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Authors

Larsen, Royce E
Shapero, Matthew WK
Striby, Karl
et al.

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Forage Quantity and Quality Dynamics Due to Weathering over the Dry Season on California Annual Rangelands☆

Royce E. Larsen[a,*], Matthew W.K. Shapero[b], Karl Striby[c], LynneDee Althouse[d], Daniel E. Meade[d], Katie Brown[e], Marc R. Horney[f], Devii R. Rao[g], Josh S. Davy[h], Craig W. Rigby[i], Kevin B. Jensen[j], Randy A. Dahlgren[k]

[a] Area Watershed and Natural Resource Advisor, University of California, Agriculture and Natural Resources, Templeton, CA 93465, USA
[b] Area Livestock and Natural Resource Advisor, University of California, Agriculture and Natural Resources, Ventura, CA 93003, USA
[c] Range Specialist, US Department of Agriculture Natural Resource Conservation Service, Templeton, CA 93465, USA
[d] Principal Scientist, Althouse and Meade, Inc., Paso Robles, CA 93446, USA
[e] Senior Environmental Scientist, Althouse and Meade, Inc. Paso Robles, CA 93446, USA
[f] Professor of Rangeland Ecology and Management, Department of Animal Science, California Polytechnic State University, San Luis Obispo, CA 93407, USA
[g] Area Livestock and Natural Resource Advisor, University of California, Agriculture and Natural Resources, Hollister, CA 95023, USA
[h] Area Livestock and Natural Resource Advisor, University of California, Agriculture and Natural Resources, Red Bluff, CA 96080, USA
[i] Agronomist, US Department of Agriculture Agricultural Research Services Forage and Range Research Laboratory, Logan, UT 83422, USA
[j] Research Geneticist, USDA ARS Forage and Range Research Laboratory, Logan, UT 83422, USA
[k] Professor of Soil Science and Biogeochemistry, Department of Land, Air and Water Resources, UC Davis, Davis, CA 95616, USA

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ABSTRACT

Livestock obtain forage by grazing on rangeland. In California annual rangelands, residual dry matter is commonly used to determine proper grazing levels. Rangeland forage biomass and quality can degrade dramatically during the dormant summer period. We examined 25 sites across an annual rainfall gradient (183–492 mm) over 3 contrasting rainfall yr (2015–2017) that varied from 57% to 152% of average annual precipitation. Overall fractional biomass loss was 54.4% (range = 46.5–61.5%) with greater fractional losses occurring in dry years. Biomass losses were related to the amount of peak standing crop and plant composition—both a function of annual precipitation. Fractional seasonal losses from the peak standing biomass in 2015 = 962 kg/ha (61.5% seasonal; 9.7% monthly), 2016 = 1 541 kg/ha (55.0% seasonal; 8.7%monthly) and 2017 = 1 923 kg/ha (46.5% seasonal; 7.3%, monthly). Forage quality metrics were strongly affected by summer weathering processes. Crude protein concentrations decreased by 33.6%, 27.7%, and 21.0% in 2015, 2016, and 2017, respectively. In contrast, relative concentrations of fiber and lignin (acid detergent fiber [ADF] = cellulose + lignin) and in the weathered biomass showed increases for ADF: 44.6% (2015), 32.2% (2016), and 24.1% (2017). Increased lignin varied: 3.4% in 2015, 23.9% in 2016, and 28.0% in 2017. While ADF and lignin concentrations (weathered biomass, kg/ha) increased during the weathering process, the standing stock decreased by 39.3% (ADF) and 46.6% (lignin), compared with overall weathered biomass loss of 54.4% and CP loss of 67.1%. The significant loss of aboveground biomass and forage quality as weathering processes occurred throughout the dry summer period affects livestock grazing strategies. Forage biomass and nutrient losses through the dry season should be considered when determining grazing strategies to achieve proper residual dry matter levels and nutrient supplementation regimes before the onset of the rainy season.

Introduction

There are an estimated 23 million ha of grazed rangelands in California (FRAP 2018). Beef cattle and sheep commonly graze these annual rangelands, helping support approximately 665 000 head of beef cattle and 570 000 sheep, making these rangelands an important economic resource (USDA-NASS 2019). In addition, rangelands serve an important role as watersheds with grazing

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* Corresponding author.
E-mail address: relarsen@ucanr.edu (R.E. Larsen).

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practices affecting wildlife habitat and water quality and quantity (runoff/infiltration and erosion) (Parker et al. 2009; USDA 2021). California's Mediterranean climate, with cool-moist winters and hot-dry summers, leads to four distinct phases of annual forage growth: break of season (germination—usually October or November), slow growth phase (December–February), rapid growth phase (March–April), and peak standing biomass (April–May) (George et al. 2001). Following peak standing biomass, the annual vegetation dies and remains dry through the summer. This forage, both grasses and forbs (broadleaf herbaceous plants), is important to the livestock industry and is the primary feed available for livestock through the summer dry period (George et al. 2001). Proper management of these rangelands is important to maintain a summer food source, sustain forage productivity, improve infiltration, and diminish soil erosion at the onset of the rainy season.

After the dry summer months, the forage that remains at the onset of the new growing season is defined as residual dry matter (RDM) (Bartolome et al. 2006). This represents the aboveground herbaceous biomass, both grasses and forbs, after it undergoes the combined effects of the previous season's production, breakdown through the summer, and any consumption by all animal types (Bartolome et al. 2006). RDM is commonly used in California annual rangelands to determine proper livestock grazing levels (George et al. 1996). Plant species composition is influenced by RDM, wherein higher RDM favors an increase in grass versus forb biomass the following spring (Bartolome et al. 2007). Further, under some conditions, total aboveground production is influenced by the previous year's RDM, although environmental factors (i.e., site conditions and weather) can overwhelm the effects of RDM on both plant species composition and total production (Bartolome et al. 2007). Even with some uncertainty on how RDM influences forage production and species composition, it is useful to determine proper grazing use on rangelands. Guidelines recommend maintaining RDM values ranging from 335 to 2 350 kg/ha depending on site-specific characteristics, such as soil type, slope, rainfall zone, and vegetation type (Bartolome et al. 2006). Because peak standing biomass levels at the end of the growing season may be substantially reduced by degradation throughout the summer dry period, grazing intensity in the spring and summer needs to be considered when trying to meet fall RDM guidelines. Thus, it is important to establish reliable forage biomass loss rates occurring over the summer dry period. Previous studies in northern California determined a linear forage biomass loss rate of ~7% per month throughout the summer dry period (Frost et al. 2005, 2008).

Along with overall forage biomass loss through the summer season, there is also a loss of nutritional quality as the annual forage completes its life cycle, senesces, and weathers (i.e., physical and chemical degradation). Nutritional quality is highest during the early vegetative state and then declines in protein and digestibility as plants mature and senesce (George and Rice 2016). As plants mature and dry, the nutritionally rich seeds are dispersed, resulting in the forage no longer meeting the nutritional levels required by livestock (George and Rice 2016). Thus, to maintain proper herd health during the summer period, livestock may require nutritional supplements to meet their dietary requirements. The amount of supplements needed depends on the loss of forage nutritional quality over the dry summer period. Mature beef cows (544 kg live weight; moderate milk production potential) need 6% (post weaning) to 11% (early lactation) of crude protein (CP) in their food to maintain body condition and health (National Research Council 2000). CP content in annual grasses on California rangelands can be as high as 15% in their early vegetative growth stage but may drop as low as 3% once they have dried and weathered (Gordon and Sampson 1939; George and Rice 2016). The CP for forbs is generally higher, with filaree (*Erodium* sp.) and bur clover *(Medicago polymorpha)* having 25–27% during their early vegetative stage compared with 5–7% once they have dried and weathered (Gordon and Sampson 1939; George and Rice 2016).

In the Mediterranean climate of California, aboveground biomass degrades and fragments following senescence, which leads to the loss of available forage and soil cover. Studies in semiarid ecosystems indicate that photodegradation is a dominant control of plant litter degradation (photochemical mineralization of organic matter), which is largely controlled by the lignin fraction of the dry forage (Austin and Vivanco 2006; Austin and Ballaré 2010; King et al. 2012; Austin et al. 2016). Microbial degradation is deemed negligible due to the lack of precipitation and low humidity during the summer months. Other factors that may contribute to loss include wind abrasion and herbivory by insects and small rodents. Photodegradation preferentially degrades lignin because it effectively absorbs radiation over a wide range of wavelengths, especially the UV wavelengths (Brandt et al. 2007; Austin and Ballaré 2010). A previous study in California grasslands showed that forage biomass lost 8–10% of its initial mass with a corresponding > 50% reduction in lignin content (Henry et al. 2008). Lignin further acts like a glue that binds other cell wall components (e.g., cellulose, hemicellulose, pectin), conferring mechanical strength to plants. The loss of lignin would therefore be expected to decrease dry forage integrity, leading to increased fragmentation by wind and fauna disturbance.

This paper examines biomass and nutritional losses of aboveground biomass production through the dry season, May through October, on the Central Coast of California. This study represents a rigorous examination of biomass and nutritional losses across a large rainfall gradient and spanning 3 contrasting rainfall yr. Results of this study fill an important knowledge gap concerning forage losses in the absence of large herbivore grazing throughout the dry season.

Methods

This study was conducted between 2015 and 2017 on California Central Coast annual rangelands. Twenty-five sites were selected, representing different annual rainfall regions between 150 and 1 000 mm (Fig. 1). Rainfall was collected at each site using a 15-cm tipping bucket rain gauge (Texas Instruments) fitted with a Hobo Pendant data logger. At each site, four plots were established using 1.27-m welded wire cattle panels arranged in 3-m diameter exclosures to exclude grazing animals. Three 0.09-m^2 quadrats (subsamples) were clipped inside each plot and averaged to provide one value. There were 25 sites for 3 yr with 4 plots per site ($n = 300$). Each exclosure was relocated each fall before the onset of the rainy season by selecting a random direction and distance, though all exclosures were kept on the same soil type, slope, and aspect.

Aboveground biomass (forage) was collected each spring at peak standing crop and then again in the fall (October−November) before the onset of the rainy season. Peak standing crop was defined as the point where forage reached its maximum growth with seed heads developing, but it was still green with no seed shatter. Weathered biomass referred to the aboveground vegetative biomass at the end of the dry summer period, before any rainfall and without any large animal herbivory. Air-dried samples were placed in a drying oven at 65^0C for a minimum of 24 h before recording the biomass weight. For this study weathered biomass was distinguished from RDM, where RDM refers to the amount of biomass remaining following both weathering and grazing. The forage quickly senesced following peak production and remained dry throughout the summer period (May−October). Sampling dates of weathered biomass varied slightly among years and sites with an average of 190 d of field weathering time. The value for weathered biomass was then standardized by dividing the difference between peak biomass and weathered biomass by the actual num-

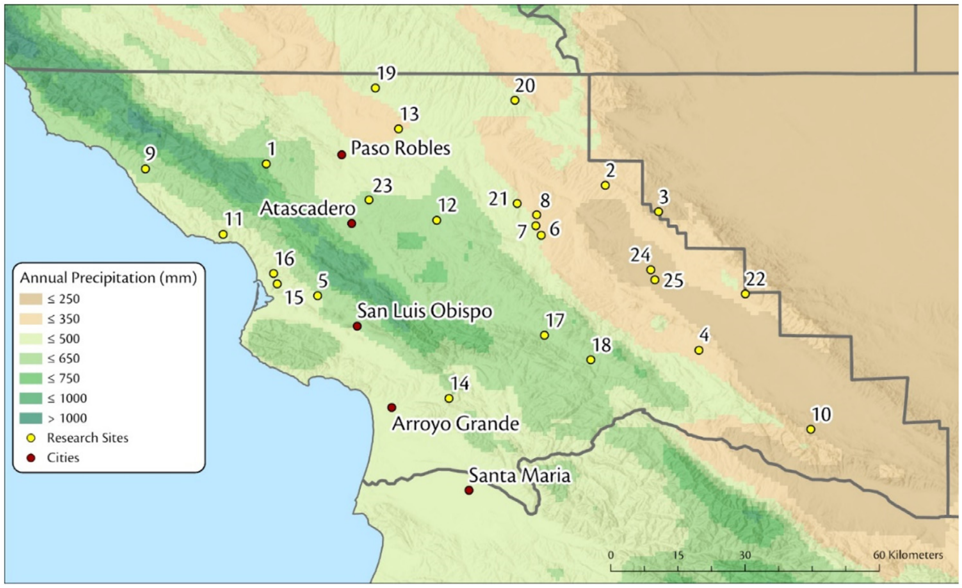

Fig. 1. Distribution of 25 sites used in this study. Precipitation data are the 30-yr average from the PRISM Climate Group. (Credit UC IGIS.)

ber of weathering days for each sample to obtain a daily-loss rate. The daily-loss rate was then used to standardize the weathered biomass values for all samples to 190 d. The dry weight rank method was used to determine species composition (Ratliff and Frost 1990). Forage functional groups, grass and forbs, were determined from the species composition.

Forage samples from 13 of the 25 sites (representative of the climate gradient) were selected for nutritional analysis by A&L Lab (Modesto, CA). CP, ADF, total digestible nutrients (TDN), and net energy lactation (NEL) were determined. CP was calculated from the nitrogen content ($CP = 6.25 \cdot N$). ADF is the percentage of the plant material that is difficult for livestock to digest and consists of cellulose, lignin, and silica. TDN was calculated as $TDN = 102.327-(1.113 \cdot ADF)$ and represents the sum of digestible crude fiber, CP, and fat. NEL was determined as $NEL = 1.085-(0.0124 \cdot ADF)$ and is a measure of feed energy available for maintenance and milk production after digestive and metabolic losses. Samples from the remaining 12 sites (representative of the climate gradient) were analyzed for lignin content using near infrared reflectance spectroscopy (Foss XDS Rapid Content Analyzer, Eden Prairie, MN) at the US Department of Agriculture–Agricultural Research Services Forage and Range Research Laboratory in Logan, Utah. The “grass hay calibration” 18GH50.eqa was used to calculate lignin content (release April 2018; NIRS Forage and Feed Testing Consortium, Hillsboro, WI).

Data Analysis

Data were tested for normality and found to be abnormal using PROC UNIVARIATE (SAS 1999). All data were subject to a $\log_{10}$ transformation before analysis and back transformed for the tables and figures. All transformed data were subject to PROC GLM (SAS 1999) using a RANDOM statement with replications (plots) and sites treated as random effects. Years and harvests were treated as fixed effects. All main effects and interactions were tested with first-order interactions and replications as the error terms. Means separation of the transformed data was done using Duncan multiple range test at $P < 0.05$ level of significance. Forage decline from peak to weathered was modeled with the linear regression function of SigmaPlot (version 14) using $\log_{10}$-transformed (Systat, San Jose, CA). Pearson’s correlation analysis was further applied to assess possible relationships among variables using SigmaPlot.

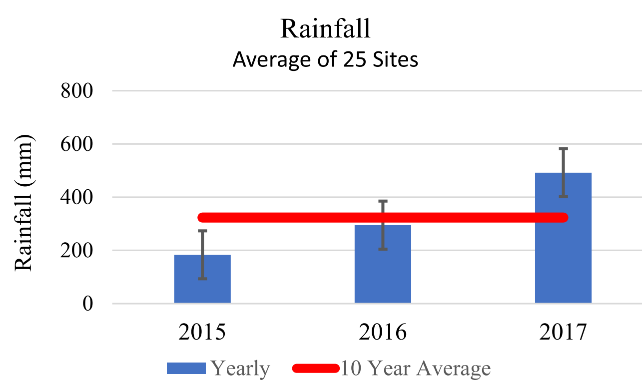

Fig. 2. Annual rainfall (mean ± 95% C.L.) for the 25 sites during the study period. The red line represents a 10-yr average for all 25 sites.

Results

Biomass Loss

This study was conducted over 3 strongly contrasting rainfall yr with the percent of average precipitation being 2015 = 57%, 2016 = 91%, and 2017 = 152% (Fig. 2). Correspondingly, average peak aboveground biomass was significantly ($P < 0.001$, Table 1) different each year (2015 = 1 562, 2016 = 2 804, and 2017 = 4 140 kg/ha) and was closely associated with annual rainfall amount (see Fig. 2). There were significant differences ($P < 0.001$, Table 2) in the dominant forage functional groups (i.e., grass vs. forbs) among years, with grasses being more prevalent in 2016 and 2017 (wetter yr) and forbs dominating during 2015 (drier yr). The dominant species within each forage functional group also changed among years (see Table 2). For grasses, rye grass *(Festuca perennis)* was dominant, but red brome *(Bromus rubens)*, wild oat *(Avena fatua)*, and annual fescue (*Festuca* sp.) were also major components, especially at the drier sites. Filaree (*Erodium* sp.) was the dominant forb, particularly during 2015 and 2016.

Table 1
Peak standing crop and weathered biomass with the accompanying biomass losses, 2015–2017. There were significant differences between peak versus weathered and between years. Means with different letters are significantly different at $P < 0.05$.[1] Small letters refer to differences between peak and weathered, while large letters denote differences between years.

Yr	Biomass		Biomass losses			
	Peak[2] (kg/ha)	WX[3] (kg/ha)	Season (kg/ha)	Daily rate (%)	Monthly rate (%)	Season (%)
Biomass averaged over all 3 yr.			*Biomass loss averaged over all 3 yr.*			
2015–2017	2 642[a]	1 203[b]	1 438	0.29	8.6	54.4
Biomass by yr.			*Biomass loss by yr*			
2015	1 562[aC]	601[bC]	962	0.32	9.7	61.5
2016	2 804[aB]	1 263[bB]	1 541	0.29	8.7	55.0
2017	4 140[aA]	2 217[bA]	1 923	0.24	7.3	46.5

[1] Duncan multiple range test $P < 0.05$.
[2] Peak, peak production, plants mature and green but done growing, seeded out but not shattered.
[3] WX, weathered forage, following senescence in late spring forage remained in the sun until fall with no precipitation events, average 190 d.

Table 2
Dominant grasses and forbs species (percent of total biomass) for 2015–2017. Values for each forage functional group with different letters are significantly different at $P < 0.05$.[1]

Scientific name	Common name	2015 (%)	2016 (%)	2017 (%)
Lolium sp.	Ryegrass	7.7	15.6	28.4
Avena fatua	Wild oats	9.5	9.9	6.8
Bromus hordeaceus	Soft chess brome	1.1	2.8	6.6
Brachypodium distachyon	False brome grass	5.3	2.4	0.5
Festuca (Vulpia) sp.	Annual fescue	1.6	4.0	12.3
Hordeum sp.	Foxtail	2.2	6.2	6.9
Bromus diandrus	Rip gut brome	1.6	1.5	2.0
Bromus rubens	Red brome	5.7	13.3	19.8
Nassella pulchra	Purple needlegrass	1.1	0.7	0.4
	Other grasses	0.7	0.3	0.5
Grass functional group		37[c]	57[b]	84[a]
Erodium sp.	Filaree	49.0	36.5	7.3
Medicago polymorpha	Bur clover	2.4	1.0	1.4
Trifolium sp.	Clover	1.9	0.3	0.4
Calystegia sp.	Owls clover	0.2	1.1	0.6
Acmispon sp.	Spanish clover	3.7	0.4	2.4
Centaurea melitensis	Tocalote	1.1	0.9	0.5
Sonchus arvensis	Sow thistle	1.1	0.0	0.0
	Other forbs	4.1	3.1	3.2
Forb functional group		63[a]	43[b]	16[c]
	Total[2]	100	100	100

[1] Duncan multiple range test.
[2] Species with < 1% presence were not listed.

Over the 3-yr study period, there was a significant ($P < 0.001$) biomass loss when comparing the peak versus weathered biomass with an average loss of 54.4% (see Table 1). There was a significant linear relationship ($R^2 = 0.88$, $P < 0.001$) between peak and weathered biomass for the combined 3-yr dataset (Fig. 3). The range of biomass losses varied by individual sites and years, with a low of 24% (2017) to a high of 74% (2015). When averaging all sites, losses were significantly different each year ($P < 0.001$) with 61.5% (962 kg/ha), 55% (1 541 kg/ha), and 46.5% (1 923 kg/ha) during 2015, 2016, and 2017, respectively (see Table 1). Correlation analysis indicated that the fraction of biomass loss was inversely related to peak biomass ($r = -0.36$; $P < 0.001$) and positively, but weakly, correlated with forb percentage composition ($r = 0.12$; $P < 0.041$).

Nutritional Losses

The CP, ADF, TDN, NEL, and lignin concentrations were all significantly ($P < 0.001$; Table 3) altered during the summer weathering season (see Fig. S1, available online at …, for data). For the overall 3-yr study, mean concentrations decreased for CP (79 → 57 g/kg), TDN (662 → 545 g/kg), and NEL (6.8 → 5.5 g/kg) and increased for ADF (321 → 428 g/kg) and lignin (49 → 57 g/kg) (see Table 3). As TDN and NEL are calculated from ADF concentrations, we focused our further reporting on ADF rather than TDN and NEL.

Table 3
Nutritional changes comparing the mean 2015–2017 values of peak versus weathered concentrations (g/kg) for crude protein (CP), acid detergent fiber (ADF), total digestible nutrients (TDN), net energy of lactation (NEL), and lignin. Means with different letters are significantly different at $P < 0.05$.[1] Standing stocks (kg/ha) for CP, ADF, TDN, NEL, and lignin were determined on the basis of changes in constituent concentrations and biomass over the weathering period.

Season	Concentration values					Standing stock values				
	CP g/kg	ADF g/kg	TDN g/kg	NEL g/kg	Lignin g/kg	CP kg/ha	ADF kg/ha	TDN kg/ha	NEL kg/ha	Lignin kg/ha
Peak	79[a]	321[b]	662[a]	6.8[a]	49[b]	209	1130	1748	18	128
Weathered	57[b]	428[a]	545[b]	5.5[b]	57[a]	69	386	656	7	69

[1] Duncan multiple range test, $P < 0.05$.

The overall average loss in CP concentration was 28% (see Table 3), with larger reductions in CP concentration occurring in drier yr (2015 = 33.6%; 2016 = 27.7%; 2017 = 21.0%; Table 4). The yr 2015 and 2016 (drier yr) had a higher percentage of forbs versus grasses and lower peak biomass. ADF concentration in weathered biomass increased by 33% for the 3-yr study period, with progressively lower percentage increases as peak biomass increased in response to greater precipitation (2015 = 44.6; 2016 = 32.2; 2017 = 24.1%). The increase in ADF concentrations in weathered biomass led to correspondingly lower values for TDN and NEL concentrations (see Table 3). On the basis of these forage quality metrics, overall forage quality was highest in 2015 when compared with 2016 and 2017 (see Table 4); even though 2015 had the lowest production, it had the highest forb composition among years. Similar to ADF, lignin concentrations were higher in weathered versus peak biomass and demonstrated an overall 17% increase in concentration for weathered biomass (see Table 3). In addition to being significantly different each year for both peak and weathered lignin values (see Table 4), the increase in concentrations was distinctly higher in the wetter yr of the study (2015 = 3.4%; 2016 = 23.9%; 2017 = 28%).

Standing stocks (kg/ha) for CP, ADF, and lignin were determined based on the changes in constituent concentrations and biomass over the weathering period (see Fig. S2, available online at …, for data). The standing stock for CP decreased (−67%) owing to both lower CP concentration and decreased weathered biomass (see Table 3). In spite of their higher concentrations in weathered biomass, both ADF (−39%) and lignin (−47%) had lower standing stocks after weathering as a result of lower weathered biomass.

Discussion

Biomass Loss

Rangeland biomass losses occur through a combination of biotic and abiotic processes, such as photodegradation (photolysis and photo-oxidation), leaching, fragmentation, and microbial decomposition (Austin and Ballaré 2010). As no rainfall occurred during the summer weathering period during this study, the roles of leaching and microbial decomposition were deemed negligible. Visual observations of fragmentation and/or herbivory by arthropods (e.g., ants, grasshoppers), rodents, and ground squirrels suggest a minor role. Persistent wind abrasion is likely to play a bigger role in fragmenting biomass, especially as the biomass becomes progressively desiccated and more brittle as the summer proceeds.

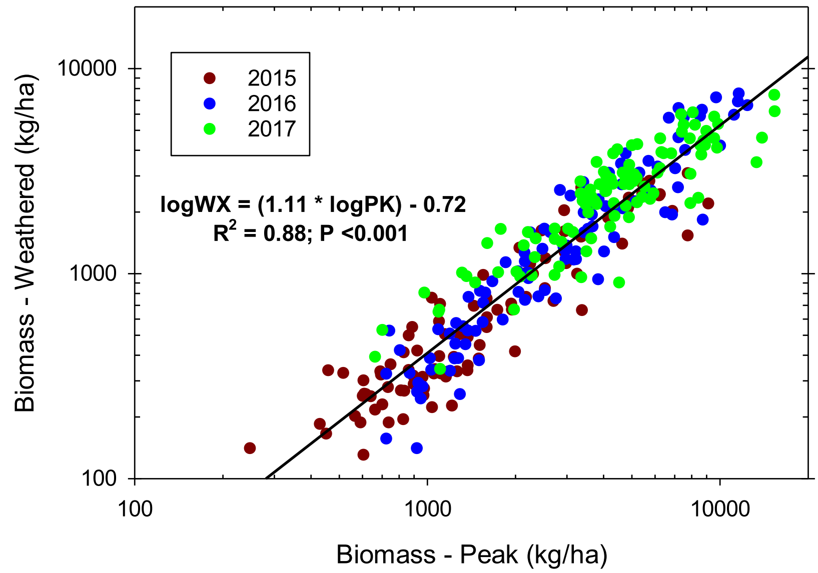

Fig. 3. Standing stocks (kg/ha) in peak versus weathered aboveground biomass for the entire 2015–2017 dataset. Note log-scale transformation necessary to conform data for normality and constant variance assumptions.

Table 4
Peak versus weathered concentrations (g/kg) and standing stocks (kg/ha) (2015–2017) for crude protein (CP), acid detergent fiber (ADF), total digestible nutrients (TDN), net energy of lactation (NEL), and lignin. Means with different letters are significantly different at $P < 0.05$.[1] Small letters refer to differences between peak and weathered, while large letters denote differences between years.

Yr	Nutritional metrics at peak production					Nutritional metrics after weathering				
	CP g/kg	ADF g/kg	TDN g/kg	NEL g/kg	Lignin g/kg	CP g/kg	ADF g/kg	TDN g/kg	NEL g/kg	Lignin g/kg
2015	99^{aA}	285^{aC}	703^{aA}	7.3^{aA}	52^{aC}	66^{bA}	412^{bB}	561^{bA}	5.7^{bA}	53^{bA}
2016	72^{aB}	327^{aB}	656^{aB}	6.8^{aB}	49^{aAB}	52^{bB}	432^{bA}	542^{bB}	5.5^{bA}	61^{aAB}
2017	69^{aB}	353^{aA}	628^{aC}	6.4^{aC}	45^{aA}	54^{bB}	439^{bA}	534^{bB}	5.4^{bB}	58^{bB}

[1] Duncan multiple range test $P < 0.05$.

In our study, the average fractional aboveground biomass loss over the summer weathering period was 54.4% (range 46.5–61.5%), with higher fractional loss occurring in years with lower rainfall and peak biomass and lower grass versus forb composition. This relates to monthly loss rates of 9.7%, 8.7%, and 7.3% for 2015, 2016, and 2017, respectively. These results were in general agreement with previous studies that reported a 7% monthly loss rate (Frost et al. 2005, 2008). Notably, though, this study refined the understanding of loss rates that showed appreciable year-to-year variability, with higher loss percentages in drier years that had lower peak standing crop. Overall, fractional biomass loss (from 3-yr data set) was negatively correlated with peak biomass and positively but weakly correlated with forb percentage, which are both related to annual rainfall. The greater peak biomass during wetter years may hinder photodegradation as greater biomass provides more shading from UV radiation, leading to less photodegradation. Further, greater peak biomass will provide additional physical support among adjacent plants to decrease wind-related fragmentation. The dominance of forbs in drier years may further contribute to greater overall biomass loss. Forbs are more susceptible to losses by photodegradation (higher lignin content) and may be selected by insect/rodent herbivory due to their higher nutritional quality. Further, some forb tissues may be more susceptible to fragmentation due to their more fragile leaf and flowering structures (Lyons et al. 2013). Overall, there is less biomass production and greater summer weathering losses during low rainfall years, leading to lower RDM at the onset of the next rainy season.

An understanding of biomass loss throughout the summer dry period is important for rangeland management decisions, such as determining proper stocking rates and erosion control RDM levels. If the grazing occurs in the springtime, a knowledge of summer biomass loss rates will enable managers to know how much forage is available for grazing, allowing them to meet RDM standards in the fall. Our results show that when you start with low peak biomass (mostly because of drought), the fractional loss rate increases over the summer dry period, which acts to perpetuate the lack of available forage/RDM over the summer/fall seasons. This is a serious concern on California semiarid rangelands, where lower seasonal rainfall amounts are expected to become more pronounced as climate extremes increase in a future with warmer climates (Larsen et al. 2014; Macon et al. 2016). For example, Griffin and Anchukaitis (2014) found that the recent 2012–2014 California drought was among the worst in the past 1 200 yr. Such extreme events are projected to increase in number and intensity in the future (Allen-Diaz 2009). Droughts occurring over several years can lead to RDM levels similar to areas experiencing wildfire loss of RDM (McDougald et al. 2001). Understanding forage loss rates over the summer dry period can assist grazing management to optimize livestock grazing while banking sufficient soil cover to meet RDM guidelines for the onset of the next rainy season.

Nutritional Losses

CP demonstrated losses in both concentration (7.9–5.7% CP) and standing stock amounts (from 209 to 69 kg/ha) (see Table 3). The loss for CP standing stock (−67. 1%) was greater than for the overall biomass loss of −54.4% and tended to be greater during 2015, a drier yr with a higher percentage of forbs versus grasses. Early work by Hart et al. (1932) along a north-south (wet-to-dry) transect of rangeland forage in the Central Valley of California found that CP concentrations were reduced twofold to threefold (20−24% to 7−12% CP) from peak to weathered biomass conditions. Further, they found that CP losses were greater for the drier sites, which is consistent with the driest year of our study having appreciably lower CP concentration. Also, CP in grasses may be lower at the same vegetative stages when comparing wet versus dry conditions, as determined by varying irrigation levels, which resulted in higher CP under drier conditions (Asay et al. 2002; Jensen et al. 2003). Forage quality differences between years in this study are most likely explained by differences in annual rainfall amounts and their effects on species composition (Bartolome et al. 2007). Drier conditions in 2015 led to higher forb (*Erodium* sp.) versus grass (*Avena fatua, Bromus rubens, Festuca [Vulpia]* sp., *Lolium* sp.) composition compared with 2016 and 2017 (see Table 2). While forage biomass was less with low rainfall (see Fig. 1), the resulting forage quality was appreciably higher in the dry yr (2015).

As annual vegetation matures, CP concentrations typically decrease in general but internally increase within the seed component of grasses and forbs. For example, up to 50% of total aboveground N can be redistributed to the seed of oats at maturity (Reeves and Sraon 1976). Thus, following maturity, shattering of seed from plants results in a disproportionately large loss of CP content and standing stocks from the residual vegetation. However, forbs have appreciably higher CP concentrations than grasses (Gordon and Sampson 1939; George and Rice 2016) but may also be more susceptible to fragmentation following senescence, contributing to higher overall CP losses during drier years. Further, the high forage quality of forbs may lead to greater selective insect/rodent herbivory of forbs contributing to a disproportionate decrease in CP concentrations. Overall, the greater percentage losses of CP standing stock (−67.1%) than overall biomass loss (−54.4%) support the role of seed shattering and plant fragmentation/herbivory as important loss mechanisms for CP.

Given the changes in CP content between grasses and forbs, it can be difficult to develop a balanced livestock ration for cattle grazing on mixed forages. Unlike a total mixed ration, it is difficult to quantify the specific plants cattle may selectively graze on rangelands. For example, when Ganskopp and Bohnert (2006) provided grazing treatments that were markedly different in protein content, the cattle balanced protein intake through changes in foraging behavior. Essentially, cattle were able to consume a higher-quality diet through foraging behavior than predicted from composite nutrient testing.

Concentrations of ADF (primarily structural cell wall components of cellulose + lignin) and lignin in the weathered biomass showed relative increases of 24.1−44.6% and 3.4−28% during the 3-yr study, respectively. The greater increases in ADF and lignin concentrations occurred in the wetter yr (2016 and 2017), which had a greater percentage composition of grasses. Thus, higher peak biomass in wetter years would be expected to have higher ADF concentrations and a correspondingly lower TDN and energy (NEL).

While ADF and lignin concentrations increased in weathered biomass, the overall standing stock of these constituents in weathered biomass decreased by 39% (ADF) and 47% (lignin) compared with an overall weathered biomass loss of 54.4% (see Table 3). This indicates that ADF and lignin are being concentrated in the weathered biomass over the summer weathering period; however, the overall standing stock of weathered biomass is also being lost. Several studies document the role of photodegradation as a dominant process regulating plant litter degradation in semiarid ecosystems (Austin and Ballaré 2010; King et al. 2012; Austin et al. 2016). Photodegradation preferentially degrades lignin as its conjugated bonds effectively absorb UV radiation, leading to formation of free radicals that break down the lignin structure. In addition, the free radicals generated from UV-lignin interactions may attack other compounds, such as hemicellulose, in the lignocellulose matrix (Schade et al. 1999). As lignin confers appreciable structural strength through binding together the lignocellulose matrix in cell walls, its breakdown decreases the physical integrity of the residual biomass, leading to enhanced potential for fragmentation by wind and fauna disturbance. Overall, our data indicate that while the ADF and lignin fractions may be lost by photodegradation, they are not being degraded as fast as other chemical components (e.g., CP) in the weathered biomass, which results in an increase in ADF and lignin relative to the total weathered biomass. However, the overall loss of ADF and lignin standing stocks (kg/ha) indicates a loss of weathered biomass along with ADF and lignin that we attribute primarily to fragmentation of the weathered biomass.

Implications for Rangeland/Grazing Management

Rangeland managers and livestock producers in California annual rangeland can optimize use of dry annual forage in terms of quantity and quality, improve next-year's forage production, and meet RDM guidelines for erosion control and nutrient cycling. Understanding changes in biomass and nutritional quality throughout the summer dry period is important for livestock producers to effectively manage stocking densities. Producers need to determine the amount of forage and supplements required to sustain grazing livestock while factoring in environmental and future season production factors (McDougald et al. 2001; Davy et al. 2016). Adequate RDM levels in the fall are important to prevent erosion and soil loss at the onset of the rainy season, especially for areas with high erosion vulnerability (Salls et al. 2018). Adequate RDM levels are also important for maintaining soil nutrient cycling that aids forage production in the following spring growing season (Allen-Diaz and Jackson 2005; Bartolome et al. 2007). As a guideline, our results showed an average aboveground biomass loss of ∼54% over the summer; however, greater losses may occur in years with lower peak biomass production.

Changes in forage nutritional quality observed in this study over the summer weathering period have direct implications to livestock and wildlife management. Since an appreciable amount of CP may be lost to seed shattering following vegetation maturity, rotational grazing before seed shatter could capture this important source of protein. Otherwise, a substantial amount of CP is lost to livestock once seed shatter has occurred. Low protein levels are a limiting factor for herds with parturition after the forage has gone through the weathering process. To match calving to changes in seasonal forage quality, lactating cows can receive sufficient nutrition in the spring when peak standing forage is available. Forage quality during the following summer weathering period is not adequate to support lactating cows but may still support nonlactating mature cows. A cost-effective approach to address protein deficiency would be to provide an adequate amount of forage biomass with appropriate protein supplements instead of energy supplements. Supplementing protein when feeding low-quality forages (similar in value to the summer weathered forage values in this study) has been shown to increase cattle dry matter intake, resulting in less cattle weight loss over those supplemented with energy (Sanson et al. 1990). Our results also raise concerns for more pronounced future climate extremes with severe droughts that decrease peak production and increase loss of summer quantity and nutritional quality of residual biomass. Seasonal reduction of forage quality in California annual rangelands likely occurs in many semiarid rangelands, especially those with Mediterranean climates.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2021.02.010.

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