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Nutritional Dynamics of Plant Growth Forms in a Forest-Grassland Mosaic[☆]



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ABSTRACT

The objectives of this study were to determine the influence of plant community type, forest stand age, and season on the forage quality of plant growth forms in a forest-grassland mosaic. We determined the forage quality of plant growth forms (graminoids, forbs, and shrubs) at 64 sites in the Blue Mountains of Oregon, over four dates between May and September over two years. Samples were analyzed for crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF). Sites were classified according to climax vegetation and grouped as either forested (ponderosa pine, *Pinus ponderosa*; Douglas-fir, *Pseudotsuga menziesii*; grand fir, *Abies grandis*) or non-forested (meadow or grassland). Forested sites were also categorized as “young” or “old” based on mean diameter at breast height of less than or greater than 37.5 cm, respectively. Graminoid and forb CP in early May were 3.5 and 2.5 points greater in the grand fir community type than the other forested types ($P \leq 0.01$) and were 2.7 and 4.9 points greater in the meadow type than the grassland type ($P \leq 0.04$). In mid-September, graminoid CP was similar between all community types ($P \geq 0.78$). In early May, forb ADF and NDF were similar between all community types ($P \geq 0.18$). In mid-September, forb ADF was 10.7 points lower in the ponderosa pine and Douglas-fir types than in all other community types ($P \leq 0.02$). Forb ADF and NDF were greater in young stands than in old stands ($P < 0.01$). Furthermore, forb ADF was 11.4 points greater in the young grand fir community type than all other forested types ($P < 0.01$). Our study characterizes forage quality across the growing season in diverse vegetation types and, in turn, can be applied to wildlife and livestock management to predict and manage animal landscape distribution.

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Introduction

Mixed-conifer forests of the inland Pacific Northwest and Northern Rockies provide a diverse array of ecosystem services, including timber production, habitat, and forage for wildlife and livestock (Brocknerhoff et al., 2017). Most of these forests are managed by the USDA Forest Service or private timber companies whose management balances for various ecosystem services (Deal et al., 2017). This region supports large populations of wild ungulates

and livestock, including, Rocky Mountain elk (*Cervus canadensis nelsoni*; Kohl et al., 2023), Rocky Mountain mule deer (*Odocoileus hemionus hemionus*; ODFW, 2024), whitetail deer (*Odocoileus virginianus*; IDFG, 2019), domestic cattle (*Bos taurus taurus*; USDA, 2024), and domestic sheep (*Ovis aries*; USDA, 2024).

The health and productivity of these species is linked to their ability to meet their nutrient requirements during late-gestation and lactation in the spring and summer (Cook et al., 2004, 2013; Richards et al., 1986; Tollefson et al., 2010). Herbivores select comparatively high-quality diets through particular patterns of landscape use (Baum et al., 2022; Clark et al., 2017; Stewart et al., 2002) and dietary preferences (Findholt et al., 2004; Kingery et al., 1996; Littleford-Colquhoun et al., 2024). However, regardless of selectivity, herbivore diets are ultimately confined by the spatial and temporal distribution of nutrients across the landscape (Ganskopp and Bohnert, 2009; Merkle et al., 2016; Raynor et al., 2016). There-

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fore, understanding how forage quality varies across the landscape and in response to land management is critical to managing wildlife and livestock populations.

Although forage quality is often the focus of investigations considering animal nutrition, the specific metrics used to quantify forage quality reflect underlying plant structural and chemical traits (Lavorel and Garnier, 2002). For example, acid detergent fiber (ADF) and neutral detergent fiber (NDF) reflect fractions of the cell wall and are associated with fiber content, carbon stock, and plant size. Crude protein (CP) is a measure of nitrogen content and is associated with photosynthetic activity and vegetative tissue. Plants are often grouped into growth form categories—graminoids, forbs, and shrubs—each of which share similar traits and exhibit similar patterns in forage quality.

Forest-grassland mosaics are common throughout the inland Pacific Northwest and Northern Rockies. For example, in the Blue Mountains of eastern Oregon and Washington, the ponderosa pine (*Pinus ponderosa* P. & C. Lawson), the Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca* [Beissn.] Franco), and the grand fir (*Abies grandis* [Douglas ex D. Don] Lindl.) forest series occur along a gradient of increasing elevation and moisture (Cooper et al., 1991; Johnson and Simon, 1987; Powell, 2007). Interspersed across the landscape, Palouse prairie grassland occurs on ridges and benches, and meadows occur alongside streams. Consequently, many forest management units contain all three forest series, grasslands, and meadows.

Although the general differences in the forage quality among plant growth forms is well established, information specific to mixed-conifer forests is limited (Clark, 2003; Skovlin, 1967). In the working forests of the region, timber harvest is the primary physical disturbance agent (Hedrick et al., 1968; Hessburg and Agee, 2003). Timber harvest removes older, larger trees, leaving younger, smaller, and fewer trees, resulting in increased light, water availability, and temperature in the understory (Bauhus et al., 2009; Long et al., 2008; Metlen et al., 2004). This process alters understory species composition and biomass (Abella and Springer, 2015; Miller and Krueger, 1976; Walburger et al., 2007), however, its influence on forage quality remains understudied (Regelin et al., 1974; Severson and Uresk, 1988).

At higher elevations, the growing season is shorter and begins later in the year, delaying plant growth and phenology. Additionally, more mesic sites often have prolonged water availability thus delaying senescence. Because of this, it is often assumed that these plant communities have higher forage quality later into the growing season. This has been evaluated at broad scales across seasonal ranges (Cook and Harris, 1968) but has not been evaluated at finer scales along a plant community gradient.

Therefore, the objectives of this study were to determine the influence of plant community type, forest stand age, and season on the forage quality of plant growth forms in a forest-grassland mosaic. We hypothesize that more mesic plant communities (e.g. meadow and grand fir communities) will maintain higher forage quality later into the season. Additionally, we hypothesize that plant communities with less understory light (e.g. forested communities and old forest stands) will have lower forage quality early in the growing season and higher forage quality later in the season due to delayed phenology.

Methods

Study area

This research was conducted in the Blue Mountains of north-eastern Oregon on a 39,530-ha block of forestland managed for timber production, 20 km north of Wallowa, OR. Elevation ranges from 900 to 1350 m ($\mu = 1170$ m) and precipitation ranges from

540 to 730 mm ($\mu = 645$ mm) with approximately 55% coming between November and March (PRISM, 2019). This portion of the Blue Mountains consists of a series of broad, rolling uplands, dissected by steep canyons. The vegetation is primarily a mosaic of coniferous forest and grasslands. Rocky Mountain elk and Rocky Mountain mule deer are common in the area throughout the year and cattle graze the area in the summer and early fall.

Site selection and vegetation

All sites in this study were developed by Yost (2005) and were designed to be representative of the vegetation of the region. We visited all of Yost's sites and selected those where the potential natural climax vegetation could be identified, resulting in a total of 175 sites. Forested sites were identified to the series level and non-forested sites were identified to the physiognomic class level (Powell, 2007). The ponderosa pine, Douglas-fir, and grand fir series were the primary forest series at the study site and represent the dominant forest vegetation of the region (Johnson and Simon, 1987). We used mean stand diameter at breast height (DBH) as a proxy measurement for stand age. Stands with mean DBH of less than 37.5 cm were classified as “young”; stands with mean DBH of greater than 37.5 cm were classified as “old”. This classification corresponds to stand age classifications used elsewhere (Yost, 2008; young = sapling and pole; old = small saw and saw). The non-forested sites were classified into either “grasslands” or “meadows” (upland herb and riparian herb physiognomic classes, respectively; Powell, 2007). From hereafter, when referred to in comparison to one-another, all plant classifications (physiognomic classes for the non-forested sites and series for the forested sites) will be referred to as “community types” (SRM, 1998).

Though understory vegetation varied between forested community types, the primary graminoids (grasses, sedges, and rushes) were elk sedge (*Carex geyeri* Boott), pinegrass (*Calamagrostis rubescens* Buckley), and Kentucky bluegrass (*Poa pratensis* L.). The dominant forbs were strawberry (*Fragaria* spp.) and western yarrow (*Achillea millefolium* L.). Common shrubs were common snowberry (*Symphoricarpos albus* [L.] S.F. Blake), birchleaf spirea (*Spiraea betulifolia* Pall.), and Oregon grape (*Mahonia repens* [Lindl.] G. Don). The grassland type was dominated by the grasses blue-bunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Å. Löve) and annual bromes (*Bromus* spp.), and the forbs parsnipflower buckwheat (*Eriogonum heracleoides* Nutt.) and fernleaf biscuitroot (*Lomatium dissectum* [Nutt.] Mathias & Constance). The meadow type was dominated by the grasses reedtop (*Agrostis stolonifera* L.), Kentucky bluegrass, and tufted hairgrass (*Deschampsia caespitosa* [L.] P. Beauv.), and the forbs lambstongue ragwort (*Senecio integerrimus* Nutt.) and slender cinquefoil (*Potentilla gracilis* Douglas ex Hook.). Shrubs were either a minor component or absent from most non-forested community types.

Field and laboratory methods

Understory production was sampled by species over three consecutive years at all 175 selected sites consisting of both age classes for each forested type and in both non-forested types using 1.8 m² caged plots installed in the early spring of each year (Damiran et al., 2008). Each caged plot was revisited at peak production in August and samples were collected. Shrubs were stripped of all herbaceous biomass and graminoids and forbs were clipped to a 1 cm stubble height. Each species was bagged separately, transported to the Eastern Oregon Agricultural Research Center in Union, OR, dried at 55°C in a forced-air oven for 48 hours, and weighed to obtain a dry matter weight.

Community composition and production data by plant growth form for each community type are presented in Table 1. Within the

Table 1

Influence of community type and forest stand age on understory community composition and production of plant growth forms in the Blue Mountains in northeastern Oregon.

	Ponderosa Pine		Douglas-Fir		Grand Fir		Grassland	Meadow
	Young	Old	Young	Old	Young	Old		
Composition (%)								
Graminoid	52 (42–66)	68 (47–80)	45 (31–60)	58 (34–78)	35 (22–50)	45 (34–62)	64 (51–79)	70 (62–78)
Forb	43 (31–53)	21 (12–36)	18 (10–27)	19 (8–29)	30 (22–39)	32 (13–35)	33 (16–47)	30 (22–38)
Shrub	5 (0–4)	12 (2–21)	37 (20–55)	23 (11–27)	34 (23–46)	23 (12–37)	3 (0–1)	0 (0–0)
Production (kg • ha ⁻¹)								
Graminoid	641 (432–700)	749 (456–1016)	446 (205–600)	607 (337–882)	464 (261–502)	629 (396–829)	776 (427–909)	2178 (1033–3001)
Forb	528 (326–708)	231 (103–324)	181 (66–206)	196 (101–207)	396 (253–497)	450 (149–418)	399 (146–493)	909 (502–1401)
Shrub	58 (2–49)	128 (30–229)	361 (140–325)	244 (98–326)	447 (254–667)	327 (131–456)	36 (0–8)	3 (0–0)
Total	1227 (910–1479)	1108 (845–1281)	988 (485–1293)	1047 (883–1239)	1307 (1026–1448)	1406 (975–1552)	1211 (636–1666)	3088 (2316–3902)
No. of Sites	19	33	25	14	22	24	18	20

Means and ranges between the upper and lower quartiles are displayed.

forested community types, graminoids were a major component of the understory plant community, reaching their greatest abundance in the ponderosa pine type. Shrubs were a small component of the ponderosa pine type but a large component of the Douglas-fir and grand fir types. Forbs were variable across forested community types and stand ages (18–43% composition). The non-forested community types were dominated by graminoids and shrubs were either a minor component or absent. This is similar to other descriptions of this area (Johnson and Simon, 1987; Crowe and Clausnitzer 1997; Johnson and Swanson 2005; Walburger et al., 2007).

Of the sites sampled for production, eight sites within each community type and age were randomly selected for nutritional quality sampling. All species that comprised the top 80% of year one production within each community type were individually sampled at each site at 4 six-week intervals from early May through mid-September in the following two years. A minimum of 100 g representing at least five individuals of each species were randomly selected at each site. Graminoids and forbs were clipped to a 1 cm stubble height and shrubs were stripped of herbaceous material. Only those species available to and consumed by wildlife and livestock were considered for nutritional quality sampling. Plant growth form composition of all species clipped for nutritional quality sampling are listed in Table S1 (available online at [insert URL here]).

Samples were collected in paper bags in the field and transported to the Eastern Oregon Agricultural Research Center in Union, OR where they were dried at 55°C in a forced-air oven for 48 hours, ground to pass a 1-mm screen, and stored in plastic bags at room temperature for subsequent chemical analysis. Samples were analyzed for CP content (AOAC, 1990), ADF, and NDF (Goering and Van Soest, 1970). All metrics are reported on a dry matter basis. All samples were run in duplicate; any sample whose coefficient of variation was greater than 5% was reanalyzed. At each site, we calculated CP, ADF, and NDF weighted means for each plant growth form using species composition within plant growth form.

Abiotic characteristics of all sites sampled were remotely derived in R using the raster package (Hijams, 2020; R Core Team, 2019). Elevation and slope were derived from a 1/3 arc-second digital elevation model aggregated to a 30-m resolution (USGS, 2019). Percentage canopy cover was derived from the University of Maryland's 30-m resolution Global Forest Cover 2000 dataset (Hansen et al., 2013). Average annual precipitation, maximum, minimum, and mean temperatures were obtained from PRISM (2019) at an 800-m resolution. Soil depth and available water storage capacity

were obtained from the Gridded National Soil Survey at a 10-m resolution (Soil Survey Staff, 2019).

Abiotic site characteristics are presented in Table S2 (available online at [insert URL here]). Within the forested communities, the ponderosa pine type occurred at the lowest elevations and driest sites, the grand fir type occurred at the highest elevations and wettest sites, and the Douglas-fir type occurred at intermediate sites. The grassland type occurred across the elevation and precipitation gradients whereas the meadow type occurred across a narrower elevational range at higher elevations but were also the in highest precipitation areas. Meadows occurred on mostly flat slopes whereas all other communities occurred across a range of slopes. Though canopy cover was quite variable within forested community types, the ponderosa pine type had the lowest cover, the Douglas-fir type had intermediate cover, and the grand fir type had the greatest cover. The grassland type had low cover. The meadow type itself had low cover, but more often occurred in smaller patches within the forest. Mean annual maximum temperature was similar among the forested communities whereas mean annual minimum was not. The ponderosa pine type had the lowest minima and the grand fir type had the highest minima. The other three communities were intermediate. The grassland type had the shallowest soils with the poorest water holding capacity whereas the meadow type had deep soils with the greatest water holding capacity. The forested community types had deep soils with intermediate water holding capacity.

Statistical analysis

Stand age only applies to forested communities, therefore we split the data into two analyses that evaluated the influence of: 1) community type (averaged across stand age within the forested community types) and sampling date on vegetation quality by plant growth form across forested and non-forested community types, and 2) forested community type, stand age and sampling date on vegetation quality by plant growth form across only forested community types. The first analysis was a repeated measures completely randomized design with 8 replications and 3 factors (community type, $n=5$; growth form, $n=3$; and sampling date, $n=4$). However, shrubs only reliably occurred in forested communities therefore data were analyzed within plant growth form. The second analysis was also a repeated measures completely randomized design with 8 replications and 4 factors (forested community type, $n=3$; stand age, $n=2$; growth form,

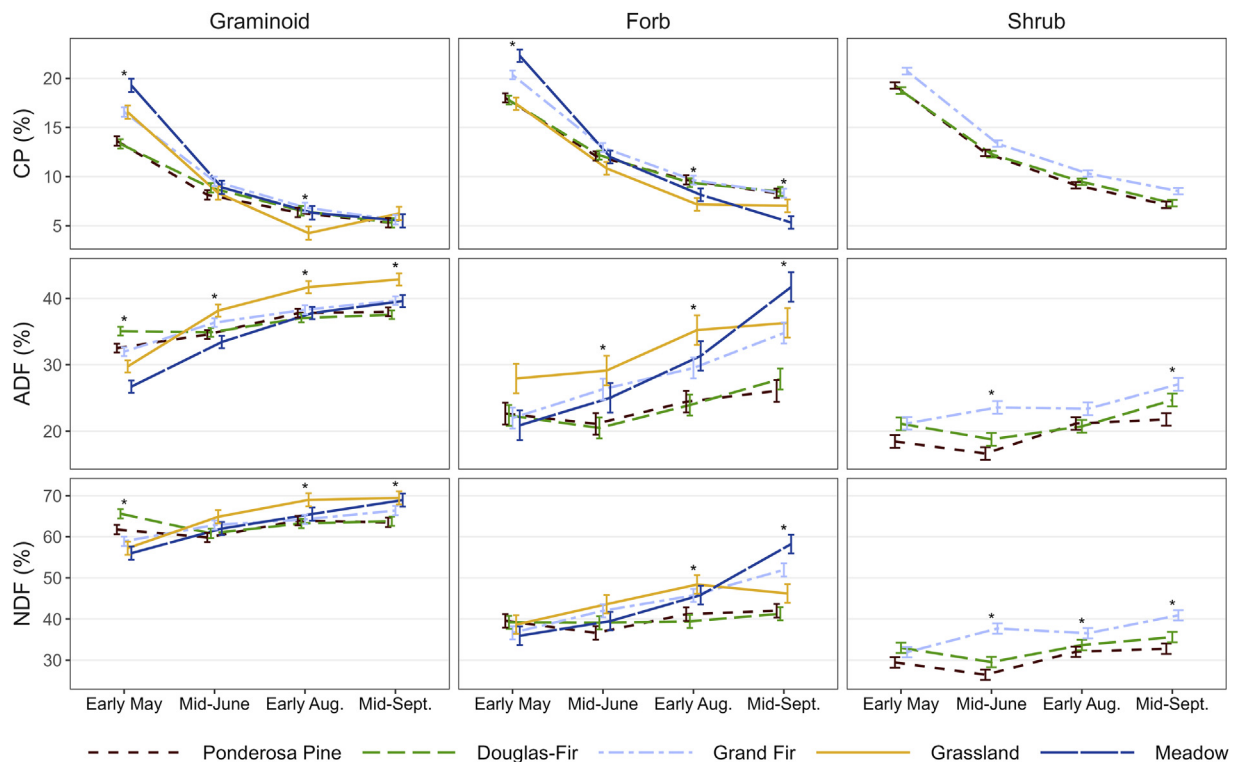


Figure 1. Influence of plant growth form and community type on crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) of clipped forage samples taken at four six-week intervals during the growing season of 2004 and 2005 in the Blue Mountains in northeastern Oregon. Means are displayed with standard error bars. P values for each community type $\times$ sampling date interaction except shrub CP were < 0.05 . The P value for the shrub CP interaction was 0.50. Within a sampling date, an asterisk indicates at least one significant difference between community types ($P < 0.05$). See Table S3 (available online at [doi:10.1016/j.rama.2025.04.004](https://doi.org/10.1016/j.rama.2025.04.004)) for the means and specific differences.

$n=3$; and sampling date, $n=4$). For both analyses, site was the experimental unit. Data were analyzed in R (R Core Team, 2019) with the lmerTest (Kuznetsova et al., 2017) and lme4 (Bates et al., 2015) packages using a linear mixed-effects model that included all factors and up to three-way interactions with site as the random effect. Means were separated with the emmeans package (Lenth, 2016, 2024) using the Tukey method. Statistical significance was accepted at $P \leq 0.05$.

Results

Community types over the growing season

All community type $\times$ sampling date interactions were significant ($P \leq 0.02$) except for shrub CP ($P=0.50$; Figure 1, Table S3; available online at [insert URL here]). In early May, graminoid CP was greatest in the meadow community type ($19.3\% \pm 0.68$; $P \leq 0.04$), and greater in the grassland and grand fir community types ($16.6\% \pm 0.68$ and $16.6\% \pm 0.48$, respectively) than the ponderosa pine and Douglas-fir community types ($13.6\% \pm 0.48$ and $13.3\% \pm 0.48$, respectively; $P < 0.01$). In mid-June, early August, and mid-September, all vegetation communities were similar in CP, except in early August where graminoid CP was 2.6 percentage points lower in the grassland type than in the grand fir type ($4.3\% \pm 0.68$ and $6.9\% \pm 0.48$, respectively; $P=0.05$). Forb CP followed a similar pattern. In early May, forb CP was greater in the meadow and grand fir types ($22.3\% \pm 0.64$ and $20.4\% \pm 0.45$, respectively) than the remaining three types ($17.7\% \pm 0.64$; $P < 0.01$). In early August, forb CP was 2.4 percentage points greater in the forested types than the grassland type ($P \leq 0.04$). In mid-September, forb CP was 3.0 percentage points greater in the forested types than

in the meadow type ($P < 0.01$). Shrub CP was 1.2 percentage points greater in the grand fir type than the ponderosa pine and Douglas-fir types ($P < 0.01$).

In early May, graminoid ADF was 5.6 percentage points greater in the ponderosa pine and grand fir types than in the meadow type ($32.3\% \pm 0.65$ vs $26.7\% \pm 0.92$, respectively; $P < 0.01$). Also, in early May, graminoid ADF was 2.8 percentage points greater in the Douglas-fir type than in the ponderosa pine and grand fir types ($P \leq 0.05$). In mid-June, graminoid ADF was greater in the grassland type ($38.2\% \pm 0.92$) than in the meadow, ponderosa pine, and Douglas-fir types ($34.3\% \pm 0.92$; $P \leq 0.03$). In early August and mid-September, graminoid ADF was 4.2 percentage points greater in the grassland type than in all forested types ($P \leq 0.04$). At every sampling date after early May, graminoid ADF in the meadow type was similar to the forested types ($P \geq 0.08$). Forb ADF was greater in the grassland type than in the ponderosa pine and Douglas-fir types in mid-June (8.3 percentage points greater ADF; $P \leq 0.04$), early August (10.5 percentage points greater ADF; $P < 0.01$), and mid-September (9.4 percentage points greater ADF; $P \leq 0.02$). In mid-September, forb ADF was 7.8 percentage points greater in the grand fir type than in the ponderosa pine and Douglas-fir types ($P \leq 0.02$). Shrub ADF in the grand fir type was 4.8 percentage points greater than in the Douglas-fir type in mid-June ($P < 0.01$) and 6.1 percentage points greater than in the ponderosa pine type in both mid-June and mid-September ($P < 0.01$).

In early May, graminoid NDF was lower in the grassland, meadow, and grand fir types than in the Douglas-fir type ($57.4\% \pm 1.61$ vs $65.6\% \pm 1.14$; $P < 0.01$). In early August, graminoid NDF was greater in the grassland type than in the Douglas-fir type ($69.0\% \pm 1.61$ vs $63.3\% \pm 1.14$, respectively; $P=0.03$). In mid-September, graminoid NDF was greater in the grassland and

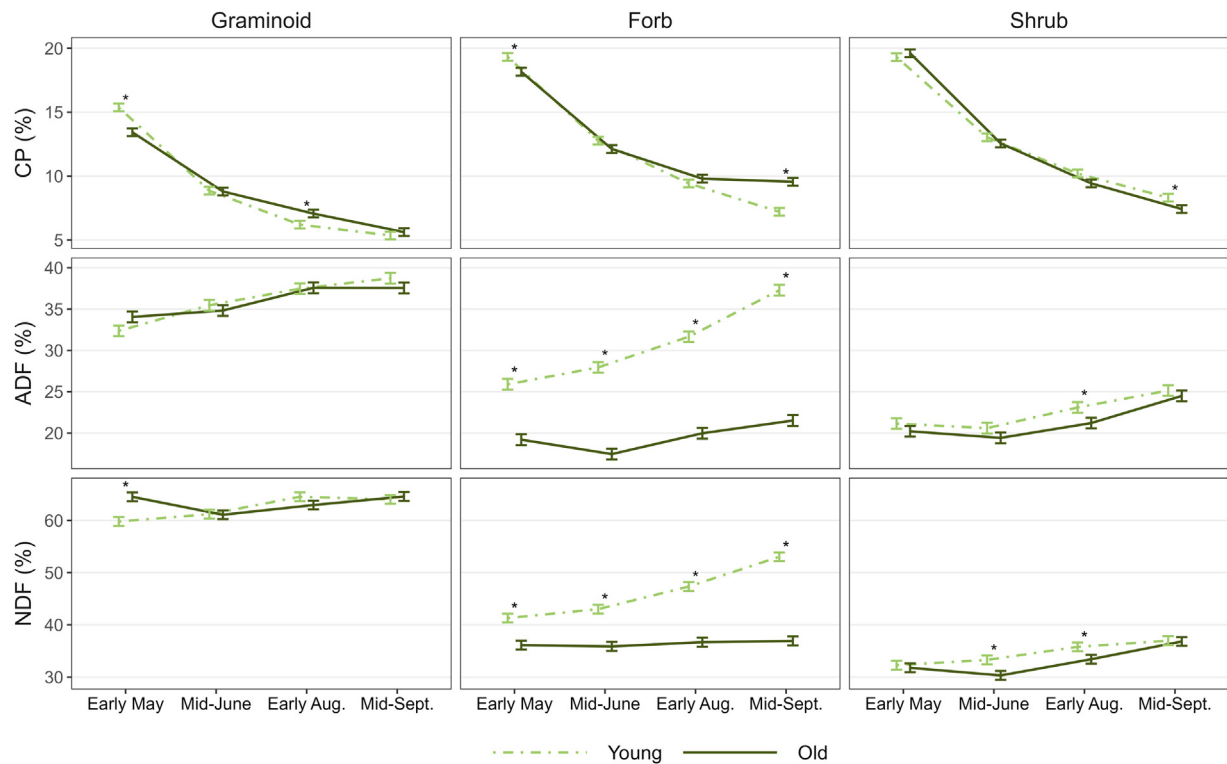


Figure 2. Influence of plant growth form and forest stand age on crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) of clipped forage samples taken at four six-week intervals during the growing season of 2004 and 2005 in the mixed-conifer forests of the Blue Mountains in northeastern Oregon. Means are displayed with standard error bars. *P* values for the stand age $\times$ plant growth form $\times$ sampling date interaction are CP: < 0.01 , ADF: < 0.01 , and NDF: < 0.01 . Within a sampling date, an asterisk indicates a significant difference between stand ages ($P < 0.05$). See Table S4 (available online at [doi:10.1016/j.rama.2025.04.004](https://doi.org/10.1016/j.rama.2025.04.004)) for the means.

meadow types than in the ponderosa pine type ($69.3\% \pm 1.61$ vs $63.5\% \pm 1.14$, respectively; $P \leq 0.05$). At every sampling date after early May, graminoid NDF in the forested community types were similar ($P \geq 0.33$). In early May and mid-June, forb NDF did not differ between all community types ($P \geq 0.10$). In early August, forb NDF was lower in the Douglas-fir type ($39.4\% \pm 1.60$) than in the grand fir ($45.7\% \pm 1.60$; $P = 0.04$) and grassland types ($48.4\% \pm 2.26$; $P < 0.01$). In mid-September, forb NDF was lower in the Douglas-fir and ponderosa pine types ($41.7\% \pm 1.65$) than in the grand fir ($51.9\% \pm 1.60$; $P < 0.01$) and meadow types ($58.2\% \pm 2.26$; $P < 0.01$). Shrub NDF in the grand fir type was greater than that in the Douglas-fir type in mid-June and mid-September (6.8 percentage points greater NDF, $P < 0.01$) and in the ponderosa pine type in mid-June, early August, and mid-September (8.0 percentage points greater NDF; $P \leq 0.03$).

Forest age and community type over the growing season

All measures of forage quality displayed stand age $\times$ sampling date $\times$ growth form interactions ($P < 0.01$; Figure 2, Table S4; available online at [insert URL here]). Graminoid CP was 2.0 percentage points greater in young stands than in old stands in early May ($15.4\% \pm 0.30$ vs $13.4\% \pm 0.30$, respectively; $P < 0.01$) but was 0.9 percentage points lower in early August ($6.2\% \pm 0.30$ vs $7.1\% \pm 0.30$, respectively; $P = 0.04$). Similarly, forb CP was 1.2 percentage points greater in young stands in early May ($19.3\% \pm 0.30$ vs $18.2\% \pm 0.31$, respectively; $P < 0.01$) but 2.4 percentage points lower in mid-September ($7.2\% \pm 0.30$ vs $9.6\% \pm 0.31$, respectively; $P < 0.01$). Shrub CP was similar between stand ages at every sampling date except mid-September where young stands were 0.9 percentage points greater than old stands ($8.3\% \pm 0.30$ vs $7.4\% \pm 0.30$, respectively; $P = 0.04$).

There were no differences in graminoid ADF between stand ages ($P \geq 0.07$) and the only difference in graminoid NDF was in early May, where old stands were 4.7 percentage points greater than young stands ($64.5\% \pm 0.84$ vs $59.8\% \pm 0.84$, respectively; $P < 0.01$). Forb ADF and NDF were greater in young stands than in old stands at every sampling date across the growing season ($P < 0.01$). In early May, forb ADF and NDF were greater in young stands by 6.7 and 5.2 percentage points, respectively ($P < 0.01$), and in mid-September by 15.8 and 16.1 percentage points, respectively ($P < 0.01$). In early August, shrub ADF was greater in young stands than old stands by 1.9 percentage points ($P = 0.04$). In mid-June and early August, shrub NDF was greater in young stands than old stands by 3.0 and 2.4 percentage points, respectively ($P \leq 0.05$).

All measures of forage quality displayed forested community type $\times$ stand age $\times$ growth form interactions ($P < 0.01$; Table 2). Graminoid CP was 1.6 percentage points greater in the young grand fir type than in all ponderosa pine and Douglas-fir types ($P \leq 0.04$). Forb CP was 1.5 percentage points greater in the old grand fir type than in the old ponderosa pine and both ages of the Douglas-fir type ($P \leq 0.05$). Shrub CP was 1.4 percentage points greater in both ages of the grand fir type than in the old ponderosa pine and Douglas-fir types ($P \leq 0.05$).

Graminoid ADF and NDF were similar across both stand ages of all forested types ($P \geq 0.37$). Within each forested type, forb ADF and NDF were greater in young stands than in old stands (11.1 percentage points greater ADF and 9.8 percentage points greater NDF; $P < 0.01$). Among old stands, forb ADF and NDF were similar between all forested types ($P \geq 0.09$). Among young stands, forb ADF was 5.9 percentage points greater in the grand fir type than in the ponderosa pine and Douglas-fir types ($P < 0.01$). Also, among young stands, forb NDF was 5.7 percentage points lower in the Douglas-fir type than in the ponderosa pine and grand fir types

Table 2
Influence of forested community type, stand age, and plant growth form on mean crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) of clipped forage samples taken at four six-week intervals between May and September of 2004 and 2005 in the mixed-conifer forests of the Blue Mountains in northeastern Oregon.

	Ponderosa Pine		Douglas-Fir		Grand Fir		SEM ¹	P values ²			
	Young	Old	Young	Old	Young	Old		CT	SA	GF	CT:SA:GF
CP (%)							0.34	< 0.01	0.50	< 0.01	< 0.01
Graminoid	8.2 ^a	8.6 ^a	8.6 ^a	8.4 ^a	10.0 ^b	9.2 ^{ab}					
Forb	12.6 ^{ab}	11.8 ^a	11.9 ^a	12.0 ^a	12.1 ^{ab}	13.4 ^b					
Shrub	12.4 ^{ab}	11.8 ^a	12.5 ^{ab}	11.8 ^a	13.2 ^b	13.2 ^b					
ADF (%)							0.74	< 0.01	< 0.01	< 0.01	< 0.01
Graminoid	35.6	35.2	36.4	35.8	36.0	36.9					
Forb	29.9 ^b	17.8 ^a	27.5 ^b	20.2 ^a	34.6 ^c	20.6 ^a					
Shrub	22.4 ^b	17.8 ^a	21.9 ^b	22.0 ^b	23.2 ^b	24.2 ^b					
NDF (%)							0.93	< 0.01	< 0.01	< 0.01	< 0.01
Graminoid	62.3	61.7	63.0	63.9	61.9	64.3					
Forb	46.3 ^c	34.2 ^a	42.4 ^b	37.5 ^a	49.8 ^c	37.5 ^a					
Shrub	34.1 ^b	27.6 ^a	33.2 ^b	34.7 ^b	36.4 ^b	36.9 ^b					
No. of Sites	8	8	8	8	8	8					

¹ SEM indicates the pooled standard error of the mean.

² P values for main effects and interaction between community type (CT), plant growth form (GF), and stand age (SA).

^{a-c} Means within a row that do not share a common superscript differ ($P < 0.05$).

($P \leq 0.04$). Shrub ADF and NDF were similar across both stand ages of all forested types, except the old ponderosa pine type, which was lower than all other types (4.9 percentage points lower ADF and 7.4 percentage points lower NDF; $P < 0.01$).

Discussion

The forage quality of plant growth forms exhibited spatial and temporal variation. At the growth form level, patterns in forage quality were consistent with the functional traits of each group. Graminoids exhibited a pronounced decline in CP and had consistently high ADF and NDF, reflecting rapid growth and senescence. Because graminoids combine photosynthetic and structural tissues, protein concentration is diluted as fibrous material accumulates over the course of the growing season. Additionally, graminoids typically have shallower root systems than forbs or shrubs (Gibbens and Lenz, 2001; Tumber-Dávila et al., 2022; Weaver, 1982), limiting access to deeper soil moisture, thus senescing when upper soil moisture is depleted. In contrast, shrubs largely separate structural and photosynthetic tissue. Woody, fibrous stems support relatively low-fiber leaves that remain photosynthetically active, resulting in less extreme seasonal changes in quality. Forbs encompass a variety of functional traits and strategies, and accordingly exhibited more variable patterns in forage quality over the course of the growing season.

In general, seasonal divergence between community types was greatest in early season for CP and in late season for ADF and NDF. Overall, CP was remarkably similar between community types. There was differentiation between community types in early May, however, at sampling dates after that, there were few differences. In contrast, there were greater differences in ADF and NDF between community types across the entire growing season. The non-forested community types exhibited a greater range in forage quality across the growing season than the forested community types. Specifically, the non-forested community types were generally higher quality early season (greater CP) and lower quality late season (greater ADF and NDF), compared to the forested types. This is consistent with observations in a similar part of northeastern Oregon (Holechek et al., 1981).

Of the non-forested community types, CP in the meadow type was greater than the grassland type only in early May and fiber was generally similar across the growing season. Similarly, in northeastern Oregon there was no difference in the quality of riparian or upland vegetation in early July or early September

(Parsons et al., 2003). The ponderosa pine and Douglas-fir types tracked closely together and were only different at one period, whereas the grand fir type was often different - being either higher quality early season or lower quality late season. Compared to the non-forested community types, graminoid forage quality in the forested community types was relatively stable over the growing season. This may be due in part to elk sedge, which was the dominant graminoid in the forested community types but absent from the non-forested community types. Relative to other graminoids, elk sedge has a lower peak forage quality, but maintains quality later into the season (Clark et al., 2013; Clark, 2003; DelCurto et al., 2019).

At the study site, stand age was controlled by periodic timber harvest. Timber harvest opens the canopy, altering plant species diversity (Clark et al., 2013; Halpern and Spies, 1995; Schoonmaker and McKee, 1988), understory biomass, and species composition (Peek et al., 2001; Young et al., 1967). We anticipated differences between young and old stands due to potential differences in light, temperature, and soil water availability (Bates et al., 2000; Walburger et al., 2007). However, in our study, stand age had little effect on graminoids or CP and primarily influenced forb and shrub fiber content, especially late season and in the grand fir community type. Likewise, in Colorado and South Dakota, others have reported no differences in CP across forest stand ages (Regelin et al., 1974; Severson and Uresk, 1988), but greater shrub ADF in younger forest stands (Severson and Uresk, 1988). In lodgepole pine (*Pinus contorta* Doug.) forests in southern British Columbia, ADF decreased as canopy cover increased (Lindgren and Sullivan, 2014), which may be related to stand age.

In young-aged, forested community types, graminoid and forb CP were greater early season and lower late season. The younger stands may have had access to more light and warmer temperatures thereby allowing them to advance phenology more rapidly. In old-aged stands, forb ADF and NDF were nearly stable over the growing season whereas in young-aged stands, not only were they greater the entire growing season, but they increased from May through September. At the study site, this trend was also observed within commonly occurring plant species (DelCurto et al., 2019), which may indicate a change in phenology or plant structure, rather than just a change in species composition. Forbs in the wetter grand fir community type may have reached more mature growth stages or grown larger, both of which are associated with greater fiber content (Van Soest, 2018). The difference in fiber content between young and old stands may also be due in part to

western yarrow. Western yarrow comprised 49% of the forb component in young stands but was absent from old stands. Relative to other forbs, western yarrow had a high fiber content: at the study site, it contained 28% ADF in May and 46% ADF in September (DelCurto et al., 2019).

In contrast, in a part of northeastern Oregon close to our study site, there were few differences in digestibility or CP of forbs between younger and older Douglas fir and grand fir stands (Long et al., 2008). However, in this study, western yarrow was present in both young and old stands and comprised a smaller portion of the sampled forb component than in our data (20% vs 62%, respectively). In this study, treatments were applied to mature stands and the authors report treated stands returning to an earlier successional stage, however, mean DBH was never reported, so comparisons between the studies are difficult.

Differences in forage quality between community types may also be influenced by western yarrow. Forb ADF and NDF were greater in the grand fir type than the other forested types during August and September. Among old stands, where western yarrow was absent, forb ADF was similar between all forested community types. In contrast, among young stands, where western yarrow was present, forb ADF in the grand fir type was greater than in the ponderosa pine and Douglas-fir types. In young stands in the grand fir type, western yarrow comprised almost two to four times as much of the forb component (81%) than in either the Douglas-fir (43%) or ponderosa pine types (22%). In another location near our study site, where western yarrow is a dominant forb species, steers selected diets containing more forbs and 3.4% greater ADF when grazing grand fir forests compared to ponderosa pine forests in June and August (Walburger et al., 2007). Despite the low quality of western yarrow, and its potential to decrease diet quality, wildlife and livestock consistently consume it on forest-grassland ranges (Damiran et al., 2019; Darambazar et al., 2013; Holechek et al., 1982a, 1982b; Mitchell and Rodgers, 1985).

Implications

Our study characterizes how the forage quality of plant growth forms changes across the growing season on a scale that has not previously been reported with ground-level data. These data provide a baseline for community-level forage quality patterns in different plant communities. However, due to shifting phenological timing (Brown et al., 2022; Chen et al., 2020; Currier and Sala, 2022) and plant biogeochemistry (Brookshire et al., 2020; McLauchlan et al., 2010), these patterns will likely change over time. Recent advances in remote sensing that have allowed the estimation of plant traits (Allred et al., 2021; Kearney et al., 2022) could be leveraged to extend and enhance the monitoring of growth form-level forage quality in this region.

While community-level averages provide valuable insight, they do not capture the complexity of the nutritional landscape. In many cases, mean forage quality at a site may be driven or skewed by a few species. In contrast, community diversity is critical as it enables herbivores to assemble diets that combine high-quality components from different species and take advantage of seasonal forage availability (Fynn and Jackson, 2022; Kluth et al., 2025). Consequently, our community-level forage quality averages likely underestimate the quality of wildlife and livestock diets.

This information is also useful for wildlife and livestock managers seeking to predict animal landscape use and allocate forage resources. The landscape distribution of large ungulates is determined by several factors (Bailey, 2005; Launchbaugh and Howery, 2005) including those considered here: community type (Johnson et al., 2000; Roever et al., 2015; Stewart et al., 2002) and forest overstory characteristics (Gillen et al., 1984; Roever et al., 2015; Walburger et al., 2009). Although the influence of landscape-scale

forage quality on animal distribution is often hypothesized (Coe et al., 2011; Raynor et al., 2016), there is relatively little research that has quantified it (Ganskopp and Bohnert, 2009; Merkle et al., 2016). As illustrated by our data, forage quality is influenced by both community type and forest overstory characteristics, indicating these factors likely influence animal distribution. Our data may be coupled with the specific dietary preferences of large herbivores (Damiran et al., 2019; Kingery et al., 1996; Torstenson et al., 2006) and used to both explain animal selection patterns in research and guide management decisions based on the distribution of forest characteristics across the landscape.

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.

CRediT authorship contribution statement

Noah G. Davis: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Samuel A. Wyffels:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation, Conceptualization. **Daalkhaijav Damiran:** Writing – review & editing, Validation, Investigation, Data curation. **Enkhjargal Darambazar:** Writing – review & editing, Investigation, Data curation. **Martin Vavra:** Writing – review & editing, Investigation, Data curation. **Robert A. Riggs:** Writing – review & editing, Investigation, Data curation. **Timothy DelCurto:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2025.04.004.

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