ORIGINAL RESEARCH

Elk forage response to prescribed fire in Boyes meadow, Prairie Creek Redwoods State Park, California

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Prescribed fire should increase plant and forage biomass for herbivores in meadows, but the response is likely to be influenced by environmental conditions. Across 15 years prescribed fires occurred every two to four years in September in Boyes meadow, Humboldt County, California. We measured the presence or absence of prescribed fires in September, climatic conditions one month later, Roosevelt elk (*Cervus elaphus roosevelti*) abundance, and the biomass of elk forage in January. From analysis of a linear mixed effects model we found that prescribed fires increased forage biomass the first January post-burn and even more so a year after the burn. Forage biomass two years post-burn decreased but was still more than three to four years post-burn. October precipitation had a positive effect on forage biomass but we detected no influence from low temperature in October or elk abundance. Given that prescribed fire increased elk forage biomass two years later, continuing to burn Boyes meadow on a three to four year rotation is suggested.

Key Words: California, forage biomass, herbivory, precipitation, temperature

Prescribed fire is becoming a widely used habitat management tool (Long et al. 2008; Starns et al. 2019). Fires facilitate nutrient cycling via the deposition of labile, burned plant material (Ojima et al. 1994), reduce coverage of senescent vegetation which increases sunlight that reaches new growth (Knapp et al. 2012), and can drive plant community composition towards species that respond favorably to disturbance (Collins et al. 1995). These changes influenced by prescribed fires can increase forage for herbivores (McNaughton 1979; Stewart et al. 2006; Long et al. 2008; Spitz et al. 2018). The rate at which fire increases forage biomass for herbivores, however, depends on the ability of the plants to compensate for loss of above-ground material. The capacity for plants to increase forage varies a great deal between ecosystems and is largely dependent on the condition and morphology of the plants, local weather following a burn, and nutrient availability in the soil (McNaughton 1979; Noy-Meir 1993; Baker 2009).

Despite the role of environmental heterogeneity on plant response to burning, many investigations of the effects of prescribed burns on forage biomass for herbivores examine one to two burns (e.g., Heisler et al. 2004; Sachro et al. 2005). Studies that track one or two burns are limited in their ability to examine the effects of weather conditions and herbivore abundance on forage biomass following a burn. Such a limited scope also makes it difficult to determine how often prescribed burns should occur to stimulate forage production.

We measured elk forage biomass in January across 15 consecutive years where prescribed fires occurred every two to four years in all or parts of Boyes meadow in Prairie Creek Redwood State Park, Humboldt County, California. We estimated change in elk forage biomass up to three to four years post-burn and examined if elk abundance, precipitation, and low temperature influenced forage biomass. Precipitation and temperature are climatic variables that have been shown to influence plant production after burns (McNaughton 1979; Stewart et al. 2006). January is shortly after burns and is also early in the plant growing season (Starns et al. 2015). Measuring forage biomass in January should reveal how quickly plants respond to fire.

Boyes meadow has a history with fire and elk. The meadow was seasonally occupied by Native American tribes, and was probably burned by Native Americans (Veirs 1987). By 1862, Boyes meadow was occupied by Europeans. The meadow was plowed, used for farmland, and also grazed by domestic livestock until it was purchased by the Save the Redwoods League in 1932 and gifted to California State Parks (Veirs 1987). Prescribed fire began in the mid-1980s by State Park personnel (Kristan 1992). Since 1994, Floyd W. Weckerly has observed when prescribed burns occurred and noted if all of Boyes meadow was burned or the part of the meadow that was burned. Elk persisted in the area after unregulated market hunting and subsistence hunting was abolished in the late 19th and early 20th century. Several elk were first documented in Boyes meadow in 1937 by State Park personnel (Harn 1958; Weckerly 2017). The elk population then appeared to increase rapidly to 100–200 in the 1940s. Thereafter, elk abundance in and around Boyes meadow seemed to range between 3 to 50 elk.

METHODS

Study area

Boyes meadow is 50-ha in size. In the mild, maritime climate there is a distinct wet season from October to early May and a dry season for the rest of the year. During the wet season, the area experiences temperatures from 10–16 C and typically receives 1500 mm of precipitation. During the dry season, temperatures range from 16–21 C and there is little precipitation. The Newton P. Drury parkway bisects the meadow into an eastern two-thirds part and western one-third area (Figure 1). Vegetation in the meadow is dominated by annual and perennial grasses, with bracken fern (*Pteridium*), some forbs, and blackberry (*Rubus*) in more well-drained areas which are prevalent west of the parkway and sedges (*Carex*) in more mesic and poorly drained areas that are evident east of the parkway (Figure 1). Since 1994, Boyes Meadow or a part of the meadow has been burned in September every 2 to 4 years.

Vegetation surveys

Every January from 2005–2019, we estimated forage biomass in 240 quarter-m² plots. Plots were spaced 10 meters apart on two randomly placed transects in each of three sectors delineating the south, middle, and north parts of Boyes meadow (Figure 1). Each transect had 40 plots. The sectors were delineated ensure that all parts of Boyes meadow were surveyed. In each plot, we used Daubenmire coverage classes to measure the cover of grasses, forbs, and shrubs palatable to elk. Elk palatability of plant species was determined

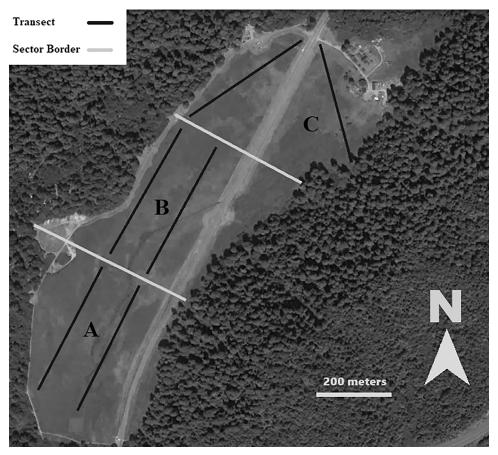


Figure 1. Aerial photograph of Boyes prairie, Prairie Creek Redwoods State Park, CA. Transects where plots were spaced 10 m apart in the three sectors (A, B, C) are delineated with black lines.

from a prior food habit study of elk conducted, in part, in Boyes meadow (Harper et al. 1967). After recording coverage, we measured the height of the vegetation to the nearest centimeter at eight different points within each plot. From the coverage and height measurements, we estimated forage biomass from calibration regressions. Calibration regressions were estimated from data collected in a different set of 129 randomly placed plots. In these plots the same coverage and plant height was measured, afterwards forage was clipped to ground level, sorted into palatable grasses, forbs, and shrubs, dried at 60 C for 48 hours, and weighed. We then estimated a multiple regression models or calibration regressions that predicted dried biomass of grasses ($r^2 = 0.84$, $F_{7,122} = 97.1$, P < 0.001) and forbs and shrubs ($r^2 = 0.33$, $F_{2,93} = 24.9$, P < 0.001; Peterson and Weckerly 2017). Estimated forage biomass in plots was the sum of predicted grass and forb – shrub biomasses.

Elk abundance

Each January from 2005–2019, we performed 10 surveys to count elk. Each survey began at sunrise and lasted 1.75 hours. The elk in Prairie Creek State Park were habituated to people, and this allowed us to collect our observations within 200 m of the elk using either the naked eye or binoculars. We took the highest count across the 10 surveys as our index of elk abundance in Boyes meadow.

Weather data

We measured mean monthly low temperature and total precipitation each October. After prescribed fires in September, October precipitation and low temperature should influence the rate that plants regrow (Williams and Biddiscombe 1964). Weather data was acquired from National Oceanic and Atmospheric Administration land-based weather stations. The Boyes station (station # 046498) was in Boyes meadow. There were many missing values, however. Consequently, we estimated the missing values using a regression that utilized data from a weather station 48km to the north near Crescent City (station # 042147). Data from the Crescent City station predicted monthly precipitation and low temperature in October ($r^2 = 0.70 - 0.71$) in Boyes meadow (Starns et al. 2014, Starns et al. 2015).

Statistical analyses

We analyzed a linear mixed-effect model using R (v. 3.5.2) to estimate forage biomass. Fixed factors were the January post-burn, the January one year post-burn, the January two years post-burn, the Januarys three to four years post-burn, elk abundance, and October precipitation and low temperature. Three to four years post-burn was the longest time between burns. Also, three to four years post-burn was the reference category. The Januarys after burns were coded as dummy variables. As recommended by Bates et al. (2015), we scaled elk abundance, October precipitation, and low temperature to have a mean of zero and standard deviation of one. Our random factors were year and sector. To meet the assumption of homoscedasticity, we took the natural log transformation of forage biomass after adding one. We added one because there was no vegetation in about one percent of plots.

RESULTS

There were four years when all of Boyes meadow was burned between 2005 and 2019. Burns in only the area west of the Newton P. Drury parkway occurred in three years and one burn occurred in only the area east of the parkway. Elk abundance ranged from 3 - 10, precipitation in October ranged from 0.45-26.5 cm, and mean low temperature in October ranged from 4.28-9.76 C. Across all 15 years the ratio of forbs-shrubs to grass elk forage was 0.15 (95% CI: 0.14 - 0.16). Post-burn estimates of forage biomass (grass, forbs, and shrubs) taken from our linear mixed-effects model were greater the January immediately after, one year later, and two years later compared to estimates of forage biomass 3-4 years post-burn (Table 1). We also found that precipitation positively impacted forage biomass, but low temperature and elk abundance were uninfluential (Table 1). The random effects of year that the survey took place and sector were similar as the 95 percent confidence

Table 1. Estimates and 95% confidence intervals (lower bound LB, upper confidence bound UB) of the fixed and random effects from analysis of a linear mixed-effects model with forage biomass as the response variable. Our fixed factors were post-burn predictors, October low temperature and precipitation, and elk abundance. The post-burn reference category was 3–4 years post-burn. The random effects (Sd – standard deviation, lower and upper 95% confidence bounds) were sector in Boyes meadow and year of survey. Data was collected in Boyes Meadow of Prairie Creek Redwood State Park, Humboldt County, CA, USA, from 2005–2018.

Fixed effects				
Predictor	Estimate	LB	UB	
Three – four years post-burn	1.282	1.070	1.478	
Three months post-burn	0.126	0.024	0.235	
One year post-burn	0.438	0.338	0.539	
Two years post-burn	0.177	0.057	0.295	
Low temperature	0.039	-0.072	0.151	
Precipitation	0.126	0.007	0.260	
Elk abundance	-0.063	-0.181	0.058	

Random effects and residuals				
Attribute	Sd	LB	UB	
Year of survey	0.255	0.129	0.315	
Sector	0.133	0.008	0.258	
Residual	0.587	0.572	0.601	

intervals overlapped. But the amount of variation in each random effect was less than the residual standard deviation.

After back-transforming forage biomass, we estimated mean forage biomass the January after the burn, one year, two years, and three to four years post-burn from the fixed effects. We controlled for precipitation, low temperature, and elk abundance by using mean values for each of these predictors. Relative to three to four years post-burn, forage biomass increased slightly the January immediately after the burn, peaked one year post-burn, and then declined two years post-burn to a value that was still marginally higher than the estimate of forage biomass three to four years post-burn (Figure 2).

DISCUSSION

Forage response three months following burns and the amount of growth in that short time in the Boyes meadow was noteworthy. Most of the forage in Boyes meadow was grass (>85 percent) with forbs making up most of the remaining 15 percent (Weckerly 2017). Most other studies measuring grass and forb production after burns were conducted in areas of continental climates. Burns were usually initiated shortly before or during the growing season (spring, summer) and forage biomass was often measured at the conclusion of growing seasons one or more years later. The amount of growth we observed in three months took one to two years at higher elevation sites exposed to winter weather that was cold with much

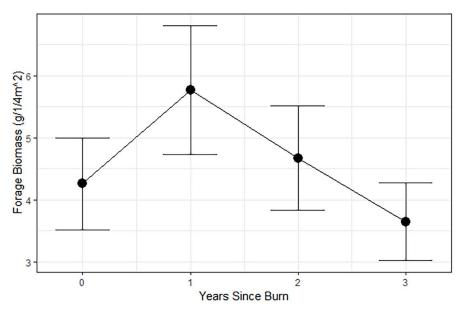


Figure 2. Predicted mean biomass of forage (g/quarter-m²), and 95% confidence intervals, in Boyes meadow of Prairie Creek Redwood State Park, Humboldt County, CA, USA. Data was collected in January 2005–2018. Year zero is the January three months post-burn.

snow (Cook et al. 1994, Sittler et al. 2019). At the scale of years our estimates indicated that prescribed burns in Boyes meadow can increase forage biomass for elk in January up to two years post-burn. Again in areas with continental climates, grass and forb biomass invariably increased one to three years following a controlled burn (Hobbs & Swift 1985, Briggs et al. 1994, Cook et al. 1994, Heisler et al. 2004, Long et al. 2008, Sittler et al. 2019). At a Montana study site, elevated grass and forb productivity was detected up to nine years after a fire (Van Dyke & Darragh 2005). In Boyes meadow, elevated grass and forb production appears to be quick. Grasses and forbs respond in a matter of months to autumn fires, but the effect to burns was undetectable three to four years after a fire.

Forage plants appeared to respond similarly across sectors to prescribed fire over the 15 years of the study. Relative to the residual standard deviation, which measures variation within a sector of Boyes meadow in a year, the random effects (i.e., standard deviations) of sector and years were smaller. There was variation in grass and forb production within sectors in each year that was noticeably greater than across sectors and years. Heterogeneity in grass and forb production that occurred even though prescribed fires are purposefully done at the end of the dry season when soil moisture is low and meadow vegetation is more likely to be senesced and dry (Underwood et al. 2003). Spatial variation in severity of burns from a fire can be considerable (Sittler et al. 2019). Across the 50 ha Boyes meadow, heterogeneity among plots within sectors in grass and forb production might be due to variation in burn severity, soil moisture, plant species, and amount of shading.

For herbivores such as elk, fire usually results in young growing plants that are nutritious because the growing plant tissue is high in protein and low in fibers that are either indigestible or take days to ferment (Van Soest 1994). After a burn forage quality for elk has been documented to range from somewhat more nutritious to noticeably more nutritious (Barker et al. 2019, Sittler et al. 2019). During rapid plant growth in late winter and early spring forage quality might indeed be high following a September burn in Boyes meadow (Weckerly 2017). In January, however, when grass and forb growth is low there might not be a noticeable increase in forage nutrition. Increased use of burned areas by elk has been noted the January after a fire however (Weckerly 2017). The increased use might be from the removal of senesced plants by burning which, in turn, should increase elk foraging efficiency on green grasses and forbs (Hobbs and Swift 1985; Peterson and Weckerly 2018; Sittler et al. 2019).

We found a positive correlation between October precipitation and forage biomass the following January. It has been established that moisture availability is an important factor in determining how plant communities respond to prescribed burns (McNaughton 1979; Frank et al. 2016). Presently, there are few published studies that directly measure the effects precipitation has on plant forage biomass production after a prescribed fire (Anderson et al. 2007). Robichaud (2000) found that prescribed burns can affect water infiltration rate through soil compaction and that the rate of water infiltration declines as temperature and duration of the burn increase. In the mild, maritime climate in the Boyes meadow it is unlikely that prescribed fires burn hot enough to create hydrophobic soil conditions that would negatively affect the ability of the soils to take in moisture.

We did not detect an influence from elk abundance on forage biomass the January after a burn. These results are atypical given that studies indicate that herbivore abundance correlates positively (Stewart et al. 2006) or negatively (Painter and Belsky 1993) with forage biomass. Our findings are similar to Sittler et al. (2019) in that no effect from elk or Stone's sheep (*Ovis dalli stonei*) was detected after burns. Both our study and that by Sittler et al. (2019) had low herbivore abundances. It is well-established that herbivores affect a myriad of factors in plant communities (McNaughton 1979; Kuijper et al. 2006; Stewart et al. 2006; Frank et al. 2016). It is likely that an effect of elk abundance on forage biomass would have been detected if elk abundance had been higher than the 3–10 elk estimated to occur in Boyes meadow during the time of our study.

We also found no correlation between low temperatures in October and forage biomass the following January. This is likely because October low temperature only ranged from 1.9 C to 5.9 C. Multiple studies have found that growth-rate of grasses and forbs varies with temperature, even when temperatures only vary from 3–4 C (Williams and Biddiscombe 1964; Peacock 1976; Durand et al. 1999). The former two studies found, however, that the strength of the relationship between temperature and plant growth rate varied based on the temperature itself and growth-phase of the plants. Williams and Biddiscombe (1964) found that plants sensitivity to changes in temperature decreased as temperature decreased, and Peacock (1976) found that grass species are more sensitive to changes in temperature during the reproductive growth stage than during the vegetative growth stage. It is possible that between October and January, which is early in the growing season when temperatures are generally low and plants are in their vegetative stage of growth, plant growth is not substantially affected by temperature. Nonetheless, there might be other metrics that we did not measure that could affect plant response in the Boyes meadow. In the cool, moist climate at Boyes meadow daily solar radiation might have a detectable influence.

Boyes meadow is a visitor attraction and is likely to be maintained in perpetuity by California State Parks (Veirs 1987). How to manage Boyes meadow to maintain produc-

tive plant communities and, in turn, food supplies for Roosevelt elk will require long-term monitoring and research. Further research is needed because of the climatic changes that are presently occurring in north coastal California (Johnstone & Dawson 2010). Our findings indicate that prescribed fires at three to four-year rotations promote forage production because plant growth is stimulated for up to two years after a burn. Nonetheless, across our 15 yearlong study there were only eight burns. Monitoring of elk and their food supplies in Boyes meadow should continue. But more detailed work is needed into ecosystem processes such as nutrient cycling, processes that impact how Boyes meadow plant communities respond to fire.

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