Comparison of a Managed and Unmanaged Quercus stellata (post oak) Community

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ABSTRACT

The woody vegetation of two equal aged, adjacent, Quercus stellata (post oak) woodlands was examined. One community was managed for the past 30 years by manual removal of encroached Juniperus ashei (Ashe juniper=mountain cedar) plants and hunting Odocoileus virginianus (white-tailed deer) and the second community was unmanaged. The communities were simple with only three tree size species found in both. In the managed community, O. stellata had the highest tree density (210 plants/ha), basal area (16.67 m²/ha) and importance (98%) with Celtis laevigata (sugar hackberry) and Ulmus crassifolia (cedar elm) being minor species. In the unmanaged community, J. ashei had the highest tree density (1.856 plants/ha), basal area (16.16 m²/ha) and importance (74%) with O. stellata second in tree density (144 plants/ha), basal area (12.67 m²/ha) and importance (25%) and Bumelia lanuginosa (gum bumelia) a minor species. Total tree density was almost ten times higher in the unmanaged community and basal area was almost twice as high, because of the presence of J. ashei density (1,856 plants/ha) and basal area (16.16 m^2/ha). Total juvenile density was more than five times higher (64.549 plants/ha) in the managed community with U. crassifolia, Smilax bona-nox (bull briar, a woody vine) and C. laevigata being the woody species with the highest density. In the unmanaged community B. lanuginosa, U. crassifolia and S. bona-nox had the highest densities. Ouercus stellata trees had a unimodal distribution in both communities, but no evidence of recruitment of juveniles into the adult population. The Weibull shape statistic (c) suggested normal distributions in both communities. Juniperus ashei had a unimodal distribution, a negative exponential function in the unmanaged community. There were six juvenile tree species including O. stellata in the managed community and five in the unmanaged community, but only J. ashei was being recruited into the adult population and only in the unmanaged community. Based on size distributions, Q. stellata and J. ashei do not seem to be ecologically compatible. Although the O. virginianus population may be influencing recruitment of O. stellata, another factor besides the presence of J. ashei, such as the biomass or density of the understory C4 grasses, may be interfering with recruitment of Q. stellata into the adult Q. stellata population. Published on-line www.phytologia.org Phytologia 97(4): 252-264 (Oct 1, 2015). ISSN 030319430.

KEY WORDS: community composition, density, basal area, community manipulation, diameter distributions, Weibull distributions, recruitment failure.

Community structure and species occurrence in a particular area are determined by the tolerance or requirements of the species to abiotic and/or biotic conditions present. However, the tolerance to or requirements for these conditions are at least slightly different for each species. Categorizing the characteristics or factors that determine why one species is present or dominant where it is found and not in another place or habitat is much more challenging (Begon et al. 2006). Several different conclusions

can be drawn when two woody species are present in the same place with one dominating the overstory and the other dominating the understory. One conclusion would be that the understory species is encroaching into the overstory species' space with the ultimate loss of the overstory species. A second conclusion could be that the overstory species encroached on the understory species, had a faster growth rate, and will result in the ultimate loss of the understory species. A third conclusion could be that they both arrived at the same time and they coexist with few adverse interactions. However, with long lived woody species the correct conclusion is difficult to clarify. The sequence of woody species is hard to determine but is occurring during community succession (Begon et al. 2006).

Central Texas plant communities, including *Quercus stellata* (post oak) communities, have no doubt been subject to current warming trends, plant community migrations, and land management practices. Land management means different things to different people including managers. One can manage for or against various species of plants and/or animals (Scifres 1980). These practices will lead to communities with a different plant and animal composition in the future.

Historically we know that plant communities worldwide have changed many times in the past (see Berner 2005). Environmental conditions appear cyclic and they have been connected to global scale fluctuations in the climate of the Earth over the past 420,000 years. Evidence of these changes have been found in ice cores and other temperature proxies taken from thick glacial ice sheets (Imbrie and Imbrie 1980). At least four cycles of warming and cooling have been found in the ice cores (Petit et al. 1999). In addition, over the last 11,000-15,000 years, the end of the last glacial maximum or cold cycle, the migration of North American plant communities has been linked to the retreat of the Laurentide glaciers (Delcourt et al. 1983; Betancourt et al. 1990; Van Devender 1995).

It is well documented that plant communities have changed; these changes also appear to be related to global climate. In addition, plant communities will continue to change in the future as they respond to changes in environmental conditions (McDowell et al. 1995; Berger and Loutre 2002; Ehleringer 2005). On a smaller scale, land management strategies can affect changes in plant communities and further complicate the picture. In most ecological studies the land management history of a particular community is not precisely known (Van Auken 2009).

Climate and plant communities are not constant and no doubt they will continue to be modified in the future. For example, plant communities are modified as woody plants encroach into grasslands, grass biomass, density and cover decline as woody plant biomass, density, and cover increase (see Van Auken 2009). In addition, there is a shift in location of the biomass, species richness, and diversity as herbaceous species are replaced by woody species. The processes involved are dynamic and the direction of the changes can be reversed. In addition to the changes in grassland communities, woodland communities change as well. Succession in central Texas woodland community has been studied (Van Auken and Bush 2013). Early woodland succession typically goes from various shade intolerant woody legumes to various shade tolerant trees. However, in the current study, a shade intolerant species (*Juniperus ashei*) (McKinley and Van Auken 2005; Van Auken et al. 2005; Grunstra 2008) is present below the canopy of a potentially shade tolerant species (*Q. stellata*). This seems to be the reverse of typical succession patterns driven by light availability (Begon et al. 2006).

Most plant community modifications in the distant past were relatively gradual compared to changes seen in the past 200-400 years. The causes of the recent modifications in plant communities could be diverse, but seem to be the result of high levels of domestic herbivory coupled to reduced fire intensity and frequency (see Van Auken 2009). We had an opportunity to examine two adjacent, equal-aged *Quercus stellata* communities on the western edge of its range with very different management histories (Figure 1). One community was unmanaged while the other was managed. Management consisted of continuous removal of all *J. ashei* plants and a reduction of large herbivores by hunting.

PURPOSE

The purpose of the present study was to ecologically describe a managed *Quercus stellata* (post oak) woodland community on the Cibolo Preserve in Boerne, Texas and to compare this community to an adjacent, unmanaged *Q. stellata/J. ashei* (post oak/mountain cedar-Ashe juniper) woodland. We hypothesize that if competition from *J. ashei* and herbivory from *O. virginianus* were affecting the recruitment of *Q. stellata* into the adult population, that we would see differences in the *Q. stellata* size class distribution.

SPECIES

Quercus stellata is widespread in central and east Texas, and across the eastern U. S. (Figure 1). In Texas it is found in a band of sandy soil called the Post Oak Savanna that extends from the Rio Grande through east central Texas north into Oklahoma (Correll and Johnston 1979). In addition, it is found in the Cross-timbers region of north Texas along with other *Quercus* species. In the Edwards Plateau Physiographic Region it is found in scattered populations usually mixed with *J. ashei* that is present throughout central Texas (Van Auken 2016). The northeastern Edwards Plateau Region, an area called the Lampasas Cut-Plane, is a partially forested area, where *Q. stellata* and various other *Quercus* species are found in woodland and forested areas (Gehlbach and Amos 1988). A study of weather patterns in southern Oklahoma, north, central and south Texas used old *Q. stellata* trees to develop a climate sensitive tree ring chronology (Stahle and Cleaveland 1988).

METHODS

Characteristics of the woody vegetation within a managed 12.1 ha *Q. stellata* woodland and an unmanaged, equal aged 4.5 ha *Q. stellata/J. ashei* woodland were determined using the quadrat procedure (Chambers and Brown 1983; Bonham 1989; Van Auken et al. 2005). The communities were adjacent but separated by a deer-proof fence. The understory of the managed community had a high cover of warmseason or C₄ grasses while the unmanaged community had little grass cover except in intermittent canopy openings of gaps. One community was on the 250 hectare Cibolo Preserve in Kendall County, central Texas (29.7691°N and 98.6935°W, Figure 1) and one was adjacent to it, but not on the preserve. Measurements for trees were done in 5 m by 5 m or 25 m² quadrats established along a belt transect line and all trees of all species were identified, counted, and measured. A tree was considered any woody plant greater than 1 cm in diameter at 1.54 m (breast height) except for *J. ashei*. Juniperus ashei had multiple stems and was measured at the base, just above ground level. If *J. ashei* plants were greater than 1.54 m tall, with a basal diameter greater than 1 cm diameter they were considered trees; otherwise, they were considered juveniles. Seedlings (< 0.5 m in height) and saplings (> 0.5 m in height, and < 1 cm in diameter) were juveniles, and identified and counted in 5 randomly placed 1 m² quadrats within each 25 m² quadrat.

Trees were sampled in a total of 204-25 m² quadrats in the managed community and 50-25 m² quadrats sampled in the non-managed community. In the managed community, juvenile woody plants were sampled in 1,020-1 m² quadrats and 250-1 m² quadrats in the unmanaged community. For trees, density stabilization curves indicated sample adequacy (Figures 2 and 3) (see Van Auken et al. 2005). Number of individual trees of each species in each 25 m² quadrat was counted and recorded and the diameter of each adult (tree) was measured with a tree caliper. The number of juveniles of each woody species in each of five 1 m² randomly distributed sub-quadrats within the larger quadrat was counted and recorded. Density of seedlings and saplings per species was calculated and pooled as juveniles. Total tree and juvenile density was calculated separately for each community by summing the density of each species. Total tree basal area was calculated by summing the basal area for each species. Density and

basal area were used to describe the plant communities as was importance (% density + % basal area/2). In addition, the density of all species of juveniles was calculated for the same purpose.

Some community characteristics were compared with a X^2 -test (Sall et al. 2012). From the tree data, diameter size class histograms were constructed. This is a quantitative way to examine population size structures using a two-parameter Weibull function fitting the diameter distributions using a maximum-likelihood algorithm (Cohen 1965; Bailey and Dell 1973; Ryniker et al. 2006; Van Auken et al. 2007). These distributions can take various shapes determined by c. If c is < 1, the plot is steeply descending and monotonic. If c =1, then the plot is a negative exponential distribution. When c is > 1, the function is unimodal. When 1 < c < 3.6 the distribution has a skew that is positive. If c = 3.6 the distribution is roughly normal. A negatively skewed distribution is indicated if c > 3.6. The scale (b) is called the "characteristic life" and is related to the mean of the distribution (Knox et al. 1989).

RESULTS

Based on the number of tree species found (Table 1), the two communities were simple, with three species of trees found in both. In the managed community, *Q. stellata* had the highest tree density (210 plants/ha), basal area (16.67 m²/ha) and importance (98%) with *Celtis laevigata* (sugar hackberry) and *Ulmus crassifolia* (cedar elm) being minor species. In the unmanaged community, *J. ashei* had the highest tree density (1,856 plants/ha), basal area (16.16 m²/ha) and importance (74%); *Q. stellata* had a tree density of 144 plants/ha, basal area of 12.67 m²/ha, and importance of 25%; and *Bumelia lanuginosa* (gum bumelia) was a minor species. Total tree density was significantly different (X² < 0.05) and 9.42 times higher in the unmanaged community. Total basal area was significantly different (X² < 0.05) and 1.7 times higher, because of the presence of *J. ashei. Quercus stellata* density in the managed community was significantly different (X² < 0.05) and 210 plants/ha compared to the unmanaged community that was 144 plants/ha, a 31% reduction. *Quercus stellata* basal area was reduced by 24% in the unmanaged community.

The total juvenile density in the managed community was significantly different ($X^2 < 0.05$) and 5.34 times higher (64,549 plants/ha) compared to the unmanaged community (12,080 plants/ha) (Table 2). In the managed community in descending order, the species with the highest juvenile densities were *U. crassifolia*, *Smilax bona-nox* (bull briar, a woody vine) and *C. laevigata*. In the unmanaged community in descending order, *B. lanuginosa*, *U. crassifolia* and *S. bona-nox* had the highest densities. *Quercus stellata* juvenile density in the managed community was significantly different ($X^2 < 0.05$) at 1,833 plants/ha, compared to the unmanaged community and fourth highest in this community at 6% relative density. In the unmanaged community it had the lowest juvenile density of the six woody species found at 120 plants/ha or a relative density of 1%.

Quercus stellata trees had a unimodal distribution in both communities (Figure 4 A and B), but no evidence of recruitment into the adult population. The Weibull shape statistic (c) suggested normal distributions in both communities, with a slightly negative skew (Figure 4A) and a slightly positive skew (Figure 4B) and very few small diameter individuals. Means were similar but 3% smaller in the unmanaged community. *Juniperus ashei* had a unimodal distribution in the unmanaged community (Figure 4 C), but the distribution was a negative exponential function with a positive skew. There were 85 *J. ashei* individuals in the two smallest diameter size classes and no *Q. stellata* plants in these size classes. There were a number of juveniles of both *Q. stellata* and *J. ashei* (Table 2) but only *J. ashei* juveniles were being recruited into the adult population and only in the unmanaged community. There were six juvenile tree species in the managed community and five in the unmanaged community, but only *J. ashei* was being recruited into the adult population and only in the unmanaged community.

DISCUSSION

No one had examined the replacement dynamics of *Quercus stellata* until this current study. The central Texas *Q. stellata* populations that we examined do not appear to be replacing themselves in either community examined (Figure 4). This is not unusual because there are a number of *Quercus* species, with many populations that are not replacing themselves (McCune and Cottam 1985; Pallardy et al. 1988; Reich et al. 1990; Beck 1992; Abrams 2003). These population changes appear to be geographically widespread (Lorimer 1992) and species independent (Loftis and McGee 1992). Many *Quercus* species have been significant components of North American forests for the last 10,000 years (Craig 1969; Watts 1979; Delcourt and Delcourt 1985; Abrams 1992; Abrams 2003). However, population changes today are associated with a lack of recruitment or replacement of the mature *Quercus* trees (Shumway et al. 2001; Cowell and Hayes 2007). Size-distributions and comparative studies have indicated recruitment failure in *Q. alba* (white oak), *Q. bucklei* (Texas red oak), *Q. gambelii* (Gambel's oak), *Q. lobata* (Garry oak), and *Q. rubra* (red oak) (Russell and Fowler 2002; Aldrich et al. 2005; Ryniker et al. 2006; MacDougall 2008). While this recruitment failure is well documented, the causes may be species or location dependent (Lorimer 1992).

Recruitment failure - the failure of juvenile plants to reach maturity - has been described for many *Quercus* species and is a major concern for conservation biologists and land managers. Recruitment failure can be due to many factors usually delineated as either pre-germination or post-germination. Previous studies have reported high *Quercus* juvenile densities, indicating that seed production and seed germination, or pre-germination factors, are not the reasons for recruitment failure (see Ryniker et al. 2006). Therefore, post-germination influences are likely the cause of recruitment failure.

Light, moisture, temperature, and fire are post-germination, abiotic factors which have been shown to influence *Quercus* establishment and growth (Nathan and Muller-Landau 2000; Collins 2003; Haas and Heske 2005; Van Auken and Bush 2009). Biotic factors, such as competition from other plants and herbivory by various animal populations have also been shown to affect establishment and growth of various *Quercus* species. Juveniles are frequently numerous under mature trees, however often these juveniles are not competitive with juveniles of other plant species (Lorimer et al. 1994). It is widely accepted that herbivores affect regeneration through a number of mechanism, including direct browsing or indirectly by browsing associated species (Shumway et al. 2001; Cowell and Hayes 2007). *Odocoileus virginianus* (white-tailed deer) populations in central Texas have increased dramatically (Doughty 1983) and at approximately one deer/5 ha populations are the highest in the United States (Armstrong and Young 2000; Fulbright and Ortega-S. 2006). However, in the managed community, *O. virginianus* populations were reduced to approximately one deer/7.2 ha. This population which is 31% lower than native communities should have a reduced effect on the population of various deciduous species, including *Q. stellata*. However, we did not find *Q. stellata* recruitment in either community.

This high *O. virginianus* population is probably because of major carnivore reductions (Beschta and Ripple 2009; Dirzo et al. 2014). Herbivory has been shown to produce a pronounced reduction in juvenile deciduous species survival and decreased sapling density in diverse North American *Quercus* savannah and woodland communities (McCune and Cottam 1985; Pallardy et al. 1988; Reich et al. 1990; Beck 1992; Abrams 2003). In spite of this recruitment failure, productivity and biomass of these communities is probably determined by the large old trees that will be present in these communities for many years (Eisen and Plotkin 2015).

We anticipated a lack of Q. stellata recruitment in the unmanaged Q. stellata/J. ashei woodland community because of potential interaction of the two species (Figure 4 B and C) and the presence of large herbivores. However, we did not anticipate a lack of recruitment in the managed community where J. ashei plants were removed and many of the large herbivores were removed as well. Odocileus

virginianus populations of one deer per 3.2 to 5.0 hectares will reduce *Quercus* seedlings (personal observation J. Jackson and wildlife biologist Kevin Meier). Consequently, the *O. virginianus* population on the preserve may still be high enough to prevent *Q. stellata* juveniles from becoming part of the adult population. This suggests another factor or series of undefined factors are controlling *Q. stellata* recruitment. If the recruitment is intermittent or cyclic, the factor controlling the recruitment will be much harder to identify. If there are multiple factors that have to be present together or in sequence they will also be difficult to identify. The presence of a high density or cover of various warm season or C_4 grasses below the *Q. stellata* canopy may require manipulation to release nutrients required by the juveniles so they can grow into the canopy as replacements. Possibly certain nutrients present in the C_4 grasses are currently unavailable to the juveniles and this could be the unknown key.

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LITERATURE CITED

Abrams, M. D. 1992. Fire and the development of oak forests. Bioscience 42:346-353.

- Abrams, M. D. 2003. Where has all the white oak gone. Bioscience 53:927-939.
- Aldrich, P. R., G. R. Parker, J. Romero-Severson and C. H. Michler. 2005. Confirmation of oak recruitment failure in Indiana old-growth forest: 75 years of data. Forest Science 51:406-416.
- Armstrong, W. E. and E. L. Young. 2000. White-tailed deer management in the Texas hill country. Texas Parks and Wildlife Department, Austin, Texas.
- Bailey, R. L. and T. R. Dell. 1973. Quantifying Diameter Distributions with the Weibull Function. Forest Science 19:97-104.
- Beck, D. E. 1992. Acorns and oak regeneration. In: D. L. Loftis and C. E. McGee (eds.) In Proceedings of the Oak Regeneration: Serious Problems, Practical Recommendations. United States Department of Agriculture, Forest Service General Technical Report SE-84. Knoxville, Tennessee.
- Begon, M., C. R. Townsend and J. L. Harper. 2006. Ecology: from individuals to ecosystems. Blackwell Publishing, Malden, Massachusetts.
- Berger, A. and M. F. Loutre. 2002. An Exceptionally Long Interglacial Ahead? Science 297:1287-1288.
- Berner, R. A. 2005. The rise of trees and how they changed Paleozoic atmospheric CO₂, climate, and geology. In: J. R. Ehleringer, T. E. Cerling and M. D. Dearing (eds.), A History of Atmospheric CO₂ and Its Effects on Plants, Animals, and Ecosystems, Springer, New York.
- Beschta, R. L. and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401-2414.
- Betancourt, J. L., T. R. Van Devender and P. S. Martin. 1990. Synthesis and prospectus. In: J. L. Betancourt, T. R. Van Devender and P. S. Martin (eds.), Packrat Middens: The last 40,000 years of Biotic Change, University of Arizona Press, Tucson.
- Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons, New York.
- Chambers, J. C. and R. W. Brown. 1983. Methods for vegetation sampling and analysis on revegetated mine lands, United States Department of Agriculture, Forest Service: 57.
- Cohen, A. C. 1965. Maximum Likelihood Estimation in the Weibull Distribution Based On Complete and On Censored Samples. Technometrics 7:579-588.
- Collins, B. 2003. Ground layer competition and herbivory effects on Cherrybark oak (*Quercus pagoda* Raf) regeneration in experimental canopy gaps. Journal of the Torrey Botanical Society 130:147-157.
- Correll, D. S. and M. C. Johnston. 1979. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner, Texas.

- Cowell, C. M. and J. J. Hayes. 2007. Structure, history and dynamics of a mature oak-beech forest in western Indiana. Journal of the Torrey Botanical Society 134:215-222.
- Craig, A. 1969. Vegetational history of the Shenandoah Valley, Virginia. Geological Society of America Special Paper 123:283-296.
- Delcourt, H. R. and P. A. Delcourt. 1985. Quaternary palynology and vegetational history of the southeastern United States. In: V. Bryant and R. Holloway (eds.), Pollen Records of Late-Quaternary North American Sediments, American Association of Stratigraphic Palynologists Foundation, Dallas, TX.
- Delcourt, P. A., H. R. Delcourt and T. Webb. 1983. Dynamic plant ecology: the spectrum of vegetation change in space and time. Quatinary Science Review 1:153-175.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401-406.
- Doughty, R. W. 1983. Wildlife and Man in Texas: Environmental Change and Conservation. Texas A & M University Press, College Station, Texas.
- Ehleringer, J. R. 2005. The Influence of Atmospheric CO₂, Temperature, and Water on the Abundance of C₃/C₄ Taxa. In: J. R. Ehleringer, T. E. Cerling and M. D. Dearing (eds.), A History of Atmospheric CO₂ and Its Effects on Plants, Animals, and Ecosystems, Springer, New York.
- Eisen, K. and A. B. Plotkin. 2015. Forty years of forest measurements support steadily increasing aboveground biomass in a maturing, *Quercus*-dominant northeastern forest. The Journal of the Torrey Botanical Society 142:97-112.
- Fulbright, T. E. and J. A. Ortega-S. 2006. White-tailed Deer Habitat. Texas A & M University Press, College Station, Texas.
- Gehlbach, F. R. and B. Amos. 1988. Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, Texas.
- Grunstra, M. 2008. Investigation of *Juniperus* woodland replacement dynamics. Doctoral Dissertation, University of Texas at San Antonio.
- Haas, J. and E. Heske. 2005. Experimental study of effects of mammalian acorn predators on red oak acorn survival and germination. Journal of Mammalogy 86:1015-1021.
- Imbrie, J. and J. Z. Imbrie. 1980. Modeling the climatic responce to orbital variations. Science 207:943-953.
- Knox, R. G., R. K. Peet and N. L. Christensen. 1989. Population Dynamics in Loblolly Pine Stands: Changes in Skewness and Size Inequality. Ecology 70:1153-1166.
- Loftis, D. L. and C. E. McGee. 1992. Oak Regeneration: Serious Problems, Practical Recommendations. United States Department of Agriculture, Forest Service General Technical Report SE-84. Knoxville, Tennessee.
- Lorimer, C. G. 1992. Causes of the oak regeneration problem. In: D. L. Loftis and C. E. McGee (eds.) Oak Regeneration: Serious Problems, Practical Recommendations. United States Department of Agriculture, Forest Service General Technical Report SE-84. Knoxville, Tennessee.
- Lorimer, C. G., J. Chapman and W. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. Journal of Ecology 82:227-237.
- MacDougall, A. S. 2008. Herbivory, hunting, and long-term vegetation change in degraded savanna. Biological Conservation 141:2174-2183.
- McCune, B. and G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. Ecology 66:1270-1278.
- McDowell, P., T. Webb, III and P. Bartlein. 1995. Long-Term Environmental Change. In: T. Powell and J. Steele (eds.), Ecological Time Series, Springer, New York.
- McKinley, D. C. and O. W. Van Auken. 2005. Influence of Interacting Factors on the Growth and Mortality of *Juniperus* Seedlings. American Midland Naturalist 154:320-330.
- Nathan, R. and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15:278-285.

- Pallardy, S., T. Nigh and H. Garrett. 1988. Changes in forest composition in central Missouri: 1968-1982. American Midland Naturalist 120:380-390.
- Petit, J. R., J. Jouzel, D. Raynaud, N. L. Barkof, J. M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V. M. Kotlyakov, M. Legrand, V. Y. Lipenkov, C. Lorius, L. Pepin, C. Ritz, E. Saltzman and M. Stievenard. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399:429-436.
- Reich, P. B., M. D. Abrams, D. S. Ellsworth, E. L. Kruger and T. J. Tabone. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71:2179-2190.
- Russell, F. L. and N. L. Fowler. 2002. Failure of adult recruitment in *Quercus buckleyi* populations on the eastern Edwards Plateau, Texas. American Midland Naturalist 148:201-217.
- Ryniker, K., A., J. K. Bush and O.W. Van Auken. 2006. Structure of *Quercus gambelii* communities in the Lincoln National Forest, New Mexico, USA. Forest Ecology and Management 233:69-77.
- Sall, J., A. Lehman, M. L. Stephens and L. Creighton. 2012. JMp Start Statistics: A Guide to Statistics and Data Analysis Using JMP. SAS Institute, Cary, North Carolina.
- Scifres, C. J. 1980. Brush management: principals and practices for Texas and the southwest. Texas A & M Press, College Station, Texas.
- Shumway, D. L., M. D. Abrams and C. M. Ruffner. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, U.S.A. Canadian Journal of Forest Research 31:1437-1443.
- Stahle, D. W. and M. K. Cleaveland. 1988. Texas Drought History Reconstructed and Analyzed from 1698 to 1980. Journal of Climate 1:59-74.
- Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management 90:2931-2942.
- Van Auken, O. W. 2016. Past, present and future plant communities of the Edwards Plateau region of central Texas. In: Proceedings of the 2012 Native Plant Society of Texas, Annual Symposium. Kerrville, Texas.
- Van Auken, O. W. and J. K. Bush. 2009. The role of photosynthesis in the recruitment of juvenile *Quercus gambelii* into mature *Q. gambelii* communities. Journal of the Torrey Botanical Society 136:465-478.
- Van Auken, O. W. and J. K. Bush. 2013. Invasion of Woody Legumes. Springer, New York.
- Van Auken, O. W., J. K. Bush and S. A. Elliott. 2005. Ecology Laboratory Manual. Pearson Custom Publishing, Boston, Massachusetts.
- Van Auken, O. W., J. K. Bush, F. A. Richter and J. Karges. 2007. Structure of Isolated Populations of *Populus tremuloides* (Quaking Aspen) in the Davis Mountains of Far-West Texas. Natural Areas Journal 27:302-312.
- Van Auken, O. W., J. T. Jackson and P. N. Jurena. 2005. Survival and growth of *Juniperus* seedlings in *Juniperus* woodlands. Plant Ecology 175:245-257.
- Van Devender, T. R. 1995. Desert grassland history: changing climates, evolution, biography, and community dynamics. In: M. P. McClaran and T. R. Van Devender (eds.), The Desert Grassland, University of Arizona Press, Tucson.
- Watts, W. 1979. Late Quaternary vegetation of central Appalachia and the New Jersey coastal plain. Ecological Monographs 49:427-469.

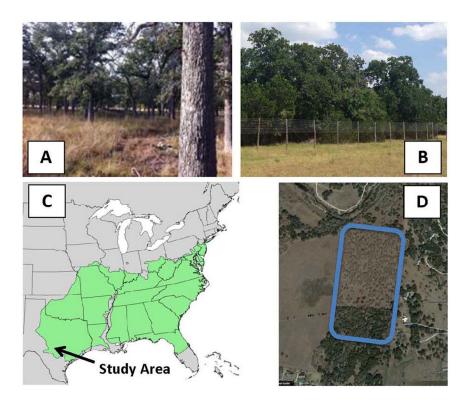


Figure 1: Two *Quercus stellata* savannas in central Texas: A) Managed with the *Juniperus* trees and shrubs removed by hand and many large herbivores removed and B) the edge of a post oak savanna in close proximity to the previous community with no manuplation. C) A map shows the distribution of *Quercus stellata* with the arrow approximately indicating the study area and D) an aerial photograph shows the *Quercus stellata* community outlined. The upper part is the managed community (light, winter, no leaves) and the lower is the non-managed community (dark, juniper folage). Upper photographs were taken by J. K. Bush.

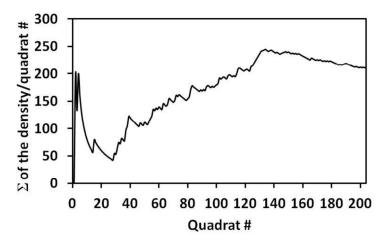


Figure 2: Density stabilization curve is presented for estimating sample adequacy for the *Quercus stellata* heavily managed community at the Cibolo Preserve, Kendall County, Boerne, Texas.

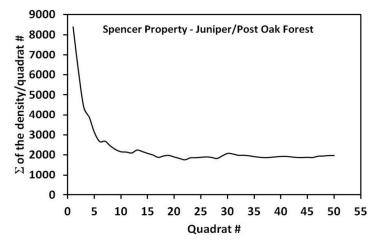


Figure 3: Density stabilization curve is presented for estimating sample adequacy for the *Quercus* stellata/Juniperus ashei unmanaged community near the Cibolo Preserve, Kendall County, Boerne, Texas.

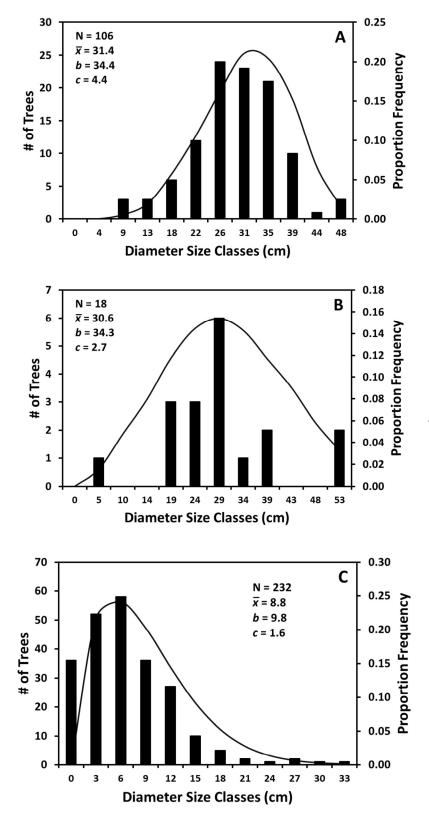


Figure 4: Diameter size class histograms and fitted Weibull distributions (solid lines) are presented. The top histogram (A) is for Quercus stellata in the managed community. The middle and lower histograms (B and C) are for Quercus stellata (B) and *Juniperus ashei* (C) in the unmanaged community. The x-axis is 3 to 5 cm in diameter depending of the community and species. The zero for J. ashei is actually > 1 cm in diameter. The *y*-axis (left) shows the number of trees counted for each size class and on the right is the proportion frequency for each bar. Sample size (N), mean community species density (x-bar), Weibull scale statistic (*b*) and the Weibull shape statistic (c) are also presented.

Table 1. Phytosociological data for trees found in a managed *Quercus stellata* community on the Cibolo Preserve, Kendall County, Boerne, Texas and unmanaged *Quercus stellata/Juniperus ashei* community adjacent to the Cibolo Preserve. Density = plants/ha, Basal area = m^2/ha , and % Importance = (% density + % Basal Area)/2. An asterisk next to a value indicates a significant difference between the managed and unmanaged communities for that characteristic.

		Μ	anaged			
Species	Density	% Density	Mean Basal Area	Basal Area	% Basal Area	% Importance
Quercus stellata	210	98	795	16.67	98	98
Celtis laevigata	2	1	1,052	0.21	1	1
Ulmus crassifolia	2	1	749	0.15	1	1
Total	214	100		17.03	100	100
		Uni	nanaged			
Species	Density	% Density	Mean Basal Area	Basal Area	% Basal Area	% Importance
Juniperus ashei	1,856	92	87	16.16	56	74
Quercus stellata	144*	7	880	12.67	44	25
Bumelia lanuginosa	16	1	114	0.18	1	1
Total	2,016*	100		29.02 *	100	100

	Managed		
Species	Juvenile De	ensity/ha	% Density
Ulmus crassifolia	21,000	65	
Smilax bona-nox	6,389	20	
Celtis laevigata	2,389	7	
Quercus stellata	1,833	6	
Juniperus ashei	222	1	
Diospyros texana	194	1	
Ilex decidua	111	0	
Bumelia lanuginosa	56	0	
Berberis trifoliata	56	0	
Parthenocissus quinquefolia	28	0	
Total	64,549		100

Table 2. Phytosociological data of juvenile woody species in a managed Quercus *stellata/Juniperus ashei* woodland community in the Cibolo Preserve, Kendall County, Boerne, Texas and an unmanaged *Quercus stellata/Juniperus ashei* woodland community adjacent to the Cibolo Preserve.

Unmanaged

Species	Juvenile Density/ha	% Density	
Bumelia lanuginosa	5,440	45	
Ulmus crassifolia	4,280*	35	
Smilax bona-nox	1,880*	16	
Juniperus ashei	200	2	
Celtis laevigata	160*	1	
Quercus stellata	120*	1	
Total	12,080*	100	