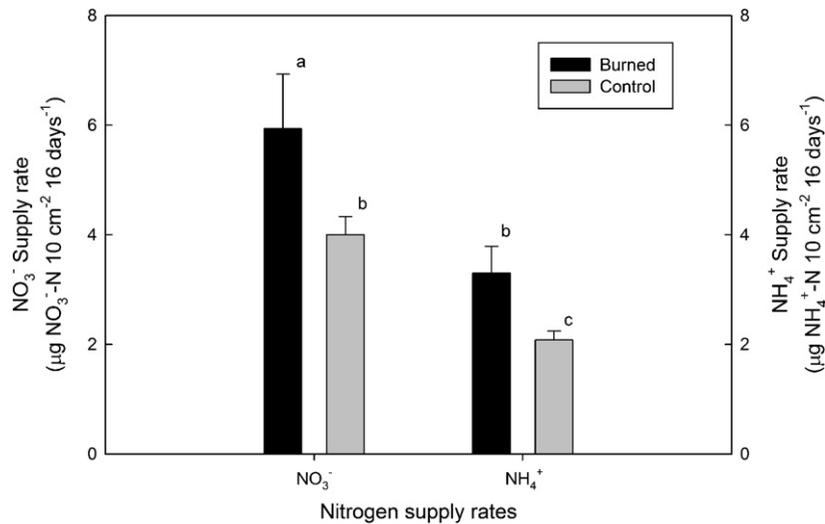


Fig. 5. Mean values (\pm SE) of soil nitrogen supply rates (pooled across installation sites) of ion exchange membranes in burned and unburned plots after fire. Differing letters indicate significant differences between treatments and soil nutrient ion, $p \leq 0.05$.

development, fire removed any vegetation (living or dead) and guaranteed increased amounts of light to new, developing sprouts. This may have resulted in morphological and physiological changes in *B. eriopoda* and *A. purpurea* that increased net photosynthesis. Additionally, increased soil nitrogen availability as a result of burning may have led to increased nitrogen content within the leaves of grasses. Greater leaf N in *B. eriopoda* and *A. purpurea* after fire may also have led to the increased net photosynthesis observed in this study (Evans, 1989).

Predawn xylem water potentials are an indication of soil water recharge during the night. Due to the removal of transpiring leaf area, we expected fire to increase predawn xylem water potentials. However, measurements of water potentials and gravimetric water content indicated that there were no differences in available soil water between burned and unburned plots. Additionally, measured water potential values suggest that severe water stress due to limited soil water did not occur. *B. eriopoda* may have considerably lower predawn xylem water potentials (-4 to -6 MPa, personal obs.). Because of the similarities in predawn water potential between treatments, gas exchange differences related to fire treatment were not a result of differences in soil moisture.

Drewa et al. (2006) hypothesized that rapid recovery of grasses to fire may be tied to ample soil moisture in the immediate post-fire environment. The year of this study, only 60% of the average amount of growing season precipitation was received, yet the plants survived fire and recovered rapidly. Additionally, prior to the burn in 2005 (this study), an above average amount of precipitation was received in May, but none in June. This was opposite in the burn of Drewa et al. (2006), in which increased precipitation was received the month of the burn. The importance of antecedent soil moisture to prescribed fires may be as relevant to plant recovery as post-fire soil moisture. More investigation is required to determine the impact of patterns of soil moisture on plant recovery after prescribed fire.

Clone size did not result in significant differences in gas exchange or predawn water potentials of *B. eriopoda* after fire. Size-dependent differences in water use efficiency, net photosynthesis and stomatal conductance have been found in desert shrubs (de Soyza et al., 1996; Donovan and Ehleringer, 1992), but is not universal (Franco et al., 1994), and is most likely related to plant age. Drewa et al. (2006) documented greater survivorship of large clones following fire, suggesting that smaller clones may be more susceptible to mortality due to a less developed root system and less resources for resprouting. Though clone survivorship was not specifically examined, all plant individuals in this study survived fire regardless of size. This was unexpected, especially since precipitation after fire in the Drewa et al. (2006) study was considerably greater than occurred after the burn in the current study. While root system development was not examined, net photosynthesis and soil water availability were similar between size classes. It seems plausible that the above average precipitation in May in the current study might have led to greater root development in small clones and facilitated post-fire recovery. Care must also be taken when comparing these results to the results of Drewa et al. (2006), as their study examined survivorship after two growing seasons, defined clone size slightly differently, and included a large sample of clones.

Our results showed that fire increased soil NO₃⁻ and NH₄⁺ concentrations, similar to other studies (Rau et al., 2007). Fire often initially increases soil NO₃⁻ and NH₄⁺ availability due to increased mineralization by altered microclimate, soil temperature, and microbial activity (Wan et al., 2001). Increased soil NH₄⁺ is usually present for some time after fire, declining with plant uptake and nitrification. Though our sampling period was short (16 days), results were comparable to other longer-term studies (Overby and Perry, 1996). Unexpectedly, soil NH₄⁺ supply rates were lower than soil NO₃⁻ rates in burned treatments. Other studies have shown immediate and substantial increases in soil NH₄⁺ after fire due to incomplete combustion or soil heating, while soil NO₃⁻ increases are not present or are significantly less than soil NH₄⁺

(Covington et al., 1991; Neary et al., 1999; Romanya et al., 2001). Soil NO_3^- will increase with time as NH_4^+ is nitrified (Williams and Melack, 1997).

In this study, decreased supply rates of soil NH_4^+ compared to NO_3^- may be a result of the method of measurement. Ion exchange membranes of PRS probes simulate roots, acting as a sink and collecting nutrients over time. Soil NH_4^+ and NO_3^- are direct measurements of soil N availability and represent a snapshot at a specific point in time. Other studies (e.g. Glass, 2006) have found differences when directly comparing ion exchange membranes with direct soil sampling. Additionally, higher supply rates of NO_3^- compared to NH_4^+ may possibly be explained by cool fire temperatures. Vegetation within the burned plots was not widespread and fire temperatures may not have been high enough to completely combust NO_3^- . Furthermore, two small precipitation events (each approximately 6 mm) occurred during the sampling period after fire. These small events may have made NO_3^- more mobile in the soil than NH_4^+ , resulting in greater accumulation on the ion exchange membrane, but were not enough water to leach NO_3^- from the root zone.

Compared to other ecosystems, knowledge and understanding of fire in the Chihuahuan desert is lacking. It is known that the use of prescribed fire as a restoration tool may be useful in reducing shrub volume, but does not often result in shrub mortality (Ansley and Jacoby, 1998; Drewa, 2003). If fire is to be useful for preservation and/or restoration, desired species should respond positively. Similar to other grasslands, our results show that fire increased physiological characteristics of dominant grasses in the Chihuahuan desert. Burned plants of *B. eriopoda* and *A. purpurea* had greater photosynthetic rates compared to unburned plants. Increases in these characteristics may result in increased plant vigor and competitive ability, helping to remediate effects of shrub encroachment and restore native desert grassland communities. Additionally, lower than average precipitation rates after prescribed fire did not appear to interact with fire to effect survivorship (of plant individuals measured in this study) or ecophysiological characteristics. Investing more effort into determining the relationship between precipitation patterns and resultant soil moisture and plant survival and recovery after prescribed fire will improve our ability to use prescribed fire as a management and restoration tool within this ecosystem.

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