Characteristics of Buckbrush Shrubs Exposed to Herbivores after Seven Years of Protection

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Abstract—In dense ponderosa pine (Pinus ponderosa Laws.) forests of northern Arizona, forage limitations may lead to severe herbivory by large ungulates on certain plant species. In 1999, we fenced 76 buckbrush (Ceanothus fendleri Gray) shrubs to protect them from herbivores and study growth and reproduction in response to forest restoration treatments implemented on the Fort Valley Experimental Forest. After seven years, we removed fences from around half the plants and examined herbivore impacts on vegetative characteristics. In spring, and again in fall, we measured stem heights and took photographs of exposed shrubs and protected controls. In fall, we also collected stems to analyze size, biomass, and leaf area. Plants exposed to herbivores had significantly less leaf area and total leaf weight than protected control plants. Stem length, diameter, and weight were statistically similar between exposed and control groups. Results from this study suggest that temporary protection from herbivores during the early stages of forest restoration may enhance rates of development and persistence of native plants such as buckbrush.

Introduction

Buckbrush (Ceanothus fendleri Gray) is a native shrub species, common in ponderosa pine (Pinus ponderosa Laws. var. scopulorum Engelm.) forests of northern Arizona. As a nitrogen-fixer, its leaves, stems, and flowers are relatively nutritious, which makes buckbrush a preferred browse plant for large ungulates such as mule deer (Odocoileus hemionus) and Rocky Mountain elk (Cervus elaphus) (Urness et al. 1975, Allen 1996). In some areas, herbivory on buckbrush can be severe and constrain growth, flowering, and stem recruitment (Huffman and Moore 2003). Large mature buckbrush plants typically have stout woody stems and spines that discourage herbivory (Kearney and Peebles 1964). Where herbivory is severe, however, plants may remain small and have reduced structural defenses. In this study,
we were interested in herbivore effects on buckbrush during the process of ponderosa pine forest restoration. Specifically, we wondered if protecting buckbrush from large herbivores for a period of several years following forest thinning would allow plants to develop resistant morphologies. If this were true, we would expect few differences between control plants (those that remained protected from herbivores) and exposed plants for which protection had been removed. Conversely, if plants did not develop adequate defenses during the protection period, exposing them to herbivores should result in measurable morphological differences compared with controls. This research was designed to provide information that could be used by forest managers to anticipate outcomes and refine restoration prescriptions for ponderosa pine forests of northern Arizona.

Methods

Study Design

We conducted our study on the Fort Valley Experimental Forest in Coconino County approximately 10 km northwest of Flagstaff, AZ. In 1998-1999, forest units of 14-16 hectares in size were thinned as part of a larger ecological restoration experiment conducted at the site (see Fulé et al. 2001 for restoration prescription details). Soon after thinning, we located 76 buckbrush plants and built “rabbit wire” exclosures around them in order to protect the shrubs from large herbivores. Exclosures were 2 x 2 m in area and 1.4 m in height. In the center of these, we established circular sample plots, each with a radius of 56.4 cm (1 m² in area). Exclosures were left in place for seven years until 2006. In spring of 2006, we randomly selected half of the exclosures (n = 33) to remove. We counted stems on plots, collected stem height measurements, and took photographs of the buckbrush shrubs within plots at the time of exclosure removal.

In October, one growing season after exclosures had been removed, we returned to the plots and again collected stem height measurements and took photographs. We also harvested stems for detailed laboratory analysis. Stems were systematically selected by harvesting the three closest to the center of each plot. Stems were stored in a cooler until processed in the laboratory. For each harvested stem, we measured leaf area, stem length and diameter, and stem and leaf biomass (dry weight) in the lab. One-sided leaf area per stem was measured by removing all leaves, placing them on a light table, and using a video projection system (AGVIS). Stem length was measured to the nearest cm and diameter was measured to the nearest mm using a digital caliper. Stems and leaves were dried at 70 °C for 48 hours then weighed to determine biomass.

Data Analyses

To test for differences between protected controls and exposed plants, we used one-way analysis of variance (ANOVA). The Shapiro-Wilk and Leven’s tests were used to test for data normality and homogeneity of variance, respectively. Raw data were transformed using natural logarithm values when the above tests indicated that ANOVA assumptions had not been met. Statistical differences were considered significant at $P \leq 0.05$. 

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Spring pretreatment differences in mean stem number and height between control and exposed groups were tested and no significant differences were found. For late summer post-treatment stem collections, parameters tested were mean leaf area per stem, leaf weight per stem, stem weight, stem length, and stem diameter. We also used simple linear regression ($P < 0.05$) to test relationships between stem length and leaf weight per stem. All tests were performed using SAS JMP Version 4.

## Results

Plants exposed to herbivores for one growing season had significantly less leaf area per stem and total leaf weight per stem than protected control plants (Table 1). Leaf area and leaf weight differed between control and exposed groups by a factor of four.

No significant differences in stem length, stem diameter, or stem weight were found between protected control and exposed plants (Table 1).

Regressions indicated significant ($P < 0.001$) positive relationships between stem length and leaf weight per stem (Figure 1). This relationship was stronger for plants protected from herbivores than those that had been exposed.

### Table 1.
Means (and standard errors) of buckbrush (*Ceanothus fendleri*) characteristics for protected control and exposed plants. $P$-values less than 0.05 indicate statistically significant differences between control and exposed means.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Exposed</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Area (cm$^2$)</td>
<td>40.63 (1.19)</td>
<td>10.13 (1.21)</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Leaf Weight (g stem$^{-1}$)</td>
<td>0.321 (1.21)</td>
<td>0.076 (1.22)</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Stem Weight (g)</td>
<td>0.836 (0.812)</td>
<td>0.829 (1.23)</td>
<td>0.9694</td>
</tr>
<tr>
<td>Stem Length (cm)</td>
<td>22.85 (1.09)</td>
<td>19.88 (1.10)</td>
<td>0.1743</td>
</tr>
<tr>
<td>Stem Diameter (mm)</td>
<td>2.90 (1.06)</td>
<td>2.91 (1.07)</td>
<td>0.9526</td>
</tr>
</tbody>
</table>

**Figure 1.** Relationships ($P < 0.001$) between stem length and leaf weight per stem for protected control (solid circles) and exposed (gray squares) buckbrush plants. Leaf weight values have been natural log-transformed to improve linearity.
Discussion and Conclusions

Results from this study suggest that short-term protection during the early stages of forest restoration may allow buckbrush plants to develop characteristics that provide resistance to herbivory. For example, stem characteristics such as length, diameter, and weight were similar between protected control plants and those that were exposed for one growing season after seven years of protection. Since buckbrush stems produce woody tissue and spines as they grow larger and older, protection for a number of years appears to allow these defensive structures to develop and increase this species’ resistance to herbivory by large animals such as Rocky Mountain elk. This conclusion is supported by earlier work done by Huffman and Moore (2003) at the Fort Valley site, which showed that buckbrush plants protected from large herbivores for two years had stem lengths averaging more than two-times longer than those of plants that had never been protected. In addition, protected plants in Huffman and Moore’s (2003) study had larger stem diameter and more current-year biomass than unprotected plants. Intensive use appeared to create a positive feedback loop by keeping buckbrush plants in a reduced form with few mechanisms to deter further herbivory. In our study, seven years may have been a long enough period of protection to allow defensive structures to develop. However, because we examined buckbrush characteristics only one year after protection was removed, it is not clear whether these plants will remain resistant if herbivore pressure continues to be high in the future. Similarly, for other species without defensive structures, longer-term protection may be needed (Shepperd and Fairweather 1994).

Although stem size and weight were similar between protected and exposed plants, we found large differences in leaf area and leaf weight between the two treatment groups. Total dry weight of leaves on individual stems may be predicted from stem length and the equations presented in this study may be used by managers to determine forage availability and for monitoring. This relationship was weaker for stems defoliated as a result of exposure to herbivory. Defoliation may lead to a variety of plant responses both detrimental as well as beneficial to persistence of populations (Maschinski and Whitham 1989); however, we did not attempt to assess such effects in our study. More work is needed to determine the effects of short-term, intensive losses of buckbrush leaf area on processes such as flowering and viable seed production. The data presented in this study suggest that treatments to restore northern Arizona ponderosa pine forests should include temporary methods to decrease herbivory in order to help conserve populations of native plants.
References


The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.