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ARTICLE

Sampling a pika's pantry: Temporal shifts in nutritional quality and winter preservation of American pika food caches

Johanna Varner[1] | **Zoe J. Carnes-Douglas**[1] | **Emily Monk**[2] | **Lauren M. Benedict**[2,3] | **Ashley Whipple**[2,4] | **M. Denise Dearing**[5] | **Sabuj Bhattacharyya**[6] | **Loren Griswold**[5] | **Chris Ray**[2,4]

[1]Department of Biological Sciences, Colorado Mesa University, Grand Junction, Colorado, USA

[2]Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, Colorado, USA

[3]Department of Biology, University of Nevada Reno, Reno, Nevada, USA

[4]Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, Colorado, USA

[5]School of Biological Sciences, University of Utah, Salt Lake City, Utah, USA

[6]Institute for Stem Cell Science and Regenerative Medicine, Bangalore, India

Correspondence
Johanna Varner
Email: jvarner@coloradomesa.edu

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Abstract

Climate change is increasing temperature, decreasing precipitation, and increasing atmospheric CO_2 concentrations in many ecosystems. As atmospheric carbon rises, plants may increase carbon-based defenses, such as phenolics, thereby potentially affecting food quality, foraging habits, and habitat suitability for mammalian herbivores. In alpine habitats, the American pika (*Ochotona princeps*) is a model species for studying effects of changing plant chemistry on mammals. To survive between growing seasons, pikas cache "haypiles" of plants rich in phenolics. Although they are toxic to pikas, phenolic compounds facilitate retention of plant biomass and nutrition during storage, and they degrade over time. Alpine avens (*Geum rossii*, Rosales: Rosaceae) is a high-phenolic plant species that comprises up to 75% of pika haypiles in Colorado. Here, we tested the hypothesis that contemporary climate change has affected the nutritional value of alpine avens to pikas in the last 30 years. Specifically, we compared phenolic activity, nutritional quality, and overwinter preservation of plants collected at Niwot Ridge, Colorado (USA), in 1992 to those collected between 2010 and 2018, spanning nearly three decades of climate change. Phenolic activity increased in alpine avens since 1992, while fiber and nitrogen content decreased. Importantly, overwinter preservation of plant biomass also increased, particularly on windblown slopes without long-lasting snow cover. Previous studies indicate that pikas at this site still depend on alpine avens for their winter food caches. Higher phenolic content in alpine avens could therefore enhance the preservation of haypiles over winter; however, if pikas must further delay consuming these plants to avoid toxicity or invest extra energy in detoxification, then the nutritional gains from enhanced preservation may not be beneficial. This study provides important insights into how climate-driven changes in plant chemistry will affect mammalian herbivores in the future.

KEYWORDS
alpine avens, climate change, *Geum*, nutritional ecology, *Ochotona*, phenolics, pika

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INTRODUCTION

Anthropogenic climate change is affecting patterns of biodiversity and habitats globally, and alpine ecosystems are thought to be among the most vulnerable to these changes due to their specialized adaptations to low temperatures, short growing seasons, and low-nutrient soils (e.g., Guisan et al., 2019; Hock et al., 2019). Increasing temperature, decreasing precipitation, and shifting seasonality have already affected plant communities in alpine ecosystems through compositional changes, distributional and range shifts, and invasions of nonnative and/or lower elevation plant species (e.g., Verrall & Pickering, 2020; Winkler et al., 2019). These changes are also likely to affect plant phenology (Inouye, 2020) and physiology (Pugnaire et al., 2020). Furthermore, if changes in climate affect plant nutrient content and/or defensive chemistry, then they could have important implications for plant–herbivore interactions (Pellissier & Rasmann, 2018; Stiling & Cornelissen, 2007; Zvereva & Kozlov, 2006).

Although many studies focus on how temperature (Fazlioglu & Wan, 2021), precipitation (Jackson & Colmer, 2005), drought (Seleiman et al., 2021), or snowpack (Rixen et al., 2022) affect alpine plant communities, another important change affecting plant physiology and defensive chemistry is the increase in atmospheric CO_2. Specifically, when atmospheric CO_2 concentrations are higher and temperatures are warmer, photosynthesis becomes more efficient, allowing plants to generate surplus carbon compounds (Drake et al., 1997). These extra carbon compounds are often invested in differentiation (including the production of fiber or secondary defensive compounds), particularly if growth is limited by nutrients or other environmental factors (Holopainen et al., 2018). Because nutrients are typically more limiting than light in alpine ecosystems, alpine plants are likely to rely on carbon-based defenses over nitrogen-based defenses (Bryant et al., 1983). In particular, phenolic compounds are typically the most common class of plant secondary compounds in alpine specialists, possibly because these compounds also play a protective role against stressful abiotic conditions at high elevations (e.g., freezing temperatures and/or high UV exposure; Defossez et al., 2021).

Several studies have highlighted changes in the concentration of phenolic compounds in alpine plants over time (e.g., Albert et al., 2009; Alonso-Amelot et al., 2007; Nybakken et al., 2008); however, few studies have investigated how this shifting plant chemistry might affect plant–herbivore interactions in alpine ecosystems. In addition to becoming increasingly toxic, many alpine plants are also likely to decrease in nitrogen content, either through "dilution" by increased carbon biomass (Zvereva & Kozlov, 2006) or through reduction in the concentration of nitrogen-rich photosynthesis machinery (Owensby et al., 1996). Mammalian herbivores are typically nitrogen limited (Karasov & del Rio, 2007; Robbins, 1992), so a reduction in nitrogen content could result in a significant decline in nutritional quality for these animals (Turunen et al., 2009). Furthermore, plants may also invest excess carbon in fiber (Rothman et al., 2015), thereby further reducing their nutritional value for herbivores. Together, such potential shifts in nitrogen, fiber, and toxicity could cause important changes in food quality, foraging habits, and ultimately habitat suitability for herbivores, particularly those in the alpine zone (Moore et al., 2015). Indeed, historical expansions of C4 grasses that replaced C3 plants in the Miocene have been implicated in range retractions and extinctions of small mammals, likely due to the nutritional differences between these two types of plants (Ge et al., 2012).

Here, we investigate changes in the defensive chemistry and nutrient content of an important food resource for American pikas (*Ochotona princeps*), hereafter "pikas." Pikas are small mammalian herbivores in the Lagomorph order that are distributed across western North America, primarily in alpine talus habitats (Smith & Weston, 1990). Pikas represent a unique system for evaluating the effects of climate change on food quality because their annual diet is partitioned between forage that is consumed immediately after harvest (the "summer diet") and forage that is stored for winter consumption (the "winter diet"; Dearing, 1996a). Unlike many alpine mammals, pikas do not hibernate during winter (Smith & Weston, 1990). Instead, they spend the short alpine summer amassing a large food cache called a haypile, which they then consume over winter (Dearing, 1996a, 1997b). Importantly, summer and winter diets differ in the plant species selected for consumption (Dearing, 1996a, 1997a, 1997b; Smith & Erb, 2013). The summer diet of pikas typically consists of graminoids and forbs that are nitrogen rich and nontoxic (Dearing, 1996a). In contrast, their winter diet is typically rich in plants known to contain high levels of secondary compounds, particularly phenolics (Dearing, 1996a, 1997b). Although phenolics are toxic to pikas (Dearing, 1996b), pikas manipulate these plant toxins by caching the most toxic species, which have antimicrobial properties that help preserve biomass through the winter (Dearing, 1997a). In addition, phenolic toxins break down during storage, making the plants more palatable when consumed later in the winter (Dearing, 1997a).

Although the response of pikas to climate change is idiosyncratic and regionally variable (Smith et al., 2019), this species is widely considered a climate sentinel species (Wilkening & Ray, 2015). Specifically, pikas have experienced population declines (Beever et al., 2013), upslope range retractions (Billman et al., 2021), and local extinctions in parts of their geographic range (Beever et al., 2016; Stewart et al., 2017). While these changes appear to be the most pronounced at lower elevations and/or in more-isolated mountain ranges (Beever et al., 2016), evidence of demographic decline is also evident in parts of the species' core range (Billman et al., 2021; Stewart et al., 2017). Although pika declines have been associated with microhabitat features and changing vegetation communities, particularly reduced forb cover (Wilkening et al., 2011, 2019), no studies have examined the effects of climate change on the nutritional quality of these plants, which could provide a key mechanistic link between changes in vegetation and changes in pika distribution, density, behavior, or physiology.

Alpine avens (*Geum rossii*, Rosales: Rosacea) is an alpine forb that is high in phenolics and comprises 50%–75% of pika winter diet in Colorado (Bhattacharyya & Ray, 2015; Dearing, 1996a). Beyond pikas, alpine avens is also an important component of the summer diet of other alpine herbivores, including mountain goats (Hibbs, 1967), elk (Baker & Hobbs, 1982), and ptarmigan (May & Braun, 1972). Here, we investigated changes in the chemistry of this plant and its overwinter preservation as they pertain to changes in food quality for pikas and other herbivores over the last three decades. Importantly, alpine avens has decreased in its relative abundance in the last 30 years but remains a preferred winter food source for pikas at this site (Bhattacharyya & Ray, 2015). We collected samples of this species from the West Knoll of Niwot Ridge, Colorado, between 2010 and 2018 to compare the phenolic activity, fiber, and nitrogen contents of these "recent" samples to "historical" samples collected in the same location in the early 1990s (Dearing, 1996a, 1997a). We also repeated an experiment by Dearing (1997a) to investigate whether changes in plant chemistry may have resulted in enhanced overwinter preservation of this plant in pika haypiles, and we extended this experiment to investigate how microhabitat (aspect and slope angle) affects preservation. We hypothesized that changes in climate have affected the nutritional value of this plant species. Specifically, in accordance with previous studies (e.g., Couture et al., 2014; Rice et al., 2021; Rothman et al., 2015), we expected to see an increase in phenolic activity, a decrease in nitrogen content, and an increase in fiber content. Understanding changes in the chemistry and nutritional profile of this species is an important step towards a more mechanistic understanding of how climate change may affect the mammalian herbivores in this changing ecosystem.

METHODS

Study sites and plant sampling

This study was conducted at the Niwot Ridge Long-Term Ecological Research site (40°03′ N, 105°35′ W, elevation 3520 m), located in the Front Range and specifically in the Roosevelt National Forest, Boulder County, Colorado. We worked on the West Knoll, the site of Dearing's previous studies on pikas and alpine avens (Dearing, 1996a, 1996b, 1997a, 1997b). At this site, the west-facing slopes are generally wind-blown and support dry-meadow and fellfield vegetation. In contrast, snow accumulates on the east-facing slopes, where scattered snow beds remain until midsummer (Suding et al., 2015).

Recent samples

In late July or early August of 2010, 2013, 2014, 2017, and 2018, we collected 1–2 leaves (0.3–0.5 g) from each of 10–15 individual alpine avens plants located in foraging areas in active pika territories on the West Knoll. Sampled plants were at least 50 m apart, and we targeted leaves that were green and fully intact. Leaves were cut just above the ground and kept on ice in the field, then transferred to a −80°C freezer until analysis. A subset of leaves was weighed fresh and then dried to measure subset water content, as described in detail below. In 2018, we also collected leaves of alpine avens from five additional locations, including one additional site in the Front Range and four other mountain ranges in the southern Rocky Mountains (San Juan, Cimarron, La Sal, and West Elk). In each of these five mountain ranges, we collected samples from at least three sampling locations (separated from one another by >500 m), and at each sampling location, we collected 1–2 leaves from each of at least three individual plants. We did not have historical samples from any of these five extra locations, but this sampling allowed us to investigate spatial variation in plant chemistry within a year.

Historical samples

We also analyzed "historical samples" of alpine avens that were collected by Dearing on the West Knoll of Niwot Ridge in 1992. These samples (frozen alpine avens leaves) had been stored at −80°C until 2014, when they were tested as described below. We analyzed these frozen leaves collected in 1992 as an assay control and compared our results to the values reported by Dearing (1996a, 1997a, 1997b).

Plant chemistry and nutrition assays

Total phenolic activity of alpine avens was measured using the Folin–Ciocalteu method (Waterman & Mole, 1994) for both recent and historical alpine avens samples. Although this method is less accurate in measuring absolute phenol content compared with more sophisticated analytical approaches (e.g., LC–MS), it provides a consistent estimate of biological activity in ecological studies where activity depends on phenolic oxidation, such as in plant–herbivore interactions (Appel et al., 2001; Moreira et al., 2020). Furthermore, we wanted to directly compare our results with those of previous studies that used the same assay (Dearing 1996a, 1997a, 1997b). Phenolic content of ~0.2 g of frozen plant material was extracted into a solution of 95% methanol by grinding with a Polytron PT3100 Mixer (Kinematica, Lucerne, Switzerland) at 12,000 rpm for 30 s. After 48 h in the dark at room temperature, samples were centrifuged for 5 min at 3300 rpm, and the supernatant was used in the Folin–Ciocalteu reaction, following the protocol of Ainsworth and Gillespie (2007). As in Dearing's previous studies, tannic acid was used as the standard for the standard curve. We used a subsample of each plant sample to calculate water content by weighing fresh samples in the field (fresh mass [FM]) and reweighing after drying for 24 h at 40°C (dry mass [DM]). All phenolic activity values were converted to phenolic activity per gram DM. Total phenolic activity is expressed as milligrams of tannic acid equivalent (TAE) per gram DM of plant material.

Total fiber content (neutral detergent fiber, NDF) and cellulose/lignin content (acid detergent fiber, ADF) of recent and historical alpine avens samples were measured in a fiber analyzer according to the manufacturer's instructions (ANKOM 200 Fiber Analyzer; ANKOM Technology, Macedon, NY). Fiber analyses required 0.5 g of dried plant material. Nitrogen content was measured by combusting 5 mg of dried, ground plant material in an elemental combustion system (Costech Analytical Technologies, Valencia, CA) coupled to a Delta Plus Advantage mass spectrometer (Thermo Finnigan, San Jose, CA) operating in the continuous-flow mode. Nitrogen analyses were conducted for both historical samples and for recent samples collected in 2013 and 2017; however, additional replicates of avens collected in 2017 failed in the instrument, leaving only one measurement of nitrogen content for that year.

Overwinter preservation experiment

We also tested whether changes in plant chemistry or microhabitat characteristics (e.g., duration of snowpack or insolation) would affect overwinter preservation of pika haypiles (i.e., the amount of biomass remaining in early summer after snowmelt). To do so, we repeated an experiment originally conducted in 1992–1993 by Dearing (1997b), in which samples of a high-phenolic plant species (alpine avens) and a low-phenolic plant species were exposed to winter haypile conditions. Specifically, we collected alpine avens and mixed graminoid samples (*Carex* spp. and *Deschampsia* spp.) in August 2017 from West Knoll. We then created two types of "artificial haypiles," each consisting of 15–25 g FM of either avens or graminoids ($n = 5$ artificial haypiles of each sample type, as in Dearing, 1997b). Each artificial haypile was contained in a bag constructed of fiberglass window-screen mesh, which was then placed in a wire suet-feeder cage, allowing sample exposure to free air while preventing damage to or theft of samples by rodents or pikas. These cages were placed in the talus to mimic the placement of pika haypiles (i.e., each was positioned under a large rock where it was exposed to air but not to direct sunlight). These cages were left in place from August 2017 to July 2018, when their contents were dried at 40°C for 48 h and reweighed. The % biomass remaining was calculated as: (DM remaining, in grams)/(starting FM, grams × dry matter, in percentage). We recognize that many other factors could affect preservation of actual pika haypiles, including the size, structure, and composition of the haypile (Jakopak et al., 2017) or pika activities, such as deposition of feces/urine or reorganization, but by controlling these extraneous factors, this simple experiment provides important insight into the basic preservation ability of the plants that comprise the pika haypile.

We placed these artificial haypiles ($n = 10$ total) at varying aspects around the West Knoll so that potential effects of microhabitat (slope aspect and slope angle, which affect insolation, microclimate, and snowpack duration) on overwinter preservation could also be investigated. Although we did not directly measure microclimate or snowpack duration at each location, we calculated an insolation index to capture the effects of incident sunlight on each artificial haypile. Following Jeffress et al. (2013), we calculated insolation as sin(aspect) × cos(slope angle). Thus, insolation values range from −1 (indicating a steep, south-facing slope with high sun exposure) to 0 (indicating a flat slope) to +1 (indicating a steep, north-facing slope with very little sun exposure).

Although Dearing's original experiment used clover (*Trifolium parryi*) as the low-phenolic plant sample, we chose to include graminoids instead in this experiment because graminoids are now much more common than *T. parryi* in haypiles and in the environment, and they make up a significant part of the pika's summer diet at this site (Bhattacharyya & Ray, 2015). Dearing (1997b) included the low-phenolic plant in her experiment to test (1) whether high-phenolic plant species preserved better than low-phenolic plant species and (2) whether high-phenolic plant species could enhance preservation of low-phenolic plant species in a mixed sample. We did not attempt to determine whether avens affected graminoid preservation in a mixed sample, nor did we compare current graminoid preservation to past clover preservation. Thus, while it is possible that pikas have shifted to using graminoids more than clover because nutritional shifts have made clover a less palatable food source (e.g., through increased phenolics), this substitution should not affect the conclusions of our experiment, which tested for changes in preservation of avens and for how microhabitat affects overwinter preservation of haypiles.

Statistical analyses

Differences in phenolic activity, nitrogen, and fiber content between historical alpine avens samples analyzed in different decades (1992 analyses reported in Dearing [1996a, 1997b] vs. analysis of additional historical samples in 2014) were assessed using a Student's *t* test. Differences in phenolic activity and nitrogen content between historical avens samples and recent avens samples with >2 years of recent sampling were assessed using ANOVA, including a Tukey honestly significant difference post hoc test. Differences in fiber between historical and recent avens samples were tested by *t* test. To assess changes in overwinter preservation, we used a *t* test to compare the percentage of biomass remaining after 1 year between recent (2017–2018) and historical (1992–1993) artificial haypile exposure experiments. All statistical analyses were conducted in R (v 4.0.1; R Core Team, 2020).

RESULTS

Analysis of historical samples

We found no difference in chemistry or nutritional value between alpine avens leaves collected and analyzed in 1992, and additional alpine avens leaves collected and frozen in 1992 and analyzed in 2014. With respect to year of analysis for these historical samples, there was no significant difference in phenolic content ($t = -0.65$, $\text{df} = 11$, $p = 0.52$), nitrogen content ($t = -2.5$, $\text{df} = 3$, $p = 0.09$), total fiber (NDF; $t = -0.32$, $\text{df} = 4$, $p = 0.76$) or cellulose/lignin content (ADF; $t = -0.28$, $\text{df} = 4$, $p = 0.79$). Hereafter, values reported for "historical samples" come from the samples that we analyzed in 2014 ($n = 10$), for which we had larger sample sizes than the original values reported in Dearing (1996a; $n = 3$).

Phenolic analyses

We observed a significant and sustained increase in phenolic activity of alpine avens in recent years (2010–2018), compared with 1992 (Figure 1; ANOVA: $F_{5,38} = 21.6$, $p < 0.001$). Phenolic activity in recent samples was generally about twice as high as in historical samples, except

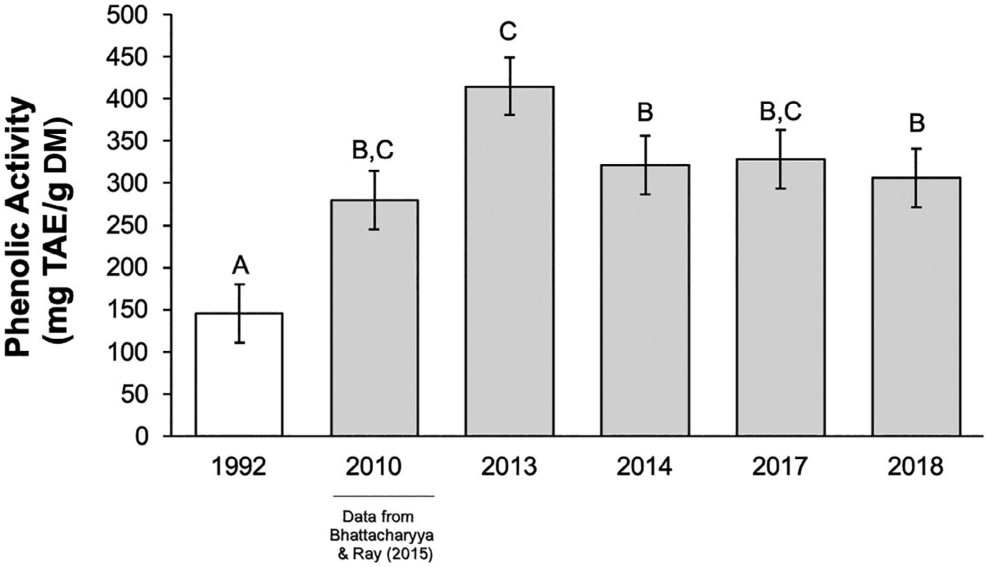

FIGURE 1 Changes in phenolic content (activity) of alpine avens on Niwot Ridge. Phenolic content is reported as milligrams of tannic acid equivalent (TAE) per gram of dry plant tissue (dry mass [DM]). Error bars indicate the 95% confidence interval. Means that do not share the same letter are significantly different by Tukey's honestly significant difference test.

in 2013, when phenolic activity was nearly three times higher. Alpine avens from Niwot Ridge also had higher phenolic activity than avens collected in several other ranges in 2018 (Appendix S1: Figure S1; ANOVA: $F_{4,21} = 7.74$, $p = 0.0005$), but phenolic activity was similar between samples collected at Niwot and those collected within the Front Range at a separate location approximately 50 km away.

Fiber and nitrogen analyses

Compared with historical samples (collected in 1992), avens collected in 2013 had significantly lower total fiber (NDF; $t = 3.04$, df = 8, $p = 0.01$; Figure 2a) and significantly less cellulose/lignin content (ADF; $t = 5.1$, df = 8, $p = 0.03$; Figure 2b). Likewise, avens collected in 2013 and 2017 had 21% lower nitrogen content compared with the historical samples (ANOVA: $F_{2,4} = 10.97$, $p = 0.02$; Figure 2c).

Overwinter preservation experiment

Alpine avens preservation in artificial haypiles significantly increased by 10% in 2017–2018, compared with 1992–1993 (Figure 3; $t = -3.5$, df = 7, $p = 0.01$). There was no difference in preservation between avens and graminoids ($t = -0.6$, df = 8, $p = 0.56$) in the 2017–2018 experiment. Insolation was not a significant predictor of overwinter preservation in haypiles for avens or graminoids ($R^2 = 0.07$, $p = 0.95$), but avens and graminoids in recent samples preserved better on west-facing slopes (>90% remaining) compared with east-facing slopes (<85% remaining; Figure 4). Overwinter exposure of avens in artificial haypiles did not result in nitrogen enhancement, as was observed for historical samples (Dearing, 1997b; Appendix S1: Figure S2).

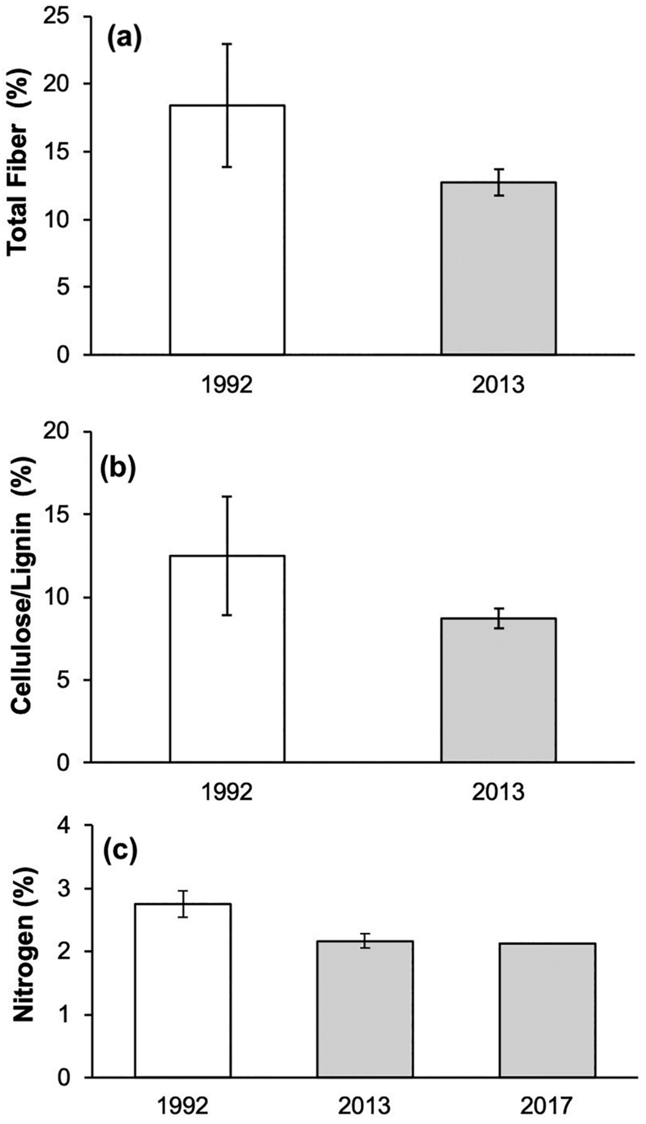

FIGURE 2 Changes in nutrient content of alpine avens collected at Niwot Ridge. Avens samples collected in 1992 and 2013 were tested for (a) total fiber content (neutral detergent fiber; % dry mass [DM]), (b) cellulose/lignin content (acid detergent fiber; % DM), and (c) nitrogen content (% DM). Mean ± 95% confidence interval for each year is shown (in 2017, $n = 1$ measurement for nitrogen due to failure of additional samples in the instrument).

DISCUSSION

Here, we document changes across nearly three decades in the nutritional profile of alpine avens (*G. rossii*), a primary food resource for pikas on Niwot Ridge. Compared with historical samples collected in 1992, we found a 21% decrease in nitrogen content and a 30% decrease in fiber content, but a clear increase in phenolic activity. Phenolic activity more than doubled between historical and recent samples, and this increase was sustained from 2010 through 2018. Furthermore, increased phenolic activity was correlated with significantly higher overwinter preservation of biomass in artificial haypiles, particularly on west-facing slopes. We hypothesized that changes in atmospheric CO_2 concentration, temperature, and/or precipitation have affected the nutritional chemistry of this plant species and its value to pikas, and each of these metrics has certainly changed at our study site. Between 1992 and 2015, monthly mean atmospheric CO_2 levels measured at Niwot Ridge increased from 356 to 397 ppm, and current levels are near 417 ppm (https://gml.noaa.gov/dv/data/index.php?site=NWR). Likewise, the average July temperature at the Niwot Ridge SNOTEL site (40°03′ N, 105°33′ W) has increased by an average of 2.5°C, from 10.2°C in 1992 to 12.7°C averaged across 2013–2018

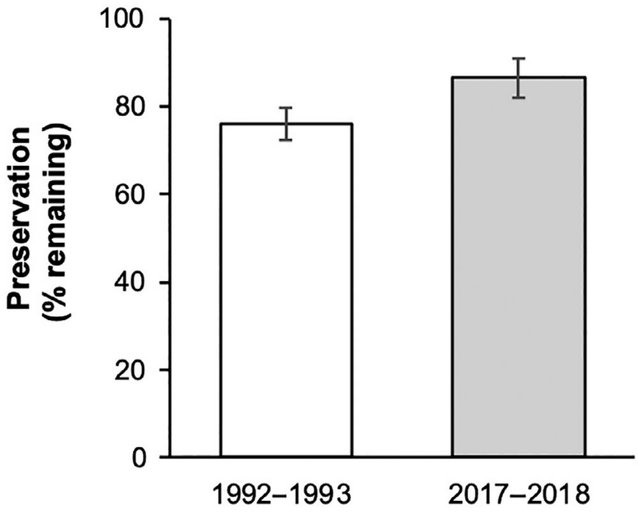

FIGURE 3 Changes in overwinter preservation of alpine avens at Niwot Ridge. Overwinter preservation is measured by percent dry matter remaining in artificial haypiles in spring. Mean ± 95% confidence interval for each year is shown.

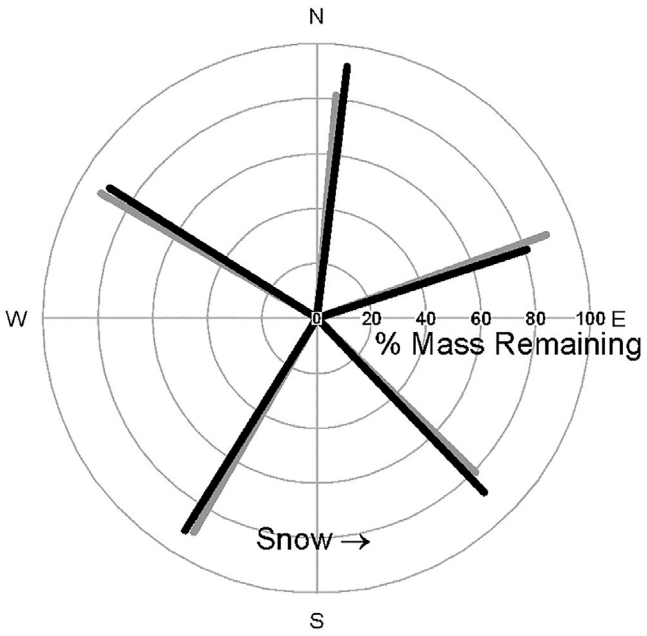

FIGURE 4 Overwinter preservation of avens (black bars) and graminoids (gray bars) as a function of slope aspect around the west knoll of Niwot Ridge, 2017–2018. The wind tends to remove snow from west-facing slopes and deposit it on east-facing slopes at this site.

(https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=663), and annual maximum temperature on Niwot Ridge has risen ~0.5°C/decade over the past 70 years (de Mesquita et al., 2018; McGuire et al., 2012).

Our results are consistent with other studies demonstrating increases in carbon-based plant secondary compounds as a response to these aspects of climate change (Rice et al., 2021). Specifically, experiments in which CO_2 concentrations were artificially elevated have reported similar increases in both phenolics (Couture et al., 2014; Lindroth et al., 1997) and other carbon-based plant secondary compounds (Zhu et al., 2015). Meta-analyses (e.g., Robinson et al., 2012) and reviews (e.g., Holopainen et al., 2018) have also shown that phenolics have increased with increased atmospheric CO_2 in a variety of plant taxa. Conventionally, increased CO_2 is thought to allow surplus photosynthesis, generating extra carbon that can be invested in differentiation (including defense metabolites), especially when growth is limited by soil nutrients or temperature (Holopainen et al., 2018).

However, our results are not consistent with predicted changes in phenolics with increased temperature. Warmer temperature is conventionally thought to *decrease* foliar phenolic contents because higher temperatures stimulate growth, tipping carbon investment towards growth rather than differentiation or defense (Holopainen et al., 2018), a result seen in several experimental warming studies (e.g., Nissinen et al., 2017). However, plant growth at this site and in alpine tundra habitats more broadly, is likely limited by a complex suite of abiotic factors as opposed to temperature alone (Suding et al., 2015). Thus, while warmer temperatures might stimulate plant growth to some degree, we suggest that investing excess carbon in defense compounds rather than growth may still be advantageous to alpine plants as a defense against herbivory or an antioxidant protectant against other abiotic stressors (Defossez et al., 2021; Moreira et al., 2020).

Although we observed a significant and sustained increase in phenolic activity among recent samples compared with historical samples, we also observed significant interannual variation in phenolic activity in recent years, which we believe might be linked to precipitation. Phenolic activity in our study was by far the highest in 2013, an abnormally dry year in which approximately 25% of the state of Colorado was in D4 Exceptional Drought conditions (http://drought.gov). Specifically, total year-to-date precipitation by August 1, 2013 was approximately 50 mm lower than in other recent years (632 mm in 2013 vs. 688 mm average between 2014 and 2018). Because the water content of alpine avens sampled in 2013 (37%) was well within the range of values of water content in other years (31%–48%), the increased phenolic activity from that year was likely not an artifact of the plants being drier, wherein more plant material would be represented per gram FM in the assay. Rather, a large body of literature indicates that dry conditions increase leaf phenolic content across a variety of plant taxa (Alonso-Amelot et al., 2007; Bautista et al., 2015; Sarker & Oba, 2018), perhaps as a protection against physiological stress caused by drought. Importantly, environmental conditions (i.e., temperature, soil nutrients, water availability, and/or sunlight) have a bigger effect on foliar phenolic content than genetics (Steen et al., 2021), suggesting that phenolic content is regulated via phenotypic plasticity and can be adjusted by plants, given the abiotic stressors of a given year. This finding is also consistent with our observations of higher interannual variation in phenolic activity (Figure 1), compared with spatial/geographic variation in phenolic activity within a year (Appendix S1: Figure S1). Since phenolics are toxic to pikas (Dearing, 1996b) and many other herbivores (Karasov & del Rio, 2007), this interannual variability in phenolic activity may require herbivores to adjust the relative amount of high-phenolic plants included in summer vs. winter diets each year. In particular, higher phenolic activity in the diet of mammalian herbivores during years of low precipitation could compound other stress associated with drought, particularly because water is critical for detoxification of phenolics and other plant toxins in small mammals (Torregrossa et al., 2011). Stress related to meeting the metabolic demands of detoxification should be considered as a potential mechanism for explaining pika losses that have been correlated with drought metrics, such as vapor pressure deficit and actual evapotranspiration (Billman et al., 2021; Johnston et al., 2019).

This increase in phenolic activity of recent samples is also consistent with the enhancement we observed in artificial haypile preservation (compared with the 1990s, Figure 3). Phenolics have antimicrobial properties, thereby slowing degradation of alpine avens in winter food caches (Dearing, 1997a). However, a variety of other factors may also be responsible for the enhanced overwinter preservation of recent samples, including changing microclimatic conditions and/or microbial processes. Interestingly, we observed a strong east–west gradient in preservation during this experiment, wherein plants on west-facing slopes preserved better than those on east-facing slopes (Figure 4). We hypothesize that this gradient may be due to differences in snowpack and humidity. Specifically, on Niwot Ridge, the typically westerly winds redistribute large amounts of snow from west to east. Thus, the west-facing slopes are typically wind-scoured and bare, whereas east-facing slopes accumulate a deeper snowpack that persists later into the summer. This pattern may have caused the haypiles placed on west-facing slopes to experience colder and drier winter conditions, whereas those placed on east-facing slopes may have experienced relatively warmer and moister conditions. Together, these conditions could have enhanced microbial degradation processes on east-facing slopes, leading to faster biomass decay and reduced preservation over winter.

The decreases that we observed in foliar nitrogen are also consistent with previous studies. Artificially elevated CO_2 concentrations produce similar decreases in foliar nitrogen (9%–18%; Couture et al., 2014; Lindroth et al., 1997). Likewise, nitrogen levels have decreased in many plant genera that serve as hosts for arthropod herbivores (Robinson et al., 2012). Conventionally, decreased nitrogen content under elevated CO_2 is thought to be caused by one of three processes: nitrogen “dilution” (i.e., due to increased carbon biomass; Robinson et al., 2012; Zvereva & Kozlov, 2006), reduction in the concentration of photosynthetic enzymes in leaf tissue (which can comprise up to 25% of total leaf nitrogen), or reduction in chlorophyll content of leaf tissue (e.g., Owensby et al., 1996). Mammalian herbivores are typically nitrogen limited, and a reduction in nitrogen content of this magnitude in an important component of their diet could be detrimental to pikas. However, the increased phenolic activity of alpine avens (and its concomitant enhanced overwinter preservation) may offset these decreases in nitrogen since this plant is not typically consumed until winter (Dearing, 1996a) and nitrogen is not depleted during storage (Appendix S1: Figure S2).

Contrary to our expectations, we also observed a 30% decrease in cellulose/lignin content of alpine avens leaves over the last 20 years. In contrast, most previous studies have shown increases in either fiber content (10%–15%; Rothman et al., 2015) or leaf toughness (a proxy for fiber content; Robinson et al., 2012). The implications of these nutritional changes for pikas and other herbivores are unclear. Importantly, because we observed similar declines in both nitrogen and fiber content, the protein-to-fiber ratio may not have changed significantly in alpine avens. The protein-to-fiber ratio is a strong driver of forage selection for many mammalian herbivores (Owensby et al., 1996; Rothman et al., 2015), so stasis in this ratio would be consistent with the observation that alpine avens has dominated pika food caches at this site for decades (Bhattacharyya & Ray, 2015; Dearing, 1997a). Our observation of higher phenolic activity in recent samples also suggests that alpine avens is investing extra carbon resources in soluble carbohydrates (e.g., defense compounds like phenolics), rather than fiber.

Although the sample size in our exposure experiment was small, if the patterns that we observed in this experiment hold across years and in different ecoregions, then these results could have important implications for pikas during continued climate change. A leading hypothesis to explain pika declines at lower elevations is that warmer summer temperatures lead pikas to restrict their summer foraging activity, thereby amassing small or insufficient overwinter food caches (Mathewson et al., 2015; Smith & Erb, 2013; Wilkening et al., 2011). However, if increased phenolic content of stored plants also results in better preservation, then smaller food caches may still provide pikas with adequate nutrition during winter. Likewise, our results suggest that changes in winter snowpack may also affect preservation of haypiles. In particular, warmer and moister conditions during the winter may accelerate degradation of haypiles, whereas colder and drier conditions may enhance preservation. Although climate models generally forecast reduced winter snowpack across the intermountain west (e.g., Ikeda et al., 2021; Mote et al., 2018), the increased frequency of rain-on-snow events (Musselman et al., 2018) could also affect sub-surface humidity and duration of snowpack, as could changes in wind that affect how snowpack is distributed across the landscape (Breslow & Sailor, 2002). These interacting factors underscore the importance of considering spatial heterogeneity when forecasting how changes in climate will affect species, particularly in topographically complex regions like the Rocky Mountains.

CONCLUSIONS

This study highlights the complex interactions between alpine plant chemistry and herbivory in the context of climate change: increased plant phenolics are likely to have both costs and benefits for mammalian herbivores. For example, pikas could benefit from increased plant preservation, but elevated phenolics could also cause alpine avens to become less digestible, particularly if these chemicals become more toxic at warmer temperatures (Dearing, 2013). Thus, pikas could be forced either to delay consuming cached plants or to expend additional energy on detoxification conjugates when consuming plants at a higher phenolic level (Dearing, 1996b). In this case, the nutritional gains from better preservation during storage might not exceed the energetic costs of detoxification or delayed consumption. Likewise, the decline in foliar nitrogen observed in this study could also be detrimental because alpine mammalian herbivores are generally nitrogen limited and may need to change their foraging strategy to maintain body mass (Stiling & Cornelissen, 2007). Food-caching herbivores, such as pikas, might avoid this trade-off if the increase in phenolic-mediated plant toxicity is countered by better retention of plant material and nutrients in the cache (Dearing, 1997a). However, the numerous herbivores that do not cache food may not have similar avenues for mitigating these changes in plant chemistry and thus may experience differing impacts under future climate change scenarios.

If the patterns that we observed in alpine avens in this study are shared among other alpine forb species, then many other herbivorous species could also be affected by increased toxicity and reduced nitrogen in their food sources. Due to the wide-ranging implications of changes in available nitrogen for any ecosystem, we encourage additional study of potential feedbacks between climate and plant chemistry that might be impacting herbivores in other environments. In particular, we suggest that alpine environments should be prime targets for such studies, given that phenolics are the most common defensive compound in alpine plants and studies of food-caching herbivores are particularly amenable to experimentation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Varner et al., 2022) are available from the Environmental Data Initiative: 10.6073/pasta/91798dccc14852d8d3db5cfca8c3a127.

ORCID

Johanna Varner https://orcid.org/0000-0001-9431-0760

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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