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The influence of the foodscape on quaking aspen stand condition and use by ungulates

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***Abstract*— *In order to study the effects of herbivory on plant communities, we determined whether the types and concentrations of chemicals present in different aspen (Populus tremuloides Michx.) stands and understories, i.e., the foodscape, are associated with aspen use by elk (Cervus elaphus L.) and with aspen regeneration and recruitment. Transects were established in aspen stands with high, medium, and low regeneration levels (N=5 locations/regeneration level; ranging from 2,331 m to 2,724 m in elevation) in Wolf Creek Ranch in northern Utah. Using non-metric multidimensional scaling (NMDS) ordination and regression analyses, we examined the relationships between aspen regeneration, recruitment, elk presence, browsing, and other landscape elements with the foodscape (e.g., biomass and chemical composition of the understory and chemical defenses of juvenile aspen trees). The foodscape was affected by elevation and canopy height but it did not explain aspen use or indicators of aspen resilience. Our findings suggest that foodscapes of lower nutrient content–occurring at lower elevations under drier climatic conditions–are more likely to foster aspen stands with less forb and grass understory, and thus lower nutritional biomass. Nevertheless, the extent of the decline in the availability of nutrients in the understory did not appear to influence aspen browsing or indicators of aspen resilience. Future research should focus on exploring the influence of additional–and more contrasting–gradients of chemical availability in the landscape on aspen use by herbivores.*

***Keywords*— Browsing, Elk, Phenolic glycosides, Plant secondary compounds, Preference.**

I. INTRODUCTION

Landscapes offer herbivores a diversity of types and concentrations of chemicals (i.e., the foodscape) packaged inside an array of forage species distributed across different temporal and spatial scales [1-6]. In turn, foraging decisions by herbivores are influenced by the heterogeneous distribution of chemicals in time and space, relative to the type of animal and its history with the foodscape [7-11]. In addition to the distribution of chemicals, foraging choices are driven by other biotic (e.g., perceived likelihood of predation, human presence, hunting, co-grazing) and physiographic (e.g., elevation, climate, slope) factors, which further influence animal movement and grazing patterns across plant communities [7,12,13].

Aspen (*Populus tremuloides* Michx.) communities represent an ideal study system to explore the influence of the foodscape on foraging decisions by herbivores because they provide a wide variety of plant diversity to consumers [14-16], and because aspen trees show substantial genetically-based variation in phytochemical traits that influence foraging behavior [17]. Despite this diversity and presence of chemical defenses, repeated foliage removal and damage to meristematic tissues from herbivory continue to impact aspen trees to the point of representing a major cause of poor aspen regeneration in some areas of North America [18] and Eurasia [19].

Herbivores are sensitive to changes in the nutritional quality of plants in a community; they modify their dietary breadth as well as the amounts and proportions of ingested plant parts and species in order to meet their nutritional needs [e.g., 20,21]. This is why wild and domestic ungulates typically prefer aspen in the fall, when the average nutritional quality offered by the understory drops below that present in aspen tissues [16,22,23]. Additionally, studies with sheep have revealed that aspen intake is dependent on the types of feed an animal has recently consumed [5], as well as on the animals' nutritional state [5,6]. For instance, ingesting foods containing high concentrations of protein enhances aspen intake, especially if plant defenses in aspen are present in low concentrations [5,6]. On the other hand, because aspen is a good source of starch, energy-restricted sheep consume greater amounts of aspen leaves than control (i.e., non-restricted) animals [6].

Herbivores also respond to plant secondary compounds (PSC) by reducing the amount of PSC-containing plants that they consume [24], a process regulated by the complementarities and antagonisms occurring across different detoxification pathways and the availability of nutrients needed for detoxification processes [24-26]. Aspen chemical defenses (phenolic glycosides and condensed tannins) have been shown to deter ungulate browsing, but when ungulate numbers increase above a certain threshold, the capacity of these defenses to deter browsing to a level that effectively restricts tissue loss to herbivores gets compromised [reviewed by 27]). Consistent with this idea, a recent study conducted at the same location where the present study was carried out reports that a majority of the aspen stands assessed were not recruiting new stems at sufficient levels to replace overstory trees [28]. This response was likely a consequence of elk numbers exceeding the carrying capacity desired by managers for the region [28], which was estimated to be below one animal km-2 [29,30]. Nevertheless, Rogers et al. (2015) [28] did not determine the types and amounts of nutrients provided by the surrounding understory or the chemical composition of aspen trees in that region.

Collectively, it follows that chemicals present in aspen, as well as those offered by the surrounding vegetation, shape herbivores' decisions on how much aspen will be incorporated into their diet. Thus, identifying the concentration of different nutrients and PSC across the landscape, i.e. the geospatial variation in the quality of food or "foodscape," is critical for understanding herbivores' preferences in diverse plant communities like those observed in aspen-dominated landscapes [4,31].

The objective of this study was to characterize the chemical composition of different aspen and accompanying understory communities across a gradient of aspen recruitment in order to determine whether the types and concentrations of nutrients and PSC in the landscape (i.e., the foodscape) are associated with aspen use by elk and with aspen regeneration and recruitment. We hypothesized that nutrients in juvenile aspen and the surrounding vegetation interact with plant secondary compounds to influence aspen use by herbivores. Thus, we predicted that (i) as nutritional biomass in the understory increased (i.e., greater amounts of crude protein), aspen use would decrease and recruitment (number of stems reaching > 2 m in height) and regeneration (number of stems growing to ≤ 2 m in height) would increase because herbivores would prefer an understory with greater amounts and concentrations of nutrients over defended aspen tissue. Additionally, we predicted that (ii) as defense content in aspen stands increased, aspen use would decrease because phytochemicals constrain food intake. If our predictions are true, aspen in areas with high understory biomass would experience less browsing, especially if they contained high concentrations of defense compounds. However, if the surrounding understory contains low understory biomass, then aspen herbivory would be less constrained by such defenses and aspen intake would increase because those animals would be more willing to consume defended foliage in order to meet nutritional requirements. This means that stands with low understory biomass may be more at risk of succumbing to herbivory pressure and would need more intensive management than stands with greater understory biomass.

II. MATERIALS AND METHODS

2.1 Study site

Wolf Creek Ranch (WCR) is located east of Park City, UT, USA (N 40° 30.6365' W 111° 14.673'), and is situated on a 5,382 hectare private parcel of land, with approximately 2,333 hectares (~43% of the property) covered by aspen forests that consist of a stable aspen community-topped plateau that borders public land to the east and private land on all other sides [28,32]. Loamy soils dominate WCR, and surface soils primarily overlay Keetley volcanic tuffs and resemble those soils found in forested areas within this region [28]. Although most of the aspen within WCR are found between 1,950 and 2,443 m of elevation, the property ranges from 1,950 to 2,750 m of elevation. The average precipitation at WCR is 694 mm (measured from 1987 to 2012 using the nearest rain gauge; SNOTEL #330), most of which occurs in the form of snow during the winter season, and with mid-summer being the driest period of the year [28].

Because elevation is variable within WCR, aspen phenology, morphology, and community composition varies markedly across the property [33]. Locations at lower elevations tend to be drier and contain aspen and conifer forests among areas of mountain big sagebrush (*Artemisia tridentata* ssp. vaseyana Rydb.) or bigtooth maple (*Acer grandidentatum* Nutt.) and Gambel oak (*Quercus gambelii* Nutt.). Wetter locations at higher elevations are dominated by stable aspen stands (single-species stands with little to no competition with conifers; also called "pure" aspen stands) [32,34,35] with some conifer cover (mainly Douglas-fir [*Pseudotsuga menziesii* Franco], subalpine fir [*Abies lasiocarpa* Nutt.], and white fir [*Abies concolor* Lindl. ex Hildebr.]) on north- and east-facing slopes [28].

Herbivores within WCR are primarily mule deer (*Odocoileus hemionus* Raf.), rocky mountain elk (*Cervus elaphus* L.), and sheep (*Ovis* spp.), although moose (*Alces alces*) are occasionally spotted in the area. Elk numbers were estimated to be moderate-to-high for the habitat found in WCR. Deer numbers are not well known on the property [28]. Hunting is not typically permitted on WCR, but a small number of guided elk hunting permits were issued in 2013. Hunting is allowed on adjacent National Forest and private properties to the west, north, and east of WCR. This proximity of hunted lands to privately restricted lands increases elk numbers seasonally as animals flee to safer zones. Property managers in WCR allow 3,000 sheep to graze for two weeks each year in June and six to seven weeks in October and November. Although sheepherders are instructed to keep sheep out of aspen stands to reduce aspen browsing, browsing sometimes occurs [28].

2.2 Preceding study

In a preceding study completed by Rogers et al. (2015) [28], the authors identified fifty random sample points from an overlaid grid and aspen cover layer using a GIS program. Seven of the locations were eliminated because aspen cover was less than 50% tree cover. Within the forty-three remaining locations, a 1-ha monitoring plot was established within each location. Within each plot, forest structure, tree composition, regeneration, recruitment, landscape elements, percent of browsed aspen, and herbivore use was measured. Tree diameters and heights were converted to estimates or classifications to accommodate non-expert field technicians. The data were collected by trained citizen scientists during June and July of 2012.

Measurements within 1-ha monitoring plots were completed within two 2 m x 30 m belt transects oriented perpendicular to each other at cardinal directions to capture differences in terrain. Aspen regeneration (number of stems < 2 m tall), recruitment (number of stems ≥ 2 m and ≤ 6 m tall), and mature canopy trees (trees > 6m tall) were determined within transects at each location. Average canopy height was estimated for the tallest layer of trees using a Biltmore stick. In addition, the number of distinct fecal piles within the transects were counted [36], and separated by species for mule deer, elk, and sheep. Fecal piles that could not be positively identified were not counted, and the frequency of these incidences was not noted. Mean values from variables measured within transects were assumed to represent the surrounding 1-ha area and were extrapolated from the area of the transects (120 m2) to 1-ha values (x 83.33) [28].

Rogers et al. (2015) [28] found that 46% of the stands analyzed were not self-replacing and 19% were marginally self-replacing using regeneration standards provided in O'Brien et al. (2010) [37]. Using browse thresholds for regeneration sustainability presented in Jones et al. (2005) [38], 72% of the stands sampled did not reach the recruitment threshold for long-term sustainability of the stand. The majority of counted fecal pellet piles within the entire 43 locations sampled corresponded to elk (96 elk fecal piles, 8 deer fecal piles, 0 sheep fecal piles), and populations were estimated to occur in a density of 7.8 elk km-2. Previous studies concluded that elk presence of < 1 elk km-2 was ideal for successful stand-replacing recruitment [29,30]. Rogers et al. (2015) [28] also found there was a negative relationship between elk presence (estimated via pellet counts) and aspen regeneration and recruitment. The same areas with high elk pellets also had poor regeneration, recruitment, and stand conditions. Elk presence did not show a relationship with slope however, in agreement with Rogers and Mittanck (2014) [39]. Hill aspect had a positive relationship with recruitment and a negative relationship with elk presence. Elk seemed to prefer drier aspects and browse impacts were greater in these areas, or fecal pellets were easier to find in the less densely covered understory.

2.3 Foodscape Assessment

Fifteen locations were chosen from the forty-three locations studied by Rogers et al. (2015) [28]. We chose fifteen stands because of sampling logistics and because five stands of each treatment was expected to provide enough power to detect differences across locations. Five high, medium, and low recruitment TPA (recruitment as a percentage of live mature aspen trees per area) locations were chosen to be surveyed and sampled, ranging in elevation from 2,331 m to 2,724 m (see Fig 1 for locations of aspen stands sampled). All locations were under different levels of browsing pressure and thus no Control area (i.e., no browsing) could be used in the study. The cut-offs for high, medium, and low recruitment TPA were developed by Rogers et al. (2015) [28] based on the ability of the aspen stand to replace itself over time under varying levels of herbivory. Stands were selected so that one stand from each recruitment TPA level was located within a distance of 1.5 km of each other in order to minimize variation in environmental conditions across the stands. Factors that disqualified locations were slopes greater than 20° (given constraints with site access), areas completely defoliated by aspen blight, and locations that were less than 100 m from a paved road or human structure.

Measurements within 1 ha monitoring plots were completed within two 1 m x 30 m belt transects oriented perpendicular to each other at cardinal directions to capture terrain variations according to the methods of

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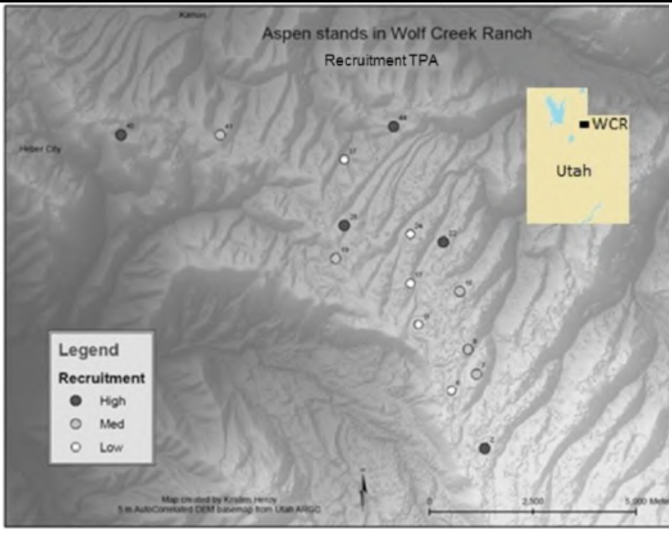

Fig.1: Locations of high, medium, and low regeneration aspen stands (five of each regeneration level to total fifteen stands) sampled during the study at the Wolf Creek Ranch (WCR).

The location of WCR within Utah is shown in the inlaid map of Utah in the upper right corner.

Rogers et al. (2015) [28]. Forage samples were taken every 5 m on alternating sides of the belt transect using a 0.1 m2 quadrat sampling square, so that twelve samples (all herbaceous plants at ground cover) were taken for each location and placed in separate paper bags. Sampling occurred during six consecutive days from 24-Aug-2015 to 29-Aug-2015, since browsing ungulates appear to consume greater amounts of aspen in the early fall [40]. We acknowledge the three-year gap between the original aspen forest data collected by Rogers et al. (2015) [28] and the chemical composition of the foodscape reported here. Nevertheless, very small-to-no-change in recruitment and very small changes in regeneration are expected under that time frame when aspen stands are under the influence of herbivory as the major agent of disturbance [41,42].

To assess shrub density and abundance, the length and width of all shrubs within the 1 m x 30 m belts were recorded [43,44]. In addition, a reference branch was chosen from a shrub of the same species that lay outside of the transects, which was used to estimate the leaf biomass of the shrubs within the lanes, using the reference unit method [45]. Briefly, leaf biomass was estimated by holding up the reference branch to the shrub in the 1 m x 30 m lane and approximating how many reference branches fit inside the shrub in the lane. The reference branch leaf biomass–later measured in the lab–was then multiplied by this number in order to estimate the leaf biomass on each shrub [45]. Reference branches were replaced at least once per day and leaves were stripped off the branch and placed into an individual paper bag, or sooner if leaves began to dry out because the reference branch leaves had to be intact for accurate estimations of dry matter. Mean values of variables measured within transects and quadrats were extrapolated to represent the surrounding 1-ha area. Shrub leaf weight was extrapolated from the area of the transects (60 m2) to 1-ha values (× 166.66).

In order to determine food type biomass, weights of all twelve clip samples were summed, then divided by 1.2 m2 to determine average weight (kg) of samples in 1 m2, and then converted to kg ha-1 (× 10,000). All forage weights were expressed as kg DM ha-1. The nutritional constituent biomass (i.e., the amount of nutrients available per unit of area) was calculated by the product of the forage biomass and the concentration of nutrients in the forages (e.g., i.e., kg crude protein ha -1, kg fiber ha -1).

Aspen leaf samples were taken from each location from trees with an approximate maximum height of 2 to 2.5 m, when possible, by stripping leaves from no more than two branches per aspen tree and placing them into paper bags. The range of 2 to 2.5 m was chosen because trees at or below this height are below the browse line and consequently used by large ungulates like elk [46]. A minimum of 25 g of leaves were harvested from each stand by collecting leaves from each tree within a 30 m radius of the center of the transect. If a location did not contain any aspen trees between 2 to 2.5 m within the 30 m radius, then trees closest in height to 2 to 2.5 m were used. Stand number and tree height for the stands that did not contain any aspen trees within the selected height range were: stand 9 (high regeneration stand; ~3 m in height), stand 6 (medium regeneration; < 1 m in height), and stand 7 (low regeneration stand; ~3 m in height).

We utilized information gathered by Rogers et al. (2015) [28] (e.g., recruitment stems ha-1, regeneration stems ha-1, recruitment TPA, live aspen stems ha-1, percent aspen cover, canopy height, percent of aspen browsed, elevation, slope, and aspect) from the fifteen sampled stands to determine their relationship with the foodscape (i.e., understory food type biomass, understory nutrient constituent biomass, aspen defense chemistry) assessed in the present study (see Table 1 for variables assessed in Rogers et al. [2015] [28] and variables assessed in the current study).

2.4 Forage analyses

All understory, shrub, and aspen leaf samples were stored at -20 °C within 60 minutes of sample collection. Frozen samples were transported in coolers to Utah State University in Logan, UT and stored in a freezer upon arrival. Freeze drying was used instead of oven-drying to

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better preserve the chemical composition of plant samples [47]. All aspen and understory samples were kept at -20 °C until they were freeze-dried. Samples were weighed before and after freeze-drying in order to determine dry matter content.

Table.1: Variables used in the study.

Variables assessed by Rogers et al. 2015:
Regeneration stems ha^{-1}
Recruitment stems ha^{-1}
Recruitment TPA percentage
Landscape (physiographic) elements
Elevation[f]
Slope
Aspect
Percent browsed aspen
Fecal pellet counts
Percent aspen canopy cover
Canopy height
Variables assessed during the current study:
Aspen leaf chemistry[g]
CP[a], ADF[b], NDF[c], TDN[d], Tremulacin, Salicortin, Total PG, Condensed tannins
Understory food type biomass[e]
Grass, Forb, Dead material, Shrubs
Nutrients within each understory food type[e]
CP[a], ADF[b], NDF[c], Hemicellulose, TDN[d]
Total understory nutrients within each location[e]
CP[a], ADF[b], NDF[c], Hemicellulose, TDN[d]
Total understory biomass within each location[e]

[a] Crude protein
[b] Acid detergent fiber
[c] Neutral detergent fiber
[d] Total digestible nutrients
[e] Kg ha^{-1} on a dry matter basis
[f] Meters
[g] Percent of dry matter

2.5 Forage separation

After drying, each forage sample obtained from the quadrats was separated into three food types. The food types consisted of grasses, forbs, and dead understory. Food types from each bag were weighed to determine the amount of forage within each sampled quadrat, and then added to obtain total dry matter harvested from all twelve quadrat squares for each stand.

2.6 Chemical analyses

After separation into food types, a composite food type sample for each stand was ground in a Wiley Mill with a 1 mm screen, and analyzed for dry matter content [48] (Method 930.15), neutral detergent fiber (NDF), acid detergent fiber (ADF) [49], and crude protein (CP) [48] (Method 990.03). Total digestible nutrients (TDN) were calculated from CP and fiber using equations from Weiss (1992) [50] as an estimate of digestible energy of the samples [51,52]. The amount of hemicellulose was determined by subtracting ADF from NDF.

Phenolic glycosides were extracted from 40 mg of freeze-dried leaf material in 1 ml of methanol. The samples were vortexed on high for 5 minutes and centrifuged at 16,000 G for 2 minutes. Supernatants were removed and placed in separate micro-centrifuge tubes. This procedure was repeated a second time, and the extracts were pooled to yield 2 ml of crude extract. Phenolic glycosides (salicortin and tremulacin) were quantified using high performance liquid chromatography (Agilent 1100 Series, Santa Clara, CA, USA) with a Luna 2, C18 column (150 x 4.6 mm, 5 µm) at a flow rate of 1 ml/min. Compound peaks were detected at 280 nm using purified salicortin and tremulacin standards isolated from aspen leaves [53].

Condensed tannins were extracted from approximately 50 mg of freeze-dried leaf tissue with 1 ml of a 70% acetone-10 mM ascorbic acid solution. Samples were vortexed on high for 20 minutes at 4 °C followed by centrifugation at 16,000 G for 2 minutes. Supernatants were removed and placed in separate micro-centrifuge tubes, and the extraction was then repeated. Condensed tannin concentrations were measured spectrophotometrically (SpectraMax Plus 384, MDS, Toronto, Canada) using the acid butanol method [54] standardized with purified condensed tannins isolated from aspen leaves [55]. Defense content of the understory forage samples was not assessed given the minimal to nil content of chemical defenses in grasses and dead plant material and uncertainties about the type of chemical defenses present in forbs.

2.7 Statistical analyses

2.7.1 Multivariate analysis–Non-metric multidimensional scaling (NMDS) ordination

An exploratory ordination of relationships between the thirteen foodscape variables within each of the fifteen stands (understory nutritional constituent biomass, understory food type biomass, aspen defense chemistry [tremulacin, salicortin, total PG, condensed tannins]) and aspen browsing indicators (percent browsed aspen, fecal pellets), indicators of aspen resilience (recruitment stems ha-1, recruitment TPA, regeneration stems ha-1, live aspen stems ha -1), stand structure (canopy height, percent aspen cover), or physiographic conditions (elevation, slope, aspect) was conducted using nonmetric multidimensional scaling (NMDS) ordinations to uncover the variable(s) that explained the most variability between

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foodscapes. Ordinations were created with subsequent fitting of smooth response surfaces of aspen browsing indicators, aspen resilience indicators, stand structure factors, and physiographic conditions over the ordination to assess the relationship of these groups of variables with the foodscape.

We used NMDS with Bray-Curtis dissimilarity as implemented by the metaMDS and ordisurf functions in the vegan package Version 2.4-1 [56] in R Version 3.3.1 using RStudio [57,58]. Scaling was automatically applied by the metaMDS command (centering, PC rotation, half-change scaling). Expanded scores were based on Wisconsin and square root transformations, as set by metaMDS. Percent stress, the percentage of variation not explained by all dimensions in the ordination and therefore the overall measure of quality of fit of the ordination to the data, was calculated using the metaMDS command in the vegan package [59]. The command envfit with 1,000 permutations was used to obtain r2 and P-values for all aspen browsing indicators, aspen resilience indicators, stand structure, and physiographic variables on each foodscape group ordination.

2.7.2 Univariate correlation analysis

Univariate correlations were conducted after completing the multivariate analysis to further explore relationships between the foodscape and indicators of aspen browsing, aspen resilience, and other biotic and physiographic conditions assessed. The objective was to obtain one r2 and P-value for each of the individual thirteen foodscape variables in relation to each of the indicators of aspen browsing, aspen resilience, stand structure, and physiographic condition variables because the vegan package in R only generates one r2 and P-value for each of these variables in relation to the entire foodscape (not to the individual variables that make up the foodscape).

Multivariate analyses (i.e., from the NMDS ordination analyses) with resulting P-values of 0.1 or lower were included in univariate regressions with foodscape variables (i.e., food type biomass, nutritional biomass constituents, and aspen defense chemical constituents). Those variables included in the univariate analysis were canopy height and elevation.

We used the xyplot command for regressions using the lattice package Version 0.20-33 [60] in R Version 3.3.1 using RStudio [57,58]. A significant correlation was defined as any variable with a P-value of 0.1 or less, and trends were defined as any variable with a P-value of 0.2 or less.

III. RESULTS

3.1 Multivariate analysis–Non-metric multidimensional scaling (NMDS)

Two convergent solutions were found after 20 runs using metaMDS analyses for understory food type biomass ha^{-1}, total understory nutritional constituent biomass ha^{-1}, and aspen defense chemistry. Two dimensions (k=2) were selected by the metaMDS function (NMDS stress value=0.129) and no outliers were removed.

Significant relationships were found between the foodscape and canopy height as well as between the foodscape and elevation (see Table 2 for r^2 and P-values). Using our significance criteria, other variables in the aspen structure and physiographic variable groupings and variables in the aspen browsing or stand resilience groupings showed no relationship with the foodscape. Areas with high forb biomass and low amounts of dead understory and low condensed tannin concentration in aspen leaves occurred in stands at high elevation (~2,700 m; see Fig 2) and in stands with high canopy heights (~85 m; see Fig 3). Total nutrient biomass and PG content in aspen leaves were greatest in stands at intermediate elevations (~2,525 m) and with intermediate canopy heights (~67 m).

Table.2: P-values and r^2 values from the NMDS analysis conducted between the foodscape and indicators of aspen resilience, aspen browsing, and other biotic and physiographic factors assessed at the Wolf Creek ranch. Significant relationships are shown in bold.

	r^2	P-value
Live aspen stems ha^{-1}	0.0636	0.6603
Percent aspen cover	0.1376	0.3826
Canopy height	**0.5286**	**0.0099**
Elevation	**0.6077**	**0.0019**
Aspect	0.0114	0.9380
Slope	0.1940	0.2667
Total pellets ha^{-1}	0.0864	0.5614
TPA recruitment stems ha^{-1}	0.0013	0.9940
Recruitment stems ha^{-1}	0.0919	0.5714
Regeneration stems ha^{-1}	0.1549	0.3626
Percent browsed aspen	0.0824	0.6093

3.2 Univariate correlation analyses

3.2.1 Canopy height

There was a positive correlation between canopy height and understory forb biomass ha^{-1}, and a negative correlation between canopy height and understory shrub biomass ha^{-1}. We also found a positive correlation between tremulacin content in aspen leaves and aspen canopy height, and a positive trend between total PG

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content in aspen leaves and aspen canopy height (see Table 3 for r^2 and P-values).

3.2.2 Elevation

A positive correlation was found between elevation and both understory grass and forb biomass ha^{-1}, and a negative correlation between elevation and both understory dead and shrub biomass ha^{-1}. A positive correlation was also found between elevation and understory ADF, NDF, hemicellulose biomass ha^{-1}, and tremulacin, salicortin, and total PG content in aspen leaves. Additionally, a positive trend was found between elevation and understory TDN and CP biomass ha^{-1} (see Table 3 for r^2 and P-values).

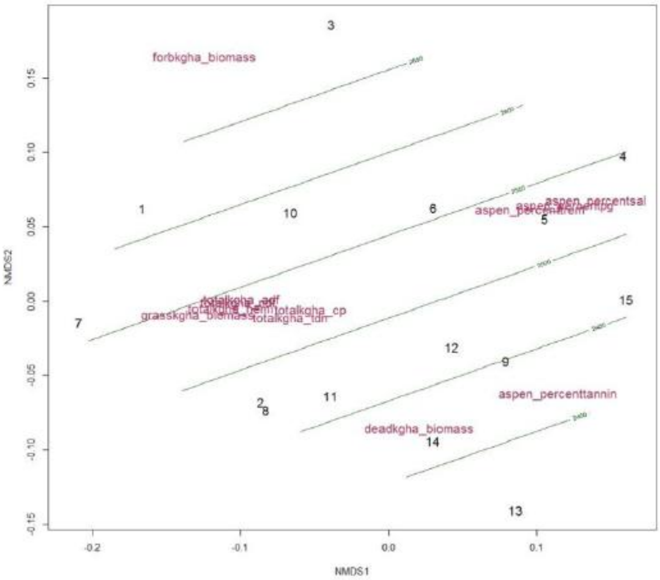

Fig.2: Organization of the foodscape variables in a nonmetric multidimensional scaling (NMDS) ordination showing the first two dimensions.

Foodscape variables were measured in each stand (fifteen values [stands] for each of the thirteen foodscape variables). Foodscape variables appear in the ordination in maroon lettering and are as follows: grasskgha_biomass (kg of grass ha^{-1}), forbkgha_biomass (kg of forbs ha^{-1}), deadkgha_biomass (kg of dead plant material ha^{-1}), shrubkgha_biomass (kg of shrubs ha^{-1}), totalkgha_cp (kg total CP [crude protein] ha^{-1}), totalkgha_adf (kg total ADF [acid detergent fiber] ha^{-1}), totalkgha_ndf (kg total NDF [neutral detergent fiber] ha^{-1}), totalkgha_hemi (kg total hemicellulose ha^{-1}), totalkgha_tdn (kg total TDN [total digestible nutrients] ha^{-1}), aspen_percenttrem (percent tremulacin), aspen_percentsal (percent salicortin), aspen_percentpg (percent total PG), and aspen_percenttannin (percent condensed tannins). Overlaid response surfaces were placed over the ordination surface representing a gradient of elevation in each of the fifteen stands (dark green topographical surface, with each topographical line labeled with values ranging from 2400 to 2650 meters). The stress value was 12.9%. Stand numbers (1 through 15) appear on the surface in black lettering.

3.3 Nutritional analyses

Crude protein (CP) content was similar between aspen leaves collected from all fifteen stands, as well as shrub leaves and forbs collected from the understory of high recruitment TPA stands (Table 4). In general, CP concentration was low in grasses and dead plant material collected from the understory, particularly for high and medium recruitment TPA locations (P>0.05), and were lower than CP content of forbs in medium and low recruitment TPA stands (P<0.05). Acid (ADF) and neutral (NDF) detergent fiber content was low in aspen and shrub leaves, with high concentrations in dead plant material and grasses. Total digestible nutrient (TDN) concentration was the greatest in aspen and shrub leaves. Concentration of TDN was lowest in dead plant material for all recruitment TPA levels, and lowest in grasses for low recruitment TPA locations (P<0.05).

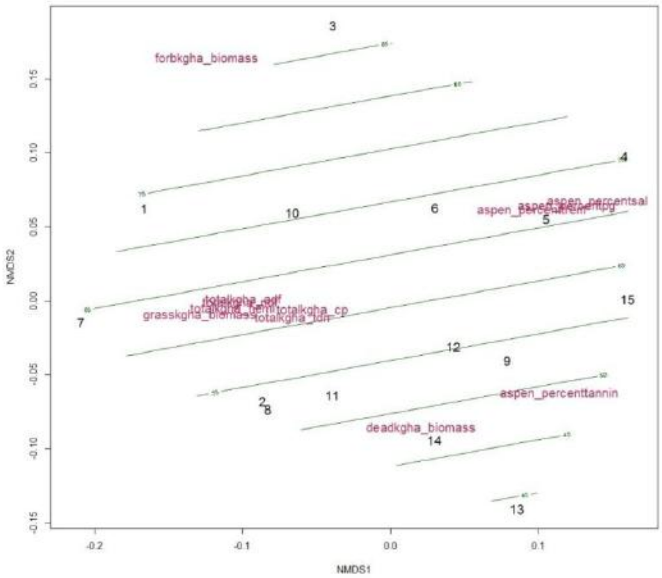

Fig.3: Organization of the foodscape variables in a nonmetric multidimensional scaling (NMDS) ordination showing the first two dimensions.

Foodscape variables were measured in each stand (fifteen values [stands] for each of the thirteen foodscape variables). Foodscape variables appear in the ordination in maroon lettering and are as follows: grasskgha_biomass (kg of grass ha^{-1}), forbkgha_biomass (kg of forbs ha^{-1}), deadkgha_biomass (kg of dead plant material ha^{-1}), shrubkgha_biomass (kg of shrubs ha^{-1}), totalkgha_cp (kg total CP [crude protein] ha^{-1}), *totalkgha_adf (kg total ADF [acid detergent fiber] ha^{-1}), totalkgha_ndf (kg total NDF [neutral detergent fiber] ha^{-1}), totalkgha_hemi (kg total hemicellulose ha^{-1}), totalkgha_tdn (kg total TDN [total digestible nutrients] ha^{-1}), aspen_percenttrem (percent tremulacin), aspen_percentsal (percent salicortin), aspen_percentpg (percent total PG), and aspen_percenttannin (percent condensed tannins). Overlaid response surfaces were placed over the ordination surface representing a gradient of canopy height in each of the fifteen stands (dark green topographical surface, with each topographical line labeled with values ranging from 40 to 85 meters). The stress value was 12.9%. Stand numbers (1 through 15) appear on the surface in black lettering.*

Table.3: P-values and r^2 values from univariate regression analyses conducted between the foodscape and canopy height and elevation assessed at the Wolf Creek ranch. Significant relationships are shown in bold.

Food type biomass[e]	Grass		Forb		Dead		Shrub	
	r^2	P-value	r^2	P-value	r^2	P-value	r^2	P-value
Canopy Height[f]	<0.001	0.97	**0.33**	**0.03**	0.02	0.65	**0.47**	**0.01**
Elevation[f]	**0.31**	**0.03**	**0.20**	**0.09**	**0.24**	**0.06**	**0.39**	**0.01**

Nutrient constituent biomass[e]	CP[a]		ADF[b]		NDF[c]		Hemicellulose		TDN[d]	
	r^2	P-value	r^2	P-value	r^2	P-value	r^2	P-value	r^2	P-value
Canopy Height	0.003	0.56	0.002	0.66	0.001	0.69	0.01	0.74	0.001	0.70
Elevation	**0.16**	**0.14**	**0.24**	**0.06**	**0.22**	**0.06**	**0.27**	**0.05**	**0.17**	**0.13**

Aspen defense chemistry[g]	Tremulacin		Salicortin		Total PG		Condensed Tannin	
	r^2	P-value	r^2	P-value	r^2	P-value	r^2	P-value
Canopy Height	**0.22**	**0.08**	0.10	0.25	**0.15**	**0.16**	0.05	0.44
Elevation	**0.45**	**0.01**	**0.37**	**0.02**	**0.43**	**0.01**	0.05	0.44

[a] Crude protein
[b] Acid detergent fiber
[c] Neutral detergent fiber
[d] Total digestible nutrients
[e] Kg ha^{-1} on a dry matter basis
[f] Meters
[g] Percent dry matter basis

3.4 Plant secondary compound analyses

Total concentration of phenolic glycosides (PG) and condensed tannins were similar in high, medium, and low recruitment TPA stands, before and after excluding stands that did not contain trees between 2 to 2.5 meters in height (i.e., stand 22 [high recruitment TPA], 16 [medium recruitment TPA], and 17 [low recruitment TPA]) (see Table 5).

IV. DISCUSSION

Previous research suggests that nutrients and plant secondary compounds (PSC) influence aspen use by ungulates [5,6,23,61,62]. However, little work has been completed on the interplay between the chemicals present in the landscape and aspen stand health and browsing by ungulates. Here we document relationships of stand resilience indicators (regeneration, recruitment, recruitment TPA), aspen browsing indicators (fecal pellets, percent browsed aspen), structural characteristics of the stand (canopy height, aspen canopy cover), and physiographic conditions (elevation) with the foodscape (understory food type biomass, nutritional constituent biomass of the understory, and aspen defense chemistry).

4.1 Nutritional constituent biomass

We predicted that as understory nutritional biomass at the sampled locations increased (e.g., greater crude protein content, lower fiber content, greater TDN content), aspen use by ungulates would decline, and consequently recruitment and regeneration would increase because ungulates would prefer a higher quality and abundant understory to less nutritious and defended aspen tissues. We did not find any significant relationships between nutritional constituent biomass and aspen use indicator variables within the ordination, but did find a relationship between nutritional constituent biomass and elevation.

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The positive relationships found with elevation in the analyses are likely due to environmental influences such as precipitation or soil moisture content. Previous studies have shown elevation is positively correlated with moisture [63,64]. Locations at higher elevation have greater soil moisture than those at lower elevations and aspen, grasses, and forbs tend to thrive in areas of high moisture versus areas with low moisture [65-67], offering a greater concentration of nutrients to herbivores. Thus, the growth and establishment of different food types at various elevations on the landscape affected the quality of the foodscape (e.g., food type biomass and therefore nutrient amount and concentration), essentially providing a resilience buffer not present at lower elevations.

Table.4: Nutritional analyses (% dry matter) of aspen leaves and understory samples collected from different aspen stands at Wolf Creek Ranch showing different levels of aspen recruitment TPA.

High recruitment TPA aspen stands- # 1[b], 9 [a], 11[e], 13[e], 15[d]

	Crude protein	ADF[f]	NDF[g]	TDN[h]
Grasses	11.5 ± 2.1	38.11 ± 1.39	61.89 ± 1.72	56.17 ± 1.82
Forbs	13.71±1.4	30.9±1.42	42.56±2.55	59.22 ± 1.16
Dead	11.11±0.54	44.64±1.01	64.71±1.04	51.01 ± 0.73
Aspen	14.73±0.31	18.39±1.52	26.26±1.65	69.12 ± 1.08

Medium recruitment TPA aspen stands- # 3[d], 4[a], 6[d], 8[e], 14[c]

	Crude protein	ADF	NDF	TDN
Grasses	8.89 ± 0.48	40.05 ± 0.57	65.76 ± 1.54	53.74 ± 0.56
Forbs	11.87±1.33	32.68±3.9	42.57±3.21	57.76 ± 3.12
Dead	8.88±0.59	45.53±0.91	65.32±2.54	49.52 ± 0.75
Aspen	14.53±0.8	17.43±0.58	24.96±2.23	69.86 ± 0.39

Low recruitment TPA aspen stands- # 2[b], 5[d], 7[c], 10[c], 12[c]

	Crude protein	ADF	NDF	TDN
Grasses	8.97 ± 0.08	40.78 ± 0.72	66.03 ± 0.29	53.21 ± 0.58
Forbs	12.26±0.41	30.33±2.94	42.21±2.99	59.62 ± 2.30
Dead	11.56±0.21	41.76±0.61	61.57±1.37	53.38 ± 0.46
Aspen	14.84±0.58	20.29±1.19	29.21±1.49	67.62 ± 0.85

Composite leaf samples from all stands sampled

	Crude protein	ADF	NDF	TDN
Shrub	13.24	17.71	27.80	69.60

[a] August 25, 2015
[b] August 26, 2015
[c] August 27, 2015
[d] August 28, 2015
[e] August 29, 2015
[f] Acid detergent fiber
[g] Neutral detergent fiber
[h] Total digestible nutrients

Table.5: Plant secondary compounds (% dry matter) of aspen leaves at Wolf Creek Ranch across stands with different levels of recruitment TPA.

High recruitment TPA aspen stands

	Tremulacin[f]	Salicortin[f]	Total PG[f]	Condensed tannins
Aspen[g]	5.13 ± 0.99	8.33 ± 1.81	13.47 ± 2.71	1.59 ±0.56
Aspen[h]	5.04 ± 0.75	7.73 ± 1.52	12.77 ± 2.18	2.42 ± 2.04

Medium recruitment TPA aspen stands

	Tremulacin	Salicortin	Total PG	Condensed tannins
Aspen[g]	6.15 ± 1.72	8.55 ± 2.95	14.7 ± 4.62	1.68 ± 0.92
Aspen[h]	6.33 ± 1.3	9.08 ± 2.29	15.41 ± 3.55	1.55 ± 1.41

Low recruitment TPA aspen stands				
	Tremulacin	Salicortin	Total PG	Condensed tannins
Aspen[g]	6.04 ± 0.9	6.05 ± 1.38	12.09 ± 2.03	2.97 ± 1.16
Aspen[h]	5.59 ± 0.84	5.5 ± 1.2	11.09 ± 1.89	2.66 ± 1.87

[a] August 25, 2015
[b] August 26, 2015
[c] August 27, 2015
[d] August 28, 2015
[e] August 29, 2015
[f] Percent of dry sample weight
[g] Excluding stands that did not contain 2 m trees for sampling
[h] Including stands that did not contain 2 m trees for sampling

4.2 Understory food type biomass

We also predicted that understory biomass would be inversely related to aspen browsing because if nutrient biomass at these locations was above the threshold required to meet nutritional needs, then animals did not need to seek extra nutrients from aspen leaves and consequently aspen use would decline. We found a significant effect of elevation on understory biomass, and as mentioned in the previous section, elevation is positively correlated with moisture [63,64]. Aspen and forbs tend to thrive in areas of high moisture (high elevations) [65-67], and grasses and forbs senesce when temperatures increase and less moisture is available to the plants. Shrubs establish in warm and dry climates [65], and therefore thrive at lower elevations. These patterns are in agreement with findings from the univariate analysis in the current study, with positive associations between elevation and understory forb and grass biomass, with negative correlations between elevation and shrub biomass. Differences in forage types across elevations may influence elk foraging distribution, as well as aspen recruitment and regeneration. For instance, elk may use more aspen at locations where understories offer lower biomass (e.g., shrubs at lower elevation), a selection process with negative impacts on aspen recruitment and regeneration. Nevertheless, our results do not provide an indication of this pattern, likely due to the influence of other intervening variables in a complex landscape, which were more consequential than the differences in biomass and chemistry observed across the gradient explored in this study. For instance, it is possible that locations at higher elevation, due to water availability, may be simply more resilient–i.e., able to replace browsed stems at a high enough rate to not experience growth limitation through compensatory growth.

4.3 Defense content in aspen

Lastly, we predicted that as defense content in aspen stands increased, aspen use would decrease because phytochemicals constrain intake. As with nutrient constituent biomass and food type biomass, aspen use indicators did not show any relationship with the foodscape but elevation and canopy height did. Although no straightforward explanations for the relationship between aspen defense content and canopy height or elevation emerged from the current study, possible explanations may be found in current understandings of the relationship between canopy height or elevation and soil microclimate or total available moisture. As canopy height increases, the amount of light that reaches the understory is reduced [68]. Understory light environments affect microclimate (e.g., solar radiation, soil and leaf temperature, soil moisture) [69,70], and increased light intensity can increase soil temperature and soil evaporation rates [70], which can influence plant establishment and growth [71,72,73]. Alternatively, the relationship between canopy height and soil moisture may be due to bottom-up effects instead of top-down effects—meaning that soil microclimate may drive canopy height differences instead of canopy height driving soil microclimate differences—or soil moisture gradients may instead be due to elevational moisture influences. Because we did not measure soil microclimates or determine the individual effects of canopy height or elevation on PSC content in aspen, we cannot conclude in which direction the effect occurs. In either case, increased light intensity (possibly from changes in canopy height) and temperature (possibly from changes in canopy height and/or elevation) has been shown to increase defense chemical content within aspen stands [27,74-76], but our findings suggest the opposite–showing increased canopy height (shading) coincided with increased aspen PG content in the sampled juvenile aspen trees. Such changes may be in response to other variables that affect PG content such as temperature, soil moisture, or soil nutrients that were not assessed in the current study [27,76].

V. CONCLUSION

Results from this study show that the foodscape is influenced by elevation and canopy height, but no relationships were found with indicators of aspen herbivory or stand condition. The abundance of forbs and grasses at higher elevation locations helped to explain the distribution of CP biomass across the foodscape. In contrast, stands with low CP and TDN concentrations in the understory were found at lower elevation locations. It is likely that foodscapes with more differences than those found in the present study may help explain greater aspen herbivory and less aspen regeneration and recruitment at low-quality locations (i.e., even lower levels of CP or TDN biomass) relative to those that offer more food alternatives with lower concentrations of plant defenses and greater nutritional quality. Moreover, aspen stands at lower elevations may be more at risk of succumbing to overbrowsing because aspen in those areas are more likely to be stressed from lack of moisture [66,67,77].

The concept of foodscape and foraging by ungulates developed in this study could be used to explore other relationships, on a wider range of landscapes–like browsing and mineral content of aspen trees and understories–to address concerns of overbrowsing in aspen-dominated communities.

VI. CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

VII. STATEMENT OF HUMAN AND ANIMAL RIGHTS

This article does not contain any studies with human participants or animals performed by any of the authors.

VIII. ACKNOWLEDGEMENTS

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