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SIZE, AGE, AND DENSITY RELATIONSHIPS IN
CURLLEAF MAHOGANY (*CERCOCARPUS LEDIFOLIUS*)
POPULATIONS IN WESTERN AND CENTRAL NEVADA:
COMPETITIVE IMPLICATIONS

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

ABSTRACT.—Size-density-age relationships in curleaf mountain mahogany communities were studied in 25 study plots, each 30 × 30 m, in western and central Nevada. The influence of total vegetation cover (site potential) and relative mahogany cover (mahogany dominance) on the observed size-density-age relationships was investigated. A positive linear relationship was found between mean mahogany height and mean mahogany age. A positive nonlinear relationship was found between mean mahogany crown volume and mean mahogany age. Negative nonlinear relationships were found between mean mahogany density and mean mahogany age, and mean mahogany density and mean mahogany crown volume. Strong negative relationships were found between the mean combined density of established seedlings, juvenile, and immature mahogany and mean mahogany age and mean mahogany crown volume. Including total cover in the regression relationships between size, age, and density never increased the r^2 value by more than .05. The addition of relative mahogany cover improved the r^2 value for the relationship between mean mahogany density and mean mahogany crown volume by .28. The strong size-density and age-density relationships found indicate that intraspecific competition is probably occurring in the communities sampled, and that established seedlings, juvenile, and immature plants are the first individuals affected. Direct tests are needed to confirm these relationships.

Key words: curleaf mahogany, size-age-density relationships, intraspecific competition, population dynamics.

An understanding of the relationships between size, density, and age in a plant population is key to understanding the processes of intraspecific competition and population dynamics (Westoby 1977, 1981, Harper 1977). These relationships can be studied based on either the individuals of a species on one site over time or data from a series of different sites of different ages. Because curleaf mountain mahogany (*Cercocarpus ledifolius* Nutt. T & G) is a slow-growing, long-lived species, the latter method was used.

Relationships between population variables of size, density, and age can be used as indicators of a population's dynamics (Harper 1977). One example is the general relationship between average plant size and the density of a species fully occupying a site. This size-density relationship has been widely represented by the allometric equation $Y = kP^a$ (White 1981, Long and Smith 1984, Westoby 1984, and Westoby and Howell 1986) where Y is mean plant size, P is plants per unit area,

and a and k are constants. When plant populations reach full site occupancy, the maximum size-density relationship possible for that site has been obtained and density reductions occur (Hutchings and Budd 1981).

The size-density relationship has been broadly applied to many types of plants but not always consistently (Weller 1987, 1989, Zeide 1987). There have also been questions about the statistical validity of the relationship, in particular the possibility of spurious correlation (Weller 1987). It has been shown in a review of the procedures by Prairie and Bird (1989) that most of the questions regarding statistical validity have resulted from misconceptions about the relationship. They provide criteria supporting these types of analyses.

Models based on size-density relationships have been used to provide a base from which to evaluate the competitive interactions between the individuals in a population (Hutchings and Budd 1981, Long and Smith 1984,

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Gaudet and Keddy 1988). Drew and Flewelling (1979) have demonstrated the practical application of the use of a size-density model in the analysis and management of stand density in Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) plantations. Size-density models have also been successfully used in stand growth models (Smith and Hann 1984, Lloyd and Harms 1986, Smith 1986).

Most research on plant competition has centered on a phenomenological nonpredictive approach (Gaudet and Keddy 1988). Additional progress requires a predictive approach that allows general principles to be deduced that apply beyond the species and conditions of a particular site or study. Gaudet and Keddy (1988) have shown that plant biomass, plant height, canopy diameter, canopy area, and leaf shape explain most of a plant's competitive ability.

Information on intraspecific competition as related to relationships between size, age, and density in curleaf mahogany communities is nonexistent. The first objective of this study was to quantify size, age, and density relationships in selected curleaf mahogany populations. The second objective was to describe possible reasons for the observed size-age-density relationships. Explanations for the often-noted poor recruitment (Scheldt and Tisdale 1970) of new individuals into mature curleaf mahogany stands were also explored.

STUDY SITE DESCRIPTIONS

Curleaf mahogany communities were sampled in 25 study plots on three mountain ranges in western (Peavine Mountain: 9 plots, Carson Range: 4 plots) and central (Shoshone Range: 12 plots) Nevada during May–August 1985.

On Peavine Mountain scattered mahogany occur near 1890 m on west, east, and north aspects but dominate stands only above 1980 m. Mahogany stands on south-facing slopes are found above 2260 m. Individual stands vary in size from 1 to over 300 ha. Smaller stands are most common along rocky ridges and as islands within low sagebrush (*Artemisia arbuscula* Nutt.) communities. Large stands occur on hillsides and are commonly surrounded by mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* [Rydb.]

J. Boivin) communities. Annual precipitation averages 36–41 cm and occurs mostly as snow. The average frost-free period is 50–80 days. Curleaf mahogany is largely restricted to the Ticino gravelly fine sandy loam (SCS 1983), with an effective rooting depth of 51–103 cm.

Sampling on the Carson Range occurred in mahogany stands between 1550 and 1890 m. The mixed conifer zone generally occurs above 1900–2000 m. Individual mahogany stands vary in size and tree density as on Peavine Mountain. Average annual precipitation is 36–51 cm and occurs mostly as snow during the winter months. The average frost-free period is 50–80 days. Soils supporting mountain mahogany are Duckhill stony loam, Apmat gravelly sandy loam, and the Fraval-Hirschdale-Jumbo association (SCS 1983). Effective rooting depth varies from 51 to over 154 cm.

Mahogany on the Shoshone Range occur as low as 2150 m on north aspects, but large stands are rarely present below 2380 m. Southern aspects have few mahogany stands below 2600 m. All other aspects have abundant mahogany stands between 2450 and 3050 m. Limber pine (*Pinus flexilis* James) is a common associate above 2900 m. Stand size is variable, ranging from less than 1 to over 300 ha. Smallest stands occur along rocky ridge lines, and largest stands on sloping mountain sides and in bowls below the mountain crest. Annual precipitation averages 41–51 cm; but unlike western Nevada, heaviest precipitation normally occurs early in the growing season (March–June), and summer rainfall is slightly more abundant (Houghton et al. 1975). The frost-free period is 50–80 days. Mountain mahogany tends to be restricted to the Fox mount soil series, specifically Foxmount gravelly loam (Carol Jett, personal communication). These soils are well drained, moderately permeable, and have an effective rooting depth of 51–103 cm.

Average understory cover in each study area is almost identical (14–15%) (Schultz et al. 1990). Average vegetative cover on the Shoshone Range (98%) is substantially greater than on Peavine Mountain (70%) and the Carson Range (68%) (Schultz et al. 1990). A similar relationship for average curleaf mahogany cover is also present: Shoshone Range 79%, Peavine Mountain 56%, and Carson Range 54% (Schultz et al. 1990).

TABLE 1. Mountain mahogany maturity classes developed from a reconnaissance of mahogany stands near Reno, Nevada.

1. Established seedling	young plants; 2–7 mm basal diameter; smooth bark; plants may be up to 30 cm in height
2. Juvenile	young plants greater than 7 mm basal diameter; smooth bark; plants to 60 cm tall
3. Immature	young plants greater than 1.25 cm basal diameter; smooth bark; plants to 1.5 m tall
4. Young-mature	cracked bark; 1.5–3.0 m tall; crown broadened; may be multitemmed from base; not suppressed
5. Mature	cracked bark; wide full crown; few dead branches; may have several stems from base; may be suppressed; greater than 3 m tall
6. Overmature	cracked bark; may be multitemmed; numerous dead branches; may be greater than 3 m tall; frequently suppressed

METHODS

Field Sampling

An initial field reconnaissance near Reno, Nevada, indicated that mahogany stands are composed of individuals categorized into six maturity classes: established seedling, juvenile, immature, young-mature, mature, and overmature (decadent) (Table 1).

Sampling occurred in 30 × 30-m study plots, each having at least one young-mature individual and placed as close to a cardinal aspect as permitted by access and mahogany distribution. Ecotones with adjacent plant communities were avoided. Upper, middle, and lower portions of the mahogany belt were sampled when the elevation range exceeded 500 m.

Mahogany density and maturity class distribution were recorded in each study plot (density/900 m²). All mahogany plants, except established seedlings, were measured to obtain crown diameters (the two longest perpendicular diameters) and height. Established seedlings had only crown measurements recorded on plants selected for growth ring analyses.

Crown measurements were used to calculate mahogany cover (%) and mahogany crown volume (m³) (Ludwig et al. 1975, Tausch 1980). All measurements were of the green

leaf portion of the canopy and were made to the nearest decimeter (dm).

Four randomly selected individuals from each maturity class present in each study plot were cut to estimate plant age. Relative growth rates (RGR), using growth ring widths (Davis et al. 1972, Brotherson et al. 1980), were also determined on each cross section. If a maturity class had less than four individuals present, all plants were cut for age and growth ring analysis. Cross sections were cut as close to the ground as possible, and from the largest living stem.

Understory vegetation within each study plot was sampled in three randomly located 30-m belt transects (Schultz et al. 1990). Cover was occularly estimated in 15 shrub quadrats (1 × 2 m) and 30 grass and forb quadrats (20 × 50 cm). Crown cover (%) was estimated for shrub and forb species, and basal area (%) for grasses. The density of current-year mahogany seedlings (density/m²) was also recorded in each 1 × 2-m quadrat. Current-year seedlings usually had 4–8 leaves and were less than 2.5 cm tall.

Data Analysis

Crown diameter, crown height, and crown area (m²) were computed for each tree measured. Total crown area and total crown cover (%) values were calculated for each maturity class and study plot by summing the area occupied by individual plants. Average values were determined on each study area.

Relative mahogany cover (mahogany cover divided by total study plot cover) was calculated for each study plot and study area. Crown volume (m³) was computed for each mahogany plant using the formula for one-half of an ellipsoid (Tausch 1980). Total and mean values for each maturity class, study plot, and study area were calculated.

Mahogany density (density/900 m²) was determined for each study area. Growth ring counts and measurements from the mahogany subsample were made along two sanded radii on each cross section. Growth rings were identified by a single row of relatively large vessels in the springwood (Schultz et al. 1990). Modifications of a technique using acetic acid and zinc oxide (Parker et al. 1976) were used to enhance the contrast between early- and latewood in each annual ring. Time and funding constraints did not allow us to

determine whether false rings were present. Reference chronologies were not available for cross dating.

Yearly growth increments were measured to the nearest 0.01 mm for the 10 years before harvest using a Craighead-Douglas dendrochronograph and a binocular microscope. Age and ring width data from the two radii were averaged to determine a mean value for each cross section. Age data were considered reliable when values from the radii were within 5% of each other. Ring width data were used to calculate the mean stem area increment ([MSAI] [$\text{cm}^2/10$ years]) of each cross section (Schultz et al. 1990). Mean age, ring width, and MSAI values were summarized for each maturity class in each study area. Estimated mean age values for all maturity classes were based on the subsampled trees. Mean study plot age values were calculated by weighting the mean value of each maturity class by its density, summing, and dividing by total plot density. Study plot means were averaged for mean study area values. Relationships between age and size were not computed for the individual mahogany in each study plot because of the subsampled age data.

Age is an important predictor of a plant's fate only insofar as it affects plant size (Westoby and Howell 1986). Size is considered the primary determinant of survival (Westoby and Howell 1986). Each of the areas we sampled had mahogany stands composed of individuals of various size and age. To focus the analyses on the full range of variation sampled, we pooled data from all three sites.

All analyses of size, age, and density were first done using linear regression techniques. The residuals from these analyses were used to determine which were nonlinear. Nonlinear relationships were then analyzed using an iterative nonlinear regression technique to fit the data to the equation $Y = aX^b$ (Caceci and Cacheris 1984), where Y is mountain mahogany density or size, X is mean mahogany age or mean mahogany crown volume, and a and b are constants. This avoided the problems associated with logarithmic transformation of the data for analysis (Payendeh 1981, Brand and Smith 1985).

Following the completion of simple linear and nonlinear regression analyses, multiple linear ($Y = a + bX + cZ$) and nonlinear ($Y = aX^bZ^c$) analyses were performed. Values for

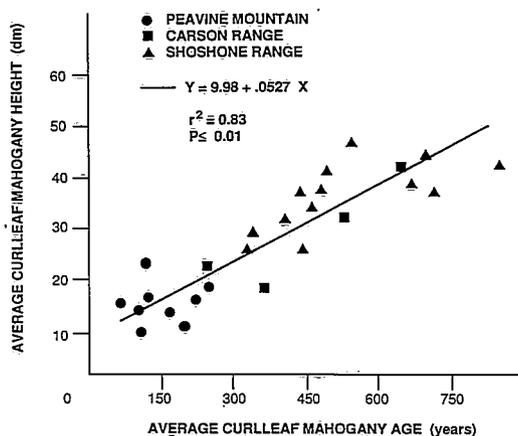


Fig. 1. Major landforms and vegetative communities on the NTS as determined by Beatley (O'Farrell 1976).

total vegetation cover and relative mahogany cover were used for Z in these analyses. These analyses provide an indication of how site potential (total plant cover) and dominance by mahogany (relative mahogany cover) in the sampled plots affected the size-age-density relationships observed. Methods for independent site potential estimates needed for direct tests of these relationships are not available for mahogany woodlands. Values for total vegetation cover, relative mahogany cover, and nonmahogany cover are from Schultz et al. (1990). The r^2 values for nonlinear analyses were computed according to the methods of Brand and Smith (1985). This r^2 has the same interpretation (% of variation in Y explained by variation in X) as for linear regression. The significance level is $P < .05$ or greater for all linear regression analyses. Significance levels are not directly available for nonlinear regression. Significance levels for the equivalent analyses using logarithmically transformed data were $P < .05$ or better.

RESULTS

Size-Age-Density Relationships

The relationship between average mahogany height and average mahogany age was the only one found to be linear (Fig. 1). The older the average age of the mahogany in a stand, the greater the average height. Including total cover in a multiple linear regression improved the results,

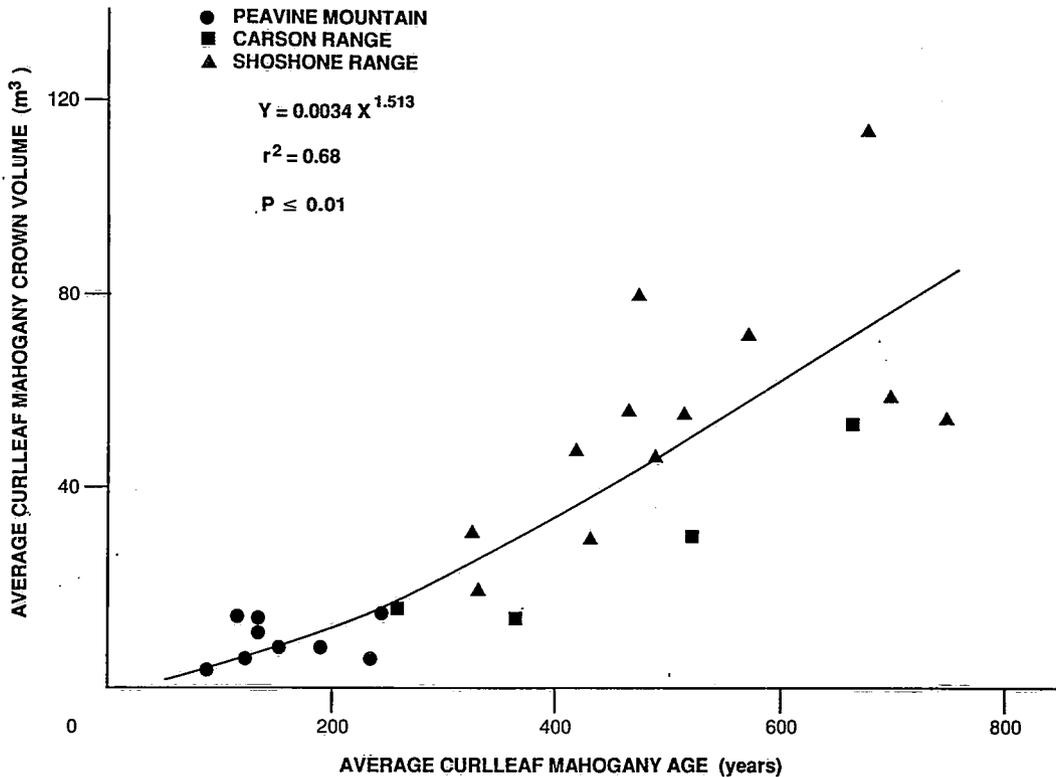


Fig. 2. Nonlinear relationship between average curleaf mahogany crown volume (m³) and average curleaf mahogany age (years) for three sites in Nevada.

$$Y = 2.71 + 0.0449X + 0.121Z, r^2 = .86, P < .001 \quad (1)$$

where Y is average mahogany height (dm), X is average mahogany age (years), and Z is the total vegetal cover (%) of the plots. The contribution of Z was significant ($P < .05$). Sites with higher total plant cover (%) tended to have taller mahogany for a given age than sites with lower total vegetal cover. This seems consistent with total cover representing site potential.

Average mahogany crown volume increased with average mahogany age (Fig. 2). Including total plant cover or relative mahogany cover for Z in a multiple nonlinear regression analysis increased the r^2 by less than .01 over that in Figure 2. The increase in mahogany crown volume with increasing stand age did not appear to be affected by either total plant cover or level of mahogany dominance in the sampled plots.

Average mahogany density had a strong nonlinear relationship with average mahog-

any age (Fig. 3). Including total plant cover or relative mahogany cover for Z in a multiple nonlinear regression analysis increased the r^2 by less than .01 over that in Figure 3. The decrease in mahogany density with increasing stand age for the sampled stands was independent of both total plant cover and mahogany dominance.

Mahogany density was highest in study plots that had an average age of less than 150 years, but it was substantially lower in study plots that had an average age of 250–300 years. Study plots with a mean age beyond 300 years had similar densities.

The density of established seedling, juvenile, and immature maturity classes had a similar, but steeper, negative relationship to average mahogany age as in Figure 3,

$$Y = 103428X^{-1.486}, r^2 = .81 \quad (2)$$

where Y is the density of established seedling, juvenile, and immature mahogany (density/900m²), and X is average mahogany age

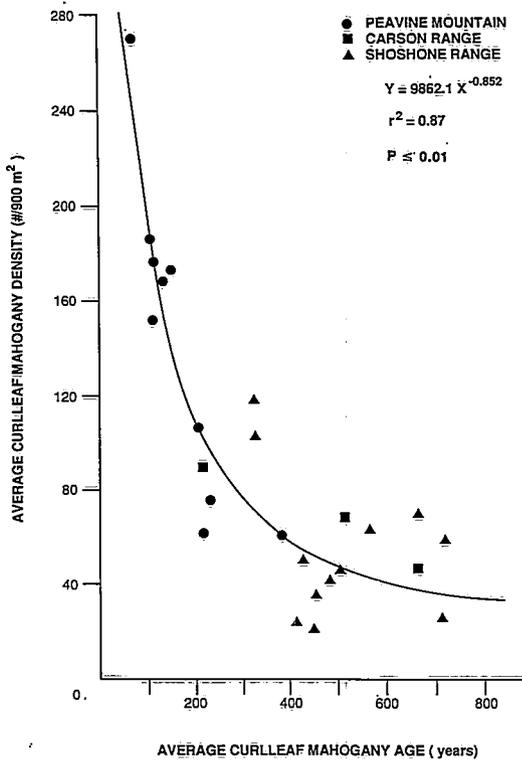


Fig. 3. Nonlinear relationship between average curleaf mahogany density (#/900 m²) and average curleaf mahogany age (years) for three sites in Nevada.

(years). The addition of total plant cover (Z) to the relationship in Equation 2 had the greatest improvement on r^2 , but the improvement was less than .02.

Mahogany density had an inverse nonlinear relationship with average mahogany crown volume (Fig. 4). Including relative mahogany cover for Z in a multiple nonlinear analysis improved the relationship,

$$Y = 0.0213X^{-1.48}Z^{3.051}, r^2 = .88 \quad (3)$$

where Y is mahogany density (density/900m²), X is average curleaf mahogany crown volume (m³), and Z is relative mahogany cover (%). For the same density, sites with higher mahogany dominance (relative mahogany cover) had larger plants than sites with lower mahogany dominance. The indication is that there may be a relationship between site potential and the ability of a given density of mahogany to dominate a site. The better the site, the larger the individual plants can be-

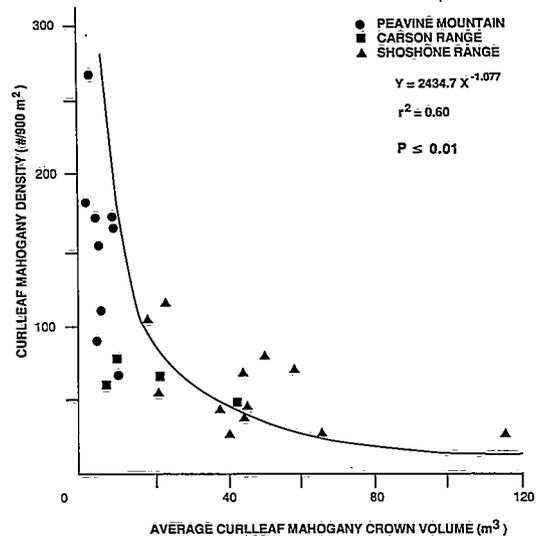


Fig. 4. Nonlinear relationship between average curleaf mahogany crown volume (m³) and curleaf mahogany density (#/900 m²) for three sites in Nevada.

come. An independent measure of site potential would be necessary to directly test this.

The density of reproduction, juvenile, and immature maturity classes had a similar, but steeper, negative nonlinear relationship with average crown volume as in Figure 4,

$$Y = 505X^{-1.15}, r^2 = .78 \quad (4)$$

where Y is the density of reproduction, juvenile, and immature mahogany (#/900m²), and X is average mahogany crown volume (m³). The addition of either mahogany or nonmahogany cover did not improve the relationship. The negative effect of large mahogany on mahogany seedlings appears generally independent of the relative levels of mahogany and nonmahogany cover. However, the addition of total plant cover (%) for Z improved the relationship:

$$Y = 0.510X^{-1.27}Z^{1.69}, r^2 = .83. \quad (5)$$

For stands with the same mean mahogany crown volume, the density of young mahogany tended to be slightly higher on plots with higher total cover. This may be a reflection of better site conditions somewhat offsetting the suppression of the younger mahogany by the dominant individuals. This possibility needs additional study.

DISCUSSION

Strong size, age, and density relationships were present in the mountain mahogany communities sampled (Figs. 1–4). Stands on Peavine Mountain, the Carson Range, and the Shoshone Range appeared to follow the same general trend. Relatively early in stand development (mean mahogany age less than 250–300 years) increases in mahogany size are accompanied by sharp declines in stand density. The change in the slope of the regression line that occurred beyond an average mahogany age of 250–300 years coincides with mahogany communities dominated by large, mature individuals (Schultz et al. 1990). These sites were mostly in the Shoshone Range. After mean mahogany age exceeded 300 years, mahogany density continued to decline with increasing stand age, but the rate of decline was reduced.

As mahogany stands increase in average age, average canopy volume and height of the individuals present increase (Figs. 1, 2, Schultz et al. 1990). As average canopy height and volume increase, stand density declines (Fig. 4, Eq. 3). This increase in plant size, together with a concomitant decrease in plant density with age, reflects the size-density relationships reported for many plant populations (Harper 1977).

Eventually, increases in individual plant size cause interference between individual plants and competition for essential resources (Hutchings and Budd 1981). As growth continues, a point is eventually reached where the habitat can support no additional biomass. Further growth can occur only when mortality occurs among existing plants. The strong size-density and age-density relationships present in Figure 4 and Equation 2, respectively, indicate that competition is probably occurring in the mountain mahogany communities sampled. Total stand density declines sharply as mean plant size increases. The density of the youngest individuals also declines, but more rapidly, as average mahogany age increases.

Gaudet and Keddy (1988) have shown that plant biomass explains a substantial part of a plant's competitive ability. Plant height, canopy diameter, canopy area, and leaf shape explain most of the residual variation. Biomass was not measured in this study, but vol-

ume measurements can be substituted for biomass, since studies have shown that volume and biomass are isometrically related (White 1981). Figure 4 indicates that average curlleaf mahogany crown volume, hence biomass, has a strong negative relationship with stand density. Average stand age, in itself, has no influence on a stand's population dynamics. As stands age, however, physical dimensions, such as average crown volume, average biomass, and average crown diameter, increase; and these physical attributes undoubtedly influence competitive interactions.

The inverse relationship of mahogany density and average mahogany crown volume (Fig. 4) was improved substantially by including relative mahogany cover (mahogany dominance) in the analysis (Eq. 3). This situation is similar to data reported by Gaudet and Keddy (1988). In their work plant height, canopy diameter, and canopy area further explained a plant's competitive ability beyond biomass alone.

A reduction of growth rates in individual plants relative to their potential can be an indication of plant competition (Long and Smith 1984). Relative growth rates, as represented by average ring width (mm), and mean stem area increment [(MSAI) ($\text{cm}^2/10 \text{ yr}$)] for each study plot for the last 10 years are reported in Schultz et al. (1990). Mountain mahogany stands on Peavine Mountain had the greatest RGR, as represented by average ring width and MSAI. If ring width and MSAI values on Peavine Mountain are assumed to be the maximum potential growth rates obtainable by curlleaf mahogany, then the RGRs in the Carson and Shoshone ranges are substantially reduced relative to the species' potential. This occurred despite similar soils and climate.

Previous work (Schultz et al. 1990) found that mean mahogany size and total mahogany crown volume are significantly ($P \leq .05$) less on Peavine Mountain than on the Carson and Shoshone ranges. Because larger individuals have a competitive influence considerably beyond what is proportional to their size (Bella 1971), it is likely that intraspecific competition is greatest in Carson and Shoshone ranges.

Since mahogany size is a function of stand age (Figs. 1, 2), we interpret the greater steepness of the regression lines in Equations 2 and 5 compared with Figure 3 to imply that

established seedling, juvenile, and immature mahogany are the first individuals in a stand affected by increasing mahogany size and, therefore, intraspecific competition. If intraspecific competition affected individuals of all sizes equally, the slope of the regression lines for all three analyses would be similar. Other research (Bella 1971, Weiner 1984, Grace 1985) has shown that the youngest and smallest individuals present in a population are the plants most affected by intraspecific competition. Schultz et al. (1990) found that Peavine Mountain has a population structure in which 62% of the plants present were from the established seedling, juvenile, and immature maturity classes. In contrast, the Carson and Shoshone ranges, respectively, had 9 and 18% of their population structure composed of individuals from these maturity classes. Mean mahogany crown volume on Peavine Mountain was 3.4 and 6.8 times smaller than on the Carson and Shoshone ranges, respectively.

As mean mahogany size continues to increase, few, if any, established seedling, juvenile, and immature mahogany are left. This situation is similar to other studies that have noted poor or absent reproduction as an indicator of competition (Long and Turner 1975, Oliver 1981).

The often-noted poor recruitment of new mahogany into mature stands can probably be explained, to some degree, by the size-density relationships observed. Data on estimated population growth rates (Schultz et al. 1990) show that mahogany communities with large average crown volumes (Shoshone and Carson ranges) have had slow population growth rates since the oldest individuals were established 500 or more years ago. Where average crown volume is relatively small (Peavine Mountain), established seedling, juvenile, and immature mahogany are abundant, and the population size has increased steadily since the oldest individuals became established.

Mahogany communities with small average crown volumes have comparatively lower mahogany cover (Schultz et al. 1990). Low mahogany cover increases the incidence of canopy gaps, which appear to be essential for the recruitment of young mahogany into the population (Schultz et al. 1990). Canopy closure has been found to indicate competition is occurring (Assman 1970). Mahogany

cover in the Shoshone Range averaged 79%, but it approached or exceeded 100% in almost half the study plots sampled. In study plots with less than 100% mahogany cover the spatial structure of the community is such that mahogany thickets with cover greater than 100% are common (personal observation). The Carson Range has a similar structural appearance.

Low densities of established seedling, juvenile, and immature mahogany can also be due to a lack of viable seed, poor seedling establishment, or poor recruitment of established seedlings into successively older maturity classes. Lack of viable seed did not appear to be a problem, since the Shoshone Range had a current-year seedling density of $2.0/m^2$. Personal observation indicates that stands with high mahogany cover and large average crown volumes have deep and persistent litter cover. Deep plant litter probably limits mahogany seedling survival and establishment (Schultz et al. 1990). Seedlings rooted in deep litter frequently do not have their roots established in mineral soil, and as soon as the litter material dries out the seedlings become desiccated and die (personal observation). Marquis et al. (1964) and Keever (1973) have observed that the establishment of relatively small-seeded species is adversely affected by continuous litter cover.

CONCLUSIONS

Curleaf mountain mahogany stands composed of large, mature individuals have lower total stand densities and lower densities of established seedling, juvenile, and immature mahogany. Over time intraspecific competition apparently occurs and probably intensifies as a result of increasing plant size. Intraspecific competition reduces the growth rates of all maturity classes below the potential growth rates for the species. Competition also appears to increase mortality in the smallest individuals present. This explains the often-noted poor recruitment (Scheldt and Tisdale 1970) of new individuals into mature mahogany stands. Increased mortality in the smallest and youngest individuals results in a maturity class structure dominated by relatively few, but very large, mature individuals. The plentiful establishment of young mahogany is probably not possible unless stands composed

of large, mature trees have their canopies opened up, and intraspecific competition is reduced.

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