The influence of forest series and stand age on individual plant species nutritional quality in a mixed-conifer forest

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INTRODUCTION

Forested ecosystems present a broad array of existing and potential plant communities based both on plant associations (sensu Daubenmire, 1952) and successional stage. These different combinations of plant associations and vegetation successional stage have been termed ecological land units in resource planning (Haufler et al., 1996). Forage quantity and quality, which theoretically vary across ecological land units, are important factors that affect habitat selection by ungulates. Managing forested ecosystems for sustainable and multiple uses requires that managers have a thorough understanding of how the type and intensity of resource dynamics influences other ecosystem components. In particular understanding how different silvicultural prescriptions affect future understory vegetation composition, production, and nutritive quality is essential to forest managers in order to maintain sustainable timber, livestock, and wild ungulate production. Numerous researchers have observed variations in habitat use as influenced by forest type within forested rangeland allotments (Parsons et al., 2003; DelCurto et al., 2005; Roever et al., 2015). Unfortunately, research designed to model secondary succession in forests affected by multiple disturbance agents is rare (Riggs et al., 2000). Likewise, research designed to describe the variation in forage quality and quantity among ecological land units (such as forest series and stand age) throughout the summer grazing period is limited.

The purpose of this study was to characterize changes in forage quality of commonly occurring plant species during the growing season for three forest series and two successional stages (stand ages) in a mixed-conifer forest. Furthermore, we hypothesized that plant species found in numerous forest types may be effective key species to evaluate the influence of overstory characteristics on understory forage quality.

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 1,100 to 1,350 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 geographic information system 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.”

Production was sampled by species in August of 2004 and 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). Of the species that occurred in all forest series, we selected the two most dominant graminoids, forbs, and shrubs for nutritional quality sampling. These species were the graminoids: elk sedge (Carex geyeri) and pinegrass (Calamagrostis rubescens), the forbs: strawberry (Fragaria spp.) and western yarrow (Achillea millefolium), and the shrubs: snowberry (Symphoricarpos albus) and birchleaf spirea (Spirea betulifolia). Of the sites sampled for production, eight sites within each forest type were randomly selected for nutritional quality sampling. Each species was individually sampled at each site, where it occurred 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 for 48 h in a forced-air oven, ground to pass a 1-mm screen, and stored in plastic bags at room temperature for subsequent chemical analysis. Samples were analyzed for crude protein (CP; AOAC, 1990) 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. This experiment was considered a repeated measures completely randomized design with eight replications and two factors (forest type, n = 6; and sampling date, n = 4). Because each species was not found in both age classes of each forest series, each forest type was treated as a unique factor level. Site was treated as the experimental unit. Each species was analyzed separately in R (R Core Team, 2018) with the lmTest (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 AND DISCUSSION

#### Graminoids

Elk sedge was the most dominant forage found across forest series and stand ages, representing 11–33% of the understory production (Table 1). CP displayed a forest type × sampling date interaction ($P < 0.01$; Table 2). In early May, the old grand fir type had higher CP ($P < 0.05$) than the old Douglas fir type with both ponderosa pine types being intermediate. No differences in Elk sedge CP content was observed in early August and mid-September. NDF also displayed a forest type × sampling date interaction ($P < 0.05$; Table 3). The old Douglas fir type was higher ($P < 0.05$) than old ponderosa pine type in early May and the old grand fir type was higher than the ponderosa pine and Douglas fir types in mid-June. Pinegrass CP content was not influenced ($P > 0.05$) by forest type at any sampling dates, averaging 15.0% in early May and declining to 4.7% by mid-September. Likewise, NDF

### Table 1. Production of the most common understory species in the forest types (forest series and stand ages) of the Blue Mountains of Oregon

| Species          | Ponderosa pine | Douglas fir | Grand fir |
|------------------|----------------|-------------|-----------|
|                  | Young | Old | Young | Old | Young | Old |
| *Graminoids*     |       |     |       |     |       |     |
| Elk sedge (Carex geyeri) | 138 (11) | 159 (14) | NS*  | 342 (33) | NS  | 177 (13) |
| Pinegrass (Calamagrostis rubescens) | 126 (10) | 121 (11) | 94 (10) | 93 (9) | NS  | 164 (12) |
| *Forbs*          |       |     |       |     |       |     |
| Strawberry (Fragaria spp.) | 62 (5) | 21 (2) | 30 (3) | 33 (3) | NS  | 31 (2) |
| Western yarrow (Achillea millefolium) | 61 (5) | NS   | 33 (3) | NS   | 26 (2) | NS   |
| *Shrubs*         |       |     |       |     |       |     |
| Birchleaf spirea (Spirea betulifolia) | 5 (0.4) | 18 (2) | NS   | 42 (4) | 51 (4) | 56 (4) |
| Snowberry (Symphoricarpos albus) | 10 (1) | 32 (3) | 22 (2) | 72 (7) | 43 (4) | 45 (3) |
| **Total**        | 1,227 | 1,108 | 988  | 1,047 | 1,307 | 1,406 |

Production is expressed as kg/ha and % of understory community (parenthesis). Data are from 137 plots clipped by species in August of 2004 and 2005. Means are only reported for plant species that were in the top 80% of the plant community based on production weight. Plant species were not in the top 80% of the understory vegetation based on 2003 peak production plots.

*NS = nonsampled.*

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content was not influenced by forest type at any sampling date.

**Forbs**

Western yarrow CP content displayed a forest type × sampling date interaction (*P < 0.01*). In early May, the young grand fir type had higher CP than the young ponderosa pine or young Douglas fir type; in mid-June, CP content was still higher (*P < 0.05*) in the young grand fir type than young ponderosa pine type but did not differ from the young Douglas fir type (*P > 0.05*). CP content was similar across forest types in early August and mid-September. Western yarrow NDF content also displayed a forest type × sampling date interaction (*P < 0.01*) with the young grand fir type having higher NDF than the young ponderosa pine type in mid-June and mid-September. Strawberry CP content was higher in the old grand fir type than the old ponderosa pine type (*P = 0.07*). In addition, strawberry CP declined with advancing maturity, averaging 18.2% CP in early May and declining to 9.4% in mid-September. NDF content was influenced by a forest type × sampling date interaction (*P < 0.01*). The old grand fir type had higher NDF than both ponderosa pine types in mid-June (*P < 0.05*) and higher NDF than the young Douglas fir type in mid-September (*P < 0.05*). Like western yarrow, NDF content of strawberry was relatively low and did not change (*P > 0.05*) over the growing season.

**Shrubs**

Birchleaf spirea CP content (*P = 0.08*) tended to be higher in grand fir understories than ponderosa pine and Douglas fir understories. Likewise,
Birchleaf spirea was influenced by sampling period \((P < 0.05)\) ranging from 20.5% CP in early May to 6.9% CP in mid-September. Birchleaf spirea NDF content displayed a forest type \(\times\) sampling date interaction \((P < 0.01)\) with both grand fir types having higher NDF than both ponderosa pine types in mid-June and mid-September. Snowberry leaf CP content was not influenced by forest series or stand age \((P > 0.05)\) and ranging from 19.6% in early May to 7.3% CP in mid-September. Snowberry NDF content displayed a treatment \(\times\) sampling date interaction \((P = 0.02)\). In early May, the old Douglas fir and old grand fir types were higher in NDF than the old ponderosa pine type. In mid-June, the young grand fir type was higher in NDF than all ponderosa pine and Douglas fir types.

Mixed-conifer forest rangelands in the interior western United States are important forage resources for the beef industry and provide critical habitat for wildlife. These areas are also diverse in respect to plant communities and present a challenge to sustainable rangeland management. We anticipated that individual plant species quality would differ as a function of overstory canopy and stand age and this difference would be most prominent in the early-August and mid-September sampling times. Instead, most of the differences in CP content occurred during the first two sampling dates with little to no differences in CP content at the end of the growing season. As expected, NDF content was highest in the graminoids.

### Table 3. The influence of forest series and stand age on the NDF concentration of the most common understory species in the mixed-conifer forests of the Blue Mountains in northeastern Oregon

| Species          | Ponderosa pine | Douglas fir | Grand fir | SEM |
|------------------|----------------|-------------|-----------|-----|
|                  | Young | Old | Young | Old | Young | Old |
|                  |       |     |       |     |       |     |
| Elk sedge*       |       |     |       |     |       |     |
| Early May        | 62.77ab | 61.31* | –     | 67.83b | –     | 65.39ab |
| Mid-June         | 61.52b | 57.99* | –     | 62.18b | –     | 70.28b |
| Early August     | 66.23 | 63.69 | –     | 63.76 | –     | 65.59 |
| Mid-September    | 61.37 | 63.93 | –     | 64.09 | –     | 68.57 |
| Pinegrass        |       |     |       |     |       |     |
| Early May        | 62.94 | 61.29 | 64.57 | 65.17 | –     | 64.59 |
| Mid-June         | 59.37 | 59.13 | 60.62 | 57.47 | –     | 62.14 |
| Early August     | 62.16 | 60.45 | 63.20 | 60.77 | –     | 62.66 |
| Mid-September    | 61.94 | 62.20 | 63.69 | 64.21 | –     | 66.19 |
| Western yarrow*  |       |     |       |     |       |     |
| Early May        | 43.11 | –     | 43.57 | –     | 38.63 | –     |
| Mid-June         | 41.09b | –     | 43.94ab | –     | 47.55b | –     |
| Early August     | 53.45 | –     | 50.46 | –     | 54.62 | –     |
| Mid-September    | 58.33b | –     | 62.62ab | –     | 64.40b | –     |
| Strawberry*      |       |     |       |     |       |     |
| Early May        | 35.63 | 34.71 | 36.74 | 37.81 | –     | 36.24 |
| Mid-June         | 33.87b | 30.60* | 35.75ab | 39.34b | –     | 39.25b |
| Early August     | 37.96 | 36.33 | 36.49 | 36.17 | –     | 36.81 |
| Mid-September    | 35.33ab | 34.58ab | 33.25a | 34.63ab | –     | 38.72b |
| Birchleaf spirea*|       |     |       |     |       |     |
| Early May        | 36.18 | 30.60 | –     | 35.09 | 30.41 | 31.55 |
| Mid-June         | 28.83b | 25.03b | –     | 32.94bc | 42.41b | 38.69ab |
| Early August     | 32.33a | 31.99a | –     | 34.81ab | 41.88b | 39.22ab |
| Mid-September    | 31.77a | 33.08ab | –     | 40.51bc | 43.67b | 46.00f |
| Snowberry*       |       |     |       |     |       |     |
| Early May        | 28.22ab | 23.68a | 27.62ab | 34.27b | 26.81ab | 33.80b |
| Mid-June         | 26.23a | 22.51a | 23.68a | 25.37a | 35.00a | 30.79ab |
| Early August     | 32.02 | 28.97 | 30.60 | 29.77 | 32.36 | 31.76 |
| Mid-September    | 32.31ab | 28.73a | 30.44ab | 35.71ab | 37.42a | 36.64ab |

Means are averaged over samples taken at four 6-wk intervals between May and September of 2004 and 2005 at eight sites of each forest type.

* A treatment \(\times\) sampling date interaction was observed \((P < 0.05)\).

* *Means within a row that do not share a common superscript differ \((P < 0.05)\).
as compared with the forbs and shrubs (Van Soest, 1994). However, we did not expect to observe higher NDF concentrations in the grand fir forest series plants as compared with the ponderosa pine and Douglas fir series. Forested habitats are important in that they provide higher forage quality later into the summer grazing period as compared with non-forested habitats. This observation is supported by other researchers who have documented the value of overstory characteristics on understory forage quality (Walburger et al., 2007; Clark et al., 2013) and the shift in beef cattle distribution to forested north aspects late in the grazing period (DelCurto et al., 2005; Roever et al., 2015).

Implications

Forest rangelands in the inland Pacific Northwest are diverse with substantial variation in vegetation types because of large pasture sizes and dramatic differences in elevation and aspect. Our data suggests that forest series and stand age influence the forage quality of plant species commonly occurring in the understories of these mixed-conifer forests. CP content differed early in the growing season, where grand fir sites had higher protein, whereas CP was not influenced by forest type later in the growing season. Plant species found in grand fir forest types contained the highest concentrations of NDF. Understanding how overstory vegetation modifies understory microclimates and, in turn, the quality of understory vegetation may provide needed insights to how large herbivores use landscapes on a space and time continuum.

Conflict of interest statement. None declared.

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