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SPATIAL RELATIONSHIPS AMONG YOUNG *CERCOCARPUS LEDIFOLIUS* (CURLLEAF MOUNTAIN MAHOGANY)

Brad W. Schultz[1], Robin J. Tausch[2], and Paul T. Tueller[3]

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 2 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 ($P \leq 0.05$) inverse relationship ($r^2 = 0.78$) 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 ($P \leq 0.05$) 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

[1]Biological Sciences Center, Desert Research Institute, University of Nevada System, Box 60220, Reno, NV 89506. Corresponding author.
[2]USDA Forest Service, Intermountain Forest and Range Experiment Station, Reno, NV 89512.
[3]Department of Environmental and Resource Sciences, University of Nevada—Reno, Reno, NV 89512.

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 1. Mean values for structural characteristics of *Cercocarpus* communities from 2 mountain ranges in western and central Nevada (data from Schultz 1987, Schultz et al. 1990). Mean values in the same column followed by the same letter are not significantly different ($P \leq 0.05$).

Mountain range	Current-year seedlings (#/m^{-2})	Established seedling, immature, and juvenile (#/ha)	Mature *Cercocarpus* (#/ha)	*Cercocarpus* crown volume (m^3/plant^{-1})	*Cercocarpus* cover (%)	Litter cover (%)	Bare ground[1] (%)
Peavine	0.1a	922a	233a	5.8a	56a	67a	10a
Shoshone	1.9b	111b	344b	39.5b	79b	76b	10a

[1]includes gravel

TABLE 2. *Cercocarpus* maturity classes. Descriptions were developed from a reconnaissance of *Cercocarpus* stands near Reno, NV.

Current-year seedling	Germinated during the current growing season; usually has 4 leaves.
Established seedling	Plants ≥ 1 year of age; 2–7 mm basal diameter; smooth bark; may be up to 30 cm tall; 8 or more leaves.
Juvenile	Young plants >7 mm basal diameter; smooth bark; plants to 60 cm tall.
Immature	Young plants >1.25 cm basal diameter; smooth bark; plants to 1.5 m tall.
Young-mature	Cracked bark; 1.5–3.0 m tall; crown broadened; may be multistemmed from base; not suppressed by adjacent larger mountain mahogany plants.
Mature	Cracked bark; wide full crown; few dead branches; may have several stems from base; >3 m tall.
Over-mature	Cracked bark; may be multistemmed; numerous dead branches; may be >3 m tall; frequently suppressed by adjacent larger mountain mahogany plants.

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 Topic Cryboroll). 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 determine 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 $P \leq 0.05$ unless otherwise noted.

TABLE 3. Elevation, slope, and aspect of each belt transect in which count data were obtained.

Transect	Elevation (m)	Slope (%)	Aspect (degrees)
1	2688	41	80
2	2688	41	80
3	2688	41	80
4	2400	29	290
5	2758	34	0
6	2758	34	0
7	2758	25	168

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 $P \leq 0.06$.

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 $P \leq 0.10$.

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

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 ($P \leq 0.05$).

Transect	Current-year seedling		Established seedling		Juvenile		Immature	
	CER	ART	CER	ART	CER	ART	CER	ART
1	20	0	1	11	1	5	0	1
2	72	15	1	15	3	3	0	5
3	75	53	0	16	0	6	5	6
4	31	39	0	2	0	7	0	4
5	337	25	0	11	0	19	0	0
6	506	28	1	11	0	4	0	0
7	33	0	1	9	0	2	0	5
Total	1074a	160b	4a	75b	4a	46b	5a	21a[1]
Percent	87	13	5	95	8	92	19	81

[1]Significantly different at $P \leq 0.06$.

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

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

Transect	Rooted under	Not rooted under
1	16	3
2	23	4
3	20	13
4	8	5
5	6	24
6	9	7
7	15	2
Total	97a	58b
Percentage	63	37

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 cm^2 (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.