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ENVIRONMENTAL ATTRIBUTES CORRELATING WITH DENSITY OF BLACKBRUSH (*COLEOGYNE RAMOSISSIMA*) SHRUBS IN THE SPRING MOUNTAINS OF SOUTHERN NEVADA

Simon A. Lei[1]

ABSTRACT.—Discovery of distinct mid-elevational bands of blackbrush (*Coleogyne ramosissima* Torr.) shrublands on desert mountain slopes in the Mojave Desert caused an investigation of the relationships between environmental factors and *Coleogyne* distribution. Environmental factors were quantitatively examined to determine which were significant predictors of *Coleogyne* density at upper-elevational limits (ecotones) in the Spring Mountains of southern Nevada. Path analysis revealed significant, direct causal effects of air temperature, soil moisture, soil depth, and percent litter cover on the distribution of *Coleogyne*. Specifically, air temperature was a significant positive predictor, while soil moisture, soil depth, and percent litter cover were significant negative predictors of *Coleogyne* density, with the effects of other environmental variables parceled out. Path analysis also indicated that indirect effects of soil pH, bulk density, compaction, percent pore space, organic matter, soil temperature, salinity, cryptogam, and percent bare soil and rock cover on *Coleogyne* density were substantially more potent than their direct causal effects. Environmental attributes associated with elevational changes correlate with and may determine the density of *Coleogyne* shrubs at upper ecotones in southern Nevada.

Key words: edaphic, soil attributes, soil surface variables, upper Coleogyne *ecotone, Spring Mountains, southern Nevada.*

Coleogyne ramosissima (blackbrush) shrublands occur along Colorado River drainages and the transition zone between the Mojave and the Great Basin Deserts (Bowns 1973). In southern Nevada, *Coleogyne* shrublands often form a distinct mid-elevational belt between *Larrea tridentata–Ambrosia dumosa* (creosote bush–bursage) shrublands below and *Pinus monophylla–Juniperus osteosperma* (pinyon-juniper) woodlands above. *Coleogyne* generally forms nearly monospecific stands in the Mojave Desert of southern Nevada (Lei 1995, Lei and Walker 1997a).

Environmental attributes that vary with elevation may determine *Coleogyne* density and distribution. Previous studies have revealed that *Coleogyne* shrublands in southern Utah are characterized by hot summers above 40°C and cold winter below –20°C (Bowns 1973). In southern Nevada, *Coleogyne* shrublands generally occur at elevations of 1200 to 1500 m (Beatley 1969), but occasionally occur below 1200 m on north-facing slopes and over 2000 m on south-facing slopes (Lei 1995, Lei and Walker 1997a). *Coleogyne* plants usually grow well on sand, sandy loam, and loam, less well on gravel and clay loam, and poorly on dense clay soils (Korthuis 1988). Soil surfaces are stony, and caliche, located approximately 30 to 50 cm below the soil surface, is a characteristic of *Coleogyne* shrubland subsoils (Lei and Walker 1997a, 1997b). Shallow soil may partially determine the abundance and distribution of *Coleogyne* shrublands (Callison and Brotherson 1985, Lei and Walker 1997a, 1997b). West (1983) stated that *Coleogyne* plants have a low tolerance to excessive soil salinity and moisture. In southern Utah, the upper elevational boundary of *Coleogyne* shrublands appears to be determined by low air temperature in winter months (Bowns and West 1976).

Coleogyne shrublands cover relatively large areas in mid-elevations of southern Nevada. I designed a study to determine which abiotic factors change with changing elevation. The objective of this study was to investigate why these abiotic factors should vary with elevation and how this variation would cause the changes observed in *Coleogyne* density. Examining various environmental parameters helped

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me discern which ecological factors *Coleogyne* requires at its upper-elevational limits in southern Nevada.

METHODS

Study Area

The study site is in the Spring Mountains (36°07′N, 115°38′W) of southern Nevada. Weather patterns are characterized by hot, dry summers and cool, wet winters. Summer and winter air temperatures sometimes reach above 35°C and into the subzero range, respectively (Lei and Walker 1997b). Although episodic monsoonal thunderstorms occur in summer, most precipitation occurs in winter seasons. Mean annual precipitation is generally <300 mm (Lei 1995). A relative humidity $\leq 20\%$ is common in summer seasons (Lei and Walker 1997a, 1997b).

Field Surveys and Laboratory Analyses

During summer 2000 and winter 2002, I conducted field studies along upper *Coleogyne* shrubland ecotones. Six canyons were selected within the Spring Mountains: Lee, Kyle, Trout, Lovell, Cold Creek, and Wheeler Pass. The elevational range of upper *Coleogyne* shrubland ecotones varied widely among the canyons, ranging from 1500 m in Trout Canyon to 1985 m in Lee Canyon. I established thirty 100-m^2 circular plots (5.6-m radius) at each of 6 elevations for a total of 180 plots. The lowest of the 6 elevations represented *Coleogyne* stands, while the highest represented *Pinus-Juniperus* stands. The remaining 4 elevations represented upper *Coleogyne* shrubland ecotones.

Within each plot, numbers of woody perennial species >10 cm tall, including subshrubs, were recorded. Subshrubs have suffrutescent stems at the base and herbaceous stems that make up the canopy. Because the composition of woody species among the 6 canyons was similar, I pooled the density of each plant species and expressed the results as the number of individuals per 100 m^2.

In open spaces within each plot, soil pits were excavated and soil samples collected from the upper 15 cm. Soil depth, soil compaction, and air and soil temperatures were measured in the field. Soils were passed through a 2-mm sieve to remove rocks and plant roots and then were transported to the Community College of Southern Nevada (CCSN). All soils were analyzed in the laboratory using sifted substrates, after which they were oven-dried at 65°C until they reached constant mass.

I estimated soil depth as the distance to which a steel rod could be pounded into undisturbed soils. Gravimetric soil moisture was determined by computing the difference between fresh and oven-dried mass. Soil pH was determined from a paste of 1:1 soil:distilled water and measured with an electrode pH meter. A set of soil cores of known volume was carefully removed from the field. Soil bulk density was determined by weighing the volume of each soil sample and dividing dry mass by volume. Average pore space was determined using the following equation:

$$\text{Pore space} = 100 - (D_b / D_p * 100),$$

where D_b is bulk density of the soil and D_p is average particle density, usually about 2.65 g $\cdot$ cc^{-1} (Hausenbuiller 1972, Davidson and Fox 1974). Soil salinity (total soluble salts) was determined by a Beckman electrical conductivity bridge, using a slurry consisting of equal parts of soil and distilled water.

Soil compaction was measured in the field using a penetrometer, which was inserted into soils in open spaces after stony surface pavements were removed. Penetrometer readings were taken at the point where the cone base reached the soil surface (point depth = 3.8 cm). Soil organic matter was determined by predrying soils for 72 hours at 65°C, and then subtracting mass loss during ignition at 550°C for 4 hours. Soil temperatures were measured with a metallic soil thermometer at the surface (0 cm) and 15 cm below surface in open spaces. Air temperatures at 1.5 m aboveground were measured during midday, concurrently with soil temperatures to ensure compatibility.

Within each plot, soil surface characteristics of litter, bare ground, gravel (2–64 mm in diameter), cobble (65–256 mm), boulder (>256 mm), and cryptogams were visually quantified using 10% increments.

Statistical Analyses

Multivariate analysis of variance (MANOVA; Analytical Software 1994) was used to detect significant effects of site (6 canyons), elevation, and seasonality (summer and winter) on environmental variables. Four-way ANOVA was also performed to detect significant effects of site, elevation, seasonality, and soil depth (at ground surface and 15-cm depth) on soil temperature. One-way ANOVA, followed by Tukey's multiple comparison test, was performed to compare differences in *Coleogyne* shrub density among elevational levels and among environmental variables.

Pearson's correlation was conducted to correlate *Coleogyne* shrub density with soil and surface variables, and to intercorrelate among these variables. Path analysis, including a path diagram, was conducted to examine proposed causal links between environmental (predictor) variables and *Coleogyne* shrub density (response variable). Path analysis, indicated by path coefficients (partial regression coefficients), was used to quantify significant, direct causal effects of environmental variables on *Coleogyne* density and on each other using correlational data. Because of similarities in environmental attributes, I pooled the data among the 6 canyons within Spring Mountains. Mean values were presented with standard errors, and statistical significance was determined at $P \leq 0.05$.

RESULTS

Coleogyne, Artemisia, Juniperus, and *Pinus* were the 4 common woody taxa along a gradient of ascending elevation (Table 1). *Ephedra nevadensis, Opuntia echinocarpa,* and *Menodora spinosa* occurred primarily in the nearly monospecific *Coleogyne* zones and disappeared with increasing elevation (Table 1). Mean *Coleogyne* density decreased significantly ($P \leq 0.001$; Table 1) with increasing elevation along upper *Coleogyne* shrubland ecotones. *Coleogyne* disappeared and was replaced by *Artemisia, Juniperus,* and *Pinus* plants at higher elevations.

A significant interaction was found between elevation and seasonality for air temperature ($P \leq 0.001$; Fig. 1). Significant interactions were found between elevation and soil depth ($P \leq 0.001$; Fig. 2), elevation and seasonality, and elevation, soil depth, and seasonality for soil temperature. A significant interaction was also detected between elevation and seasonality for gravimetric soil moisture ($P \leq 0.001$). However, there were no significant interactions ($P > 0.05$) between site and elevation, elevation and seasonality, and site, elevation, and seasonality for the remaining soil and surface variables. Soil pH, soil moisture, soil compaction, bulk density, air temperature, and soil temperature decreased, while percent pore space and organic matter increased significantly with increasing elevation ($P \leq 0.05$; Table 2, Figs. 2, 3).

Coleogyne density was positively correlated with soil pH, soil compaction, bulk density, and soil and air temperatures ($P \leq 0.05$; Table 3), but was negatively correlated with soil depth, soil organic matter, percent pore space, and gravimetric soil moisture ($P \leq 0.05$; Table 3). Percentages of ground cover of gravel, cobble, and cryptogam were positively correlated,

TABLE 1. Density of woody and subwoody taxa along upper *Coleogyne* shrubland ecotones in the Spring Mountains ($n = 30$ per elevation). The lowest elevation represented *Coleogyne* vegetation zones, while the highest represented *Pinus-Juniperus* zones. Mean values in rows followed by different letters are significantly ($P \leq 0.05$) different by 1-way ANOVA and post-hoc Tukey means comparison test.

	Mean density					
		Upper *Coleogyne* ecotones				
Species	*Coleogyne*	Ecotone 1	Ecotone 2	Ecotone 3	Ecotone 4	*Pinus-Juniperus*
Artemisia tridentata	0a	0a	13.8b	45.7c	92.1d	87.8d
Cercocarpus ledifolius	0a	0a	0a	0a	1.1b	1.5b
Coleogyne ramosissima	98.9a	93.2ab	87.0b	70.8c	37.7d	0e
Ephedra nevadensis	1.6a	0.9b	0c	0c	0c	0c
Ephedra viridis	0a	1.2b	2.4c	2.2c	0a	0a
Fallugia paradoxa	1.4b	2.1bc	2.8c	3.1c	0a	0a
Gutierrezia sarothrae	9.3b	8.9b	10.1ab	13.2a	5.0c	4.7c
Juniperus osteosperma	0a	2.3b	4.9bc	8.9c	17.1d	12.4cd
Menodora spinosa	4.9a	2.7b	0c	0c	0c	0c
Opuntia echinocarpa	0.8a	0b	0b	0b	0b	0b
Pinus monophylla	0a	0a	0a	2.1b	4.8bc	5.9c
Yucca baccata	8.8a	4.7b	4.5b	2.3c	0d	0d

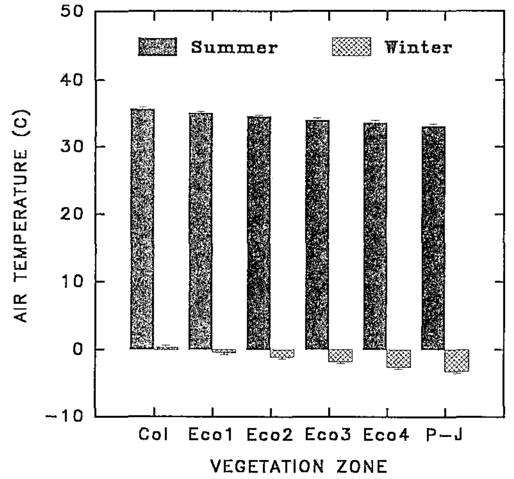

Fig. 1. Air temperature (mean ± $s_{\bar{x}}$) at 1.5 m aboveground in August 2000 and January 2002 in the Spring Mountains. The lowest elevation represented *Coleogyne* vegetation zones, and the highest represented *Pinus-Juniperus* zones. Narrow vertical bars denote standard errors of the means. Symbols of vegetation zones: Col = *Coleogyne*; Eco1 = upper ecotone 1; Eco2 = ecotone 2; Eco3 = ecotone 3; Eco4 = ecotone 4; and P-J = *Pinus-Juniperus*.

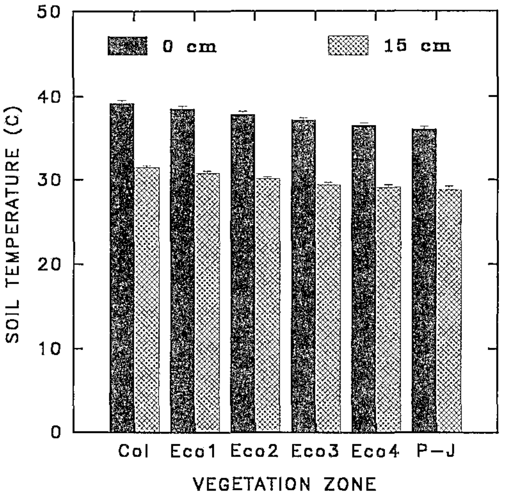

Fig. 2. Soil temperatures (mean ± $s_{\bar{x}}$) at the soil surface (0 cm) and at 15-cm depth in open spaces during midday in August 2000 along upper *Coleogyne* shrubland ecotones in the Spring Mountains. The lowest elevation represented *Coleogyne* vegetation zones, and the highest represented *Pinus-Juniperus* zones. Narrow vertical bars denote standard errors of the means. Symbols of vegetation zones: Col = *Coleogyne*; Eco1 = upper ecotone 1; Eco2 = ecotone 2; Eco3 = ecotone 3; Eco4 = ecotone 4; and P-J = *Pinus-Juniperus*.

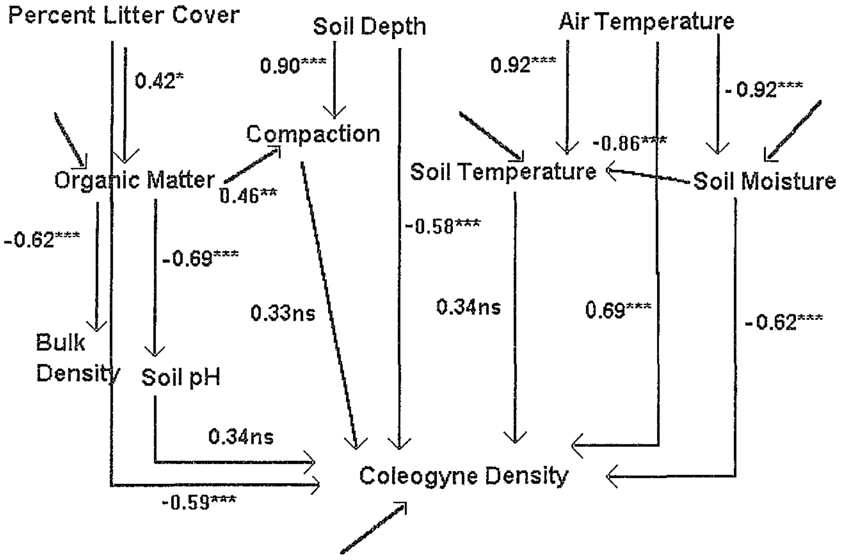

Fig. 3. Path diagram depicting hypothesized relationships (partial regression coefficients) among environmental attributes, and between environmental attributes and *Coleogyne* shrub density. Significance levels: $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$, and ns = nonsignificant.

TABLE 2. Soil properties at the upper 15 cm along upper *Coleogyne* shrubland ecotones in the Spring Mountains (n = 30 per elevation). The lowest elevation represented *Coleogyne* vegetation zones, while the highest represented *Pinus-Juniperus* zones. Soil moisture, organic matter, and pore space were expressed in percentages. Soil moisture was measured in August 2000, and a similar pattern was observed in January 2002, with a significantly greater percentage. Mean values in columns followed by different letters are significantly ($P \leq 0.05$) different by 1-way ANOVA and post-hoc Tukey means comparison test.

Vegetation zone	Moisture (%)	Organic matter	pH	Pore space	Bulk density (g · cm^{-3})	Compaction (kg · cm^{-2})	Depth (cm)
Coleogyne	1.23a	2.72ab	7.8ab	50.6a	1.31a	9.65a	20.8a
Upper ecotone	1.41ab	2.56a	7.9a	52.1ab	1.27ab	8.39ab	22.3a
Upper ecotone	1.69b	3.01b	7.8ab	52.8ab	1.25b	6.55bc	23.7a
Upper ecotone	1.82bc	3.64bc	7.7b	54.3b	1.21bc	4.98c	24.6ab
Upper ecotone	2.05c	3.82c	7.5c	55.6bc	1.18cd	3.06d	25.9b
Pinus-Juniperus	2.16c	4.29d	7.4c	56.6c	1.15d	2.87d	33.4c

TABLE 3. Relationship between *Coleogyne* density and environmental attributes along upper *Coleogyne* shrubland ecotones in the Spring Mountains. The direct causal effect of each attribute on *Coleogyne* density is the standardized partial regression coefficient (path coefficient). The indirect causal effect of each attribute is equal to Pearson's correlation r (total causal effect) minus the corresponding path coefficient. Significance levels: *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, and ns = nonsignificant.

Attribute	Direct effect	Indirect effect	Total effect
Litter	–0.59***	–0.26ns	–0.85***
Bare soil	–0.01ns	–0.88***	–0.89***
Gravel	0.14ns	0.75***	0.89***
Cobble	0.25ns	0.52***	0.77***
Boulder	–0.30ns	–0.51**	–0.81***
Cryptogam	0.09ns	0.75***	0.84***
Soil depth	–0.58***	–0.38*	–0.96***
Soil moisture	–0.62***	–0.28ns	–0.90***
Soil pH	0.34ns	0.63***	0.97***
Soil bulk density	–0.21ns	0.73***	0.94***
Compaction	0.33ns	0.57***	0.90***
Percent pore space	–0.004	–0.94***	–0.94***
Soil organic matter	–0.25ns	–0.64***	–0.89***
Soil temperature (open space)			
at surface	0.34ns	0.50**	0.84***
at 15-cm depth	0.33ns	0.42**	0.75***
Air temperature	0.69***	0.28ns	0.97***
Total soluble salt	0.17ns	0.50**	0.67***

while litter, bare soil, and boulder were negatively correlated with *Coleogyne* density ($P \leq 0.05$; Table 3).

Path analysis proposed that air temperature is a significant positive predictor of *Coleogyne* density, while soil moisture, soil depth, and percent litter are significant negative predictors ($P \leq 0.001$; Fig. 3), with the effects of other environmental variables parceled out. Air temperature was a significant positive predictor of soil temperature, whereas soil moisture was a significant negative predictor ($P \leq 0.001$; Fig. 3). Soil depth was a significant positive predictor of soil compaction ($P \leq 0.001$), while soil organic matter was a significant negative predictor of soil compaction and bulk density ($P \leq 0.01$; Fig. 3). Percent ground cover of litter was a significant positive predictor of soil organic matter, which in turn was a significant negative predictor of soil pH and bulk density (Fig. 3). Path analysis also suggested that indirect effects of percent bare soil and rock cover, cryptogam, soil pH, bulk density, compaction, percent pore space, organic matter, soil temperature, and salinity upon *Coleogyne* density are substantially more potent than their direct causal effects (Table 3).

Significant intercorrelations ($P \leq 0.05$; Table 4) were detected among soil and surface variables. Specifically, soil compaction and bulk

TABLE 4. Intercorrelations among soil attributes along upper *Coleogyne* shrubland ecotones in the Spring Mountains. Soil temperatures were measured at the surface (0 cm) and at 15-cm depth in open spaces during August 2000. All r–values (Pearson's correlations) are significantly different at $P \le 0.001$.

Attribute	Depth	Moisture	pH	Bulk density	Compact.	Pore space	Organic matter	Temp.		Salinity
								0 cm	15 cm	
Depth	—									
Moisture	0.86	—								
pH	–0.88	–0.88	—							
Bulk density	–0.89	–0.99	0.90	—						
Compaction	–0.83	–0.99	0.89	0.98	—					
Pore space	0.89	0.98	–0.90	–0.99	–0.99	—				
Organic matter	0.89	0.94	–0.95	–0.96	–0.95	0.96	—			
Soil temperature										
at surface	–0.84	–0.98	0.81	0.96	0.97	–0.96	–0.93	—		
at 15 cm	–0.74	–0.94	0.76	0.91	0.94	–0.91	–0.90	0.98	—	
Salinity	–0.56	–0.81	0.81	0.75	0.84	–0.75	–0.84	0.79	0.85	—

TABLE 5. Percent ground cover of litter, bare soil, gravel, cobble, boulder, and cryptogam along upper *Coleogyne* shrubland ecotones in the Spring Mountains (n = 30 per elevation). The lowest elevation represented *Coleogyne* vegetation zones, while the highest represented *Pinus-Juniperus* zones. Mean values in columns followed by different letters are significantly ($P \le 0.05$) different by 1-way ANOVA and post-hoc Tukey means comparison test.

Vegetation zone	Litter	Bare soil	Gravel	Cobble	Boulder	Cryptogam
Coleogyne	15.5a	8.6a	58.2a	8.0a	2.4a	7.8a
Upper ecotone	22.8b	12.0ab	47.5b	6.6a	2.2a	8.3a
Upper ecotone	25.7b	18.6b	40.1c	5.7ab	2.0a	7.9a
Upper ecotone	28.8bc	37.1c	18.8d	5.4ab	2.5a	7.4a
Upper ecotone	31.9c	43.7cd	9.7e	6.1ab	2.4a	6.4a
Pinus-Juniperus	33.3c	45.7d	7.1e	4.1b	3.1a	6.8a

TABLE 6. Intercorrelations among soil surface variables along *Coleogyne* shrubland ecotones in the Spring Mountains. Significance levels: $*P \le 0.05$, $**P \le 0.01$, $***P \le 0.001$, and ns = nonsignificant.

Variable	Litter	Bare soil	Gravel	Cobble	Boulder	Cryptogam
Litter	—					
Bare soil	0.94***	—				
Gravel	–0.97***	–0.99***	—			
Cobble	–0.88***	–0.76***	0.80***	—		
Boulder	0.49**	0.66***	–0.63***	–0.53**	—	
Cryptogam	–0.75***	–0.89***	0.87***	0.45**	–0.61***	—

density, soil moisture and percent pore space, compaction and soil temperature, and organic matter and percent pore space revealed significant positive correlations ($P \le 0.01$; Table 4). Alternatively, soil depth and organic matter, soil moisture and temperature, bulk density and percent pore space, soil compaction and percent pore space, and soil pH and organic matter revealed significant negative correlations (Table 4).

Moreover, soil surface characteristics showed significant differences with increasing elevation (Table 5) and significant intercorrelations ($P \le 0.01$; Table 6). Percent cover of litter and cryptogam and percent cover of litter and cobble were negatively correlated ($P \le 0.05$; Table 6). Conversely, both percent cover of gravel and cobble and percent cover of bare soil and boulder were positively correlated ($P \le 0.05$; Table 6).

DISCUSSION

A number of environmental attributes varied with elevation, and such variation would cause the changes observed in *Coleogyne* shrub density at upper ecotones in the Spring Mountains of southern Nevada. This study explained how correlations among these environmental factors help yield the ecological requirements of *Coleogyne*. Path analysis suggested that indirect effects of percent bare soil and rock cover, cryptogam, soil pH, bulk density, compaction, salinity, organic matter, soil temperature, and percent pore space upon *Coleogyne* density are substantially more potent than their direct causal effects. Short, unlabeled (residual) arrows shown in the path diagram (Fig. 3) indicate that these environmental variables are also subject to additional influences not examined in this study, such as climatic, edaphic, geomorphic, and biological factors.

Air temperature was a significant negative predictor of the density of *Coleogyne* shrubs, producing a considerably more direct than indirect effect on *Coleogyne* density. Weather extremes are a recognized, important environmental element in the survival and natural selection of plants (Nelson and Tiernan 1983). During occasional frigid winter days, air temperatures can drop to below –35°C, which may prevent *Coleogyne* plants at mid-elevations from migrating upslope. Low winter air temperatures may largely determine the upper-elevational boundaries of *Coleogyne* in southern Utah (Wright et al. 1979). From a functional perspective, upper elevational distribution limits of woody plant species along the elevational gradient are primarily a response to air temperature in central Nevada (Smith et al. 1995a). Snow is fairly common at upper *Coleogyne* ecotones in the Spring Mountains, and spring snowmelt can lengthen the recharge period and provide additional soil water, both of which partially limit *Coleogyne* seed germination (Lei 1997) and limit long-term *Coleogyne* establishment. Greater precipitation at higher, cooler elevation can also have the same effect. In general, precipitation is positively correlated, while air temperature is negatively correlated, with ascending elevation in southern Nevada (Lei and Walker 1997a).

Soil depth was a significant negative predictor of *Coleogyne* density in this study. The direct effect of soil depth upon *Coleogyne* density was considerably more potent than its indirect effect. Shallow soils are a characteristic of *Coleogyne* shrublands in southern Utah (Bowns and West 1976) and southern Nevada (Lei and Walker 1997a, 1997b). *Coleogyne* density was negatively correlated with soil depth and soil moisture, which increased significantly with depth. *Coleogyne* seeds generally did not germinate well under high quantities and frequencies of water in a laboratory experiment (Lei 1997). In the lab experiment (Lei 1997), excessive watering promoted fungal growth, which became considerably more evident 4 weeks after the initial germination experiment. Mature *Coleogyne* plants also do not establish well in soils with high water content in southern Utah (West 1983). Deep soils of *Pinus-Juniperus* woodlands have a higher water content than shallow soils of *Coleogyne* shrublands in southern Nevada, presumably due to less evaporation loss of soil moisture and more potential storage of soil water at depth (Smith et al. 1995b).

Soil moisture, soil temperature, and *Coleogyne* density were hypothesized to have several causes, which in turn were hypothesized to influence each other. The path coefficients linking *Coleogyne* density with soil moisture and soil temperature were –0.62 and 0.34, respectively (Fig. 3). The direct causal effect of soil moisture on *Coleogyne* density was considerably more potent than its indirect effect. On the other hand, the indirect effect of soil temperature upon *Coleogyne* density was considerably more potent than its direct effect. Additionally, soil moisture was a significant negative predictor of soil temperature in this study. Much of the fluctuation in soil temperatures can be accounted for by changes in soil water content (Bowns 1973) and climatic variables.

Soil compaction, bulk density, organic matter, and *Coleogyne* density were hypothesized to have several causes, and these in turn were hypothesized to influence each other (Fig. 3). The path coefficient linking soil organic matter and *Coleogyne* density was considerably lower than Pearson's r for the same variables, implying that soil organic matter had some direct effect (–0.25) on *Coleogyne* density, but more of its effect was indirect (–0.64). Indirectly, soil organic matter affected *Coleogyne* density by contributing to soil compaction and bulk density.

A combination of relatively high soil organic matter and percent plant litter cover in the *Pinus–Juniperus* woodlands greatly enhances water storage capacity in soil. Although *Pinus, Juniperus,* and *Artemisia* plants are evergreen, some individuals have fairly high leaf turnover rates, thus producing an enormous amount of litter and organic matter in soils. In this study soil organic matter was a significant negative predictor of soil pH. *Coleogyne* shrub density was significantly positively correlated with soil pH. Although soils are calcareous and alkaline, soil pH declines with increasing elevation (Wright et al. 1979). The acidic coniferous leaf litter and abundant plant root biomass, along with excretions of living organisms and decomposition of dead organisms in *Pinus-Juniperus* woodlands, were likely to lower soil pH.

Loose, porous soils have low bulk densities and less compaction (Brady 1974). Abundant plant litter and organic matter in *Pinus-Juniperus* woodlands decrease soil compaction and bulk density because organic matter is less dense than a corresponding volume of mineral soil (Barbour et al. 1999). In this study soil organic matter was a significant negative predictor of soil compaction and bulk density. Although the organic content of a soil is not the sole determinant of its bulk density, it has been shown to be a reliable empirical predictor (Jeffrey 1987).

Soils at higher elevations in southern Utah and Nevada tend to have lower compaction because of higher infiltration and greater permeability to air and water (Bowns 1973, Lei 1995). Frost-heaving also likely decreases compaction, especially in surface soils. Additionally, percent pore space was higher with ascending elevation and was significantly negatively correlated with *Coleogyne* density. A combination of increasing percent pore space, organic matter content, and percent litter cover, and decreasing soil compaction and bulk density would allow greater water infiltration and retention in the soil at higher rather than at lower elevations. *Coleogyne* plants have a low tolerance to excessive soil moisture (West 1983), which partially limits the distribution of *Coleogyne* at its upper ecotones.

Among the soil surface characteristics, percent litter and bare soil cover increased, while percent gravel and cobble cover decreased significantly along the elevational gradient. In this study *Coleogyne* plants had a high density where rocks were abundant on soil surfaces. Dense woodland vegetation generally does not establish well with abundant rocks, regardless of size, on the soil surface in desert mountains at high elevations (Batanouny 1973).

This study examined significant relationships of selected environmental variables on the distribution of *Coleogyne* at its upper-elevational limits in the Spring Mountains, with the effects of other edaphic variables parceled out. Nevertheless, relationships between environmental attributes and density of *Coleogyne* shrubs are purely correlative. Correlative data can only address relationships and permit development of hypotheses about cause and effect. Definitive identification of cause and effect requires controlled experiments. Establishing long-term ecological research plots at various sites and using both physiological and ecosystem approaches to research are necessary to further delineate critical biotic and abiotic factors that determine the upper *Coleogyne* shrubland ecotones in southern Nevada.

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