FOOD SUPPLY EARLY IN THE PLANT GROWING SEASON: INFLUENCES

FROM ELK ABUNDANCE AND PRECIPITATION

by

Lee H. Williamson, B.A.

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Committee Members:

Floyd (Butch) W. Weckerly, Chair

Mark Ricca

M. Clay Green

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ABSTRACT

Large herbivores interact with plant communities via grazing and trampling, and the response of plant communities to these disturbances is influenced by available moisture. Whether herbivore disturbances and available moisture influence biomass of plant communities additively or multiplicatively, however, can vary based on the temporal and spatial scale at which these factors are observed. Examining these relationships is needed to understand the dynamics of plant and herbivore populations. Early in the plant growing season, many plants put most of their energy goes towards above ground growth, and herbivore disturbances can accelerate this growth given adequate soil moisture. The relationship between these factors can also vary spatially as conditions for plant growth differ. I measured the entire food supply for a non-migratory population of elk (*Cervus elaphus*) in a temperate rainforest over a 15-year period when population abundance and total precipitation varied. The food supply was a 50-hectare meadow complex that was divided into 7 sectors, 2-10 hectares in size. I compared linear mixed effect models using Aikaike Information Criterion to determine whether elk abundance and total precipitation had an additive or multiplicative influence on the herbivore food supply. The selected model included elk abundance and precipitation as additive, not multiplicative, predictors of food supply. Also, the relationship between food supply and precipitation varied across sectors. Forage biomass in some sectors showed a positive asymptotic relationship with precipitation but in other sectors showed

little increase with precipitation. Even in this temperate rainforest, elk herbivory

influenced meadow plant communities independently of precipitation.

I. FOOD SUPPLY EARLY IN THE PLANT GROWING SEASON: INFLUENCES FROM ELK ABUNDANCE AND PRECIPITATION

Introduction

Estimating relationships between herbivores and climatic factors on plant communities is needed to understand population dynamics of both the plants and herbivores. As more herbivores inhabit an area, disturbances to plant communities caused by trampling and grazing increase in magnitude. These disturbances can reduce the herbivore populations food supply and, consequently, negatively affect abundance of the herbivore population (Mysterud 2006). Plant-herbivore interactions, however, are mediated by other environmental factors such as precipitation (Fuhlendorf and Smeins 1999, Stewart et al. 2006). While precipitation can influence plant community response to herbivore disturbances, it is difficult to predict how this relationship will affect forage biomass in most ecosystems. This is because the effects of herbivory and precipitation on forage biomass may act independently or through an interaction between the two whereby the effect of herbivory depends on the amount of precipitation (Fuhlendorf and Smeins 1999, Stewart et al. 2006, Cook et al. 2016).

Grazing and trampling by large herbivores immediately decreases aboveground plant material (McNaughton 1985, Plumptre 1993). These disturbances, however, can create conditions that facilitate plant growth and even compensatory growth (McNaughton 1979). Because large herbivores trample vegetation when grazing, overstory senescent plant material is removed which increases the amount of sunlight that reaches new growth (Jameson 1963, Langer 1972). Additionally, the loss of plant material stimulates photosynthetic activity in remaining leaves (Macedo et al. 2007) and

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can prompt physiological responses that promote leaf development (Gifford and Marshall 1973). These responses can allow the plant to elevate growth or compensate for and even benefit from herbivore disturbances (Stewart et al. 2006).

Plant compensation for herbivore disturbances is regulated by available moisture (McNaughton 1979, Belsky 1985). Allocating resources towards above-ground primary production (NAPP) requires water to be diverted from the plants root system (Sosabee and Wiebe 1971), and this can limit root development (Sosabee and Wiebe 1971, Volesky and Anderson 2007). In areas with abundant moisture, however, plants can increase NAPP without compromising root development (Belsky 1985).

Compensatory response by plants to herbivory can lead to higher overall NAPP (Hik and Jeffries 1990, Stewart et al. 2006). Nonetheless, a review of 236 grazing studies showed that herbivores increased NAPP in only 17% of studies (Milchunas and Lauenroth 1993). This indicates that, at the plant community level, the effects of moisture and herbivory vary between systems. Generally, ecosystems composed of herbaceous, grazing-tolerant plants with abundant precipitation are more likely to benefit from herbivory (McNaughton 1979, Hik and Jeffries 1990, Stewart et al. 2006). In these ecosystems, plant communities can compensate more readily for grazing because the abundant moisture facilitates the compensatory response while also increasing the rate of nutrient fixation and assimilation of fecal derived nutrients (Bardgett and Wardle 2003). These ecosystem characteristics select for rapid growing herbaceous plant communities that are composed of more labile plant material (Bardgett and Wardle 2003). The high proportion of labile plant material allows for a higher portion of the plant to be ingested by herbivores which means the majority of nutrients in the plants is returned to the soil in

the form of easily assimilated fecal material and not plant litter that decomposes slowly (Bardgett and Wardle 2003). In most studies, however, plant community response to herbivory was either neutral or negative (Milchunas and Lauenroth 1993). This review indicated that ecosystems that have only moderate NAPP, moisture, and soil nutrients do not benefit from any amount of herbivory. These ecosystems select for slow growing and grazing-resistant vegetation that is less palatable to herbivores because of chemical defenses and low amounts of digestible plant material (Bardgett and Wardle 2003).

Even within ecosystems that facilitate plant compensation to herbivory, factors that affect the rate of compensation can vary. Soil productivity can vary over the course of several meters with variance increasing with spatial scale (Cain et al. 1999). Additionally, herbivores do not graze all plants equally (McNaughton 1979, Beck and Peek 2005). Selectivity by herbivores can lead to increased grazing of certain plants while largely ignoring others. At spatial scales inhabited by herbivore populations, animals rarely utilize all available forage patches equally (Fortin et al. 2002). These factors may lead to a non-uniform response of plant communities to herbivory within an ecosystem and necessitate comparisons across multiple spatial scales to draw conclusions about the effects of moisture and herbivore disturbances on forage biomass. Furthermore, several studies have found that plant response to herbivory varies over time as well as across a landscape (Tomanek and Albertson 1957, Grant 1971). These studies found that plant community responses to herbivory can vary across years of continuous grazing as herbivore grazing pressure brings about either more grazing-tolerant or grazing-resistant vegetation. Additional studies have found that plant community response can also vary seasonally (Stewart et al. 2006, Cook et al. 2016). The effects of season on plant

production are well understood for individual plant species, but how season affects total forage biomass of an entire plant community will vary as plant life-histories, available moisture, and grazing pressure vary spatially.

While making long-term predictions about herbivore food supply is crucial for ensuring the persistence of herbivore populations, estimating the effects of herbivory and precipitation on herbivore food supply must account for temporal and spatial variation of factors that affect plant growth within an ecosystem (Fuhlendorf et al. 2001, Cook et al. 2016). This requires a dataset that has estimates of the entire herbivore food supply, a challenge because herbivores typically forage across a large area. Probably because of these associated challenges, no study has directly estimated the effects of herbivory and precipitation on food supply for a population of large herbivores.

In my study area, Redwood National and State Parks, the meadow ecosystems are dominated by a single large herbivore, the Roosevelt elk (*Cervus canadensis roosevelti*). Compared to most populations of Roosevelt elk, the herd in my study area forages within a relatively small area (Weckerly 2017). Additionally, this area consists of a simple matrix of dense forests with little forage intermixed with meadow forage patches. This setting makes it feasible to reliably estimate the bulk of the food supply. Herein, I measured elk abundance, precipitation, and forage biomass across 15 years early in the growing season when precipitation should mediate plant responses to herbivory. I evaluated whether precipitation and elk abundance had an additive or interactive (i.e., multiplicative) influence on plant communities that were the food supply for an elk population. Furthermore, I examined whether responses differed between two scales, the meadow and within the meadow. Elk abundance and precipitation varied 3.9- and 12.6-

fold, respectively, over the course of the 15-year study, which allowed for a robust examination of the influence of these two factors on the food supply of the elk population.

Materials and Methods

Study Area

Data was collected in the Davison meadow complex along the Prairie Creek drainage in Redwood National and State Parks (41º24' N, 124º02'W) in Humboldt County, California, USA (Figure 1). This area is a temperate rainforest that has a maritime climate with temperatures that typically range from 10-20°C year-round (Starns 2015). On average, the area receives 165 cm of annual precipitation, most of which occurs from late fall through early spring (Starns et al. 2015). Vegetation in the Davison meadow complex is dominated by perennial and annual grasses such as California oatgrass (*Danthonia californica)*, redtop (*Agrostis gigantica*), and softchess (*Bromus horeaceus*). Forbs such as buttercup (*Ranunculus*) and clover (*Trifolium*) were also present. Reed canary grass (*Phalaris arundinacea*) has become abundant since the early 2000s. This plant is, however, unlikely to be palatable to elk at any stage of growth (Weckerly 2017). The Davison meadow complex is surrounded by old-growth and second growth coastal redwood (*Sequoia sempervirens*) forest. Common conifers include Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*). Dense canopy cover in the surrounding forest prevents many grasses and forbs from growing. Predators of elk are mountain lions (*Puma concolor*) and black bear (*Ursus americanus*).

The Davison meadow complex covers 51 ha. Cattle grazing began in the late 1890s after forest was removed and meadow vegetation was established (Weckerly 2017). Cattle were the only herbivores that grazed the Davison meadow complex until 1991 when the area was purchased by the Save the Redwoods League and gifted to the National Park Service (Starns et al. 2015). After 1991 cattle grazing ceased, and elk colonized and began grazing the meadow complex (Weckerly 2017). Two elk herds have used the Davison meadows. A herd is comprised of females, juveniles, and subadult males that form a cohesive group (Weckerly 1999) that rarely coalesce with other elk herds (Weckerly 2017). The Davison herd has grazed the Davison meadow complex as its source of forage in winter across the length of the study (Weckerly 2017). The Levee herd, which usually occupied meadows to the south of the Davison complex, also grazed the southern part of the Davison meadow complex from 2007 to 2012. In 2016, another 10-ha cattle pasture, immediately south of the Davison meadow complex, was purchased by Save the Redwoods League and became available to elk (McGuire 2018).

Black-tailed deer (*Odocoileus hemionus columbianus*) are the only other large herbivore in the Davison meadow complex. Deer, however, were scarce. Other herbivores of meadow vegetation include the California vole (*Microtus californicus*) and phytophagous insects.

Vegetation Data

Vegetation data was collected each January between 2005 and 2019. Differences in soil productivity and access to sunlight can cause plant community responses to herbivory and precipitation to vary within an ecosystem. In order to account for the effects of this variation on herbivore food supply, and ensure that all parts of the Davison

meadow complex were measured, I divided the Davison meadow complex into 7 sectors, ranging from 2-10 has in size, when measuring forage biomass (Figure 1) (Weckerly 2017).

I estimated forage biomass within 270 ¼ m^2 plots (250 plots in 2005) located along transects that were randomly placed in each of the 7 sectors. The sectors grazed by herds across the 15 years of the study were horsebarn, sectors A, B, and C, WPC, picnic, and south Davison (Figure 1). Vegetation in fish hatchery and cattle pasture was not included in analyses because these two sectors began being grazed in 2016 when the Davison herd expanded its home range (McGuire 2018). The number of transects within each sector, and the number of plots within each transect, was proportional to the size of the sectors. Each transect had 10-30 plots spaced 10 meters apart. Transects were at least 20 meters apart. In each plot I estimated vegetation height to the nearest centimeter in 8 equidistant places. I also estimated coverage of palatable grasses, forbs, and shrubs using Daubenmire coverage classes: 0-5%, 6-25%, 26-50%, 51-75%, 76-95%, and 96-100% (Daubenmire 1968). From 2005-2007, these measurements were taken in 129 additional plots distributed throughout the 7 sectors. Vegetation within these plots was then clipped to ground level and sorted into palatable grasses, forbs, and shrubs. These samples were then dried for 48 hours at 60°C and weighed to measure dried biomass (Weckerly 2017). Following this, multiple regressions were estimated using average vegetation height within each plot and Daubenmire coverage classes to predict dried biomass of grasses (g ¼ m^2) ($r^2 = 0.84$, $F_{7, 122} = 97.1$, $P < 0.001$) and the other vegetation categories ($r^2 = 0.33$, $F_{2, 93} = 24.9$, $P < 0.001$) (Weckerly 2017). These regressions were used to estimate forage biomass within each plot in every year of the study.

Weather and Elk Data

Precipitation can limit plant growth, but cold temperatures might also be influential. I measured average monthly low temperature and monthly precipitation (cm) in 3 months that were early in the growing season: October, November, and December. Weather data was acquired from National Oceanic and Atmospheric Administration land-based weather stations. Initially, weather data was obtained from the Prairie Creek State Park station (station # 046498) located 3 km north of the Davison meadow complex. There were many months of missing data, however. I estimated these missing values from a regression that used data from a weather station 48km to the north near Crescent City, California, USA (station # 042147). Data from the Crescent City station predicted monthly precipitation ($r^2 = 0.61$) and low temperature ($r^2 = 0.70$) in the Davison meadow complex (Starns et al. 2014, Starns et al. 2015).

Previous work has shown that the time spent grazing by the Davison herd is directly proportional to food availability in the sectors of the Davison meadow complex (Weckerly 2017), so it is likely that elk abundance is a reliable index of herbivory across the Davison meadow complex. To estimate elk abundance, I conducted 10 population surveys each January. Each survey began at sunrise and lasted 1.75 hours. For each survey, I drove a pre-determined route through the Davison meadow complex and recorded the number of adult and subadult females, subadult males, and juveniles. The herds were habituated to people, and so all observations were carried out within 200 meters using binoculars or the naked eye. I did not include adult males because they do not graze the Davison meadow complex to the same degree as female herds (Weckerly 2007). I used the highest count across the 10 surveys as my estimate of population

abundance for each year. The high count was adequate to index abundance because detection probabilities of females was high (> 0.8) in the Davison meadow complex (Weckerly 2017).

Evaluation of Predictors

I estimated Pearson's correlation coefficients to measure the associations between forage biomass (kg) in the Davison complex with elk abundance, average low temperature, and precipitation. Precipitation was natural log transformed because a positive, asymptotic relationship with forage biomass was evident in scatterplots. I estimated forage biomass at the scale of Davison meadow complex because multiple studies have found that relationships between environmental factors are more pronounced at a larger scale (Fortin et al. 2002, Christianson and Creel 2008, Cook et al. 2016). Thus, I was more likely to find the environmental factors that had the strongest influence. For my predictors of average low temperature and precipitation, I used values from each of the months of October, November, and December, the sum of November and December, and sum of October through December of each year. I chose October through December because it was when the rainy season usually began and the climatic conditions were most likely to influence vegetation in January (Starns et al. 2015, Weckerly 2017). I used the weather predictor that had the highest correlation with forage biomass in the model selection process.

I analyzed linear-mixed effect models that were built in the lme4 package in R version 3.6.1. Each model had forage biomass within quadrats (g ¼ m^2) as the response variable and included elk abundance and my selected weather variable as fixed numeric predictors. Sector and year data were collected were random factors and included in each

model as intercepts random effects. Sector was included as an intercepts random effect because environmental heterogeneity may lead to different responses to herbivory and precipitation across the Davison sectors. Year data was collected was included as an intercepts random effect to account for variation caused by variables not considered in my study. I scaled each value of herbivore abundance and the selected weather variable by subtracting the mean and dividing by the standard deviation of the dataset as recommended by Bates et al. (2015). Additionally, the relationship between precipitation and forage biomass was positive and asymptotic (Starns et al. 2015), and so I natural log transformed precipitation.

Model Selection

The effects of weather and herbivory on plant communities can vary within an ecosystem (Stewart et al. 2006), and thus it is possible that the influence of weather and herbivore abundance on forage biomass may vary among the 7 sectors in the Davison meadow complex. To test this, I considered models that had the same set of all possible fixed factors that might be influential, but each model differed in random effects. I compared log likelihoods of models that included my selected weather variable, herbivore abundance, or both as slopes random effects with sector random intercepts. When these models had the same number of random components, I compared log-likelihoods. I then used a likelihood ratio test to compare the model with the largest log likelihood to a model with only random intercepts. I included random effects from the model that best fit the data when comparing models to identify influential fixed effects.

I considered whether the selected weather variable and herbivory had an additive or multiplicative influence on forage biomass within the 1/4 m^2 plots. Furthermore, the

addition of the cattle pasture and fish hatchery into the home range of the Davison herd

may also influence forage biomass, and so I included the addition of these two areas as a

binary, categorical factor. To determine whether my selected weather variable and

herbivore abundance had an additive or multiplicative influence on forage biomass, and if

the addition of the cattle pasture and fish hatchery influenced forage biomass, I fit four

linear-mixed effect models. Model 1 included my selected weather variable and herbivore

abundance as fixed additive predictors, and model 2 also included an interaction between

the two predictors. Models 3 and 4 also used my selected weather variable and herbivore

abundance as fixed additive and interacting effects but also included a dummy variable

for the years the Davison herd expanded its home range. I used Akaike Information

Criterion (AIC_c) to determine which model had the strongest fit to the data considering

parsimony. Models compared via AIC_c were estimated with maximum likelihood

estimators, but restricted maximum likelihood estimation was used when estimating and

reporting parameter and random effect estimates of the selected model (Wolcott et al.

2015). For the selected model, I estimated 95 percent confidence intervals of fixed and

random effects from 1000 parametric bootstrap simulations.

Results

From 2005 to 2019, forage biomass in the Davison meadow complex ranged from

8,257 (SE = 365) kg in 2014 to 19,432 (6,277) kg in 2006 and averaged 14542 (138) kg.

Elk abundance ranged from 17 individuals in 2006 to 67 individuals in 2012 and

averaged 49 individuals. Elk abundance correlated negatively with forage biomass in the

Davison meadow complex ($r = -0.40$, $p = 0.014$, Figure 2). Precipitation from October

through December correlated positively with forage biomass ($r = 0.70$, $p = 0.003$)

(Figure 3) and had the strongest association with forage biomass among all weather variables (Table 1). Precipitation from October through December each year ranged from 17.6 centimeters in 2014 to 222.4 centimeters in 2013 and averaged 137.9 centimeters.

To address what should be the random effects with sector, I first estimated a model that included both elk abundance and precipitation from October through December as slopes random effects with random intercepts for sector (model A). The model, however, did not converge (probably because of insufficient data) and was excluded from further consideration (Table 2). Model B that had precipitation from October through December as a slopes random effect had a log-likelihood of -10938 ($df =$ 9). Model C, that had elk abundance as a slopes random effect, had a log likelihood of -10963 ($df = 9$). Model B had a stronger fit as the log-likelihood was 25 units higher than model B. A likelihood ratio test comparing model B to model D ($df=8$), the model that did not include any slopes random effects, indicated model B was a better fit (Table 2) ($\chi^2 = 121.26$, $df = 9$, $p < 0.001$). My findings indicated that model B had the best fit, and so I included precipitation from October through December as a slopes random effect in all subsequent models.

The AIC_c analysis to examine influential fixed factors indicated that all models had similar log-likelihoods and $\Delta AIC < 2.0$ (Table 3). Whether elk abundance and total precipitation from October through December were included as fixed additive factors (model 1) or fixed interacting factors (model 2) did not significantly affect the fit of the model, nor did including the addition of the cattle pasture and fish hatchery (models 3 & 4). Therefore, I selected the most parsimonious model, model 1, which had elk abundance and total precipitation from October through December as fixed additive

factors. Increasing elk abundance had a negative effect on forage biomass and increasing precipitation had a positive effect (Table 4). The residual standard deviation was larger than random effects for slopes and both intercepts. This indicates that most of the variation in the data was caused by factors not included in our random effects. Sector intercept standard deviation was notably larger than year standard deviation.

From the selected model I estimated sector-specific regressions between precipitation in October through December and forage biomass within each quadrat ($g\frac{1}{4}m^2$). The regressions indicated that forage biomass in WPC, horsebarn (HB), and the picnic sectors did not increase or only increased slightly with precipitation (Figure 4). Conversely, forage biomass in sectors A, B, C, and south Davison (Sdav) increased with precipitation.

Discussion

The results of this study are novel in that they measured the entire herbivore populations food supply to investigate the relationships between the food supply and elk abundance and precipitation. Past studies have found that, following herbivory, different species of grass are capable of translocating water away from the roots and crown and towards young leaves, effectively increasing the rate at which these plants develop new leaves (Sosabee and Wiebe 1971, Macedo et al. 2007). The degree to which this response occurs is dictated by available soil moisture (Sosabee and Wiebe 1971, Macedo et al. 2007), and so I expected to detect a multiplicative relationship between herbivore abundance and precipitation in this temperate rainforest. The model that had the strongest fit to the data, however, included precipitation and elk abundance as additive predictors. This indicates that the plant community response to elk abundance is little affected by

available moisture. The average precipitation early in the growing season was 137.9 centimeters for this study, and so there was likely adequate moisture to facilitate plant compensation. It is possible, however, that the plant growth stage early in the growing season precluded any possible interaction between herbivore abundance and precipitation. Previous studies have found that, in annual grasslands, grazing early in the plant growing season can prompt a physiological response from the plant community that leads to increased tiller initiation and seed production (Briske and Noy-Meir 1998), but these changes do not become evident until later in the plant growing season. In the short-term, however, grazing early in the plant growing season can reduce the already limited photosynthetic surfaces of juvenile plants and reduce carbon allocation towards root development (Belsky 1985, Huntly 1991, Briske and Noy-Meir 1998). These changes make it difficult for plants to fix carbon and absorb soil moisture and can thus limit plant growth early in the growing season. Early in the plant growing season, a large amount of available forage biomass for herbivores consists of plants in early developmental stages and even a low rate of herbivore disturbances may reduce root development and prevent these plants from benefitting from precipitation.

Absence of an interaction between herbivore abundance and precipitation may indicate a shift in plant community composition. A plant community characterized by grazing tolerant plants would be less affected by herbivory as precipitation increased (McNaughton 1979, Stewart et al. 2006). In a plant community that is grazing resistant, however, forage biomass is less palatable and should be less affected by changes in herbivore abundance, and this might make for difficulty in detecting an interaction between herbivore abundance and precipitation. While some studies have shown that

grazing by resident populations year-round can select for grazing tolerant plant communities (Grant 1971, Leege et al. 1981), a comprehensive review of grazing studies showed that intensive grazing led to declines of grazing tolerant plants in over 80% of the studies included in the review (Milchunas and Lauenroth 1993). The studies that demonstrated increases in yields of palatable grasses were characterized by either low stocking rates or rotational grazing in productive ecosystem. Even in grazing tolerant plant communities, plant compensation for herbivory requires plant resources to be diverted from the plant's roots toward aboveground biomass (McNaughton 1979). While this response may initially increase aboveground growth rates, consistent grazing can lead to a reduction in root development (Volesky and Anderson 2007). As root development of palatable grasses is hampered, their ability to compete for resources diminishes (Brink et al. 2013). This can give unpalatable plants an advantage, and lead to the proliferation of grazing resistant plants (Augustine and McNaughton 1998). Such a shift in plant community composition is likely in the Davison meadow complex, where species such as invasive reed canary grass has become more abundant (Weckerly 2017).

My findings are similar to those of Milchunas et al. 1994. Both studies found that cool-season precipitation had a greater influence on forage biomass than either temperature or grazing regiment. Milchunas et al. (1994) hypothesized that lower temperatures during cooler months of the year decreased evaporation rates, and enabled plant communities to utilize a greater portion of precipitation. Evidence for this hypothesis is provided by Patton et al. (2007) who found that forage biomass was more strongly influenced by precipitation than herbivory in sites with lower evaporation rates than in sites with higher evaporation rates. This relationship was also strongest for grass

species. It is likely that cooler temperatures early in the plant growing season in the Davison Meadow Complex contribute to lower rates of evaporation and more pronounced benefits from precipitation. It is also possible, however, that the growth stage of the plant community early in the growing season may allow the plants to benefit more from precipitation. Plants at a younger growth stage tend to have more shallow roots than those of fully developed plants, and their growth rate is influenced more by changes in precipitation patterns than by available ground water (Weaver 1968, Sims et al. 1978). This relationship has been found even in mesic grasslands characterized by high soil moisture levels (Knapp et al. 2001). While the Davison Meadow Complex includes many perennial grass species with deep root systems, it also includes annual grass species (Weckerly 2017). These annual species would have shallow root systems and should benefit from precipitation. This relationship should be especially pronounced near the beginning of the plant growing season when cool temperatures facilitate low evaporation rates.

While cooler temperatures early in the plant growing season may allow for increased soil moisture, they may also slow the rate at which plants grow by suppressing soil microbial communities that mineralize nitrogen for these plants. Woodmansee and Duncan (1980) showed that soil nitrogen and phosphorous was lower in the early winter than in the late winter and early spring in California annual grasslands (Woodmansee and Duncan 1980).The authors concluded that cooler temperatures in the early winter months slowed the rates at which microbial communities were able to assimilate soil nutrients. As temperatures became warmer in the late winter and early spring, however, these microbial communities became more active and were able to assimilate soil nutrients

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from plant litter and animal feces that had built up during the cooler period. This relationship likely exists in the Davison Meadow Complex and may explain why I found the asymptotic relationship between precipitation and forage biomass in the cool, early winter months.

According to my selected model, the picnic area, WPC, and horse barn sectors had almost no increase in forage biomass as precipitation increased. A history of anthropogenic disturbances may have resulted in the relationship between precipitation and forage biomass in the picnic area, WPC, and horse barn. The horse barn was used to store heavy equipment in the past 30 years, and part of the area was covered by asphalt. Likewise, west PC was the site of the Davison family homestead. The picnic area was previously a logging deck that also had large asphalt pads in the past 30 years (Richey and Wheeler 2001). Previous studies have shown that deposition of gravel and asphalt can degrade soils (Gudin and Syratt 1975) and damage native microbial communities (Wang et al. 2007). The time it takes for a former mesic grassland to be restored can take anywhere from 5 to over 25 years depending on the length of time the gravel or asphalt was present (Řehounková 2007).

Results of my selected model indicate that there was a great deal of variability in forage biomass from plot to plot. This indicates that vegetation community attributes that contribute to forage biomass, like ground cover and aboveground primary production, vary over short distances within this ecosystem. Differences in available soil nutrients likely contribute to this variation. Previous work has shown that soil nitrogen levels can vary significantly over distances as short as 10 meters (Cain et al. 1999), and can lead to differences in ground cover, root development, and primary production (Hutchings and

John 2004). These differences in plant attributes would be increased during the growing season as plants with more developed root systems take in and utilize moisture at a greater rate than plants with less-developed root systems. All of this could lead to a non-uniform distribution of forage with certain patches containing relatively more forage than others within the same sector. Over several years, this non-uniform distribution could lead to declines in total forage biomass within each sector. This is because meadow selection by the herd is largely determined by available forage biomass in this area (Weckerly 2017). Distribution of individuals within each meadow, however, is influenced by social factors. Members of a herd can act aggressively towards each other, and the rate of aggressive behaviors likely increases with resource competition (Weckerly 1999, Weckerly et al. 2001). Competition for forage would increase in meadows where palatable forage is not evenly distributed. This increased competition could lead to a few socially-dominant individuals grazing areas of higher production and the majority of the herd grazing less productive areas.

It is likely that the relationship between elk abundance and forage biomass was affected by the presence of phytophagous insects. There are over a dozen species of grasshoppers in the genus *Melanoplus* that inhabit grasslands along the northern California coast (Strohecker et al. 1968). No study, to my knowledge, has evaluated the effect of *Melanoplus* populations on forage biomass in northern California, but results from studies in other grasslands throughout the United States indicate that this genus can significantly reduce aboveground forage biomass, ground cover, and canopy height across a large area (Onsager 1983, Porter et al. 1996). Several species of *Melanoplus in* northern California reach adulthood by the end of September (Dingle et al. 1990), right at

the beginning of this areas growing season and the time of year when forage biomass is at its lowest (Starns et al. 2015). Due to its phenology, and the numerous studies that have cited the potential of *Melanoplus* species to affect vegetation communities, it is likely that *Melanoplus* species affect the herbivore food supply early in the plant growing season.

It is possible that two other mammalian herbivores, black-tailed deer and the California vole may have affected the relationship between elk abundance and the herbivore food supply. Previous work has shown that wild populations of black-tailed deer and Roosevelt elk exhibit some dietary overlap, especially in the fall and winter months when forage is less abundant (Leslie et al. 1984). Nonetheless, diet quality of each species was similar across the seasons of the year. This indicates that strong competition for diet quality is unlikely between black-tailed deer and Roosevelt elk. California voles, however, consume grass and can substantially reduce standing crop of grasses in northern California during fall and winter (Batzli and Pitelka 1971). I did not measure California vole abundance during this study. It is possible that California voles might have influenced forage biomass in January. Considering the variety of herbivores that might have influenced forage biomass in the Davison meadow complex, Roosevelt elk herbivory had to be pervasive for me to detect a decline in forage biomass with an increase in elk abundance.

My selected model allowed the relationship between precipitation and forage biomass to vary among the 7 Davison sectors, but this model had a log likelihood that was only marginally greater than that of the model which allowed the relationship between elk abundance and forage biomass to vary across sectors. The Davison meadow complex represents a heterogeneous ecosystem where soil drainage, plant access to

sunlight, and other ecosystem attributes vary. Thus, it is likely that the relationship between elk abundance and forage biomass should also vary among the Davison sectors. While this may be the case, previous work has found that time spent foraging by elk in north-coastal California is associated with grass abundance and meadow size (Weckerly 2005). This indicates that the Davison herd is grazing each of the Davison sectors relative to the amount of forage biomass within each sector. The Davison herd spends less time grazing each sector as available forage biomass decreases, and this could make it more difficult to detect differences in plant community response between sectors. Elk also select meadows to forage based on proximity and accessibility (Fortin et al. 2002, Weckerly 2005) and the Davison herd likely grazes some sectors more or less than would be expected based solely on available forage. Thus, the Davison herd is not grazing each sector purely based on forage availability, and differences in plant community response within each sector should be evident. It is possible that a model that allowed the relationships between precipitation and elk abundance both with forage abundance may fit the data better than my selected model. This model, however, would not converge, likely due to a small sample size of only 7 sectors.

As would be expected for a California annual grassland, I found that precipitation early in the growing season was the most influential predictor of forage biomass. In spite of this, I was unable to detect a multiplicative relationship between early winter precipitation and elk abundance in their effects on forage biomass. This is likely because compensation for herbivory by annual plants would likely not become evident until later in the growing season when aboveground production is higher. This may also indicate, however, that the plant communities of the Davison meadow complex have shifted

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towards a more grazing resistant composition as *P. arundinacea* increases in abundance. I also found that, while their plant communities superficially resemble those of sectors A, B, and C, forage biomass in west PC, horse barn, and the picnic area did not increase with increasing precipitation. This indicates that the remedial action done by the park in these areas may not have been effective. To better understand the interactions between the Davison herd and the plant communities of the Davison meadow complex, and to ensure that the Davison herd's food supply persists in the years to come, biologists of Redwood National Park should take steps to limit the spread of *P. arundinacea*. Furthermore, park biologists should investigate what factors may be limiting plant growth in the west PC, horse barn, and picnic areas.

Table 1. Pearson's correlation coefficients of precipitation and low temperature with forage biomass. Data was collected in the Davison Meadow Complex Climatic variables were considered by each month, November and December, and October through December. Precipitation was the total for the month(s). Low temperature was averaged across days of each month.

Correlation Coefficients of Weather Variables		
Variable	Precipitation	Average low temperature
October	0.66	0.21
November	0.42	0.10
December	0.70	0.44
November – December	0.72	0.35
October – December	**0.77**	0.35

Table 2. A summary of the different random effects and their log likelihoods. The fixed effects for each model were female abundance, total precipitation in October and December, and expansion of the Davison herd, and forage biomass was the response variable. The bold numbering indicates the model with the lowest log likelihood; this model was selected. There was no correlation of fixed effects.

| | | Random Effects | | |
Model	Intercepts	Slopes	LL	nPar
A*	Sector, Year	Abundance, Oct-Dec Precipitation	n/a	10
B	Sector, Year	Oct-Dec Precipitation	**-10938.02**	9
C	Sector, Year	Abundance	-10963.09	9
D**	Sector, Year	N/A	-11000.06	8

* Model A did not converge

** Model B and C had the same number of parameter estimates, so a log-likelihood test could not be conducted between these two models. A likelihood ratio test between model B and D indicated that model B was a stronger fit ($\chi^2 = 121.3$, df $= 1$, P < 0.001).

Table 3 AICc model selection of models with different fixed effects. Each model estimates forage biomass ($g\frac{1}{4}m^2$) in the Davison Meadow Complex. Reported for each model are log likelihoods (LL), number of parameters estimated (nPar), and difference in AIC_c between a model and the model with the smallest AIC_c (Δ).

Summary of Fixed Effects				
Model	Fixed effects	LL	nPar	Δ
1	Abundance, Oct – Dec precipitation	-10940.39	7	0.00
2	Abundance, Oct – Dec precipitation, abundance X Oct – Dec precipitation	-10939.54	8	0.32
3	Abundance, Oct – Dec precipitation, expansion	-10939.75	8	0.73
4	Abundance, Oct – Dec precipitation, abundance X Oct – Dec precipitation, expansion	-10939.35	9	1.94

Table 4. Estimates and 95% confidence intervals of the selected model. The tables below include all fixed and random effects of the selected linear-mixed effects model estimating forage biomass ($g\frac{1}{4}m^2$). The fixed effects were abundance, and Oct-Dec precipitation. The random effects were intercepts for year and sector, and slopes for Oct-Dec precipitation among sectors.

Fixed effects			
Predictor	Estimate	LB	UB
Intercept	-0.08	-0.44	0.27
Abundance	-0.11	-0.21	-0.02
Oct-Dec precipitation	0.18	0.02	0.36
Random effects and residuals			
Attribute	Sd	LB	UB
Intercepts - year	0.18	0.11	0.26
Intercepts - sector	0.43	0.26	0.76
Slopes - Oct-Dec precipitation	0.18	0.11	0.33
Residual	0.84	0.82	0.86
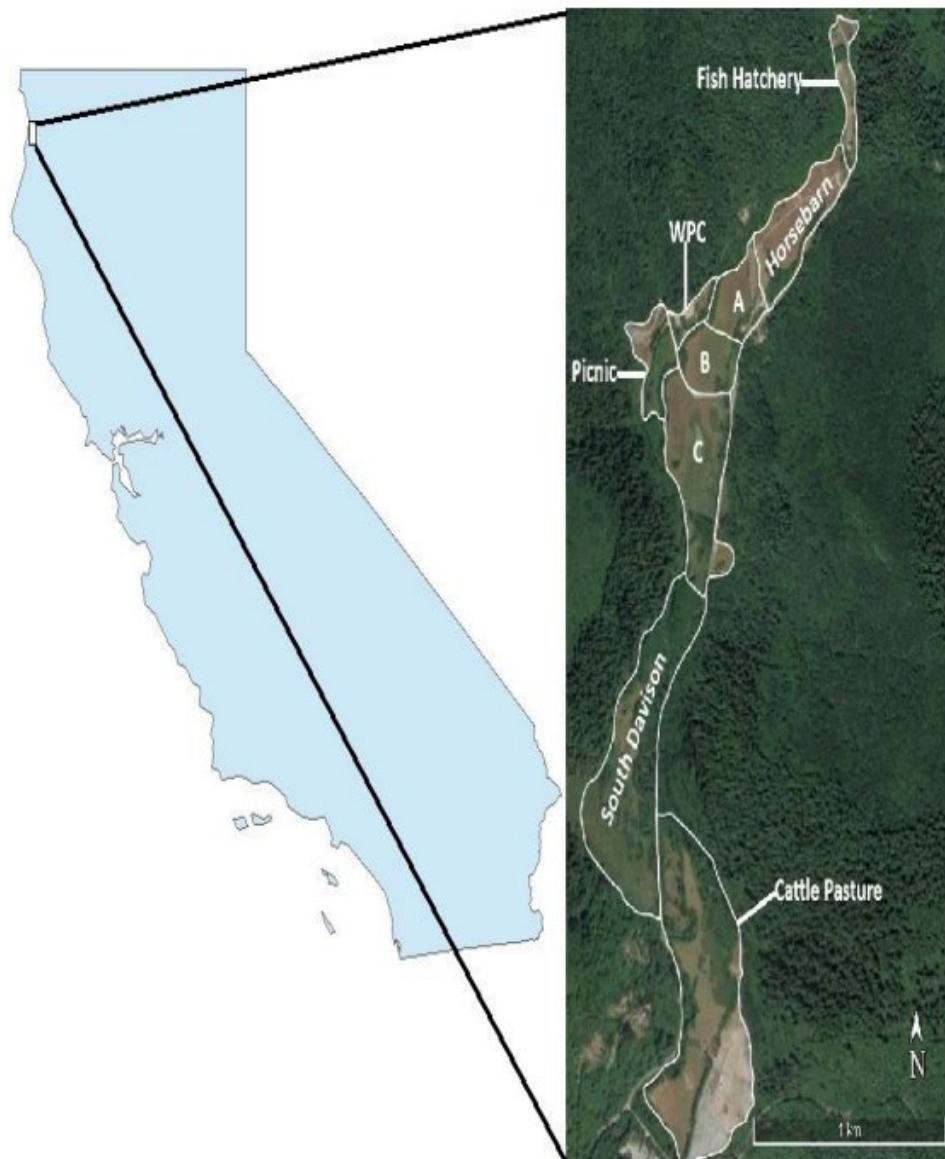
Figure 1. Map of the Davison meadow complex in Redwood National and State Parks and location of the parks in California. Within the meadow complex are the sectors. Map was figure 1 in MCGuire (2018).
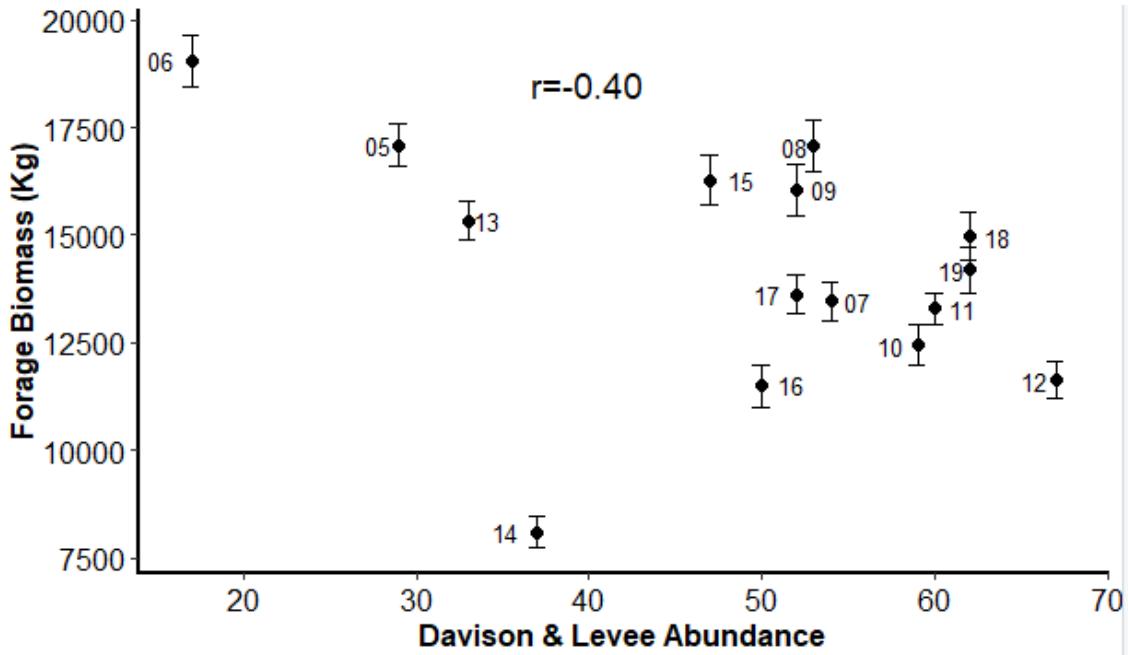
Figure 2. Scatterplot of elk abundance and January forage biomass, 2005 - 2019. Also shown is the correlation coefficient. Forage biomass estimates, with one standard error bars, are for the Davison meadow complex. Elk abundance is the sum of abundances of the Davison herd and the Levee herd when it inhabited parts of the Davison meadow complex. The numbers next to estimates and error bars reference years (e.g., 06 is 2006).
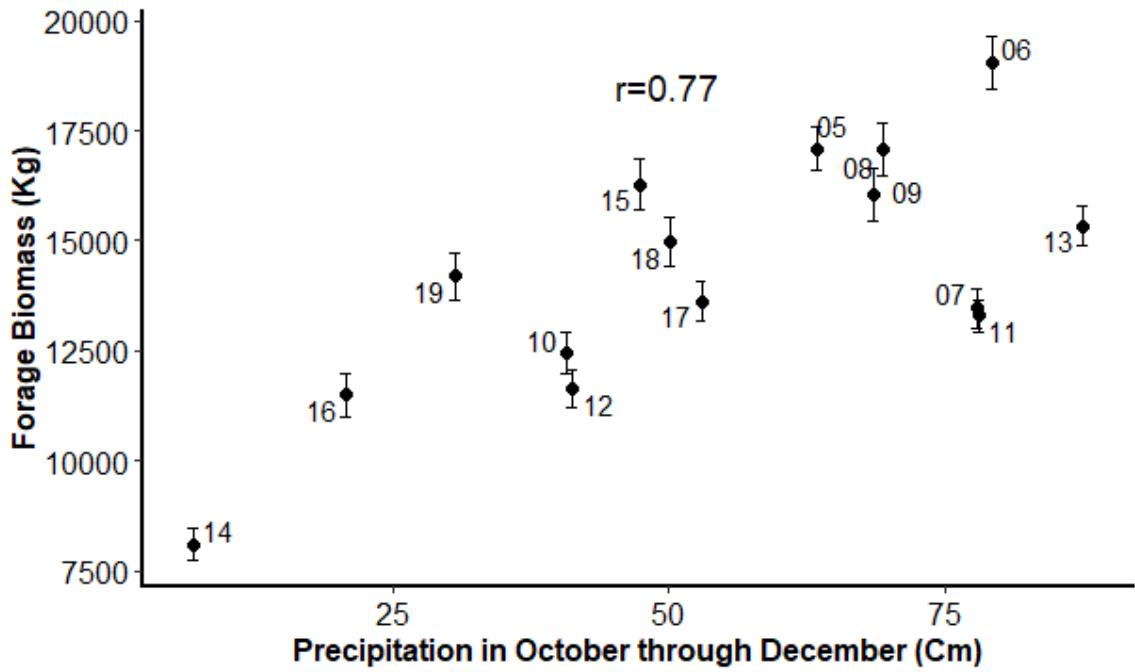
Figure 3. Scatterplot of precipitation and forage biomass, 2005 - 2019. Also shown is the correlation coefficient. To estimate correlation, precipitation was natural log transformed. Forage biomass estimates, with one standard error bars, are for the Davison meadow complex in January 2005 - 2019. The numbers next to estimates and error bars reference years same as in figure 2.

Sector Specific Regression from Selected Model
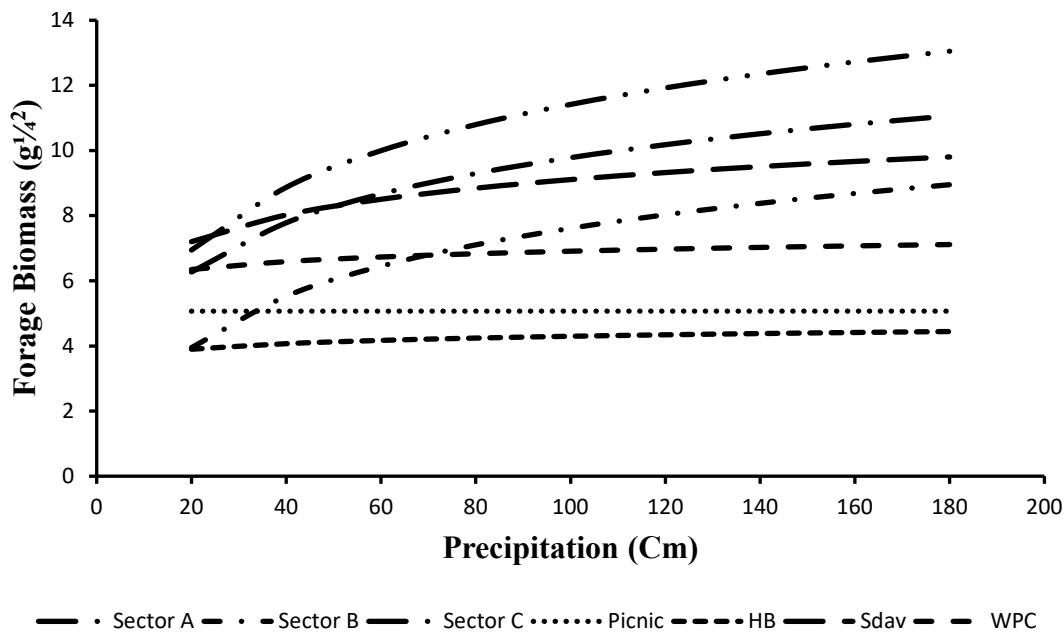
Figure 4. Plot of regressions predicting forage biomass as precipitation increases in the Davison meadow complex. Coefficients were taken from the selected model. All values of precipitation were natural log transformed. Precipitation values represent the range in total precipitation from October through December.
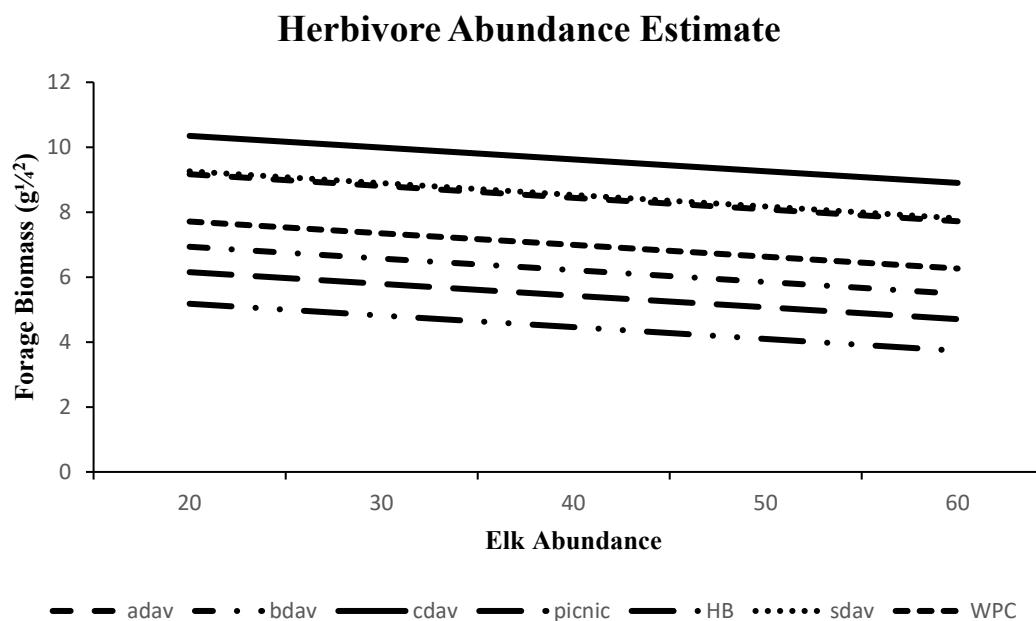
Figure 5. Plot of regressions predicting forage biomass as elk abundance increases in the Davison meadow complex. Coefficients were taken from the selected model. Elk abundance values represent the range in abundance from 2005 to 2019.

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