Spatial relationships among young *Cercocarpus ledifolius* (curlleaf mountain mahogany)

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SPATIAL RELATIONSHIPS AMONG YOUNG CERCOCARPUS LEDIFOLIUS
(CURLLEAF MOUNTAIN MAHOGANY)

Brad W. Schultz¹, Robin J. Tausch², and Paul T. Tueller³

ABSTRACT.—This study analyzed spatial location patterns of Cercocarpus ledifolius Nutt. (curlleaf mountain mahogany) plants, classified as current-year seedling, established seedling, juvenile, and immature individuals, at a central Nevada study site. Most current-year seedlings were located in mahogany stands in which large, mature individuals had the greatest abundance. These stands had greater litter cover and a thicker layer of litter than areas with few current-year seedlings. Most established young Cercocarpus were located in adjacent Artemisia tridentata ssp. vaseyana (mountain big sagebrush) communities, or in infrequent canopy gaps between relatively few large, mature Cercocarpus. We discuss potential roles of plant litter, root growth characteristics, nurse plants, and herbivory in the establishment and renewal of Cercocarpus communities.

Key words: Cercocarpus, litter, mountain mahogany, seedling, recruitment, spatial relationships, maturity class.

Cercocarpus ledifolius Nutt. (curlleaf mountain mahogany; hereafter Cercocarpus) is a desirable browse species in the Intermountain West (Smith 1950, Smith and Hubbard 1954, Hoskins and Dalke 1955). Attempts to revegetate wildlife habitat with Cercocarpus have had little success. Common problems have been competition from annual weeds (Holmgren 1954), sensitivity to frost and drought (Plummer et al. 1957, 1968), slow growth (Plummer et al. 1957), and impaired germination (Liacos and Nord 1961, Young et al. 1978).

Cercocarpus does not sprout from root crowns following removal of the canopy (Ormiston 1978, Austin and Urness 1980). Reproduction must occur from seed. Limited research has addressed the structure of Cercocarpus stands (Scheldt 1969, Duncan 1975, Davis 1976, Davis and Brotherson 1991) or how stand structure may influence regeneration. Except for Duncan’s (1975) work in Montana, past studies concluded that most stands have few young Cercocarpus and that older individuals have the greatest abundance. These studies (Scheldt 1969, Duncan 1975, Davis 1976, Davis and Brotherson 1991) also found few seedlings, low seedling survival, and irregular seed production (Plummer et al. 1968). The few current-year Cercocarpus seedlings that emerge apparently have rapid elongation of their taproot (0.97 m after 120 days; Dealy 1975). Rapid root growth should benefit Cercocarpus seedlings in the Great Basin, where a semiarid climate predominates. Previous studies indicate land managers require additional information about processes in Cercocarpus communities: (1) the dynamics of current-year Cercocarpus seedlings in relationship to the rest of the vegetative community, and (2) conditions that permit current-year seedlings and established young Cercocarpus to be recruited into the population structure.

Schultz et al. (1991) presented the first predictive relationships about the structure of Cercocarpus stands. Their study in western and central Nevada found that mean Cercocarpus crown volume had a significant (P < 0.05) inverse relationship (r² = 0.78) with density of Cercocarpus in established seedling, juvenile, and immature maturity classes. Schultz (1987) also found that Cercocarpus canopy cover and mean Cercocarpus crown volume had significant (P < 0.05) positive correlations with density of current-year Cercocarpus seedlings. This dichotomy, along with other patterns observed by Schultz (1987), may offer valuable insight into the regeneration of Cercocarpus stands. Additionally, Schultz (1987) observed that (1) locations with large canopy gaps between widely scattered mature individuals generally had more Cercocarpus in established seedling, juvenile, and immature maturity classes than...
did locations with small canopy gaps; (2) locations with small canopy gaps, and hence greater Cercocarpus canopy cover and crown volume, had a greater abundance of young Cercocarpus in adjacent Artemisia tridentata ssp. vaseyana (mountain big sagebrush) communities; (3) established Cercocarpus in the Artemisia community were often rooted under the protective canopy of another shrub or shrub skeleton; and (4) most current-year Cercocarpus seedlings were found where thick plant litter had accumulated under mature Cercocarpus. Table 1 summarizes differences (patterns) in Cercocarpus stand structure from locations in western (Peavine Mountain) and central (Shoshone Range) Nevada. Table 2 defines the maturity classes mentioned throughout this study.

Based on observations about the spatial location of current-year Cercocarpus seedlings and established Cercocarpus in the youngest maturity classes, we implemented a brief descriptive study on the Shoshone Range in central Nevada to quantify the spatial distribution of current-year Cercocarpus seedlings and Cercocarpus in established seedling, juvenile, and immature maturity classes. We integrate data from this study, the Schultz et al. (1990, 1991) studies about stand structure, which were conducted at the same location as this study, and other relevant literature to describe possible processes, mechanisms, or factors that influence survival of current-year Cercocarpus seedlings and their subsequent recruitment into established seedling, juvenile, and immature maturity classes. Our goal is to stimulate thought that can guide research about the regeneration of this desired browse species.

**METHODS**

Initial measurements describing the structure of Cercocarpus stands occurred on the Shoshone Range and Peavine Mountain in June and July 1985. Relevant results are presented in Table 1. Measurements describing the spatial location of individuals in current-year Cercocarpus seedling, established seedling, juvenile, and immature maturity classes were made on the Shoshone Range in early August 1985. Abundant rainfall in central Nevada during June and July allowed current-year Cercocarpus seedlings to survive until we initiated this study. Similar data could not be collected from Peavine Mountain in western Nevada because a dry spring and summer resulted in the early desiccation and disappearance of most Cercocarpus seedlings.

Seven 1 × 40-m belt transects (BT) were located at 4 of the 13 Cercocarpus stands in the Shoshone Range measured by Schultz et al. (1990, 1991). None of the BTs were placed in study plots sampled by Schultz et al. (1990, 1991; also described in Schultz 1987) because those study plots were located in the interior of the stands, not near the ecotone with the adjacent Artemisia community. The 4 stands sampled were selected because (1) they were near access roads and time was limited, and (2) their respective topographic positions allowed at least 1 transect (of the 7) to be located at each cardinal aspect.

The following criteria were used to select transect locations: (1) a Cercocarpus stand dominated by mature individuals was present, (2) a sharp ecotone existed between the Cercocarpus stand and adjacent Artemisia community, (3) the transect remained on the same landform.
TABLE 2. Cercocarpus maturity classes. Descriptions were developed from a reconnaissance of Cercocarpus stands near Reno, NV.

<table>
<thead>
<tr>
<th>Maturity Class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current-year seedling</td>
<td>Germinated during the current growing season; usually has 4 leaves.</td>
</tr>
<tr>
<td>Established seedling</td>
<td>Plants 2-7 mm basal diameter; smooth bark; may be up to 30 cm tall; 8 or more leaves.</td>
</tr>
<tr>
<td>Juvenile</td>
<td>Young plants &gt;7 mm basal diameter; smooth bark; plants to 60 cm tall.</td>
</tr>
<tr>
<td>Immature</td>
<td>Young plants &gt;1.25 cm basal diameter; smooth bark; plants to 1.5 m tall.</td>
</tr>
<tr>
<td>Young-mature</td>
<td>Cracked bark; 1.5-3.0 m tall; crown broadened; may be multistemmed from base; not suppressed by adjacent larger mountain mahogany plants.</td>
</tr>
<tr>
<td>Mature</td>
<td>Cracked bark; wide full crown; few dead branches; may have several stems from base; &gt;3 m tall.</td>
</tr>
<tr>
<td>Over-mature</td>
<td>Cracked bark; may be multistemmed; numerous dead branches; may be &gt;3 m tall; frequently suppressed by adjacent larger mountain mahogany plants.</td>
</tr>
</tbody>
</table>

and had the same aspect throughout its length, and (4) all transects located in the same stand were 40 m or more apart. Table 3 describes the elevation, slope, and aspect of each transect. Cercocarpus in the Shoshone Range are largely restricted to the Foxmount soil series (Carol Jett personal communication), which is a gravelly loam (specifically, a Loamy-skeletal, mixed Typic Cryquoll). This soil is well drained and moderately permeable. Depth to a paralithic contact averages 60–100 cm.

All transects were located such that 20 m occurred in the Cercocarpus stand and 20 m in the adjacent Artemisia community. Each transect was divided into forty 1 × 1-m quadrats. Every Cercocarpus rooted in each quadrat was classified by maturity class. For Cercocarpus in established seedling, juvenile, and immature maturity classes, we determined whether the plant was rooted under the protective canopy of a live or dead shrub.

Distribution of current-year seedling, established seedling, juvenile, and immature Cercocarpus was summarized for 10 classification categories (populations). These were (1) the number of Cercocarpus in current-year seedling, established seedling, juvenile, and immature maturity classes rooted in either the Cercocarpus community or the adjacent Artemisia community, and (2) the number of established seedling, juvenile, and immature Cercocarpus rooted under and not under the canopy of a live or dead shrub. The Wilcoxon signed rank test was used to examine if there was a significant difference in the distribution of individuals in the Cercocarpus and Artemisia communities, respectively, for each maturity class. The significance level is P ≤ 0.05 unless otherwise noted.

RESULTS

Current-year Cercocarpus seedlings were not distributed evenly between Cercocarpus stands and adjacent Artemisia communities (Table 4). Significantly more current-year seedlings were rooted in the Cercocarpus community.

At least 81% of established seedling, juvenile, and immature Cercocarpus were rooted in the adjacent Artemisia community (Table 4). For established seedling and juvenile maturity classes the difference in spatial distribution was significant; the significance level for immature Cercocarpus was P ≤ 0.06.

More established seedling, juvenile, and immature Cercocarpus were rooted under the protective canopy of a live or dead shrub than in the open (Table 5). Only 1 transect had more plants without a protective canopy, but the significance level was P ≤ 0.10.

DISCUSSION

Spatial distribution of current-year Cercocarpus seedlings and established young Cercocarpus had an inverse relationship (Tables 1, 4). Current-year seedlings were most abundant in Cercocarpus stands dominated by large, mature Cercocarpus and least abundant in adjacent Artemisia communities. Young, established
Cercocarpus were virtually absent from mature Cercocarpus stands but had a greater abundance in adjacent Artemisia communities (Tables 1, 4). Young Cercocarpus were also abundant in stands with low Cercocarpus crown cover or relatively few large Cercocarpus (Table 1). The low density of current-year seedlings in adjacent Artemisia communities (Table 4) has 2 possible interpretations: (1) viable Cercocarpus seeds were not dispersed into the Artemisia community, or (2) germination of Cercocarpus seed was impaired. Because data about seed densities are lacking, a definitive conclusion cannot be made. Cercocarpus seed, however, is primarily wind dispersed (USDA 1948); therefore, it is unlikely that few seeds were present in the Artemisia community, particularly since all data were collected within 20 m of the Cercocarpus stands. Most likely, over 85% fewer Cercocarpus seedlings were in the Artemisia community (Table 4) because seed germination was substantially lower than in the Cercocarpus stands.

The inverse relationship for distribution of current-year seedlings and established young Cercocarpus indicates that locations with a high abundance of current-year seedlings are not necessarily locations with the best seedling survival. Populations perpetuate when seedlings survive and advance into successively older maturity classes, eventually producing new seedlings. The pattern for spatial distribution of current-year seedling, established seedling, juvenile, and immature Cercocarpus derived from this study and that conducted by Schultz et al. (1990, 1991) indicates that 4 factors may influence survival of current-year seedlings as well as plants in the youngest maturity classes: (1) presence or thickness of plant litter, (2) root growth characteristics, (3) presence of nurse plants, and (4) herbivory.

Moderate levels of litter can favor seed germination and seedling establishment by decreasing soil temperature and increasing soil moisture (Evans and Young 1970). Thick litter, however, can reduce seedling establishment and survival by preventing or restricting contact between soil and seed or soil and root (Fowler 1986).

High litter cover (Table 1) and a thick layer of litter (personal observation) were common in Cercocarpus stands in the Shoshone Range. Litter cover and litter thickness were not measured in adjacent Artemisia communities; however, litter cover in high-elevation (>2200 m) Artemisia communities ranges from 15% to 50% (Tueller and Eckert 1987). Extensive and deep litter in Cercocarpus stands may promote seed germination but decrease seedling survival because roots from Cercocarpus seedlings seldom make contact with the mineral soil. Less litter in the Artemisia community may reduce Cercocarpus seed germination but enhance survival of seeds that germinate. Root growth characteristics may play an important role.

Rapid root growth that current-year Cercocarpus seedlings experience (Dealy 1975) should enhance survivorship of Cercocarpus seedlings during seasonal drought, a common phenomenon in the Great Basin. Root systems that undergo rapid elongation should be able to follow a retreating zone of soil moisture (downward) better than root systems that elongate slowly. We excavated several Cercocarpus seedlings rooted in thick plant litter and found that root growth was extensive (20+ cm) but not...

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**Table 4.** Number of current-year seedling, established seedling, juvenile, and immature mahogany rooted in Cercocarpus (CER) stands dominated by mature individuals, and in adjacent Artemisia (ART) communities. Within each maturity class, total values between community types with different letters are significantly different ($P \leq 0.05$).

<table>
<thead>
<tr>
<th>Transect</th>
<th>Current-year seedling</th>
<th>Established seedling</th>
<th>Juvenile</th>
<th>Immature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CER</td>
<td>ART</td>
<td>CER</td>
<td>ART</td>
</tr>
<tr>
<td>1</td>
<td>20</td>
<td>0</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>2</td>
<td>72</td>
<td>15</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>3</td>
<td>75</td>
<td>53</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>4</td>
<td>31</td>
<td>39</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>337</td>
<td>25</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>6</td>
<td>506</td>
<td>28</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>7</td>
<td>33</td>
<td>0</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td>1074</td>
<td>160b</td>
<td>4a</td>
<td>75b</td>
</tr>
<tr>
<td>Percent</td>
<td>87</td>
<td>13</td>
<td>5</td>
<td>95</td>
</tr>
</tbody>
</table>

1Significantly different at $P \leq 0.05$.  

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downward toward or into the mineral soil. Root growth was largely lateral. Following germination in early spring, available moisture in both mineral soil and plant litter is probably high, since cool temperatures and abundant precipitation are common (Houghton et al. 1975). Because moisture is not limiting early in the growing season, root growth probably follows the path of least resistance. When thick litter resides on top of mineral soil, the path of least resistance would be laterally through the litter, not downward through the mineral soil. The loamy soil that *Cercocarpus* stands inhabit undoubtedly stores and retains more water than plant litter does, and thus should desiccate more slowly. If thick plant litter prevents or retards roots of current-year *Cercocarpus* seedlings from reaching or penetrating moist mineral soil, seedling mortality should be high when litter desiccates rapidly later in the summer. We observed high mortality for current-year *Cercocarpus* seedlings in August in *Cercocarpus* stands with thick accumulations of litter. Less litter on Peavine Mountain (Table 1) and in the *Artemisia* community (see Tueller and Eckert 1987) may enable root systems of *Cercocarpus* seedlings at these locations to grow downward into mineral soil immediately following germination. This should increase survivorship of current-year seedlings, which may account (at least partially) for the greater abundance of established seedling, juvenile, and immature *Cercocarpus* on sites with less surface litter.

Herbivory may also play a role in seedling survival. Current-year *Cercocarpus* seedlings have an average leaf surface area of only 4 cm² (Dealy 1975), which herbivores can easily consume. Herbivory can adversely affect establishment of woody species (Marquis 1974, McAuliffe 1986), including *Cercocarpus* (Scheldt and Tisdale 1970). The presence of protective nurse plants, therefore, may be important for regeneration of *Cercocarpus* seedlings.

*Cercocarpus* stands in the Shoshone Range had a mean shrub canopy cover of 11% (Schultz et al. 1990). Total shrub canopy cover was not measured in adjacent *Artemisia* communities; however, it generally ranges from 41% to 50% (Tueller and Eckert 1987). Thus, shrub cover in adjacent *Artemisia* communities is 3.5 to 4 times greater than that in *Cercocarpus* stands. Since more established seedling, juvenile, and immature *Cercocarpus* were rooted under a shrub or shrub skeleton than not (Table 5), the difference in shrub canopy cover between *Cercocarpus* stands and adjacent *Artemisia* communities may influence survival of current-year seedlings, established seedlings, juvenile, and immature *Cercocarpus*. *Artemisia* and other short-statured shrubs may serve as nurse plants and protect small *Cercocarpus* (including current-year seedlings) from herbivores until their photosynthetic surface is large enough to cope with frequent browsing. Since shrub cover is low in *Cercocarpus* stands, more young *Cercocarpus* are probably exposed to herbivores than in *Artemisia* communities. This may help explain the near absence of young *Cercocarpus* in *Cercocarpus* stands and their greater abundance in adjacent *Artemisia* communities.

**CONCLUSIONS**

Abundance of current-year *Cercocarpus* seedlings is greatest in *Cercocarpus* stands that have high *Cercocarpus* canopy cover, large mean *Cercocarpus* crown volume, and an extensive layer of plant litter. These stand attributes also result in a low density of plants in established seedling, juvenile, and immature maturity classes. Established young *Cercocarpus* are most abundant where gaps occur in the *Cercocarpus* canopy, or in adjacent *Artemisia* communities. Survival of current-year seedlings appears best at locations that permit roots of seedlings to make contact with mineral soil. Survival of current-year seedlings and progression of individuals from established seedling maturity class into successively older maturity classes appear to be enhanced by the presence of a shrub canopy that protects small *Cercocarpus* from herbivores.

### Table 5: The number of established seedling, juvenile, and immature *Cercocarpus* rooted under and not under another shrub or shrub skeleton. Significance level is $P \leq 0.10$.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Rooted under</th>
<th>Not rooted under</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>16</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>23</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
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<td>13</td>
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<td>4</td>
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<td>5</td>
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<td>6</td>
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<td>7</td>
</tr>
<tr>
<td>7</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>97a</td>
<td>58b</td>
</tr>
<tr>
<td>Percentage</td>
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LITERATURE CITED


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