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Recommended citation

Russell, Francis Leland. and Norma L. Fowler. 2002. Failure of Adult Recruitment in *Quercus buckleyi* Populations on the Eastern Edwards Plateau, Texas. *American Midland Naturalist* 148(2): 201-217.

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Failure of Adult Recruitment in *Quercus buckleyi* Populations on the Eastern Edwards Plateau, Texas

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ABSTRACT.—In many semiarid regions woodlands, savannas and grasslands form an unstable landscape mosaic; the physiognomy of a particular patch in the mosaic changes over time. To explain such temporal and spatial variation in tree abundance in semiarid landscapes, greater understanding of woodland tree population dynamics and factors that affect population dynamics of trees in woodlands is required. We examined the apparent failure of adult recruitment in *Quercus buckleyi* (Spanish oak) populations in woodlands on the Edwards Plateau, Texas. To verify adult recruitment failure, we quantified age structures of adult stems (stems taller than 150 cm) in five *Q. buckleyi* stands. We found that adult recruitment has been low to absent for 35 to 60 y in four of our five sites. At the fifth site, some stems recruited above 150 cm (the browse line) in the past 30 y. Most recruitment of adult stems occurred between 1900 and 1935, a period of low deer abundance. At the one site with recent adult stem recruitment, relatively low deer densities have been maintained since 1970 by hunting and by a perimeter fence that prevents immigration. Based on coincidence of adult stem recruitment with low deer populations, we hypothesize that intense browsing pressure or the interaction between fire suppression and intense browsing pressure is limiting adult recruitment of *Q. buckleyi*. If the documented patterns persist, many *Q. buckleyi* stands on the eastern Edwards Plateau are unlikely to replace themselves.

INTRODUCTION

Woodlands, defined as stands of trees less than 10 m tall that do not form a closed canopy, are characteristic vegetation in many parts of the world, usually in areas too dry to support true forests (Whittaker, 1975). Patches of woodland often form an unstable mosaic with patches of savanna or grassland (Belsky, 1989; Callaway and Davis, 1993). Research on factors driving temporal changes in patch physiognomy in semiarid landscape mosaics largely has focused upon woodland establishment in grasslands and savannas. Herbivory, fire regime, water availability and interactions among these factors have all been shown to be important in determining the timing and quantity of woody regeneration in savannas and grasslands (Archer, 1989; Savage and Swetnam, 1990; Prins and van der Jeugd, 1993; Villalba and Veblen, 1997; Weltzin *et al.*, 1997; Weltzin and McPherson, 1997). In contrast, relatively little is known about population dynamics of trees in existing woodlands or factors that affect these population dynamics. Understanding temporal variation in adult recruitment of woodland trees and identifying factors that limit tree adult recruitment in woodlands would enhance our understanding of causes of temporal changes in woodland physiognomy, including reversion of woodlands to savannas or grasslands.

The vegetation of the Edwards Plateau of central Texas is an example of a semiarid landscape mosaic of woodlands, savannas and grasslands. *Quercus buckleyi* Dorr & Nixon is

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often the most abundant woody species in woodlands on the eastern Edwards Plateau. However, populations of this species contain many fewer saplings and small adults than larger adults (Van Auken, 1988, 1993; Russell and Fowler, 1999). In fact, rarity of saplings and small adults is not restricted to *Q. buckleyi*, but also is typical of populations of *Prunus serotina* Ehrh. (black cherry) and *Fraxinus texensis* (Gray) Sarg. (Texas ash), both secondary components of Edwards Plateau woodlands (Van Auken, 1993). Such size structures may indicate that recruitment of adults (stems taller than 150 cm) has not occurred in recent decades and may be insufficient to maintain existing populations (Van Auken, 1988, 1993; Russell and Fowler, 1999). Alternatively, adult recruitment may be occurring, but saplings and small adults may be rare because individuals may grow rapidly through these size classes.

We quantified age structures of *Quercus buckleyi* stands on the eastern Edwards Plateau, based upon cores, to test our hypothesis (Russell and Fowler, 1999) that adult recruitment has been low or absent in recent decades. We use these age structures, together with other available evidence, to generate hypotheses about factors causing temporal variation in rates of adult recruitment in *Q. buckleyi* populations.

STUDY SPECIES AND HABITAT

Quercus buckleyi is a small to moderate-sized tree that is endemic to the Edwards Plateau (Correll and Johnston, 1979). It is most abundant in woodlands on canyon slopes on southern and eastern portions of the plateau, but also occurs in savannas (Buechner, 1944). When the trunk is damaged, *Q. buckleyi* generally sprouts from the root crown, resulting in genetic individuals composed of multiple stems. Typically, stems belonging to the same genet readily can be identified because connections to the decaying stump are visible aboveground or, if the connections are belowground, the stems occur in a circle around the decaying stump. Sprouting can allow a genet to survive after the original stem dies and provides a mechanism by which the species can persist in a community, at least temporarily, even without recruitment from seed.

Quercus buckleyi-dominated woodlands on the southern and eastern Edwards Plateau are "mixed woodlands" composed of a mixture of deciduous and evergreen canopy trees. These mixed woodlands are most extensive on canyon slopes, where they frequently occur as a narrow strip (less than 50 m wide) immediately below the canyon rim. *Prunus serotina*, *Fraxinus texensis* and *Juniperus ashei* Buchholz (Ashe juniper) are important canopy species, but are usually less abundant than *Q. buckleyi*. Canopy trees rarely exceed 10–15 m in height (Correll and Johnston, 1979). The understory is sparse with the exception of isolated but dense patches of *J. ashei* saplings.

Mixed woodlands are an important component of a landscape mosaic that includes savannas and grasslands. Grasslands and the herbaceous layer of savannas are dominated by mid and short grasses, such as *Schizachyrium scoparium* (Michx.) Nash. (little bluestem), *Bouteloua rigidisetata* (Steud.) Hitchc. (Texas grama) and *Buchloe dactyloides* (Nutt.) Engelm. (buffalo grass) (Fowler and Dunlap, 1986). The most common savanna trees are *Quercus fusiformis* Small and *Q. stellata* Wangh.

METHODS

Age and size structures of adult *Quercus buckleyi* stems were quantified at five study sites, each a discrete patch of mixed woodland, between 1995 and 1997. We selected study sites according to five criteria; each site: (1) contained at least 200 *Q. buckleyi* genetic individuals, (2) had land-use history available, (3) showed no evidence of clearing, (4) contributed to geographic representation across the Edwards Plateau and (5) had access

assured. These study sites were at Barnes Hollow (30°32'N 97°59'W), Coldwater Austin City Preserve (30°22'N 97°49'W), Hill Country State Natural Area (29°38'N 99°10'W), Pedernales Falls State Park (30°20'N 98°15'W) and Kerr Wildlife Management Area (30°06'N 99°24'W). All study sites were strips along hillsides or canyon slopes and were 0.4–1.0 km long and 10–80 m wide. Sites varied in area because boundaries of each site were natural edges of mixed woodland patches.

Structure of *Quercus buckleyi* populations can be described using either genetic individuals or individual stems as sampling units. Hereafter, "genet" refers to a genetic individual (possibly composed of multiple stems sprouted from the same root crown), whereas "stem" refers to a single *Q. buckleyi* stem that may have originated either as a stump sprout in an existing genet or from seed. We do not refer to individual stems as "ramets" because the extent to which stump sprouts produce their own root systems and, therefore, are capable of independent survival is unknown.

We quantified both genet-based and stem-based population structures. Using genets as the sampling unit has the advantage of representing statistically independent sampling units. A constraint in using a genet-based sampling design in which one stem is selected randomly from each multistemmed genet is that such a sampling design is more likely to include stems that originated from seed, which may occur singly, vs. sprouts, which must always originate in a multistemmed genet. Because most small, and therefore presumably young, *Quercus buckleyi* stems are sprouts in multistemmed genets that include at least one large stem (Russell and Fowler, 1999) this sampling design is likely to underestimate the abundance of young stems in the population. Alternately, a stem-based sample can include several stems from a single genet, yet stems of a single genet are not statistically independent because they may be connected through a common root system. The advantage of using individual stems as the sampling unit is that it better represents the population potential for persistence via resprouting. The majority of our conclusions, and all statistical analyses, are based on genet-based population structures. Stem-based population structures are presented to address the possibility that populations may persist through sprouting.

We randomly sampled *Quercus buckleyi* stems at each study site. We systematically walked through each study site and blindly drew slips of paper marked "Yes" or "No" from a bag when we encountered a stem. A separate slip of paper was drawn for each stem in multistemmed genets. If we drew a slip marked "Yes," we extracted two cores and measured stem diameter at 150 cm in height and then counted the number of stems in the genet to which the stem belonged. If a stem was too narrow to core (<1.25 cm), the number of years since it grew above 150 cm was estimated by measuring the length of the current or past year's growth and assuming the stem had grown an equal amount in previous years. If we drew a slip marked "No," we did not collect data on that stem. At Pedernales Falls we sampled dead stems, as well as live stems, to estimate adult mortality rates.

We cored stems at 150 cm, near the browse line, rather than at the base to estimate the rate at which stems become reproductive adults, providing a better predictor of future population growth or decline than the rate at which seedlings recruit to the population. Because seedlings and small saplings may be disproportionately affected by browsing and shading and, therefore, may never reach reproductive size, we believe that adult recruitment provides a better predictor of future population growth. *Quercus buckleyi* stems do not usually reproduce when they are 150 cm tall, but we believe that juveniles taller than 150 cm have a high probability of becoming reproductive adults because they probably have escaped mortality factors causing most juvenile mortality.

To age stems, or to determine the year of death for dead stems cored at Pedernales Falls, we sanded increment cores with 80 grit sand paper followed by a final sanding with 220 grit sand paper. Growth rings were counted and ring widths measured using a dissecting microscope with a 10× micrometer. Cores were cross-dated using ring sequences from 1957–1962 and 1967–1972. Cross-dating of cores was confirmed using the computer program COFECHA of the International Tree-Ring Data Bank Program Library (Holmes, 1994). Although deciduous oaks rarely produce false or missing rings (Schweingruber, 1993), cross-dated cores ensured that our estimates of time since stems became adults were not affected by anomalies in ring production (Fritts and Swetnam, 1989).

We estimated the number of years since the stem grew above 150 cm from ring counts for cores that could not be cross-dated. If a stem had heart rot, we estimated the number of years since the stem grew above 150 cm from its diameter. For each site, predictive relationships for stem age based on diameter were developed from stems at the site that could be cross-dated using least squares linear regression. Stem diameter accounted for much of the variation in stem age at three sites (Fig. 1). At the other two sites heart rot probably did not affect our ability to detect recent adult recruitment failure. At Coldwater few stems (8.9%) had heart rot and at Hill County heart rot primarily occurred in large stems (>15 cm), which were invariably older (>45 y since growing above 150 cm) stems.

We quantified the genet-based population structure for each site by resampling the stem-based data set. The probability of a genet being represented in the stem-based data set from its site depended on the number of stems in the genet. Therefore, to ensure that all genets in a site had an equal probability of inclusion, we weighted genets by probability of being selected when we resampled the stem-based data set. If a genet that was chosen in resampling was represented by more than one stem in the stem-based data set, we randomly selected one of those stems to represent the genet in genet-based population structures for that site. Genet-based samples included 6.3% (stems from 44 genets), 11.9% (45), 19.9% (58), 19.9% (57) and 45.0% (54) of genets at Hill County, Coldwater, Barnes Hollow, Pedernales Falls and Kerr, respectively.

We compared genet-based *Quercus buckleyi* age and size structures with negative exponential, uniform and normal distributions using Kolmogorov-Smirnov one sample tests for all sites except Coldwater. Because many stems were of the same age in the Coldwater population, we used the G-test for goodness of fit to compare the observed age structure with the three distribution types. A negative exponential distribution is one possible model of a population that maintains a constant stage structure and size through time. Specifically, it describes the stage structure of a population with a constant rate of adult recruitment and stage-specific mortality rates that are identical for all stages and constant through time. We compared *Q. buckleyi* stage structures with uniform distribution models because previous studies of oak woodlands (Mensing, 1992) and xeric oak forests (Ruffner and Abrams, 1998) have documented continuous, if not constant, adult recruitment before European settlement resulting in age structures that approximate uniform distributions. We compared *Q. buckleyi* stage structures with normal distribution models because Veblen and Lorenz (1987) hypothesized that normal distributions would describe age structures of young tree populations where shading reduces juvenile survival and growth following prolific adult recruitment.

Because tree regeneration in some semiarid landscapes is higher in sites or years with greater water availability (White, 1966; Reid and Ellis, 1995; Villalba and Veblen, 1997), we statistically compared timing of *Quercus buckleyi* adult recruitment with annual precipitation. For each site we used one-way ANOVA to compare annual precipitation during adult recruitment episodes with precipitation during intervals with no adult recruitment.

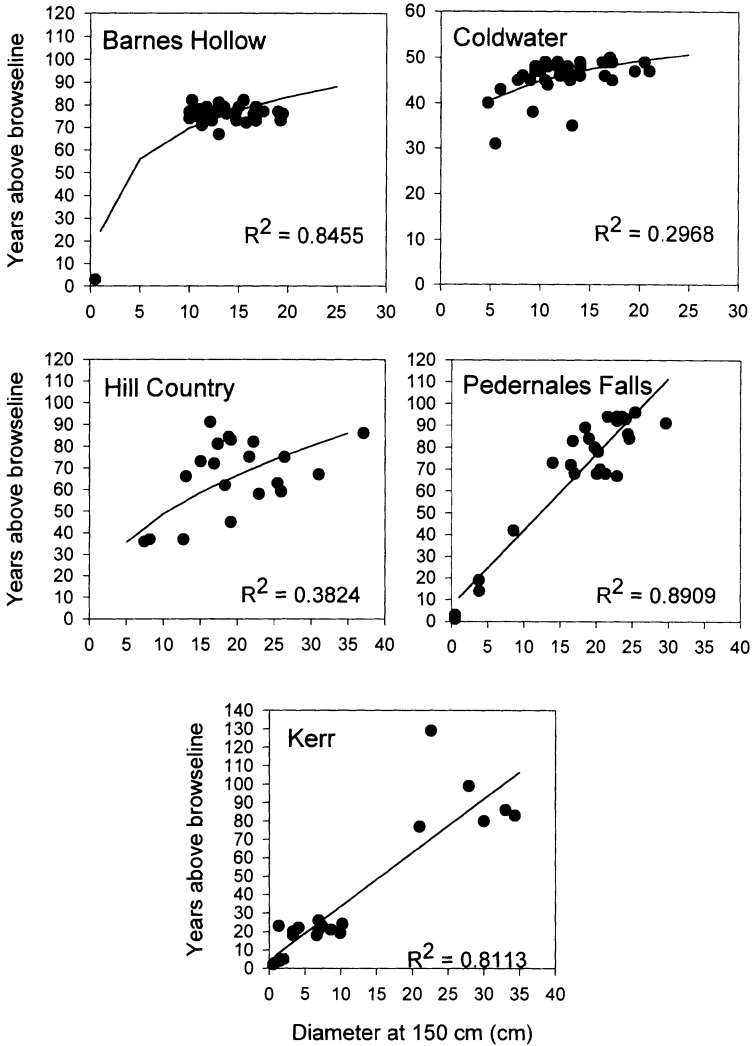


FIG. 1.—Diameter-age relationships for *Quercus buckleyi* stems at the five study sites. Regression equations are; Barnes Hollow: $y = 23.903 + 19.890 (\ln(x))$; Coldwater: $y = 30.571 + 6.234 (\ln(x))$; Hill Country: $\ln(y) = 2.848 + 0.451(\ln(x))$; Pedernales Falls: $y = 7.187 + 3.473x$; Kerr: $y = 4.436 + 2.917x$

Durbin-Watson tests were used to detect serial autocorrelation in annual precipitation. In addition, autocorrelation values with a 30 y time lag were inspected visually to detect patterns other than first-order autocorrelation. Historical precipitation at Barnes Hollow, Coldwater and Pedernales Falls was represented by precipitation data from Austin, Texas (United States Department of Commerce, 1896–1996). Historical precipitation at Hill Country and Kerr was represented by precipitation data from San Antonio, Texas. Barnes Hollow, Coldwater and Pedernales Falls were 50 km, 15 km and 60 km from Austin,

Texas, respectively. Hill Country and Kerr were 74 km and 100 km from San Antonio, Texas, respectively.

Water availability may affect seed production or germination (Reid and Ellis, 1995). Thus, episodes of adult recruitment may result from favorable climate many years before stems grow above 150 cm. Therefore, we also used one-way ANOVA to test whether annual precipitation differed during time intervals when stems that became adults germinated and intervals when acorns did not become adults. Because the time required for a *Quercus buckleyi* seedling to grow above 150 cm is unknown, we conducted multiple one-way ANOVAs, assuming 5, 10, 15 and 20 y time lags between germination and growth above 150 cm. For example, for Barnes Hollow, we compared precipitation between 1911 and 1934, when stems grew above 150 cm, to precipitation during intervals without adult recruitment; then, we also compared precipitation for 1906–1929, 1901–1924, 1896–1919 and 1891–1914, when stems that became adults may have germinated, with intervals when seedlings did not grow into adults.

Using the sample of live and dead stems from Pedernales Falls, we estimated adult mortality rate for the decade 1986–1995. Over-all adult mortality rate was calculated as the proportion of living adult stems in 1986 that died before 1995. We estimated diameter of stems in 1986 by subtracting the sum of widths of annual rings produced between 1986 and 1995 from the stem's diameter in 1995 or at the time of death. Because we extracted solid cores from stems that died in the 1970s, decomposition most likely did not affect our estimate of adult mortality between 1986 and 1995.

RESULTS

Genet-based population structures.—At all sites except Kerr, age and size structures differed significantly from negative exponential models. At all sites, age and size structures differed significantly from uniform distribution models. Young and small stems were significantly underrepresented in observed stage structures relative to stage structures predicted by negative exponential and uniform distribution models, except at Kerr. At all sites except Hill Country, observed age structures differed significantly from normal distribution models (Fig. 2). Size structures at Pedernales Falls and Kerr differed significantly from normal distributions, but no significant differences were found at the other three sites (Fig. 3).

Few or no *Quercus buckleyi* stems have grown above 150 cm in the past 35–60 y at four of the five sites (Fig. 2). No more than 8.9% of stems in genet-based data sets grew above 150 cm in the past 40 y at any of these four sites. *Quercus buckleyi* age structures at these sites are characterized by brief periods of adult recruitment that lasted no more than 40 y, and sometimes much less, during which 66.3% to 99.2% of adult stems recruited. Episodes of extensive adult recruitment occurred at three sites (Barnes Hollow, Hill Country and Pedernales Falls) between 1900 and 1935. At Coldwater, adult recruitment occurred between 1945 and 1955.

In contrast to recent low rates of adult recruitment at the other four sites, at Kerr 31.5% of stems in the genet-based data set grew above 150 cm since 1970. Extensive adult recruitment at Kerr also occurred between 1895 and 1930.

Stem-based population structures.—Stems that grew above 150 cm in the past 35 y are much rarer than stems that grew above 150 cm between 35 and 90 y ago at four of the five sites (Fig. 4). However, at two sites, Barnes Hollow and Pedernales Falls, limited recruitment of adult stems in existing genets has occurred in the past 10–15 y. Stem-based size structures reflect recent low rates of adult recruitment (Fig. 5).

Analyses of precipitation data.—Mean annual precipitation did not differ significantly between periods of adult recruitment and intervals without adult recruitment. Furthermore,

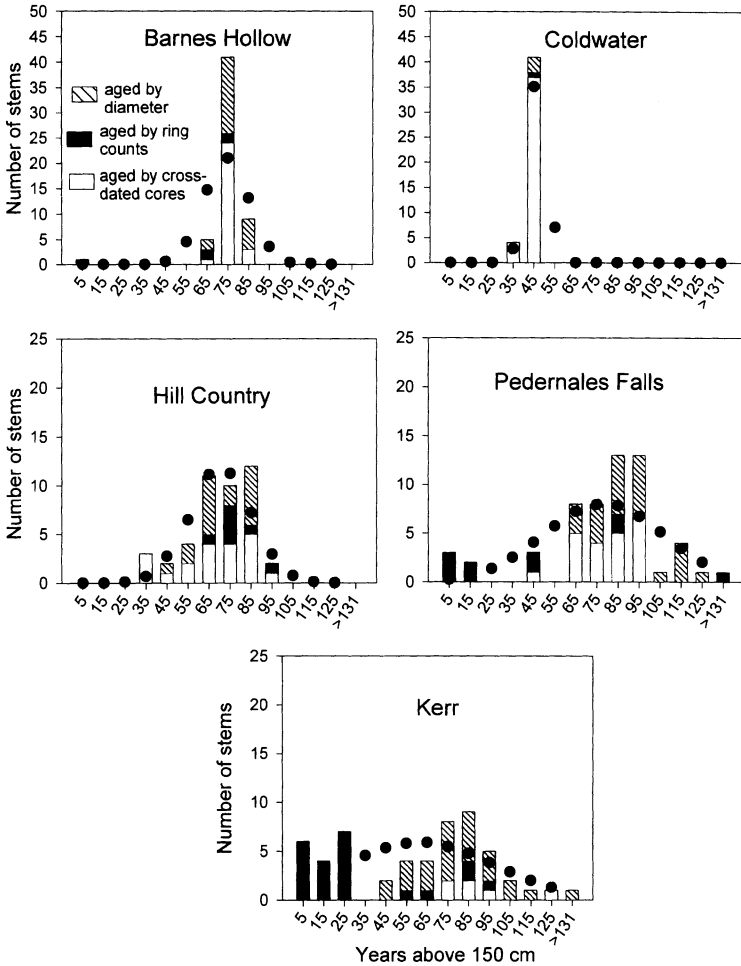


FIG. 2.—Genet-based age structures of adult *Quercus buckleyi* stems from the five study sites. 150 cm height represents the average browseline for the Edwards Plateau. Mid points of age categories are shown. Five year age categories are used for Coldwater to accommodate the narrow range of ages in this population. Solid dots indicate expected abundances for each age category based on normal distribution models

when 5, 10, 15 or 20 y time lags between germination and adult recruitment were assumed, no significant differences in mean annual precipitation were detected between intervals when existing adults may have germinated and intervals when seedlings did not grow into adults. Annual precipitation at San Antonio showed marginally significant serial autocorrelation ($P = 0.0998$).

Adult mortality rates.—Over-all mortality rate of adult stems at Pedernales Falls was 3.79% (3 of 79 stems) between 1986 and 1995. Dead stems were estimated to have been in 10.01–15.00 cm, 20.01–25.00 cm and >25.01 cm dbh size classes in 1986. Mortality rates of stems 15.01–20.00 cm dbh and 20.01–25.00 cm dbh were 0% (0 of 26) and

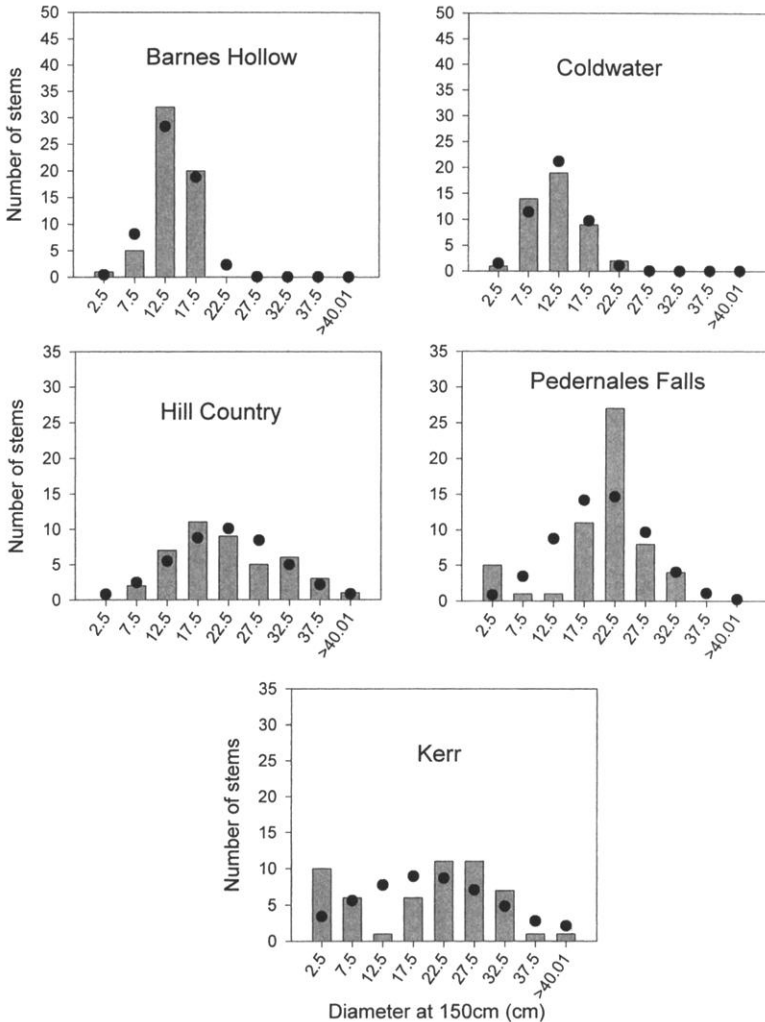


FIG. 3.—Genet-based size structures of adult *Quercus buckleyi* stems from the five study sites. Mid points of size categories are shown. Solid dots indicate expected abundances for each size category based on normal distribution models

3.85% (1 of 26), respectively. Sample sizes of less than ten stems, limit reliability of estimates of size-specific mortality rates in smaller and larger size classes.

DISCUSSION

Adult recruitment failure in Quercus buckleyi populations.—Age structures presented above support our hypothesis that adult recruitment is entirely absent or occurs at a much reduced rate in most *Q. buckleyi* populations (Russell and Fowler, 1999). In four of five sites in this study (all but Kerr) there has been either no recruitment of adults, or a very low rate of recruitment, in the previous 35–60 y. Because size structures of these four

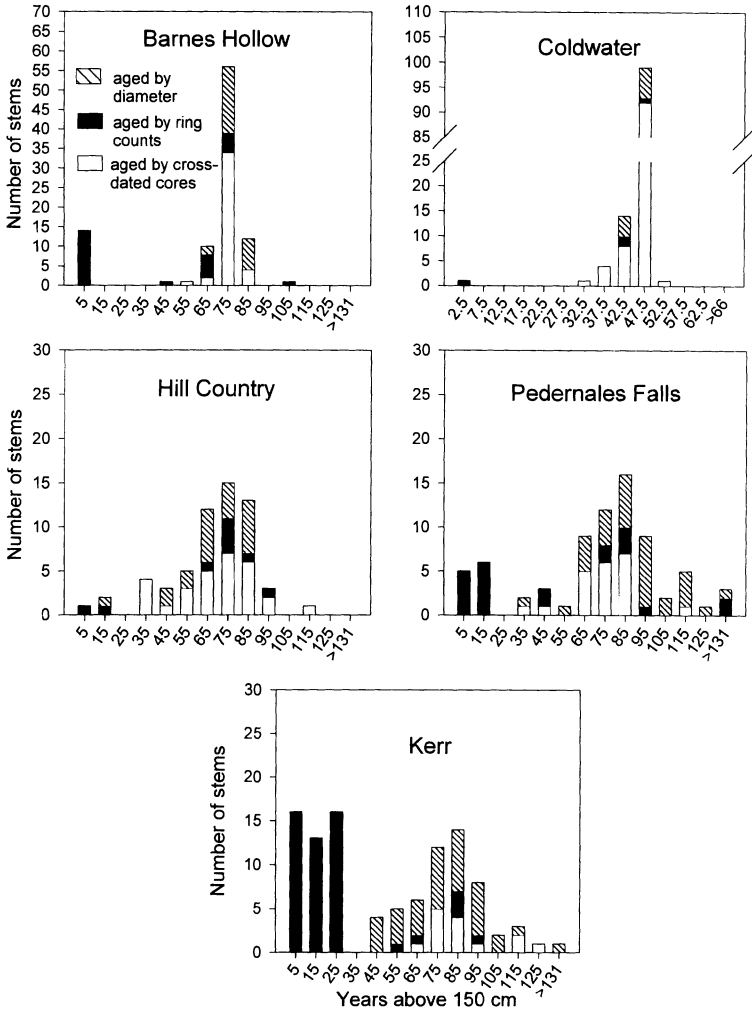


FIG. 4.—Stem-based age structures of adult *Quercus buckleyi* stems from the five study sites. Mid points of age categories are shown. Five year age categories are used for Coldwater to accommodate the narrow range of ages in this population

populations are similar to size structures previously reported for many *Q. buckleyi* populations (Van Auken, 1988; Van Auken, 1993; Russell and Fowler, 1999), we conclude that absence of adult recruitment or greatly reduced adult recruitment in *Q. buckleyi* populations is widespread.

Pronounced changes in stage structures, and possibly pronounced decreases in sizes, of *Quercus buckleyi* populations will occur in the future. Significant underrepresentation of adults in young age classes relative to negative exponential and uniform distribution models demonstrates that young adults are too rare to replace the large cohorts that currently occupy age classes between 60 and 100 y as these individuals move into older age classes.

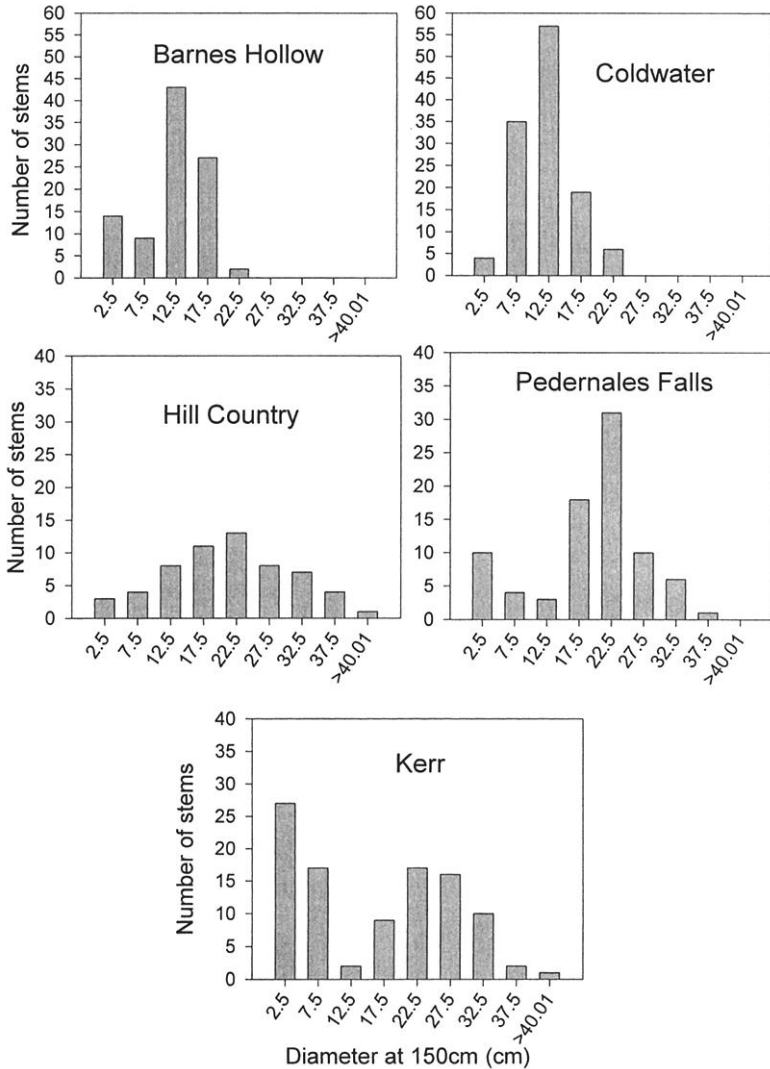


FIG. 5.—Stem-based size structures of adult *Quercus buckleyi* stems from the five study sites. Mid points of size categories are shown

Furthermore, if the rate of adult recruitment does not increase before individuals that recruited between 1900 and 1935 reach their maximum (unknown) lifespan, many *Q. buckleyi* populations will decline. At three of five sites studied *Q. buckleyi* populations already may be declining as adult stem mortality rates, estimated to be 3.8% per decade at Pedernales Falls, likely exceed rates of adult recruitment. At Barnes Hollow, Coldwater and Hill Country, adult recruitment rates were approximately 1.8%, 0% and 0% per decade, respectively, for the most recent decade represented in age structures.

Quercus buckleyi populations could persist despite the current absence of adult recruitment if recruitment resumes within the lifespan of existing adults. Adult recruitment

would be expected to resume if shade from *Q. buckleyi* adults that recruited between 1900 and 1935 currently prevents survival or growth of *Q. buckleyi* seedlings (a "stem exclusion phase" in stand development) (Oliver, 1981). When these canopy adults die greater light availability to seedlings might increase their survival or growth. Adult recruitment also might be expected to resume if *Q. buckleyi* adult recruitment has been episodic historically. The current absence of adult recruitment might be a low recruitment phase between periods of prolific adult recruitment.

We believe that the current absence of adult recruitment is not caused by shade from the large *Quercus buckleyi* cohorts that recruited between 1900 and 1935 because high light environments are available, but do not contain *Q. buckleyi* saplings and small adults. In other woodland, savanna and grassland landscape mosaics where shading is hypothesized to limit adult recruitment of trees in woodlands, saplings and small adults are found at the woodland-savanna ecotone (Veblen and Lorenz, 1988; Mensing, 1992). Our sampling included individuals at the woodland-savanna ecotone, yet *Q. buckleyi* age structures still show an absence or very low number of recent recruits. In addition, adult *Q. buckleyi* occur in savannas neighboring mixed woodlands (Buechner, 1944), but saplings are no more common in savannas than they are in mixed woodlands (L. Russell; N. Fowler, pers. obs.). Competition from grasses should not prevent *Q. buckleyi* colonization of savannas because most savannas in this region have much bare ground (Fowler and Dunlap, 1986). Finally, although quantitative models of age structures of tree populations undergoing stem exclusion are rare, Veblen and Lorenz (1987) predicted that these age structures would approximate normal distributions. At three of four sites with little recent *Q. buckleyi* adult recruitment, age structures differ significantly from normal distributions; young age categories are underrepresented relative to normal distribution models.

Quercus buckleyi age structures provide no evidence that episodes of adult recruitment have alternated with intervals of little adult recruitment in the past. We found no evidence for more than one episode of adult recruitment in any population. Furthermore, at Pedernales Falls and Kerr adult stems are present in each age class between 90 y and 130 y, suggesting that at these sites adult recruitment may have occurred at a continuous, low rate historically; they also do not show episodic adult recruitment.

If *Quercus buckleyi* populations do decline, the former oak-dominated woodlands might become dominated by *Juniperus ashei*, which is replacing itself (Van Auken, 1988). A second, although less likely, possibility is that mixed woodlands might become savannas. In some sites stump-sprouting may slow the rate of decline of *Q. buckleyi*, but present rates of adult recruitment of *Q. buckleyi* from stump sprouts appear too low to maintain current populations.

Possible causes of adult recruitment failure.—Why is there so little recruitment of adults into these *Quercus buckleyi* populations? We review the key plausible mechanisms, including inappropriate climatic conditions, changes in the fire regime and herbivory and conclude that browsing by white-tailed deer or interaction effects of deer browsing and fire suppression most likely cause the documented adult recruitment failure.

Comparisons of timing of *Quercus buckleyi* adult recruitment with historical precipitation records provide no evidence that altered or inappropriate climatic conditions inhibit *Q. buckleyi* recruitment. In some semiarid woodlands tree adult recruitment is greater during periods of above-average precipitation or in moist sites (White, 1966; Reid and Ellis, 1995; Villalba and Veblen, 1997). However, we found no evidence that adult recruitment of *Q. buckleyi* is related to or limited by precipitation. Mean annual precipitation did not differ significantly between periods without *Q. buckleyi* adult recruitment and periods with adult recruitment. Furthermore, mean annual precipitation did not differ significantly

between periods when current *Q. buckleyi* adults may have germinated and periods when seedlings did not grow into adults. Comparisons of timing of *Q. buckleyi* adult recruitment across the Edwards Plateau with annual precipitation records from Austin and San Antonio, Texas, also do not suggest coincidence of adult recruitment and above-average precipitation (Figs. 6, 7).

Fire frequency on the eastern Edwards Plateau has decreased since ranching began in the mid 19th Century (Bray, 1904; Foster, 1917). Unfortunately, we cannot infer historical effects of fire on *Quercus buckleyi* population dynamics directly from our data because we found no fire scars on any cores we collected and, therefore, cannot construct fire histories for our sites. However, we argue that lack of fire is not the primary cause of *Q. buckleyi* adult recruitment failure based on existing knowledge of immediate and long-term effects of fire suppression in other plant communities.

Where fires have been suppressed for decades, lack of fire may inhibit oak adult recruitment if low light levels, caused by prolific tree regeneration in the early years of fire suppression, reduce survival and growth of shade-intolerant oak seedlings (Lorimer, 1985; Abrams, 1992). Light levels may be reduced by adult oaks, a possibility we discussed above, or by increased densities of fire-intolerant understory tree species. In eastern forests, increased densities of shade-tolerant, fire-intolerant understory species, principally *Acer saccharum*, *A. rubrum*, *Fagus grandifolia* and *P. serotina*, are primarily responsible for light limitation of juvenile oak survival and growth (Lorimer *et al.*, 1994; Abrams, 1996). In contrast, understories of most mixed woodlands, including our five study sites, remain sparse in the absence of fire. Of the understory species inhibiting oak regeneration in eastern forests, only *Prunus serotina* occurs in Edwards Plateau mixed woodlands and, like *Quercus buckleyi*, *P. serotina* saplings and small adults are rare or absent (Van Auken, 1993). Therefore, it seems unlikely that shading by fire-intolerant understory species limits *Q. buckleyi* adult recruitment in mixed woodlands.

Fire suppression may inhibit oak regeneration where juvenile oaks are heavily browsed because fires, which top-kill seedlings and small saplings, may produce rapidly growing sprouts that quickly grow above the browseline. This interaction seems a plausible mechanism by which fire suppression may contribute to *Quercus buckleyi* adult recruitment failure. As we describe below, white-tailed deer populations on the Edwards Plateau are large (Young and Richards, 1996), suggesting that rapid elongation would enhance the probability that a stem would grow above the browseline. Relative growth rates of *Q. buckleyi* seedlings and sprouts that grow from top-killed seedlings have not been quantified. However, accelerated growth by sprouts is common in oaks (Moore and Johnson, 1967; McClaran and Bartolome, 1989).

We hypothesize that browsing by white-tailed deer is important in causing adult recruitment failure based on the coincidence of *Quercus buckleyi* adult recruitment with periods of low deer populations. At four sites (all but Coldwater), most present adults grew above the browseline between 1900 and 1935 and regeneration has been low or absent since the mid 1930s. Between 1900 and 1930 deer were nearly extirpated from the eastern Edwards Plateau by intense commercial hunting (Hahn, 1945). Not until effective enforcement of game laws in the early 1930s did deer numbers increase. As early as 1940 die-offs of deer from starvation due to overpopulation were reported in this region (Van Volkenberg and Nicholson, 1943; Taylor and Hahn, 1947). Deer populations peaked in the 1980s and have remained very large. In 1995 deer densities in the four counties of this study were 36.9 deer/km² (Blanco Co.), 33.8 deer/km² (Kerr Co.), 29.8 deer/km² (Bandera Co.) and 15.7 deer/km² (Travis Co.) (Young and Richards, 1996). Deer densities in western Travis County (the portion on the Edwards Plateau) are considerably higher than

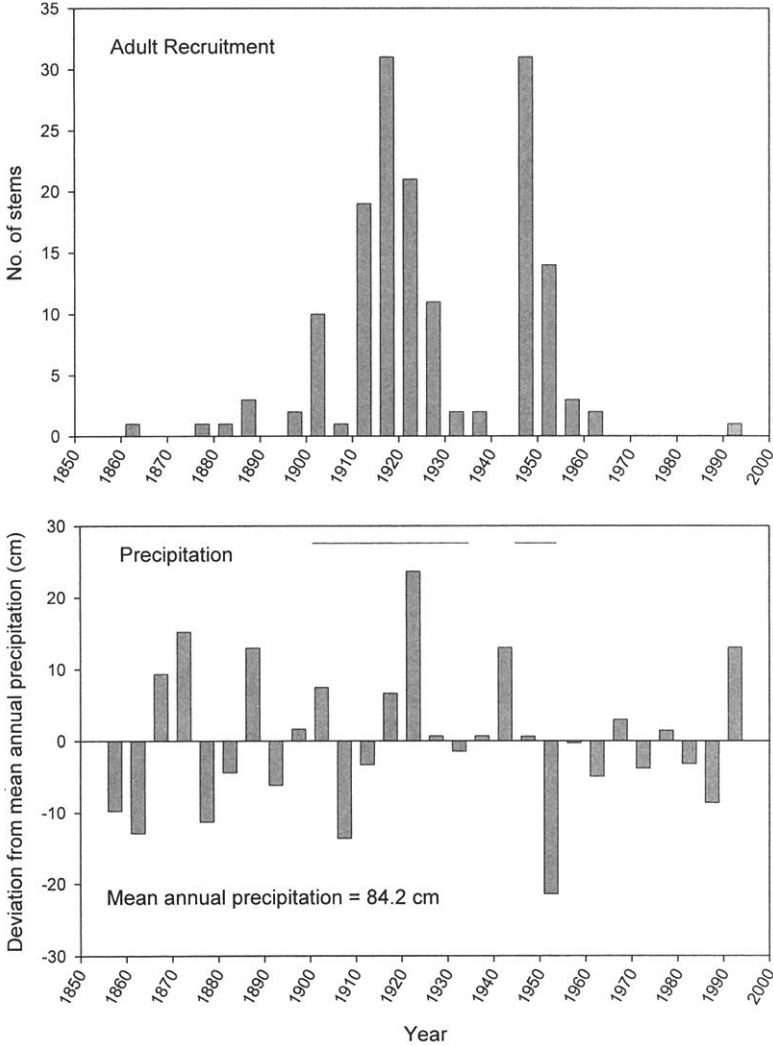


FIG. 6.—Timing of *Quercus buckleyi* adult recruitment at Barnes Hollow, Coldwater and Pedernales Falls compared with annual precipitation at Austin, Texas. For the combined age structure, bars represent number of stems that grew above 150 cm during the five year interval. For the precipitation graph, bars represent mean annual precipitation during the five year interval. Lines at the top of the precipitation graph indicate periods of much *Q. buckleyi* adult recruitment

the county-wide average density. Thus, a large increase in deer populations in the 1930s corresponds with a large reduction in recruitment of adults into four of five *Q. buckleyi* populations studied.

Successful *Quercus buckleyi* adult recruitment at Kerr since 1970 provides a further example of coincidence of adult recruitment and low deer populations. In 1968 a fence was constructed around Kerr to limit deer immigration. Previous efforts to lower deer densities

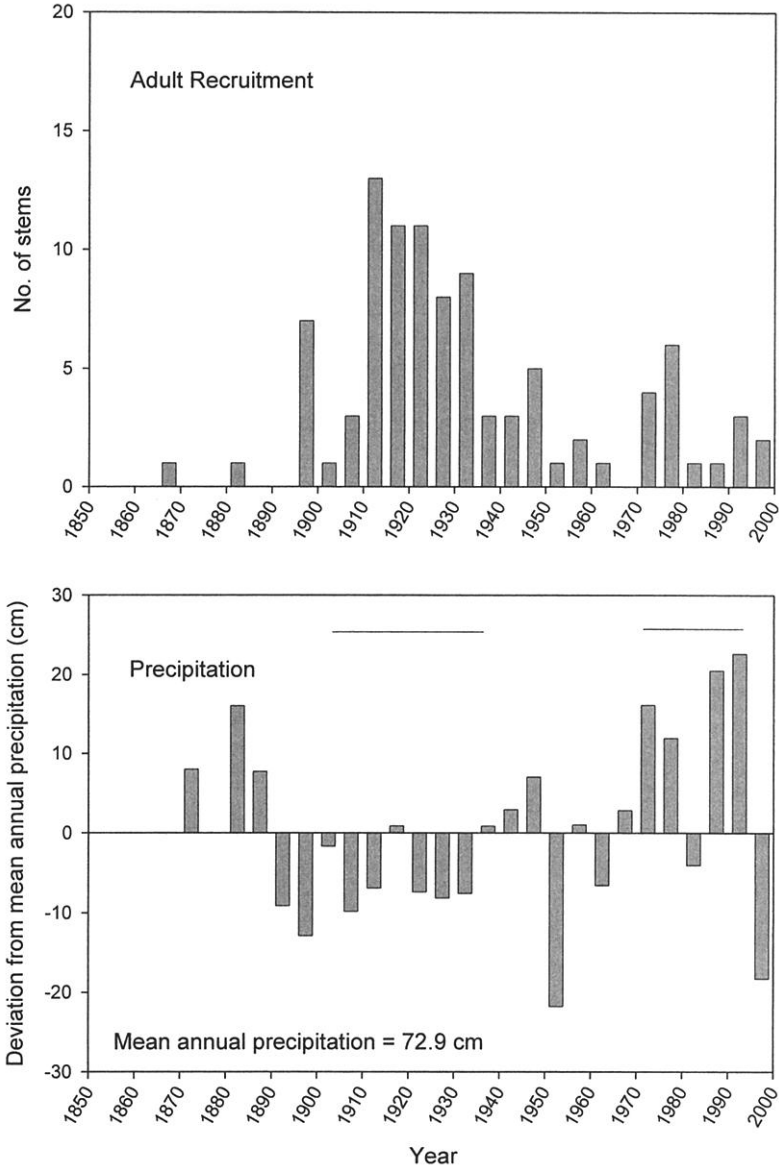


FIG. 7.—Timing of *Quercus buckleyi* adult recruitment at Hill Country and Kerr compared with annual precipitation at San Antonio, Texas. For the combined age structure, bars represent number of stems that grew above 150 cm during the 5 y interval. For the precipitation graph, bars represent mean annual precipitation during the 5 y interval. Lines at the top of the precipitation graph indicate periods of much *Q. buckleyi* adult recruitment

through hunting alone had not succeeded because deer migrated to the site from surrounding ranches where deer densities remained high. Following construction of this fence, deer densities declined from 46.5 deer/km² in 1968 to 19.5 deer/km² in 1972 (Harmel and Litton, 1981). Deer densities at Kerr have remained lower than densities at Hill Country and Pedernales Falls since 1972 (Texas Parks and Wildlife Department, pers. comm.). Long-term deer density data were not available for Barnes Hollow and Coldwater.

The pattern of *Quercus buckleyi* adult recruitment at Coldwater differed from the other four sites both in its timing, which was 1945–1950 after deer populations in the region had increased, and in the brevity of the period of successful adult recruitment. If deer densities at this site were high, as they were for the region generally in the 1950s (Young and Richards, 1996), synchronous prolific sprouting that satiated the local deer population may have allowed successful adult recruitment. Both the short duration of adult recruitment (80% of stems in the genet-based sample recruited within 5 y) and the high proportion of multistemmed genets (68.2% of genets were multistemmed as compared to 41% at the site with the second highest abundance of multistemmed genets (Kerr)) indicate that most adult stems originated as stump sprouts. The high density of stump sprouts may have been greater than the local deer could consume in the short time that sprouts were vulnerable. (Stump sprouts grow much more quickly than seedlings, especially in high light conditions (L. Russell, pers. obs.)). Cutting or a crown fire could have stimulated synchronous prolific sprouting (Huss, 1954).

Interestingly, deer browsing preferences correspond closely with interspecific patterns of adult recruitment failure, or apparent adult recruitment failure based on size structures, in mixed woodlands. For example, *Quercus buckleyi* is a highly preferred browse species on the Edwards Plateau (Armstrong *et al.*, 1991). *Prunus serotina* and *Fraxinus texensis* also are preferred deer browse (Armstrong *et al.*, 1991) and saplings of these species are rare (Van Auken, 1988). Only *Juniperus ashei*, which is among the least palatable species on the Edwards Plateau (Armstrong *et al.*, 1991), appears to be replacing itself (Van Auken, 1988).

Previous historical studies have suggested that changes in population sizes of browsing mammalian herbivores can affect establishment of woodlands in savannas and grasslands directly (Prins and van der Jeugd, 1993) as well as indirectly via interactions with fire (Pellew, 1983; Mensing, 1992). Age structures we quantify here lead us to hypothesize that mammalian herbivory is also important in limiting tree populations in some existing woodlands and, ultimately, may cause changes in the physiognomy of woodland patches. Once again, the degree of limitation of woody regeneration by herbivores is likely to be influenced by the fire regime. To rigorously test these hypotheses, as well as to evaluate management strategies for woodland conservation, exclosure experiments are needed.

Acknowledgments.—We gratefully acknowledge the City of Austin Parks and Recreation Department, the Texas Parks and Wildlife Department and the United States Fish and Wildlife Service, all of whom provided access to tracts used in this project. We thank Bill Armstrong, Donnie Harmel and Sean Heavey of the Texas Parks and Wildlife Department for land use history information for the tracts owned by TPWD. We thank Sheldon Kennedy and Gladin Turner for land use history information for tracts in the Balcones Canyonlands NWR. We thank Max Traweck of the Texas Parks and Wildlife Department for information on the history of deer populations on the Edwards Plateau. We thank Kate Bradley, Svata Louda, Annie Paradis, Tatyana Rand, Lauren Young, David Zippin and three anonymous reviewers for insightful comments on drafts of this manuscript. This project was supported by The Nature Conservancy (to L. Russell) and NSF (to N. Fowler).

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