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TREE SIZE AND UNDERSTORY PHYTOMASS PRODUCTION IN A WESTERN JUNIPER WOODLAND

Milda R. Vaitkus and Lee E. Eddleman

ABSTRACT.—Understory phytomass production in a western juniper (Juniperus occidentalis) woodland was examined relative to tree size in central Oregon in 1983 and 1984. Vegetation was sampled in two zones, the canopy zone (beneath the canopy) and the intercanopy zone (the space between canopies), on two adjacent sites—a lower slope site with shallow soil and an upper slope site with deeper soil. Sampling was stratified into three tree size classes. Individual species production was significantly affected by tree size and location relative to tree canopy. Production of bottlebrush squirreltail, bluebunch wheatgrass, cheatgrass, miscellaneous annual grasses, perennial forbs, and annual forbs increased with increasing tree size. Sandberg bluegrass production was greater in the intercanopy than the canopy zone, while production of bottlebrush squirreltail, bluebunch wheatgrass, miscellaneous annual grasses, and both perennial and annual forbs was greater in the canopy zone. Production of cheatgrass was determined by the interaction of tree size and zone. Phytomass relationships were expressed to a greater degree on the upper slope site, where total production exceeded that of the lower slope site by approximately 50% the second year of the study.

Individual trees appear to exert a great influence on associated vegetation as western juniper woodlands progress from the seedling (tree establishment) phase to closed stands of mature trees. Original community dominants appear to be spatially segregated beneath tree canopies and associated with large trees, while formerly less common species, such as cheatgrass, come to dominate the entire site.

Key words: Juniperus occidentalis, western juniper, phytomass production, understory, tree size.

Western juniper (Juniperus occidentalis Hook., subsp. occidentalis) was historically associated with desert-grassland vegetation and primarily occurred in open stands, on plateaus, or on edges of ponderosa pine (Pinus ponderosa) forests (Sowder and Mowat 1958). A dramatic increase in establishment and density of western juniper in much of the Intermountain West seems to have occurred in the late 1800s and early 1900s (Burkhardt and Tisdale 1969, Adams 1975, Young and Evans 1981). Western juniper woodlands are presently concentrated in central and eastern Oregon, with extensions into northern California, northern Nevada, southwestern Idaho, and eastern Washington (Dealy et al. 1978). Expansion of western juniper into sites originally dominated by mountain big sagebrush (Artemisia tridentata spp. vaseyana) and perennial bunchgrasses in southwestern Idaho was found to be directly related to cessation of fire (Burkhardt and Tisdale 1976). Overgrazing has also been proposed as a factor contributing to increased western juniper density (Dealy et al. 1978).

Effects of increased western juniper frequency and density on associated vegetation are poorly understood. In pinyon-juniper woodlands, increases in frequency and density of trees have been shown to reduce the quantity and diversity of associated species (Dwyer 1975). Pinyon and juniper begin to exert their influence over the understory at the stage of community development characterized by an abundance of seedlings and saplings, and a few vigorous, mature trees (Blackburn and Tueller 1970). In 60–70 years, although height of trees at this point is only double that of shrubs, understory species decline at an increasingly rapid rate. As tree density increases, the understory is yet further reduced (Blackburn and Tueller 1970, Dwyer 1975, West et al. 1979, Tausch et al. 1981, Schott and Pieper 1985). Seed reserves of primary understory species decline and species diversity decreases (Koniak and Everett 1982).

Spatial patterns of understory vegetation may also develop beneath individual woodland trees. Patterns of plant cover relative to
distance from the bole have been found for singleleaf pinyon (Pinus monophylla), Utah juniper (Juniperus osteosperma) (Everett and Koniak 1981), and one-seed juniper (Juniperus monosperma) trees (Arnold 1964). Such patterns may vary with tree size, as found by Everett et al. (1983) in singleleaf pinyon–Utah juniper stands.

Climax stands of western juniper contain trees of mixed ages, ranging from first-year seedlings to trees several hundred years old, with most individuals in an intermediate age class (Burkhardt and Tisdale 1969). Seral stands are usually composed of predominantly younger age classes with a maximum age of nearly 100 years. Personal observations, as well as data from Driscoll (1964), suggest that as western juniper stands increase in age, size, and density, understory production is reduced and species composition changes. This vegetation suppression by western juniper at particular stages of woodland development has not been closely examined.

This study was begun to determine the relationship between individual trees of various sizes (ages) and the phytomass production of associated vegetation beneath and immediately adjacent to the canopy. Specifically, we wanted to identify phytomass production patterns of associated vegetation relative to western juniper tree size and location within seral stands.

**METHODS**

The study area is located 8.8 km southeast of Prineville in central Oregon, on a gentle north-northwest–facing slope. Long-term precipitation in Prineville (elevation 868 m), the nearest recording station, averages 254 mm annually, 89% of which occurs from October to June.

The area is representative of the Juniper Zone described by Driscoll (1964) and is characterized by the dominance of western juniper and associated shrubby vegetation, most commonly Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis), mountain big sagebrush (Artemisia tridentata ssp. vaseyana), and scattered low sagebrush (Artemisia arbuscula). Native perennial grasses include Idaho fescue (Festuca idahoensis), bottlebrush squirreltail (Sitanion hystrix), bearded bluebunch wheatgrass (Agropyron spicatum), and Sandberg bluegrass (Poa sandbergii). Cheatgrass brome (Bromus tectorum) and many forbs, both annual and perennial, comprise the remainder of the herbaceous component.

The study area showed no evidence of fire in the last 100 years and had been used for much of the past decade as pasture, grazed heavily during the winter and early spring. Mixed tree size classes (Burkhardt and Tisdale 1969), continuing recruitment of western juniper seedlings, the presence of locally isolated areas of vigorous bunchgrasses, along with soil characteristics, indicated the area was at an early to mid-seral successional phase.

Study sites at two elevations were selected in this area—one at an elevation of approximately 1140 m and another at 1220 m. Precipitation on each site was measured with U.S. Forest Service rain gauges. Lower site soils were relatively shallow (330 mm), clayey, mesic Aridic Durixerolls, while upper site soils were moderately deep (740 mm), clayey-skeletal, frigid Pachic Argixerolls. The soils, vegetation, fire, and grazing history are typical of the western juniper communities on soils of basaltic origin described by Driscoll (1964). Canopy cover of western juniper, determined using the line-intercept method (Canfield 1941), was 21% on the lower site and approximately 40% on the upper site.

On each site an area representative of general woodland conditions (i.e., tree size and density) was identified and a 50 × 40-m plot arbitrarily placed within it. In each plot all trees were inventoried as to height and canopy diameter and then separated into three canopy diameter size classes—small (1–3 m), intermediate (3–5 m), and large (5–9 m), corresponding to approximate average ages (determined from core samples) of 40, 55, and 75 years, respectively. From each of these three canopy size classes, five trees without overlapping canopies were randomly selected for sampling.

During June and July in both 1983 and 1984, phytomass production in the herbaceous layer was measured. The five individual trees within each size class were used as replications. Production was determined on an individual tree basis by clipping vegetation to ground level in small plots along transects corresponding to the cardinal directions.
Each transect was established within a 90-degree quadrant radiating from the bole of the tree and extending at least 1.2 m beyond the edge of the canopy. Samples were designated into two zones: the canopy zone (from the bole outward to the edge of the canopy) and the intercanopy zone (the area beyond the edge of the crown extending into the open space between tree canopies). Because each interstitial area was of different size and configuration, the intercanopy zone was restricted to an area immediately adjacent to an individual tree's canopy. Plot number and size varied with tree size to insure sampling at least 10% of each of these zones ($n = 2$ to $n = 7$; $20 \times 20$-cm to $50 \times 60$-cm plots). Samples were dried at 100 C for 24 hours and weighed. Productivity comparisons were made on the basis of grams of dry matter per square meter.

Data was log-transformed to stabilize variance, and a split-split-plot analysis of variance was used. Main plots were years (1983, 1984) and tree size (small, intermediate, large). Subplots were zones (canopy, intercanopy), and sub-subplots were quadrants (not addressed in this paper). Where interactions were not significant, main effects means were separated using Tukey's w-procedure at $P = .05$ (Steel and Torrie 1980). When interactions were significant, multiple comparisons were made by computing an adjusted comparison-wide probability using the Bonferroni inequality (Miller 1986). All analyses were performed using the Statistical Analysis System (SAS Inc. 1988).

RESULTS

In 1983 and 1984 total precipitation at Prineville, Oregon, was above the 30-year average, with precipitation on the study sites even higher. On-site precipitation from October to June was 420 mm and 480 mm on the lower site and 454 mm and 494 mm on the upper site for 1983 and 1984, respectively. This compared with 235 mm for the 30-year average at Prineville during the same period. Total production on the lower slope site, which showed a significant year-by-size interaction (Table 1), was 38.9 g/m$^2$ in 1983 and 18.3 g/m$^2$ in 1984. Sandberg bluegrass, bottlebrush squirreltail, cheatgrass, and annual forb production comprised the greatest part of this production on the lower slope site. Production of these individual species was significantly greater in 1983 than in 1984 (Fig. 1).

On the upper slope site, total production was 42.4 g/m$^2$ in 1983 and 36.2 g/m$^2$ in 1984 and showed no between-year differences or interactions (Table 2). Species contributing most to total production on the upper slope site were Sandberg bluegrass, Idaho fescue, and perennial and annual forbs. In contrast to the lower slope site, only miscellaneous annual grasses and annual forbs showed any year-to-year differences (Fig. 1); both had significantly greater production in 1984 than in 1983.

Other relationships on both sites were confounded by interactions between main effects (Tables 1, 2). Perennial forb and total production showed significant year-by-size interactions on the lower slope site, while cheatgrass production on the upper slope site had a significant year-by-zone interaction. Because of these interactions and between-year differences in precipitation patterns, we analyzed data by individual years to examine the main effects of tree size and zone.

Tree size had a significant effect on the phytomass production of individual species on both sites (Tables 1, 2). On the lower slope site, production of bottlebrush squirreltail (1983) and perennial forbs (both years) was significantly greater associated with large trees than with small trees (Fig. 2). On the upper slope site, production of bottlebrush squirreltail (1983), bluebunch wheatgrass (1983), cheatgrass (1983), miscellaneous annual grasses (both years), perennial forbs (both years), and annual forbs (1983) was greater associated with large than small trees (Fig. 3). These relationships were reflected in significantly greater total production associated with large than with intermediate and small trees in 1984 (data not shown).

Location relative to the tree canopy also significantly affected production on both sites (Tables 1, 2). On the lower slope site (Table 1) there were significant differences in production between canopy and intercanopy zones for Sandberg bluegrass (both years), bottlebrush squirreltail (1983), bluebunch...
Table 1. ANOVA results of log-transformed mean phytomass production on the lower slope site.

<table>
<thead>
<tr>
<th>Species</th>
<th>1983</th>
<th>1984</th>
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<tbody>
<tr>
<td></td>
<td>Size Zone</td>
<td>Size Zone</td>
</tr>
<tr>
<td>Sandberg bluegrass</td>
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<tr>
<td>Bottlebrush squirreltail</td>
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<td>Bluebunch wheatgrass</td>
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<td>Cheatgrass</td>
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<td>Misc. annual grasses</td>
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<tr>
<td>Perennial forbs</td>
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<td>Annual forbs</td>
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<td>Sagebrush</td>
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<tr>
<td>Total</td>
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</tbody>
</table>

*p < .05.
**p < .01.

Table 2. ANOVA results of log-transformed mean phytomass production on the upper slope site.

<table>
<thead>
<tr>
<th>Species</th>
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<tbody>
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<td>Size Zone</td>
</tr>
<tr>
<td>Sandberg bluegrass</td>
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<tr>
<td>Idaho fescue</td>
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<tr>
<td>Bottlebrush squirreltail</td>
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<td>Bluebunch wheatgrass</td>
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<td>Cheatgrass</td>
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<td>Misc. annual grasses</td>
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<td>Perennial forbs</td>
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<td>Annual forbs</td>
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<td>Sagebrush</td>
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<tr>
<td>Total</td>
<td>**</td>
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</tbody>
</table>

*p < .05.
**p < .01.

wheatgrass (both years), and annual forbs (1984). On the upper slope site (Table 2) Sandberg bluegrass (both years), bottlebrush squirreltail (1983), cheatgrass (1983), miscellaneous annual grass (1984), perennial forb (both years), and annual forb (1984) production differed significantly between zones. All species, with the exception of Sandberg bluegrass, had significantly greater production in the canopy than the intercanopy zone (Figs. 4, 5). Sandberg bluegrass production was greater in the intercanopy than in the canopy zone.

Interaction between tree size and zone affected the production of several species (Tables 1, 2). Cheatgrass production on both sites was closely tied to both tree size and zone. The interaction of size and zone was significant both years on the lower slope site and in 1984 on the upper site. On the lower slope site cheatgrass production in the canopy of large trees was greater than production associated with small and intermediate trees. On the upper slope site production of cheatgrass in both zones was greater associated with large and intermediate trees than with small trees. Bottlebrush squirreltail production also showed significant interaction between size and zone. On both sites (1984) bottlebrush squirreltail canopy production was greater associated with large and intermediate trees than with small trees. These species may have contributed to significantly greater total production in the canopy zone of large versus small and intermediate trees in 1984 on the lower slope site (data not shown). Sagebrush production on the upper slope site in 1983 also showed a significant tree size-by-zone interaction (Table 2). Production of sagebrush was greater in the canopy of large than
in small and intermediate trees, and in the intercanopy of large and intermediate than in small trees.

**DISCUSSION**

In this study we found that phytomass production was influenced by both tree size and zone (location relative to the tree canopy). Tree size significantly affected production of most species, especially on the upper slope site (Fig. 3). Bottlebrush squirreltail, bluebunch wheatgrass, cheatgrass, miscellaneous annual grass, and perennial and annual forb production increased as tree size increased. Sandberg bluegrass production, on the other hand, showed no relationship to tree size.

In community level studies, influences of increasing tree size have been found to negatively impact production of associated vegetation. West et al. (1979), working in singleleaf pinyon-Utah juniper communities, found that as tree size increased, understory biomass declined. Blackburn and Tueller (1970) found a reduction in the number of species present in a black sagebrush (*Artemisia nova*) community as pinyon and Utah juniper increased in size and density. Everett et al. (1983) discovered similar negative species-specific responses to tree size in singleleaf pinyon-Utah juniper communities. In these studies an increase in tree size resulted in greater competition between trees and understory vegetation, with trees outcompeting other species. Conversely, in our study large trees had a positive influence on associated vegetation. On our study site large trees appeared to act as “refuges” for most species, with greatest production associated with the largest tree size.

This importance of microsite in determining species’ distribution and production was also reflected in zone relationships. Lower light levels and temperatures, higher humidity, and, possibly, greater nutrient concentrations in the canopy zone (Doescher et al. 1987) favored production of bottlebrush squirreltail, bluebunch wheatgrass, cheatgrass, miscellaneous annual grasses, and perennial forbs. Sandberg bluegrass production was always greater in the drier, warmer intercanopy zone. These patterns of individual species production relative to tree canopy are not unique to western juniper. Singleleaf pinyon (*Pinyon monophylla*) and Utah juniper (*Juniperus osteosperma*) understory plant cover (Everett and Konia 1981) and one-seed juniper (*Juniperus monophylla*) understory
Fig. 2. Mean phytomass production (g/m²) of the three tree size classes in 1983 and 1984 on the lower slope site. For each species, the three tick marks indicate the three tree size classes—small, intermediate, and large. Vertical error bars represent the 95% confidence intervals of the means. (*) indicates a significant difference between tree size at p < .05, ~ indicates a significant size-by-zone interaction, p < .05.

Fig. 3. Mean phytomass production (g/m²) of the three tree size classes in 1983 and 1984 on the upper slope site. For each species, the three tick marks indicate the three tree size classes—small, intermediate, and large. Vertical error bars represent the 95% confidence intervals of the means. (*) indicates a significant difference between tree size at p < .05, ~ indicates size-by-zone interaction, p < .05.)

production (Arnold 1964) were found to occur in species-specific patterns, dependent upon distance from the bole of the tree.

Composition differences in understory species between the upper and lower site may be traced to differences in elevation, the original plant community, soil depth, and, perhaps, long-term grazing. The upper site also appears to receive slightly more October through June precipitation and may be cooler during the growing season (personal observation). The shallower soils of the lower site, in combination with warmer and drier conditions, supported more squirreltail and cheatgrass. Proximity to a water source may have also resulted in heavier grazing pressure on the lower site. Idaho fescue, on the other hand, was found only on the upper slope site.

Total production tended to be greater and less variable on the upper than on the lower site. Year-to-year differences in precipitation patterns may affect species production more on the lower slope site, where soil depth precludes much storage of soil moisture.
Spatial and tree size relationships observed in this study indicate the significant role microenvironments play in species distribution and production. As individual trees increase in size (or as western juniper communities progress from tree invasion to closed stands), they exert a greater influence on associated vegetation. Original community dominants appear to become spatially segregated beneath tree canopies of large trees, while less common species, such as cheatgrass, increase across the entire site.

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