Stand Development and Population Dynamics of Curlleaf Mountain Mahogany (*Cercocarpus ledifolius* Nutt.) Woodlands in Utah's Bear River Mountains

Seth A. Ex, R. Justin DeRose, and James N. Long

ABSTRACT

Curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) is a little-studied woodland tree that occurs in pure stands throughout the Intermountain West. Stand development and population dynamics of this species are poorly understood, despite their relevance to management. We describe here the development of stand age structures and population dynamics of mahogany woodlands in northern Utah using tree ages and measurements representing five structurally diverse stands. Establishment periods in all stands lasted decades, and regeneration continued intermittently in the absence of stand-replacing disturbance, eventually creating multiaged structure. Height, crown size, and basal area varied among older mahogany, which may reflect more intense intraspecific competition or increased likelihood of crown damage in older stands. Mahogany woodland managers face significant challenges. It is difficult to characterize historic stand conditions using current age structures because aging mature trees is generally unfeasible. Furthermore, there is little precedent for regenerating mahogany using silvicultural methods. Results suggest that the biggest risk in regenerating mahogany woodlands is low seedling survival, leading to the prolonged absence of mature trees. Consequently, multiaged methods that retain mature trees are recommended.

Keywords: crossdating, dendrochronology, multiaged stands, stand dynamics, vegetation management

Despite the large geographic extent of curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt., hereafter mahogany) woodlands in the Intermountain West (Preston 1968) and their importance as winter browse and cover (Davis 1990), relatively little is known about stand development and population dynamics of this vegetation type. Basic understanding of stand development allows historic stand structures, which often guide restoration and management, to be inferred from extant stands. Development of successful management strategies for mahogany also requires knowledge of population dynamics. In this study, age structures and tree measurements from five structurally diverse stands were used to characterize stand development and population dynamics of mahogany woodlands in the Bear River Mountains of northern Utah.

Mahogany is a small broadleaf evergreen tree common throughout the Great Basin that usually grows in monotypic stands on harsh sites at elevations between the mountain conifer zone and the desert steppe (Davis and Brotherson 1991). Stands may be patches tens of meters across or large enough to dominate mountain slopes. Mahogany woodlands are prominent in Utah's Bear River Mountains on southern to western aspects at elevations above 1,000 m (Lanner 1983, Russell 1997). Although mahogany is often associated with dry, rocky sites (Scheldt and Tisdale 1970), stands of particularly large trees have been found on moist, nonrocky sites (Schultz et al. 1990). Nitrogen fixing root nodules may help mahogany thrive on harsh sites (Youngberg and Hu 1972, Lepper and Fleschner 1977).

Mahogany trees are relatively long-lived, and seedlings are often rare in mature stands. Previous studies have found trees >100 years old to be commonplace (Brotherson et al. 1980, Arno and Wilson 1986, Banner et al. 1990). A Nevada study found a number of several-hundred-year-old trees and one individual more than 1,000 years old (Schultz et al. 1990). Mahogany is a weak sprouter, and sexual reproduction is the norm (Gruell et al. 1985, Austin 1990, Davis and Brotherson 1991). Regeneration rates are slow largely because good seed crops occur only one to several times per decade (Shaw et al. 2004), and seedlings often succumb to summer drought and winter browsing (Scheldt and Tisdale 1970, Ibáñez and Schupp 2002). However, mahogany's longevity implies that slow regeneration rates are sufficient for overstory replacement and do not necessarily indicate population decline (Schultz et al. 1990, Davis and Brotherson 1991), though this is uncertain (Gruell et al. 1985, Ross 1999).

Mahogany is browsed by mule deer (*Odocoileus hemionus* Rafinesque), elk (*Cervus canadensis* Erxleben), and rabbits (*Sylvilagus* spp.), especially during winter (Scheldt and Tisdale 1970).

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Seth A. Ex (seth.ex.442@gmail.com), R. Justin DeRose, and James N. Long, Department of Wildland Resources, Utah State University, 5230 Old Main Hill, NR 206, Logan, UT 84322-5230; Seth A. Ex current: Department of Forest and Rangeland Stewardship, Colorado State University, 1472 Campus Delivery, Fort Collins, CO 80523; R. Justin DeRose current: Rocky Mountain Research Station, Forest Inventory and Analysis, 507 25th Street, Ogden, UT 84401. *This work would not have been possible without funding from the Utah State University Undergraduate Research and Creative Opportunity Fund, Academic Opportunity Fund, and College of Natural Resources. Antonin Kusbach, the Forest Ecology-Silviculture Laboratory of the Utah State University College of Natural Resources, the Utah State University Ecology Center, and the Logan Ranger District also contributed resources and expertise essential to the success of this project. We thank Lindsay Ex and Dana Perkins for technical assistance and Richie Gardner and Donovan Birch for field assistance. This article was greatly improved by revisions suggested by three anonymous reviewers. Approved as Utah Agricultural Experiment Station, Utah State University, journal paper no. 8211.*

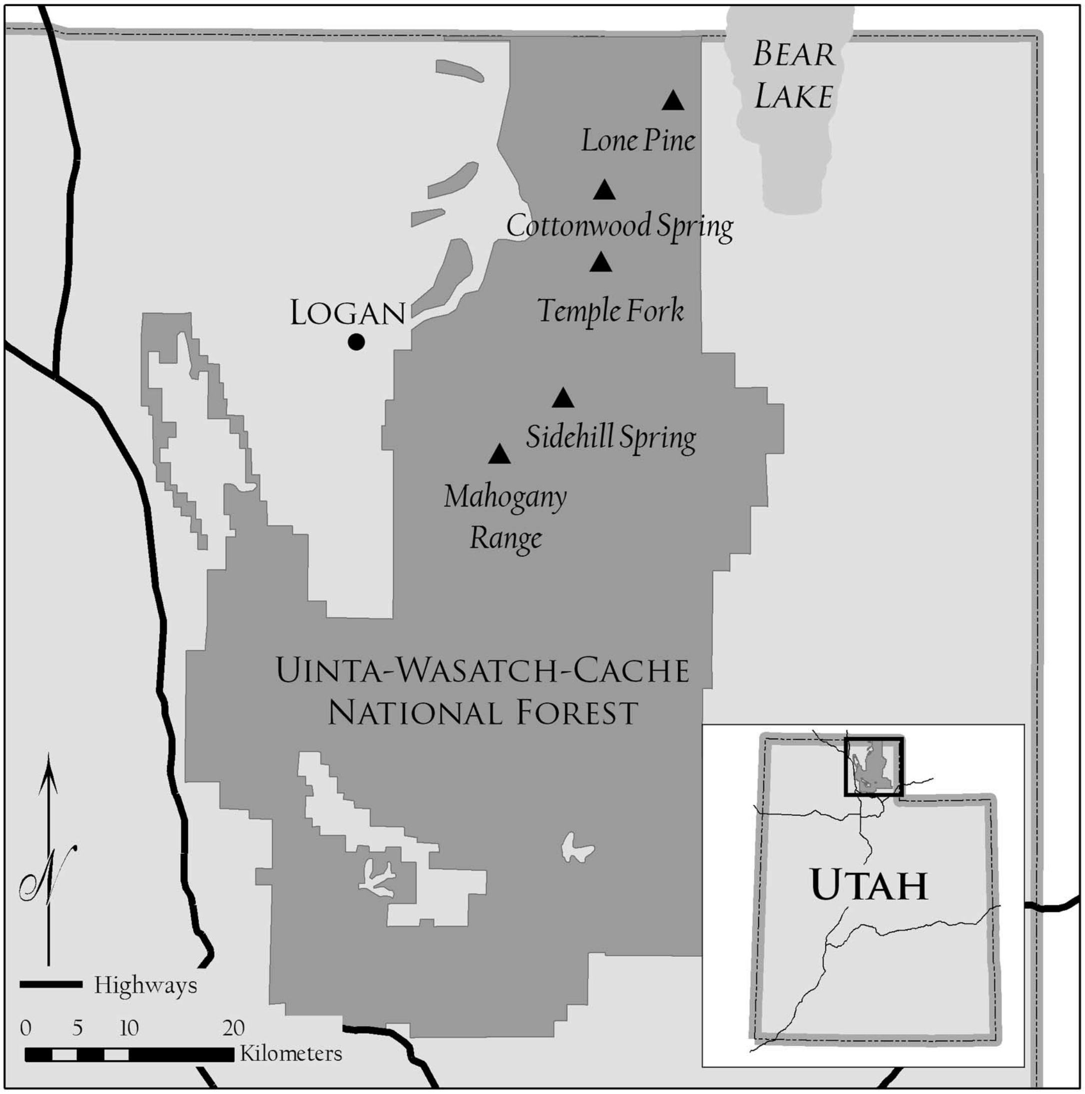

Figure 1. Map of study plots.

However, foliage of mature trees is often out of reach, escaping consumption (Davis and Brotherson 1991). This can result in a distinct browse line. Scheldt and Tisdale (1970) described morphological effects of browsing, referring to tall "umbrella"-shaped trees with elevated foliage, versus shorter "basketball"-shaped trees (presumably shaped by repeated browsing). Management-oriented research on mahogany has generally focused on browse production for wildlife use (Scheldt and Tisdale 1970, Austin 1990, Banner et al. 1990).

Silvicultural methods are not typically used to manage mahogany woodlands, and there is no consensus on appropriate regeneration methods. However, natural stand development patterns could be used as templates for silvicultural intervention. This research used age structures and physical characteristics of trees to infer stand development and population dynamics of mahogany woodlands in Utah's Bear River Mountains. Basic relationships among mahogany age, height, canopy size, and basal area across a spectrum of stand ages and tree sizes were interpreted in terms of stand development, whereas establishment dates reflected temporal patterns of reproduction.

Methods

Study Area

We established five study plots during the fall of 2008 in mahogany woodlands in the Uinta-Wasatch-Cache National Forest in northern Utah (Figure 1). Plot elevations were between 2,000 and 2,500 m, and aspects were between 180° and 270°. Slopes ranged from 12 to 42%. Average annual precipitation for the study area is approximately 121 cm (USDA Natural Resources Conservation Service) and generally falls as snow; summers are comparatively dry.

Study Design

Plots were selected to capture a spectrum of stand ages, creating a chronosequence. We used space for time substitution to mimic change over time (Cowles 1899) by comparing stands that appeared to be different ages based primarily on tree size. This method is widely used in ecology (Pickett 1989) and has been used previously with mahogany (Schultz et al. 1991). Space for time substitution permitted study of structural changes that are difficult to observe in a single stand because they occur over extremely long periods of

Table 1. Stand summary statistics.

Stand	Plot size (m^2)	n^a	Mean age	Median age	Range	SD
Temple Fork	225	14	222	224	136–338	46
Sidehill Spring	330	14	196	157	53–447	135
Cottonwood Spring	360	13	108	99	75–198	32
Mahogany Range	225	15	73	72	52–90	12
Lone Pine	375	31	43	39	11–105	23

Summary age statistics reflect overall stand age and variation in ages within stands.
[a]Values in the n column are the number of live mahogany stems included in analysis and do not include other species (Douglas-fir and Rocky Mountain juniper in Cottonwood Spring) or stems excluded from analysis because they were projected to have more than 10 missed rings.

Table 2. Master chronology summary information.

Number of dated series	24
Master series length (years)	257
Total dated rings checked	3,130
Series intercorrelation	0.417
Average mean sensitivity	0.325
Mean ring width (mm)	0.95
Number of missing rings	9
Percentage of total missing rings	0.288

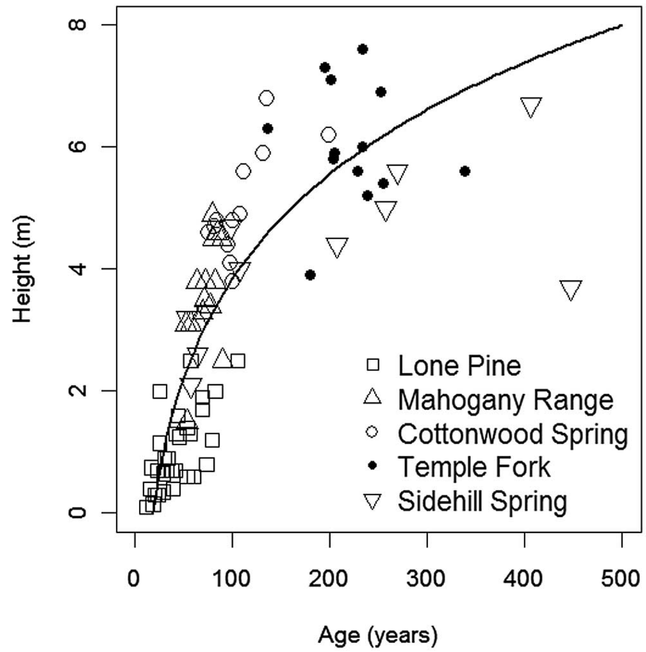

Figure 3. Mahogany height as a function of age. The fitted trend line is as follows: Height = −24.137 + 18.830 × Age$^{0.086}$. The oldest tree was an outlier and was omitted before the trend line was fitted.

time. We sized plots to include at least 13 live mahogany trees from often irregularly shaped stands of varying density. Plots ranged in size from 225 to 375 m^2 (Table 1). Age, basal diameter, height, and canopy projection area were recorded for all living mahogany trees in each plot. Tree ages were determined from ground-level stem cross-sections because extremely hard wood, irregular radial stem growth, and rot pockets made age sampling with increment borers impossible. Canopy projection area was calculated using the mean of four canopy projection measurements at cardinal directions from estimated stem center to a plumb bob at the canopy margin.

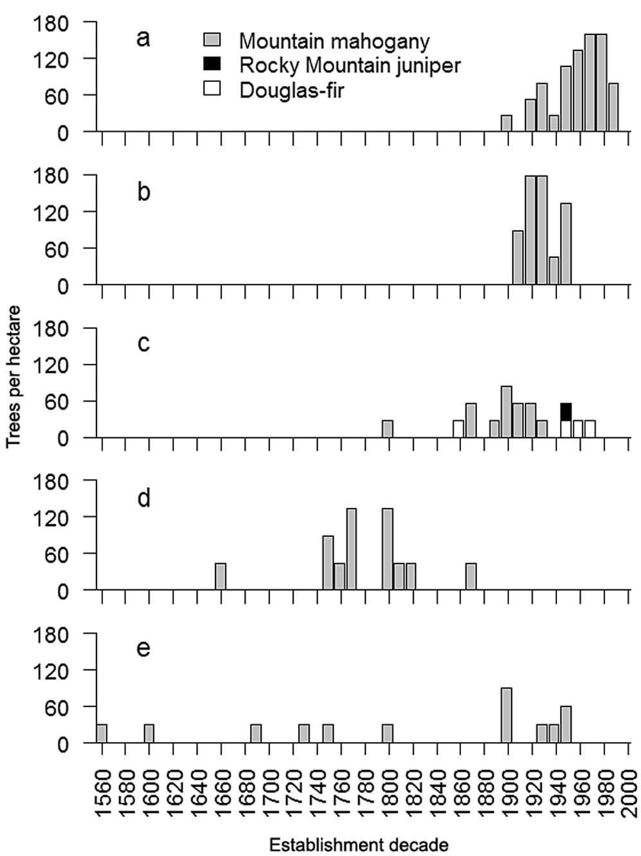

Figure 2. Establishment by decade for each plot. Lone Pine (a), Mahogany Range (b), and Cottonwood Spring (c) were characterized by single, long establishment periods, whereas Temple Fork (d) and Sidehill Spring (e) were multiaged.

Processing and Analysis

A large belt sander was used to remove chainsaw marks from cross-sections prior to final polishing for growth ring analysis using 1,500-grit sanding discs. Rings were counted, measured to the nearest 0.001 mm, and digitized using a binocular microscope, digital measuring device, and Measure J2X software (VoorTech Consulting, Holderness, NH). Where possible, ring counts and measurements were obtained on two radii for each cross-section to increase the likelihood of obtaining true ages; however, cryptic growth rings and stem damage made this impossible in some cases. A master chronology was constructed from tree-ring series showing high ring-width sensitivity. The master consisted of 24 series and was verified using COFECHA (Holmes 1983), which indicated a relatively high intercorrelation coefficient (Table 2). The master chronology was used to help identify and correct measurement and counting errors in series with low ring-width sensitivity and to select the most accurate series from cross-sections with more than one measured radius. Because the oldest individuals predated the master chronology, their ages should be regarded as conservative estimates. However, the overall low percentage of missing rings in the master implies that they were probably binned in the appropriate establishment decade. Some cross-sections had rotten centers and were consequently missing piths. The likely number of missed rings to the pith was estimated using techniques adapted from Duncan (1989). The number of missed rings was estimated on the basis of the length to height ratio of the arc described by the ring nearest the pith and the average width of the three full rings nearest the pith. Cross-sections projected to have 10 or more missed center rings were excluded from analyses.

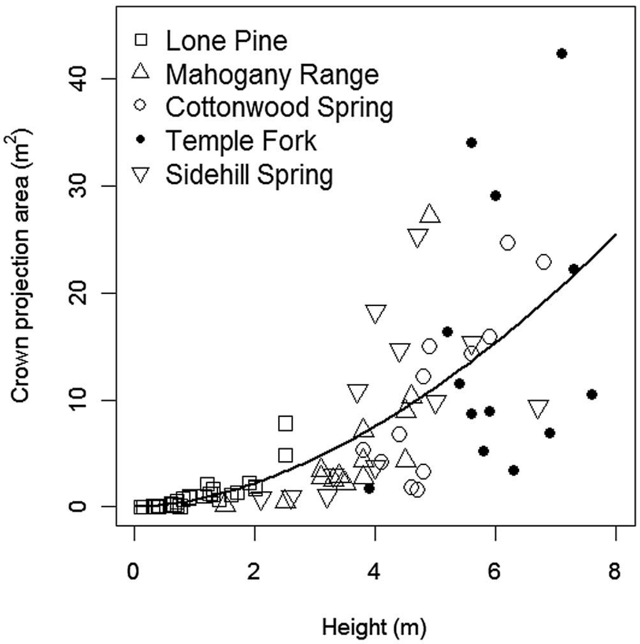

Figure 4. Mahogany crown projection area as a function of height. Note the increasing variation in crown size as individuals increase in height. The fitted trend line is as follows: Crown projection area = 0.665 × Height$^{1.752}$.

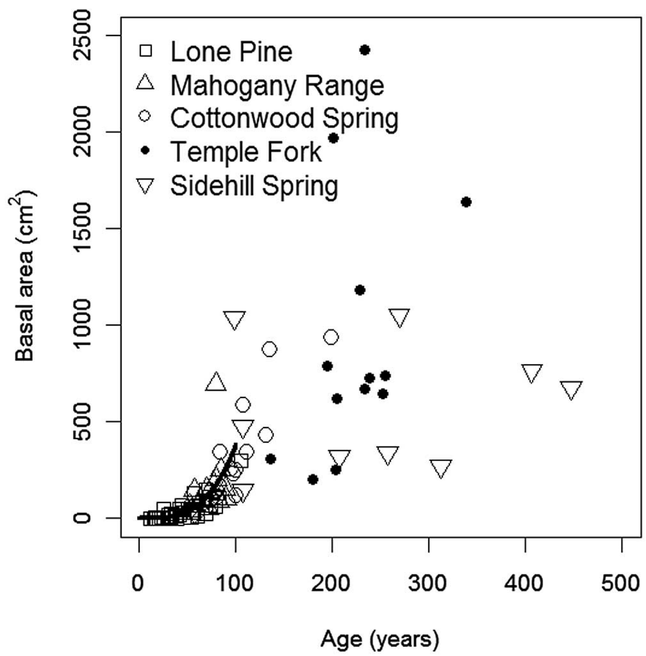

Figure 5. Mahogany basal area as a function of age. Basal area was strongly predictable up to approximately 100 years. The fitted trend line is as follows: Basal area = 0.0007 × Age$^{3.369}$. It was plotted only for ages up to 100 years.

Results

Age structures were variable between stands (Figure 2). However, a nonparametric Kruskal-Wallis test showed only that Lone Pine was significantly younger than all other stands ($\alpha = 0.05$). The oldest two stands (Figure 2d and 2e) had mahogany establishment dates spanning more than 200 years, which implies successful regeneration in the presence of mature overstory trees. By contrast, the three youngest stands (Figure 2a–2c) had relatively discrete establishment periods, suggesting that mature mahogany were rare or absent during establishment. Although establishment periods for young stands were discrete, they were lengthy. Establishment period duration is reflected in the range of tree ages occurring on a given site (Table 1). All stands were pure mahogany except Cottonwood Spring, which had minor Douglas-fir (*Pseudotsuga menziesii* subsp. *glauca* [Mirbel] Franco) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) components (Figure 2c).

Mahogany height increased markedly during early life but slowed substantially and became more variable after 100–150 years (Figure 3). Crowns generally remained small until trees neared 4 m in height, after which both the average size and the amount of variation relative to height increased (Figure 4). It is unclear from these results whether increased average crown size was associated with decreased density. Individual tree basal area increased slowly among young trees prior to accelerating and becoming variable as trees approached approximately 100 years old (Figure 5). Overall, tree size increased predictably during early life, whereas size differentiation increased after maturity.

Discussion

We interpreted results in terms of population dynamics and stand development. Age structures clearly indicated prolonged establishment periods followed by ongoing intermittent regeneration, suggesting development of multiaged structure in the absence of stand-replacing disturbance. Differentiation of mahogany height, basal area, and canopy projection area increased in older stands; very young stands consisted of uniformly small trees, whereas tree sizes in older stands were both larger on average and more variable. Taken together, age and size relationships were consistent with development of structural complexity over time.

Population Dynamics

The most striking feature of age structures was the long duration of establishment periods. Even in putatively even-aged stands (Figure 2a–2c), establishment took many decades. Prior work suggests that although large numbers of seedlings may germinate during good seed years, survival rates are typically low (Schultz et al. 1996, Ibáñez and Schupp 2002). Establishment periods may therefore reflect overall low survivorship over a decades-long series of establishment pulses. Our sample trees most likely represent a small fraction of successful recruits out of a much larger number of seedlings, most of which died before reaching maturity. This is consistent with previous research that found stem density declined rapidly as age increased in young mahogany stands before slowing once trees grew large (Schultz et al. 1991).

Age structures indicated successful regeneration in the presence of mature mahogany (Figure 2d and 2e). Young trees survived despite competition from larger neighbors, suggesting some tolerance to shading and belowground intraspecific competitive pressure (Oliver and Larson 1996). This demonstrates that mahogany is able to regenerate in the absence of stand-replacing disturbance, an important management consideration. Successful reproduction in mature stands also implies that stands became multiaged over time. Our results are consistent with work by Shultz et al. (1990), who concluded that gap-forming processes reduced stand density and relaxed light competition in older stands, allowing recruitment of new individuals into the overstory. The necessity of canopy gaps for reproduction among mature trees may explain decades-long periods with no successful regeneration in four stands (Figure 2b–2e).

Stand Development

Changes in tree height, basal area, and crown projection area reflected development of structural complexity as stands aged. Tree height and basal area increased predictably with age for mahogany less than approximately 100 years old (Figures 3 and 5). Similarly, crown projection area was consistently small until trees neared 4 m in height (Figure 4). These relationships suggest stands were relatively homogenous in terms of tree size and appearance for the first century after establishment. Age and size relationships were considerably more variable in older stands. Increased within-stand basal area variation among old trees (Figure 5) may reflect differences between dominant and suppressed individuals common among many forest types (Oliver and Larson 1996). Similarly, increased crown projection area variation as mahogany approached 4 m in height (Figure 4) could reflect differential acquisition of canopy growing space by more or less successful competitors.

Although the size relationships described in this study suggest structural complexity developed through competitive interaction, other processes may be at play. For example, variable crown projection area in older stands could reflect increased likelihood of crown breakage as trees grew old. Crown breakage from snow loading appears to be common among mature trees (Ross 1999). Similarly, large crowns among relatively tall trees could have resulted from factors independent of competition. Height growth could have released foliage from browse pressure, resulting in crown expansion (Scheldt and Tisdale 1970).

Management Implications

The results of this work apply to mahogany management in northern Utah. However, similarity to prior work on drier sites in Nevada (Shultz et al. 1990, Shultz et al. 1991) implies that they may apply across a range of site conditions. One major problem facing managers of mahogany woodlands is that ascertaining historic stand conditions from extant stands is problematic because trees are difficult to age. Accurate aging of mature trees requires cross-sections, which are invasive and labor-intensive to collect. Even with cross-sections, successful aging requires extensive sample preparation because rings are often tiny and indistinct. The difficulty of aging mature trees means that stand age structures are essentially unavailable to managers. When ages are unknown, tree size and morphology are the best indicators of stand history. In this study, apparently homogeneous stands of short (<2 m) trees were less than 100 years old and probably represented either initial site invasion or reestablishment following stand-replacing disturbance. In older stands, tree height, basal area, and canopy projection area were variable, making tree appearance an unreliable indicator of age. For example, Cottonwood Spring and Sidehill Spring were superficially similar in appearance, despite vastly different age structures (Figure 2c and 2e). Our work implies that tree appearances are a poor indicator of stand age structure.

Stand development and population dynamics described in this work suggest that silvicultural alternatives for mahogany woodlands should be developed under two assumptions: (1) regeneration will proceed slowly, and (2) in the absence of stand-replacing disturbance, stands will eventually become multiaged. Lengthy establishment periods identified in this work likely resulted from high seedling mortality over a series of regeneration events. Prior work suggests slow natural regeneration rates are a product of intermittent seed availability and low seedling survival, which potentially depends on interactions among a number of factors, including summer moisture, availability of suitable germination sites, and protection from herbivory (Ross 1999, Ibáñez and Schupp 2002, Shaw 2004). Even-aged methods remove all mature trees prior to regeneration and would probably result in a prolonged absence of mature trees unless seedling survival was increased. Seed tree and shelterwood methods maintain a seed source on site and may be a viable alternative for regenerating mahogany. Multiaged regeneration methods such as individual tree or group selection emulate canopy gap formation in old stands and are probably the closest analog to natural regeneration in the absence of stand-replacing disturbance.

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