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Rarity of Oak Saplings in Savannas and Woodlands of the Eastern Edwards Plateau, Texas

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RARITY OF OAK SAPLINGS IN SAVANNAS AND WOODLANDS OF THE EASTERN EDWARDS PLATEAU, TEXAS

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ABSTRACT—Anecdotal evidence suggests that *Quercus fusiformis* and *Quercus buckleyi*, two dominant trees of central Texas savannas and woodlands, are not recruiting to adult size classes on the eastern Edwards Plateau. To evaluate this hypothesis, size distributions of *Quercus fusiformis* and *Quercus buckleyi* populations are described. In the majority of savannas and live oak/juniper stands surveyed, *Quercus fusiformis* saplings and sapling-sized root sprouts (40 cm tall to 5 cm dbh) and small adults (5 to 15 cm dbh) were rarer than mid-sized adults (15 to 25 cm dbh) suggesting that adult recruitment of this species is below replacement rate at most sites. *Quercus buckleyi* saplings were much rarer than small adults in all mixed woodlands surveyed, suggesting that adult recruitment of this species from seed is not occurring on the eastern Edwards Plateau. Seedlings of *Quercus buckleyi* and seedlings and seedling-sized root sprouts of *Quercus fusiformis* (0 to 40 cm tall) frequently were abundant, suggesting that high seedling mortality rates may contribute greatly to poor adult recruitment. Intense browsing pressure by white-tailed deer may be the primary cause of poor adult recruitment of both species. It is unlikely that episodic adult recruitment will maintain populations of either *Quercus fusiformis* or *Quercus buckleyi*, as a reduction in seedling mortality rates over many years would be necessary to allow the slow-growing seedlings to escape their vulnerability to browsing herbivores.

RESUMEN—Evidencia anecdótica sugiere que *Quercus fusiformis* y *Quercus buckleyi*, dos árboles dominantes de sabanas y bosques del centro de Texas, no reclutan individuos hasta el tamaño adulto en el este del Edwards Plateau. Para probar esta hipótesis, describimos la distribución de tamaños en poblaciones de *Quercus fusiformis* y *Quercus buckleyi*. En la mayoría de las sabanas y parcelas de *Quercus fusiformis/Juniperus ashei* examinadas, los arbolitos y retoños de raíz del tamaño de arbolito de *Quercus fusiformis* (40 cm de altura a 5 cm de dap) y los adultos pequeños (5 a 15 cm dap) fueron más escasos que los adultos medianos (15 a 25 cm dap), sugiriendo que el reclutamiento de adultos de esta especie está por debajo de la tasa de reemplazo en casi todos los sitios. Los arbolitos de *Quercus buckleyi* fueron mucho más escasos que los adultos pequeños en todos los bosques mixtos examinados, indicando la falta de reclutamiento de adultos de esta especie desde la semilla en el este del Edwards Plateau. Se hallaron abundantes plántulas de *Quercus buckleyi* y abundantes plántulas y brotes de raíz del tamaño de plántulas (0 a 40 cm de altura) de *Quercus fusiformis*. Esto sugiere que la alta tasa de mortalidad de este tamaño de plantas quizás contribuya mucho a la escasez de adultos. El ramoneo intenso de venados de cola blanca puede ser la causa primaria del escaso reclutamiento de adultos de ambas especies. No es probable que el reclutamiento de adultos en episodios aislados mantenga las poblaciones de *Quercus fusiformis* o de *Quercus buckleyi*. Para ello sería necesario que la tasa de mortalidad de plantas que miden menos de 40 cm y que tienen crecimiento lento bajara durante muchos años para que estas plantas escaparan al ramoneo de herbívoros.

In many North American savannas and woodlands the quantity, frequency, and species composition of trees that are recruited to adult size classes appear to have changed following European settlement (White, 1966; McPherson, 1997; Scholes and Archer, 1997). In some savannas and woodlands there has been a failure of adult recruitment of previously dominant woody species (White, 1966; Mensing, 1992) although in other regions there has been prolific adult recruitment of previously sparse species (Madany and West, 1983; Archer, 1989). These changes are geographically widespread and could have large effects on species compositions and physiognomies of savannas and woodlands. Therefore, understanding historical patterns of tree recruitment and the processes that affect timing and quantity of recruitment of adult trees in these community types is of conservation interest. In this study, we use size distribution data to make inferences about the population dynamics, past and future, of one dominant savanna species, *Quercus fusiformis* (Plateau live oak), and one dominant woodland species, *Quercus buckleyi* (Spanish oak), on the eastern Edwards Plateau in central Texas.

Casual observations suggested to us that *Quercus fusiformis* is not recruiting to adult size classes. Although seedlings or root sprouts are abundant, saplings are almost non-existent (Fowler, 1988). Similarly, in populations of *Quercus buckleyi* on the southern Edwards Plateau (Bandera Co.), individuals less than 15 cm in basal diameter are much rarer than larger individuals (Van Auken, 1988). A loss of either species would greatly alter the composition of many of the plant communities of the eastern Edwards Plateau. *Quercus fusiformis* is the most common true tree found in savannas of this region. It appears to play a key role in the conversion of savannas to *Juniperus ashei* (Ashe juniper) stands, as juvenile *Juniperus ashei* are most abundant under *Quercus fusiformis* (Fowler, 1988). *Q. buckleyi* is of particular conservation concern because its presence is an indicator of suitable habitat for the endangered Golden-cheeked Warbler (Pulich, 1976). It is not known, however, whether *Q. buckleyi* is essential to this warbler.

The first goal of this study was to verify or refute the observation that there are very few saplings of either oak species on the eastern Edwards Plateau. The second goal was to infer, from observed size distributions, some characteristics of age distributions, so as to determine whether these populations are in decline. We also discuss possible causes of the scarcity of young trees, especially herbivory by white-tailed deer (*Odocoileus virginianus*).

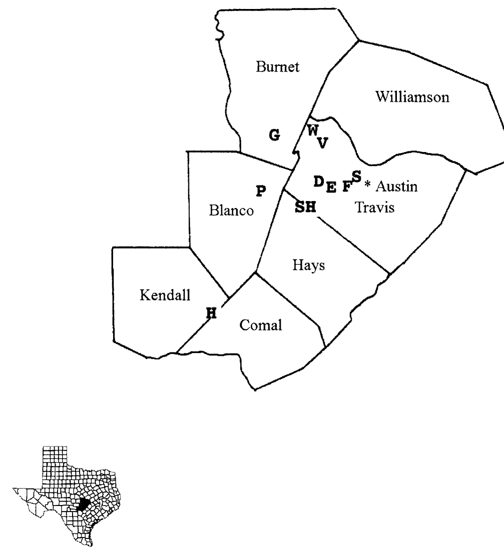

FIG. 1—The eastern Balcones Escarpment with locations of tracts containing sample sites and county names. The locations are as follows: D = Double J and T Ranch City Preserve, E = Emma Long City Park, F = Forest Ridge City Preserve, G = Grelle Primitive Area, H = Honey Creek State Natural Area, P = Pedernales Falls State Park, S = St. Edwards City Park, SH = Shield Ranch, W = Webster Tract of the Balcones Canyonlands National Wildlife Refuge, V = Victoria Tract of the Balcones Canyonlands National Wildlife Refuge.

STUDY SPECIES AND COMMUNITIES—The Edwards Plateau is a region of uplifted limestone in south-central Texas. This study was conducted on the eastern portion of the Edwards Plateau (Fig. 1). Topography there is characterized by flat plateaus dissected by sharp canyons. July average high temperature of this six county region (Burnet, Travis, Hays, Comal, Blanco, and Kendall) is 35°C and January average low temperature is 3°C. Average annual rainfall totals for these six counties vary from 71 to 91 cm. Precipitation occurs throughout the year with monthly means from 10 to 11.5 cm (May, September) to 4 to 5 cm (July, January). Mean annual gross lake surface evaporation exceeds mean annual precipitation by at least 76 cm (Larkin and Bomar, 1983). *Quercus fusiformis* (Plateau live oak) varies in size and habit from a large shrub to a large tree (Correll and Johnston, 1979). Acorns fall between late August and early November. Epicotyl emergence occurs January through March. Prolific root sprouting frequently forms a carpet of root sprouts that can extend slightly beyond the dripline of the adult's canopy. These root sprouts do not appear to increase in height while the parent is alive, but they could allow the genet to survive after the death of the original stem. In this study, size distributions of *Q. fusiformis* populations in upland savannas and in live oak/juniper stands are described. Populations in these two quite different communities are treated separately because the two communities may have quite different patterns of adult recruitment. *Quercus fusiformis* is the dominant tree of most savannas of the Edwards Plateau, but *Q. stellata* (post oak) and *Ulmus crassifolia* (cedar elm) are abundant at some sites. *J. ashei* saplings frequently occur beneath the larger trees, sometimes forming dense thickets. Many landowners mechanically remove invading *J. ashei.* Savannas of the eastern Edwards Plateau have an extensive history of grazing by cattle and sheep and browsing by goats. *Q. fusiformis* and *J. ashei* are co-dominants of the live oak/juniper stands, occurring in nearly equal proportions. Canopy cover is almost 100%. The canopy is short, rarely exceeding 10 m in height. Understory vegetation is sparse to non-existent.

Quercus buckleyi is a small to moderate-sized tree (Correll and Johnston, 1979). Acorns fall between late August and early November. Epicotyl emergence occurs between late February and late March. Sprouting from the root collar of both stumps and living stems produces genetic individuals composed of multiple stems. Sprouting appears to allow a genet to survive after the death of the initial stem. Size distributions of *Q. buckleyi* populations in mixed woodlands are described. Mixed woodlands are most extensive on mesic north- and east-facing canyon slopes. *Q. buckleyi* frequently is the dominant tree, and *Prunus serotina* (black cherry), *Fraxinus texana* (Texas ash), and *J. ashei* occur in lesser abundances. On the southern Balcones Escarpment, mean canopy cover in mixed woodlands is 91% (Van Auken et al., 1981). The canopy rarely exceeds 10 m in height. The understory is sparse with the exception of isolated but dense patches of juniper saplings.

MATERIALS AND METHODS—Savannas, live oak/juniper stands, and mixed woodlands were each represented by several study sites (Table 1). All sites overlie Pennsylvanian or Lower Cretaceous limestone. Data were collected between August and October 1994. The unit of observation in *Q. fusiformis* populations was the individual stem because it was impossible to determine in the field whether stems taller than 1.5 m belonged to the same genet. Because *Q. buckleyi* stems that belonged to the same genet could be identified by the proximity of their

TABLE 1—Land-use history of the study sites. Habitats are symbolized as follows: 1 = savanna, 2 = *Quercus fusiformis/Juniperus ashei* woodland, 3 = mixed woodland.

Site	Communities sampled	Most recent use by livestock	Most recent fire	Most recent juniper clearing	Deer hunting history
Double J and T	1	1993	unknown, but before 1993	unknown, but before 1993	prohibited since 1993
Emma Long	1, 2, 3	unknown, but before 1920	late 1970s, part of savanna	unknown	unknown
Forest Ridge	2	unknown, but before 1983	unknown	unknown	prohibited since 1983
Grelle	2	1990	unknown, but before 1934	little clearing since 1934	unknown
Honey Creek	1, 2	1980	managed burn, 1988	unknown	annual hunts since 1986
Pedernales Falls	1, 2	unknown, but before 1970	unknown	unknown	annual hunts since 1986
St. Edwards	3	unknown, but before 1988	unknown, but before 1988	unknown, but before 1988	prohibited since 1988
Shield Ranch	1	current use, cattle	unknown	unknown	annual hunts
Victoria	2, 3	1990	unknown, but before 1990	unknown, but before 1990	prohibited since 1990
Webster	1, 2, 3	1990	unknown, but before 1990	unknown, but before 1990	prohibited since 1990

bases, observations of the sizes of both genets and individual stems were made.

Quercus fusiformis stems and *Q. buckleyi* genets and individual stems were sampled using 4 m wide belt transects. One transect was used in each community type in each site. The point of origin and direction of each transect were determined randomly. When a community edge was encountered a direction was chosen randomly to continue the transect. Bearings that did not lead into an appropriate community type were discarded. Bearings between 160° and 200° of the preceding bearing also were discarded to prevent re-sampling individuals. A transect was followed until 25 *Q. fusiformis* stems or *Q. buckleyi* genets 10 to 20 cm dbh (diameter at breast height) or >20 cm dbh were sampled. The dbh of *Q. fusiformis* stems taller than 1.5 m was measured. The height of *Q. fusiformis* stems shorter than 1.5 m was measured. The high density of root sprouts beneath many adults prohibited an exact count of stems <40 cm tall in savannas. For the same reason, an exact count of stems <20 cm tall in live oak/juniper stands was not obtained.

Because adult recruitment from seed may have different implications for growth rate and spatial structure of *Q. fusiformis* populations than does vegetative reproduction, the origin of stems shorter than 1.5 m tall as seed or root sprout was recorded. In contrast to *Q. fusiformis* stems taller than 1.5 m, the connections between root sprouts shorter than 1.5 m and the parent could be revealed readily by pulling at the base of the stem. Stems shorter than 1.5 m that originated from seed could be identified by excavating to locate a bulge corresponding to the seedling's hypocotyl.

Quercus fusiformis stems were categorized according to size and, for the two smallest size categories, according to whether they were produced by seed or by sprout. Categories were seedlings 0 to 40 cm tall (these included suppressed saplings), root sprouts 0 to 40 cm tall (seedling-sized root sprouts), saplings 40 cm tall to 5.0 cm dbh (these included stems of unknown origin), root sprouts 40 cm tall to 5.0 cm dbh (sapling-sized root sprouts), all stems 5.1 to 15.0 cm dbh (small adults), all stems 15.1 to 25.0 cm dbh (mid-adults), and three categories of large adults (25.1 to 35.0 cm dbh, 35.1 to 45.0 cm dbh, and >45.1 cm dbh). The exact diameters of *Q. fusiformis* stems >20 cm dbh in savannas at Emma Long City Park and Double J and T Ranch City Preserve were not recorded and therefore all stems >15.0 cm dbh in these sites were pooled.

Diameter at breast height of *Q. buckleyi* stems taller than 1.5 m was measured. To quantify the size of multi-stemmed genets, the genet was assigned a diameter that was equivalent to a hypothetical single stem with a cross-sectional area equal to the sum of the cross-sectional areas of the individual stems. The height of *Q. buckleyi* genets containing no stems taller than 1.5 m was measured. Such genets were invariably single-stemmed and originated from seed. The size categories that were used for *Q. fusiformis* stems also were used for *Q. buckleyi* genets, but *Q. buckleyi* does not root-sprout. To determine the contribution of stump-sprouting to the replacement of *Q. buckleyi* stems in existing genets, size distributions of individual stems taller than 1.5 m were also described. These stems were categorized by dbh in 5-cm increments.

Stems and genets in the size distributions described here were sampled using transects and, therefore, are not a random sample of the stems and genets in a site. Given this non-random sampling technique, it is likely that the stems or genets are not independently and identically distributed among size categories. Therefore, results of statistical analyses comparing observed proportions of stems or genets in different size categories with the predicted size distribution of a stable population are likely to be unreliable (Garson and Moser, 1995). Inferences made about the stability of *Q. fusiformis* and *Q. buckleyi* populations from observed size distributions are based on visual comparisons with negative exponential distributions. Size structure of a population would conform to a negative exponential distribution if recruitment to the population was constant through time, mortality rate was constant across all size classes, and size accurately represented age.

RESULTS—*Quercus fusiformis* saplings were less abundant than small adults in five of the six savanna sites (Fig. 2) and five of the six live oak/juniper stands (Fig. 3). All stems 40 cm tall to 5.0 cm dbh, including sapling-sized root sprouts and saplings, were less abundant than small adults in half of the savanna sites and four of the six live oak/juniper stands. Small adults were less abundant than mid-sized adults in three of the four savanna sites in which stems >15.0 cm dbh were not pooled (Fig. 2). Small adults were less abundant than mid-adults in half of the live oak/juniper stands (Fig. 3). In all sites seedlings/seedling-sized root sprouts were much more abundant than stems in any other size class.

Quercus buckleyi seedlings were between 0.9 × and 14.1× as abundant as the next most abundant size class of genetic individuals (Fig. 4). In all sites saplings were less than 27% as abundant as small adults when multi-stemmed genets were assigned a diameter equal to a hypothetical stem with an area equal to the sum of

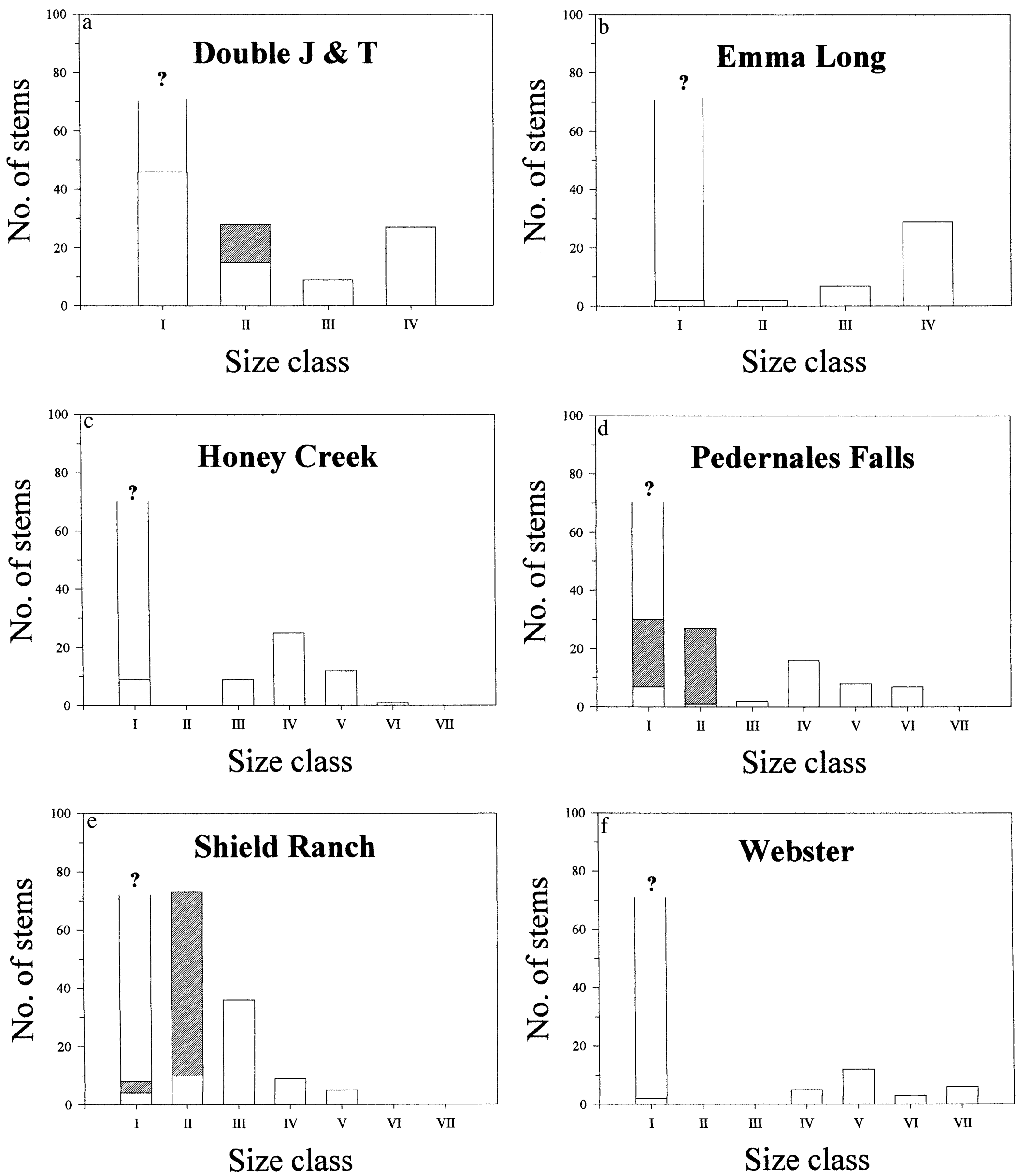

FIG. 2—Size distributions of *Quercus fusiformis* stems in savannas. Size classes are: I = 0.0 to 40.0 cm tall, II = 40.1 cm tall to 5.0 cm dbh, III = 5.1 to 15.0 cm dbh, IV = 15.1 to 25.0 cm dbh (except for the Double J and T and Emma Long sites for which IV = >15.0 cm), V = 25.1 to 35.0 cm dbh, VI = 35.1 to 45.0 cm dbh, and VII = >45.0 cm dbh. Open bars denote stems originating from seed or of unknown origin. Hatched bars denote stems originating from root sprouts. The question mark above the smallest size class indicates that an exact count of stems shorter than 40 cm was not made.

the areas of the component stems. Individual *Q. buckleyi* stems between 0 and 5.0 cm dbh were less than 10% as abundant as stems between 5.1 and 10.0 cm dbh in all sites (Fig. 5). Furthermore, in two sites stems between 5.1 and 10.0 cm dbh were less abundant than stems between 10.1 and 15.0 cm.

There were no consistent differences be-

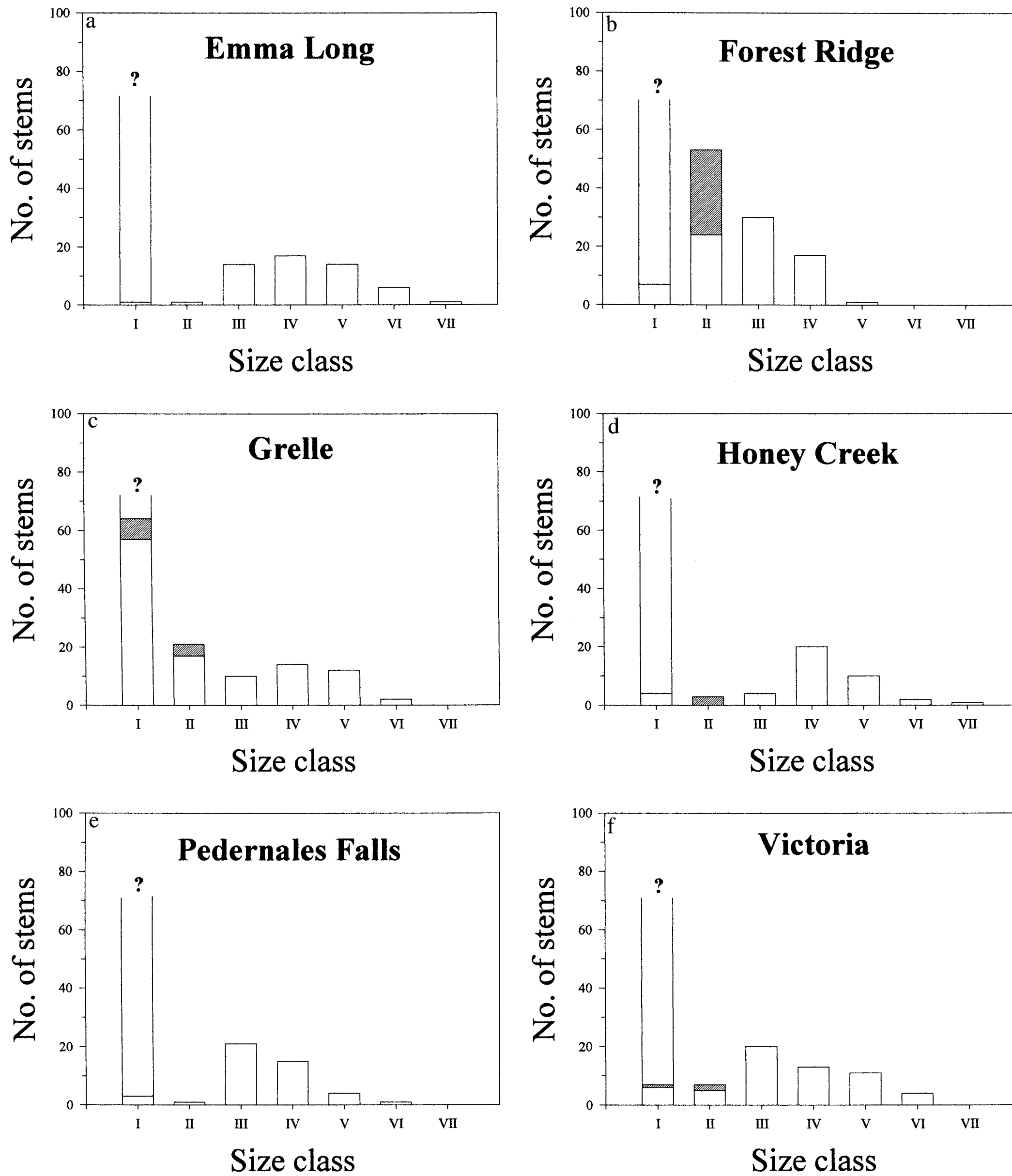

FIG. 3—Size distributions of *Quercus fusiformis* stems in live oak/juniper stands. Size classes are: I = 0.0–40.0 cm tall, II = 40.1 cm tall-5.0 cm dbh, III = 5.1–15.0 cm dbh, IV = 15.1–25.0 cm dbh, V = 25.1–35.0 cm dbh, VI = 35.1–45.0 cm dbh, and VII = >45.0 cm dbh. Open bars denote stems originating from seed or of unknown origin. Hatched bars denote stems originating as root sprouts. The question mark over the smallest size class indicates that an exact count of stems shorter than 20 cm was not made.

tween sites with different hunting histories. Only in the Shield Ranch savanna site (continuous hunting history) and the Forest Ridge live oak/juniper site (no hunting since 1983) was each *Q. fusiformis* size class less frequent than the next smaller size class, as one might expect in a population with continuous recruitment. The size distribution of stems from the Double J and T savanna site (no hunting since 1993) may also represent continuous re-

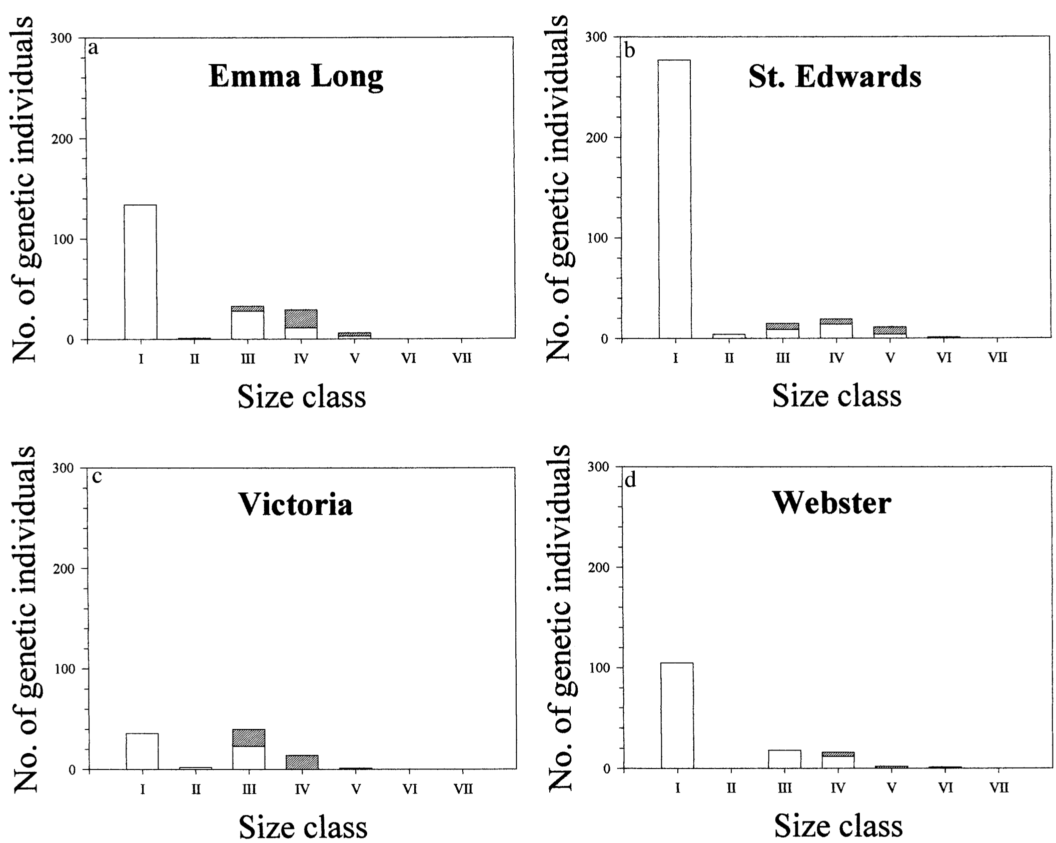

FIG. 4—Size distributions of *Quercus buckleyi* genetic individuals in mixed woodlands. Size classes are: I = 0.0–40.0 cm tall, II = 40.1 cm tall–5.0 cm dbh, III = 5.1–15.0 cm dbh, IV = 15.1–25.0 cm dbh, V = 25.1–35.0 cm dbh, VI = 35.1–45.0 cm dbh, VII = >45.0 cm dbh. Open bars denote single-stemmed genetic individuals. Hatched bars denote multi-stemmed genetic individuals.

cruitment if the relatively large abundance of stems >15.0 cm dbh is the result of pooling these larger stems. At each of the other *Q. fusiformis* sites and at all *Q. buckleyi* sites, at least one of the intermediate size classes was very rare or altogether absent, regardless of hunting history.

DISCUSSION—*Quercus fusiformis* saplings and small adults are much less numerous than mid-sized adults and large adults in savannas and live oak/juniper stands of the eastern Edwards Plateau. *Q. buckleyi* saplings are much less numerous than small adults and mid-sized adults of this species in mixed woodlands in the same region. These data suggest, although they do not prove, that neither species is recruiting to adult size classes in the region. Recruitment of saplings, if as rare as suggested by these data, is too infrequent to maintain the existing populations of either species. Furthermore, juvenile stems of vegetative origin that could prolong the life-span of existing genets are generally rare. In fact, if recruitment of saplings remains as infrequent as these data suggest and vegetative replacement of stems in existing genets remains low, both species will become extremely rare as soon as the existing adults die.

However, size distributions alone cannot provide sufficient evidence that adult recruitment of these species is not occurring because a stem's growth rate may change during its life span. Even if stem growth rates were constant, height-based size categories used for juveniles and diameter categories used for adults might not represent equal time intervals. Nevertheless, it is difficult to imagine that new genets

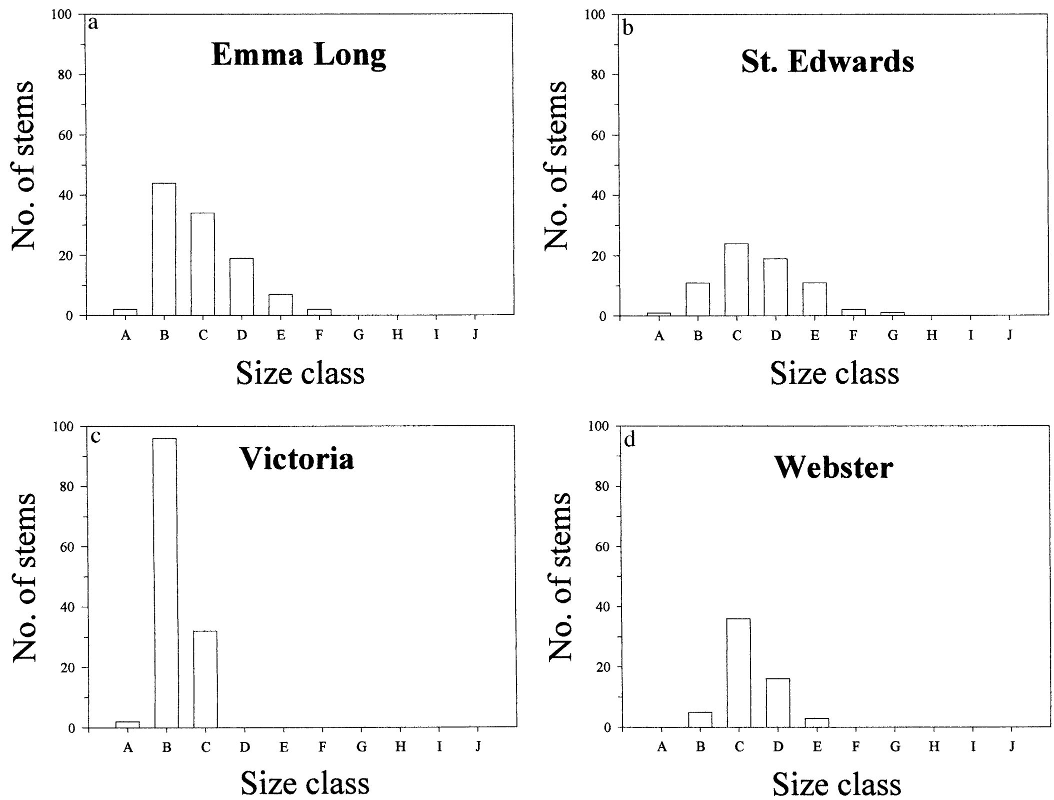

FIG. 5—Size distributions of individual *Quercus buckleyi* stems taller than 150 cm in mixed woodlands. Size classes represent 5 cm dbh increments.

of either species grow through the sapling and small adult size categories so rapidly that present size distributions of plants originating from seed represent stable populations. Root-sprouting may allow persistence of existing *Q. fusiformis* genets in the Double J and T and Shield Ranch savanna sites and the Forest Ridge and Grelle live oak/juniper stand sites, but in most sites vegetative reproduction does not increase the abundance of stems 40.0 cm tall to 5 cm dbh sufficiently to suggest complete replacement of existing *Q. fusiformis* adult stems. Stump-sprouting in *Q. buckleyi* also is unlikely to maintain existing populations of this species as stump-sprouts 0.0 to 5.0 cm dbh are very rare.

The rarity of *Q. fusiformis* and *Q. buckleyi* saplings and small adults may be due, in part, to a high mortality rate before plants become saplings. High rates of seed and seedling mortality (75 to 100%) are typical of many plant species (Harper, 1977), including oaks of savannas and semi-arid woodlands (Griffin, 1976; Allen-Diaz and Bartolome, 1992; Callaway, 1992; Hall et al., 1992; McPherson, 1993). *Q. buckleyi* and *Q. fusiformis* in the study sites may have had very high rates of seed and seedling mortality. For *Q. buckleyi* this is suggested by ratios of seedling to adult abundance in three of the four sites, which were much lower than is common in stable plant populations (Harper, 1977). Similarly, ratios of *Q. fusiformis* seedlings outside adult canopies to small adults is much lower than expected. It is likely that the rarity of seedlings results from seed and seedling mortality rather than low adult fecundity since the seed set per adult appeared high in both species (L. Russell, pers. obser.).

Although episodic adult recruitment on a time interval shorter than the life-span of adults could maintain current adult abundance and produce the observed size distributions, it seems unlikely that episodic adult recruitment will occur in either *Q. fusiformis* or

Q. buckleyi on the eastern Edwards Plateau. Slow seedling growth rates, frequently <5 cm per year (L. Russell, pers. obser.), suggest that one or even several years of enhanced seedling and sapling survival would be insufficient to ensure recruitment to adult size classes. Instead, a long series of many favorable years would be necessary for these species to grow through the vulnerable seedling and sapling size classes. Only if adult recruitment were limited by germination could a single favorable year allow a cohort to escape the vulnerable stage (Reid and Ellis, 1995).

Poor recruitment of adult oaks on the Edwards Plateau is likely to be a consequence of changes in landscape-level ecological processes that followed European settlement in the mid-19th century (Tilghman, 1989; Lorimer et al., 1994). Introduction of livestock, reduced fire frequency, and large increases in white-tailed deer populations are believed to be the greatest of these changes; any one of these could have caused regional changes in tree regeneration patterns (Foster, 1917; Hahn, 1945; Doughty, 1983). Of these three factors, intense browsing pressure by the large deer population seems the most probable cause of current failure of adult recruitment in these two oak species.

Low adult recruitment of both *Q. fusiformis* and *Q. buckleyi* on sites that have been free of browsing livestock for decades suggests that domestic browsers, particularly goats, are not responsible for failure of adult oak recruitment. Emma Long City Park, which contained sample sites in all three community types, has been free of browsing livestock since at least the 1920s, yet adults of neither species are recruiting more vigorously at this site than in the other sites. Likewise, Pedernales Falls State Park has been free of browsing livestock since at least 1970 yet *Q. fusiformis* small adults are rare in the savanna site and saplings/sapling-sized root sprouts of this species are rare in the live oak/juniper stand site there.

Grazing on the Edwards Plateau may have reduced fire frequency. Typically, reduced fire frequency is believed to increase adult recruitment of woody plants in savannas and woodlands rather than to inhibit it (Crow, 1988; McPherson, 1997; Scholes and Archer, 1997). After an extended period without fire, however, light penetration to ground level can be so reduced by the encroachment of woody understory species or by increased canopy density that seedlings and saplings of shade-intolerant species can not survive (Crow, 1988; Mensing, 1992; Lorimer et al., 1994). The high understory light levels that persist in savannas and in mixed woodlands of the eastern Edwards Plateau in the absence of fire suggest that light is not limiting adult oak recruitment in these communities. In savannas large areas of grassland still separate woody clusters, and in mixed woodlands extensive areas lack understory trees or shrubs. Furthermore, although mean canopy coverage in these woodlands was found to be 91% on the southern Edwards Plateau (Van Auken et al., 1981), the canopy is short and has few layers. In contrast, live oak/juniper stands have a densely shaded understory due to the large juniper component of the canopy. Low light levels may contribute to the lack of adult recruitment of *Q. fusiformis* in live oak/juniper stands.

Intense browsing pressure by white-tailed deer seems the most likely explanation for the failure of adult recruitment of *Q. fusiformis* and *Q. buckleyi* on the eastern Edwards Plateau. There was a large, prolonged increase in the abundance of deer on the Edwards Plateau between the 1930s and 1980s (Hahn, 1945; Reagan, 1992). By 1940 cycles of die-offs followed by rapid rebounds in deer population size were widely reported (Van Volkenberg and Nicholson, 1943). Thus there have been deer populations large enough to have been browsing palatable species heavily for at least 50 years. *Q. buckleyi* is a highly preferred browse species and, therefore, might be expected to have been browsed intensely during this period (Armstrong, 1991). *Q. fusiformis* is not preferred but is utilized heavily by deer when food is scarce. Van Auken (1993) also attributes the rarity of *Q. buckleyi* and *Q. glaucoides* saplings on the southern Edwards Plateau to intense deer browsing.

The degree of temporal coincidence between growth of deer populations and failure of adult recruitment of *Q. fusiformis* and *Q. buckleyi* cannot be determined from the data presented here. However, anecdotal evidence suggests that populations of both oak species were expanding into grasslands as recently as 1915 (Foster, 1917). Although this evidence does not prove that failure of adult recruitment in either oak species coincided with increasing deer populations, it is consistent with this hypothesis because deer were not effectively protected from hunting until the 1930s (Hahn, 1945). Descriptions of age distributions of *Q. fusiformis* and *Q. buckleyi* stands will be necessary to date precisely the beginning of the failure of adult recruitment.

A rarity of saplings of *Q. fusiformis* on sites where deer are hunted could suggest that deer have little effect on the adult recruitment of this species. However, hunting probably has not caused sustained reductions in deer densities on the tracts in this study because none of these tracts are protected from migration of deer from neighboring properties. Therefore, a comparison of the vigor of *Q. fusiformis* adult recruitment between sites which have and have not been hunted is not a strong test of the effects of deer on oak adult recruitment. To determine conclusively the effects of deer on adult recruitment of *Q. fusiformis* and *Q. buckleyi* exclosure experiments are required. Exclosure experiments that determine the effects of deer on the germination rate and seedling survival and growth rates currently are being conducted with *Quercus buckleyi.*

To summarize, *Q. fusiformis* saplings and small adults are rare in many savannas and live oak/juniper stands of the eastern Edwards Plateau. *Q. buckleyi* saplings are virtually absent from populations on the eastern Edwards Plateau. Furthermore, juvenile stems produced by vegetative reproduction frequently appear to be too rare to replace adult stems in existing genets of either species. These size distributions strongly suggest that current adult recruitment of *Q. fusiformis* in savannas and live oak/juniper stands and of *Q. buckleyi* in mixed woodlands is insufficient to maintain the number of individuals in larger adult size classes. Browsing by white-tailed deer is suggested as the probable cause of oak recruitment failure. If the situation persists dramatic changes in the community composition of savannas and woodlands on the eastern Edwards Plateau can be expected.

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