Influence of forest series and stand age on the growing season nutritional dynamics of plant growth forms in a mixed-conifer forest

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Transl. Anim. Sci. 2019.3:1724–1727
doi: 10.1093/tas/txz067

INTRODUCTION

Mixed-conifer forests of the inland Pacific Northwest and Northern Rockies are diverse ecosystems that provide a number of products, most conspicuously, timber, wildlife, and livestock grazing. Most of these forests are managed by the USDA Forest Service or private timber companies. It is the mandate of the Forest Service and often in the economic and social interest of private timber companies to manage for multiple uses. Forest managers desiring to manage for multiple uses must understand how differences in the landscape, both innate and silviculturally induced, influence the value of habitat and forage for wildlife and livestock.

Though it has been well established how the forage quality of plant growth forms (graminoids, forbs, and shrubs) fluctuate over the growing season, this information is limited for mixed-conifer forests (Skovlin, 1967; Clark, 2003). Timber harvest sets back succession, resulting in younger forest stands and increased understory forage production (Miller and Krueger, 1976; Walburger et al., 2007), however, little information is known about how stand age influences forage quality (Regelin et al., 1974; Severson and Uresk, 1988).

The growing season at higher elevation sites is shorter and begins later in the year, therefore, plant growth is delayed and phenology advances later. Because of this, it is often assumed that forage quality remains high at higher elevation or more mesic sites 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.

Of the dominant forest vegetation in the Blue Mountains of Oregon, the ponderosa pine series occurs at the lowest elevations and most xeric sites, the grand fir series at the highest elevations and most mesic sites, and the Douglas fir series occurs at intermediate sites (Johnson and Simon, 1987). In many forest allotments, all three of these series can occur in close proximity in a mosaic pattern across the landscape. Domestic cattle, elk, and deer are the most common ungulates that use these landscapes, all of which have specific dietary habits (Kingery et al., 1996). Understanding how the differences in forest series and stand age influence the kind, amount, and quality of forage produced will help inform managers of the value of the forage for each species and how each will use the landscape.

The preliminary analysis and report of this data has only focused on the broad differences between forest series and stand age (DelCurto et al., 2013); here, we seek to expand upon that. The objective of this study was to determine how forest series and stand age influence the forage quality of plant growth forms over the growing season in a mixed-conifer forest.

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Received April 4, 2019.
Accepted May 20, 2019.
MATERIALS AND METHODS

This study was conducted in the Blue Mountains in northeastern Oregon on a 36,245 ha block of forestland formerly owned by Boise Cascade Corporation (BCC) 20 km north of Wallowa, OR. Elevation ranges from 1100 to 1350 m and precipitation averages 650 mm with approximately 55% coming in the winter. All sites in this study were developed by Yost (2005) using BCC GIS data. Sites were selected based on potential natural climax overstory species (forest series) and stand age. The ponderosa pine (Pinus ponderosa), Douglas fir (Pseudotsuga menziesii), and grand fir (Abies grandis) series were the primary forest series at the study site and represent the dominant forest vegetation of the region. Stands with mean diameter at breast height (DBH) of less than 23 cm were classified as “young”; stands with mean DBH of greater than 23 cm were classified as “old.” Though vegetation varied across the study area, the primary graminoids were elk sedge (Carex geyeri), pinegrass (Calamagrostis rubescens), and Kentucky bluegrass (Poa pratensis). Dominant forbs were strawberry species (Fragaria spp.) and western yarrow (Achillea millefoilum). Common shrubs were snowberry (Symphoricarpos spp.), birchleaf spirea (Spirea betufolia), and Oregon grape (Berberis repens) (Damiran et al., 2008).

Production was sampled by species in August of 2003–2005 at randomly selected sites in each forest series-stand age combination (forest type) using 1.8 m² caged plots installed in the early spring of each year (Damiran et al., 2008). Sample size for production in 2004 and 2005 is listed in Table 1. Of the sites sampled for production, 8 sites within each forest type were randomly selected for nutritional quality sampling. All species that comprised the top 80% of 2003 production within each forest type were individually sampled at each site over four 6-wk intervals from early May through mid-September in 2004 and 2005.

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 h, ground to pass a 1-mm screen and, and stored in plastic bags at room temperature for subsequent chemical analysis. Samples were analyzed for crude protein content (CP; AOAC, 1990), acid detergent fiber (ADF), and neutral detergent fiber (NDF; Goering and Van Soest, 1970). All samples were run in duplicate; any sample whose coefficient of variation was greater than 5% was reanalyzed. At each site, species level CP, ADF, and NDF were averaged by weighted means into growth forms based on 2004 and 2005 production data. CP, ADF; and NDF are reported on a dry matter basis.

This experiment was considered a repeated measures completely randomized design with eight replications and four factors (forest series [n = 3], stand age [n = 2], growth form [n = 3], and sampling date [n = 4]). Site was treated as the experimental unit. Data were analyzed in R (R Core Team, 2018) with the lmerTest (Kuznetsova et al., 2017) and lme4 (Bates et al., 2015) packages using a mixed model analysis of variance that included site as the random effect. Means were separated with the emmeans package (Lenth, 2018) using the Tukey method. Statistical significance was accepted at $P \leq 0.05$.

RESULTS

Community composition and production data are presented in Table 1. Across all forest types, graminoids were a major component of the understory plant community, reaching their highest abundance in the ponderosa pine series. Shrubs were a minor component of the ponderosa pine series but comprised an important component of the

| Table 1. Influence of forest series and stand age on understory community composition and production of plant growth forms in the mixed-conifer forests of the Blue Mountains in northeastern Oregon |
|---------------------------------------------------------------|
| **Ponderosa pine**                                          | **Douglas fir**                          | **Grand fir**                             |
| Community composition, %                                    | Young | Old | Young | Old | Young | Old |
| Graminoid                                                   | 52    | 68  | 45    | 58  | 35    | 45  |
| Forb                                                        | 43    | 21  | 18    | 19  | 30    | 32  |
| Shrub                                                       | 5     | 12  | 37    | 23  | 34    | 23  |
| Production, kg/ha                                          |       |     |       |     |       |     |
| Graminoid                                                   | 641   | 749 | 446   | 606 | 464   | 628 |
| Forb                                                        | 528   | 231 | 181   | 196 | 396   | 450 |
| Shrub                                                       | 58    | 128 | 361   | 244 | 447   | 327 |
| Total                                                       | 1,227 | 1,108 | 988 | 1,047 | 1,307 | 1,406 |
| No. of sites                                                | 19    | 33  | 25    | 14  | 22    | 24  |

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community in all Douglas fir and grand fir types. Forbs were variable across forest types. This is similar to other descriptions of this area (Johnson and Simon, 1987; Walburger et al., 2007).

Both fibers (ADF and NDF) displayed a forest series × growth form × sampling date interaction ($P < 0.01$; Figure 1). CP did not display this interaction ($P = 0.46$) however, for ease of presentation, it is included in Figure 1. Graminoid ADF and NDF displayed no pattern of differences between forest series across the growing season. Forb ADF and NDF were higher in the grand fir series than

![Figure 1](image)

**Figure 1.** Influence of plant growth form and forest series on CP, ADF, and NDF of clipped forage samples taken at four 6-wk 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 95% confidence intervals. $P$ values for the forest series × plant growth form × sampling date interaction were CP: 0.46, ADF: <0.01, and NDF: 0.05.

**Table 2.** Influence of forest series, stand age, and plant growth form on mean CP, ADF, and NDF of clipped forage samples taken at four 6-wk 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* | $P$ values† |
|----------------|-------------|-----------|------|-------------|
|                | Young       | Old       | Young| Old        | FS | SA | GF | FS:SA:GF |
| CP, %          |             |           |      |            |    |    |    |          |
| Graminoid      | 8.19a       | 8.57a     | 8.67b| 8.39a      | 9.99b| 9.21ab|
| Forb           | 12.55ab     | 11.84a    | 11.89b| 12.01a     | 12.10ab| 13.46b|
| Shrub          | 12.34abc    | 11.78a    | 12.51bc| 11.83b     | 13.23b| 13.18bc|
| ADF, %         |             |           |      |            |    |    |    |          |
| Graminoid      | 35.59       | 35.21     | 36.39| 35.75      | 35.99| 36.89|
| Forb           | 29.92b      | 18.59a    | 27.54b| 20.01a     | 34.63b| 20.77a|
| Shrub          | 22.36b      | 17.95a    | 22.95b| 22.07b     | 23.14b| 24.10b|
| NDF, %         |             |           |      |            |    |    |    |          |
| Graminoid      | 62.30       | 61.70     | 62.89| 63.92      | 61.91| 64.28|
| Forb           | 46.30b      | 34.26a    | 42.38b| 37.29b     | 49.82b| 37.60b|
| Shrub          | 34.15b      | 27.51a    | 33.21b| 34.76b     | 36.51b| 36.84b|
| No. of sites   | 8           | 8         | 8    | 8          | 8   | 8   |

*SEM indicates the standard error of the mean.
†$P$ values for main effects and interaction between forest series (FS), plant growth form (GF), and stand age (SA).
*Means within a row that do not share a common superscript differ ($P < 0.05$).
the ponderosa pine and Douglas fir series from mid-June through mid-September ($P < 0.05$), across these dates, averaging 5.5% higher ADF and 6.0% higher NDF. Forb ADF and NDF were similar at ponderosa pine and Douglas fir sites across all sampling dates ($P > 0.08$). Shrub ADF and NDF were higher in the grand fir series than the ponderosa pine series in mid-June and mid-September ($P < 0.01$), at these dates, averaging 5.6% higher ADF and 9.0% higher NDF. Shrub ADF and NDF in the Douglas fir series were intermediate or similar to the grand fir and ponderosa pine series at all sampling dates.

All measures of forage quality displayed significant forest series × stand age × growth form interactions ($P < 0.01$; Table 2). For all growth forms, CP displayed no clear pattern of difference across forest series and stand ages. Graminoid ADF and NDF were similar across all forest types ($P > 0.36$). Forb ADF and NDF were higher in young stands than old stands in all forest series ($P < 0.01$), averaging 10.9% higher ADF and 9.8% higher NDF. Shrub ADF and NDF were lower in the old ponderosa pine type than all other forest types ($P < 0.01$), averaging 5.0% lower ADF and 7.6% lower NDF.

**DISCUSSION**

Managers often assume that forage quality remains higher later into the growing season in more mesic plant communities, however, this pattern was not observed. Fiber content (ADF and NDF) of forbs and shrubs in the grand fir series was lowest, specifically later in the growing season. Though no statistical analyses were completed, Walburger et al. (2007) reported steer diets with 3.4% higher ADF when grazing grand fir forests compared with ponderosa pine forests.

Stand age has little effect on graminoids or CP and primarily influences forb and shrub fiber content. Similarly, other researchers have been unable to detect differences in CP in forest stands differing in age (Regelin et al., 1974; Severson and Uresk, 1988). Severson and Uresk (1988) also reported higher ADF of a shrub species in older stands of a ponderosa pine forest.

Forest managers must understand how differences in the landscape, both innate and silviculturally induced, influence the value of habitat and forage for wildlife and livestock. The forage quality of understory plant communities of forests along a moisture or elevation gradient may differ in ways not often considered by managers or researchers. Timber treatments that open the canopy and reduce stand age may improve forage production but may also result in reduced forage quality.

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