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Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of Quercus buckleyi

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Abstract

To measure the effects of white-tailed deer (*Odocoileus virginianus)* herbivory on seeds, seedlings, and young saplings of *Quercus buckleyi* on the eastern Edwards Plateau of central Texas, USA, experimental fenced deer exclosures were constructed. Acorns or small *Q. buckleyi* transplants were placed in each exclosure and in each unfenced control plot. Deer did not significantly affect acorn survival and germination, but did significantly reduce transplant survival and growth rates. The results support the hypothesis that deer are responsible for the failure of recruitment into adult size classes in *Q. buckleyi* populations in this region. Without adult recruitment of *Q. buckleyi*, the species composition and possibly even the physiognomy of woodlands on the eastern Edwards Plateau will change markedly. The results of this experiment also indicate that, although juniper (*Juniperus ashei*) and *Q. buckleyi* presumably compete for water, light, and nutrients, in the presence of deer junipers can have a positive effect on seedlings and saplings of *Q. buckleyi*, a case of facilitation. In the presence of deer the transplants increased in height significantly more slowly away from juniper saplings than they did beneath juniper saplings, probably due to the physical protection from browsing that junipers provided to the transplants.

Introduction

Understanding factors that determine sizes of plant populations is a central goal of plant population ecology. Well-documented cases of herbivores limiting plant population sizes are relatively few (Louda 1982; Louda and Potvin 1995; Kelly and Dyer 2002). However, the greater number of studies showing large effects of herbivores on stage structures (Anderson and Loucks 1979; Tilghman 1989; Prins and van der Jeugd 1993) and spatial structures (Parker 1985; McAuliffe 1986; Louda 1996) of plant populations suggests that herbivory may be important in limiting sizes of many plant populations. Selective herbivores that limit populations of only a subset of the plant species in a community can have large effects upon the species composition and physiognomy of plant communities (Brown and Archer 1989; McPherson

and Wright 1990; Prins and van der Jeugd 1993; Weltzin et al. 1997; Bond et al. 2001).

Herbivory is thought to be an especially important factor in determining spatial and temporal patterns in the abundance of woody plants in landscapes that are a mosaic of patches of grassland, savanna, and woodland (White 1966; Pellew 1983; Yeaton 1988; Belsky 1989; Weltzin et al. 1997; Bond et al. 2001). Grazing herbivores can cause increases in woody species, even to the extent of converting grasslands and savannas to woodlands, by reducing competition from herbaceous species and by removing fine fuels, thus reducing the frequency and intensity of fires (Caughley 1976; Yeaton 1988; Dublin et al. 1990). Browsing herbivores can prevent savannas and grasslands from becoming woodlands by killing juvenile trees through repeated browsing or by so reducing growth rates of juvenile trees that they remain vulnerable to

surface fires for a long time (Pellew 1983; Belsky 1989; Mensing 1992; Weltzin et al. 1997). In theory, the direct consumption of seedlings and saplings of woody species by browsing herbivores could cause woodlands to become savannas or grasslands if the recruitment of adult trees was prevented throughout the lifetimes of existing adults (Lange and Willcocks 1980; Lange and Graham 1983; Callaway and Davis 1993). Quantifying effects of browsing herbivores on rates of recruitment into adult size classes in woodland tree populations is a first step in understanding effects of browsers on the species composition and physiognomy of existing woodlands and the possible conversion of these woodlands to grasslands and savannas.

In this study, we examined effects of browsing by *Odocoileus virginianus* Boddaert (white-tailed deer) on seeds, seedlings, and sapling of *Quercus buckleyi* Dorr and Nixon (Spanish oak) to determine whether deer are preventing recruitment into adult size classes in *Q. buckleyi* populations on the Edwards Plateau in central Texas, USA. The vegetation of the Edwards Plateau is a mosaic of savannas and woodlands. *Quercus buckleyi* is a dominant tree of woodlands in this region, but recruitment of saplings of this species into adult size classes is insufficient to replace existing adults, and is often altogether absent (Russell and Fowler 2002). Similarly, populations of other deciduous trees in these woodlands, including *Prunus serotina* Ehrh. and *Fraxinus texensis* (Gray) Sarg., lack saplings and small adults (Van Auken 1988). The only exception to this pattern among canopy tree species is *Juniperus ashei* Buchholz, which appears to be replacing itself. The decline in the rate of adult recruitment in *Q. buckleyi* populations coincided with the beginning of a large and prolonged increase in deer populations during the 1930s, suggesting that deer are preventing the recruitment of *Q. buckleyi* adults in these populations (Russell and Fowler 2002). Eradication of natural predators and parasites likely allowed the increase in deer populations (Hahn 1945). If adult recruitment of *Q. buckleyi* continues to be this rare, the species composition of woodlands on the Edwards Plateau, and possibly the relative abundances of savannas and woodlands in this region, are likely to change markedly.

Here we report the results of exclosure experiments designed to quantify the effects of deer on the survival and germination rates of acorns and the survival and growth rates of seedlings and small saplings of *Q. buckleyi*.

Study species and habitat

Quercus buckleyi is a small to moderate-sized tree endemic to the Edwards Plateau of central Texas (Correll and Johnston 1979). It is most abundant in woodlands on mesic canyon slopes in the southern and eastern portion of the Plateau. Acorns fall between late August and mid-November. Seedling epicotyls emerge in March. We refer to *Q. buckleyi* juveniles as 'seedlings' during the first year following germination and as 'saplings' after the first year.

Quercus buckleyi acorns are subject to pre-dispersal herbivory by weevils and by *Cyanocitta cristata* Linneaus, *Aphelocomma coerulescens* Vigers, and *Sciurus niger* Linneaus. After dispersal, acorns are eaten by *S. niger*, *Spermophillus variegatus* Erxleben, *Neotoma floridana* Ord., *Peromyscus maniculatus* Wagner, *P. leucopus* Rafinesque, *P. pectoralis* Osgood, *P. attwateryi* Allen, *Procyon lotor* Linneaus, and *Canis latrans* Say, as well as by white-tailed deer (Davis 1978). Seedlings and saplings are browsed by white-tailed deer and eaten by invertebrate folivores and stem borers. *Quercus buckleyi* is a preferred browse species of white-tailed deer on the eastern Edwards Plateau (Armstrong et al. 1991).

Woodlands dominated by *Q. buckleyi* are 'mixed woodlands', containing both deciduous and evergreen trees. Mean canopy cover in these woodlands on the southern Edwards Plateau is 91% (Van Auken et al. 1981); the canopy rarely is taller than 10 m. *Prunus serotina*, *Fraxinus texensis* and *Juniperus ashei* are important canopy trees, but frequently are less abundant than *Q. buckleyi*. The understory is sparse, with the exception of isolated but dense patches of *J. ashei* (hereafter, 'juniper') saplings.

This study was conducted in a mixed woodland in Barnes Hollow, Travis County, Texas (30°33' N, 98°W) that is typical in its species composition and physiognomy. This site is on the eastern Edwards Plateau, approximately 55 km northwest of Austin, Texas, USA. It is on a northeast facing canyon slope and elevations within the site range from 350 m to 375 m. Soils are shallow, less than 35 cm deep, gravelly clay loams mixed with 5–10 cm limestone fragments over a parent material of interbedded limestone and marl (Werchan et al. 1974). Mean annual precipitation for western Travis Co. is 810 mm. Mean annual gross lake surface evaporation exceeds mean annual precipitation by at least 760 mm in Travis Co. (Larkin and Bomar 1983). Before 1992 the site was grazed by cattle, but livestock were removed when it

was purchased by the United States Fish and Wildlife Service. The site is part of the Balcones Canyonlands National Wildlife Refuge.

Methods

Pre-dispersal seed predation

We randomly located 15 seed traps beneath canopies of *Q. buckleyi* trees in the study site. Seed traps were plastic funnels made of 6 mil polyethylene sheet plastic, each hung from four T-posts with half of a plastic bottle to collect acorns positioned at the base of the funnel. We removed acorns from traps twice weekly between September 17 and October 29, 1995 and between September 10 and November 12, 1996. Acorn viability was tested by flotation (floating acorns are not viable) and by a germination test in a 3:1 mixture of vermiculite and perlite. Acorns in the germination test were kept in a growth chamber and watered twice per week for two months. After two months the number of acorns producing roots was counted and acorns without roots were squeezed to determine whether they remained solid, and, therefore, might still be viable. All acorns that had not produced roots were easily cracked and, therefore, very likely inviable.

Small mammal trapping

To identify mammal seed predators at the study site, we trapped small mammals on seven nights between February 21 and April 15, 1997 and identified squirrel species by observation (Davis 1978). On four nights, we placed Sherman traps, baited with rolled oats, at 10 m intervals in a 5×7 grid. We trapped in 5×4 and 5×3 grids on either side of the original grid on three nights. Trapped animals were identified to species (Davis 1978; C. Malcom, pers. comm.) and released.

Experimental study of post-dispersal acorn survival and germination

In 1995 this exclosure experiment included two levels of deer herbivory (present or absent) and two levels of juniper (present or absent) in a 2×2 factorial design, with four replicate plots per treatment combination, for a total of 16 2.75 m$\times$2.75 m (7.56 m^2) plots. Eight plots were randomly placed amid juniper saplings ($+$juniper plots) and eight plots were randomly placed at least 1 m away from all juniper saplings ($-$juniper plots). In the $+$juniper plots, at least 50% of the surface area of the plot was under juniper branches that were within 1 m of the ground. Plots in each level of the juniper treatment were randomly assigned to the two levels of the deer treatment. Fences 1.5 m high of welded wire fabric with a mesh size of 5 cm$\times$10 cm were constructed around the eight $-$deer plots. Eight 20 cm$\times$20 cm holes at the base of each fence permitted access by granivores other than deer.

In 1996, four experimental plots, each 2.35 m$\times$2.35 m (5.52 m^2), were used. No plots were placed amid junipers in 1996. Two of the four new plots were randomly assigned to the $-$deer treatment and fenced. Fewer plots were used in 1996 because the low viability rate of acorns at dispersal limited the number of acorns we could sow. Plots were smaller in 1996 to achieve a similar sowing density to 1995.

We collected *Q. buckleyi* acorns from the ground in October 1995 and 1996. Viable acorns (judged by the flotation test) were refrigerated at 3°C until we sowed them in experimental plots. We randomly assigned 360 viable acorns in 1995 and 295 viable acorns in 1996 to each plot. To identify acorns after secondary dispersal, the base of each acorn was marked with a dot of red fingernail polish. Experimental acorns were sown on the soil surface in a grid pattern in the central 2.25 m$\times$2.25 m of each plot (71.1 acorns/m^2) in 1995 and in the central 2.1 m$\times$2.1 m of each plot (66.9 acorns/m^2) in 1996. We sowed acorns between December 7 and 20, 1995 and on January 7 and 8, 1997.

We monitored 22.8 m$\times$22.8 m (518 m^2) zones centered in each 1995 experimental plot for newly germinated *Q. buckleyi* seedlings at two-week intervals between March and June 1996. Circles 50 m in radius (7854 m^2) centered in each 1996 experimental plot were monitored for newly germinated seedlings once each month between March and July 1997. In August 1996 and 1997, plots were searched for labeled acorns and any whole, labeled acorns were cracked to determine viability.

To calculate the acorn germination rate in each plot, we multiplied the proportion of acorns that were viable at dispersal by the germination rate of viable acorns. The proportion of viable acorns removed also was calculated. The effects of the deer and juniper treatments on the germination rate and on the removal rate of acorns that fell in 1995 and in 1996 were ana-

lyzed with Kruskal-Wallis tests and Mann-Whitney U tests, respectively.

Experimental study of seedlings and saplings: design

Deer (+deer and −deer) and understory juniper (+juniper and −juniper) treatments to study herbivory of seedlings and saplings were established in a 2×2 factorial design. In 1995 and again in 1996 we randomly located 100 5.31-m^2 circular plots (2.6 m diameter) amid juniper saplings and 100 plots at least 1 m from all juniper saplings. Each plot had a circular transplant zone (0.6 m diameter) surrounded by a 1 m buffer zone. Plots in each level of the juniper treatment were randomly assigned to levels of the deer treatment. Cylindrical fences 1.5 m high were constructed around the transplant zones of −deer plots.

Experimental seedlings were grown from acorns collected in the study site and germinated in a 3:1 mixture of vermiculite and perlite. Newly germinated seedlings were grown in sleeves containing a 3:1 mixture of Metro-Mix[TM] and Bacto[TM] (bwi Companies, Inc., Schulenburg, Texas, USA) until transplanting. We randomly selected 200 seedlings for transplanting each year and randomly assigned them to plots. Before transplanting, the total leaf area of each seedling was measured from digitized photographs of leaves, using NIH Image, an image analysis computer program. After transplanting, height, length of the longest stem, and total stem length of each seedling were measured. Transplant height was the vertical distance from the highest meristem to the soil surface. Transplant height differed from length of the longest stem if transplants were leaning, a result of rodent digging, or if the longest stem was crooked, a result of browsing the apical meristem. Analyses of randomly sampled, naturally occurring juveniles (n = 43) in the study site indicated that longest stem length and total leaf area provided the best non-destructive estimate of transplant aboveground biomass (Russell and Fowler, unpubl. results). In both 1995 and 1996, we transplanted seedlings in March. Seedlings were watered every three days for two weeks after transplanting. Seedlings that appeared sickly during this two-week period and died soon after were excluded from analyses.

Censuses of transplants were conducted at the beginning (April or May), middle (July or August), and end (November) of each growing season until May 1998. During each census, we recorded the presence or absence of each transplant and its height, longest stem length, total stem length, number of leaves and browsing damage. The leaves of each transplant were photographed to measure its total leaf area and to estimate its aboveground biomass during each census except July 1996, August 1997, and April 1998.

We harvested surviving transplants in May 1998, measured the diameter of the taproot at 5 cm in depth and measured each transplant's final aboveground biomass (after drying at 60 °C for three days). Analyses of haphazardly sampled, naturally occurring small saplings (n = 17) indicated that taproot diameter at 5 cm depth provided the best estimate of taproot biomass (Russell and Fowler, unpubl. results).

Experimental study of seedlings and saplings: analyses

For +deer plots, effects of neighboring juniper saplings and cohort on the number of transplants that were browsed were analyzed with a contingency table analysis.

Effects of deer and junipers on the numbers of transplants that survived until harvesting were analyzed using a contingency table analysis. Treatment effects on the survivorship curves of transplants were examined using Wald tests of the hypothesis that the coefficients of the treatment and interaction variables, generated through Cox proportional hazards models (PROC PHREG, SAS version 6.07 1992), did not differ from zero (Fox 1993; Allison 1995).

We analyzed treatment effects on total proportional changes in height and biomass. Total proportional changes were calculated as:

$$\text{Prop}\,\Delta S = \left(S_{\text{harvest}} - S_{\text{transplant}}\right)/S_{\text{transplant}}$$

where S_{harvest} is height or mass at harvest and $S_{\text{transplant}}$ is height or mass at transplanting. For these analyses, we used only transplants that survived until harvest, Kruskal-Wallis tests for the 1995 cohort and two-way ANOVA for the 1996 cohort.

We also analyzed the effects of deer, junipers, and date on the monthly rates of proportional change in height and aboveground biomass of transplants in both cohorts using repeated measures ANOVAs (PROC MIXED, SAS version 6.07 1992). The monthly rate of proportional change in height or biomass is the proportional change during the census in-

terval divided by the number of months of growing season (March 1 to December 1) during the interval. If the interaction of a treatment and census date significantly affected the monthly rate of proportional change in height or aboveground biomass, single degree of freedom contrasts were constructed to examine the effect of the treatment during each census interval. To explore significant three-way interactions, we constructed the appropriate contrast to test the juniper×deer interaction effect during each interval with a significant juniper×date or deer×date interaction effect. Significance thresholds for contrasts were adjusted using Bonferroni corrections to account for multiple comparisons.

Treatment effects on the estimated final taproot biomass of transplants were analyzed using a 2-way ANOVA for the 1995 cohort and a Kruskal-Wallis test for the 1996 cohort.

Additional analyses of transplants in the +deer/−juniper plots

These plots had enough browsed transplants to allow some additional analyses. Logistic regressions were used to examine the effect of a transplant's initial aboveground biomass on the probability that it would be browsed (each cohort separately) and on its probability of survival until harvest (1995 cohort only; 1996 cohort sample sizes were too small for this analysis).

Sample sizes also permitted an examination of the direct, short-term effect of browsing on height in these plots. These short-term effects were changes that occurred between pre- and post-browse censuses. For each census interval during which transplants were browsed we randomly selected an equal number of transplants that had not been browsed during or before the census interval and combined these individuals from all census intervals to produce a data set of changes in height for unbrowsed plants. T-tests were used to compare the monthly rate of proportional change in height between browsed and unbrowsed transplants.

To examine effects of browsing over the course of the experiment, we compared browsed and unbrowsed individuals in these plots at the end of the experiment. Survival was tested with a 2×2 contingency table analysis. T-tests were used to compare total proportional change in transplant height and final taproot mass between browsed and unbrowsed plants. Effects of browsing on the total proportional

change in aboveground biomass, total leaf area per individual, and leaf number per individual were analyzed with Wilcoxon rank sum tests.

Results

Pre-dispersal seed predation

The flotation test of acorn viability indicated that 40.8% (n = 103) and 5.1% (n = 99) of acorns in seed traps were viable upon dispersal in 1995 and 1996, respectively; 32.6% and 1.0% of acorns from traps germinated in the growth chamber in 1995 and 1996, respectively. Weevil larvae frequently caused acorn inviability. Some acorns that did not germinate were indicated to be viable by the flotation test (they sank) because the weevil larvae in them had consumed little endosperm before the acorns fell into the seed traps.

Small mammal trapping

We caught four *Peromyscus pectoralis*, six *P. attwateryii*, two *P. leucopus*, one *P. maniculatus* and four mice that were either *P. leucopus* or *P. maniculatus* in 151 trap-nights. We observed *Sciurus niger* and *Spermophillus variegatus* individuals in the study site; both of these species not only eat acorns, but also disperse them by carrying them away, burying them, and failing to retrieve some of the buried acorns (Davis 1978).

Experimental study of post-dispersal acorn survival and germination

Neither deer nor junipers significantly affected the rate at which sown acorns survived to become seedlings, nor the rate at which these acorns were removed from the plots, in spring 1996. The juniper treatment having been dropped from the experiment, deer did not significantly affect either the rate at which sown acorns became seedlings or their removal rate in spring 1997. The mean rate at which acorns survived and germinated was less than 0.4% in each treatment combination in spring 1996 and in each level of the deer treatment in spring 1997. These survival and germination rates include acorns that were removed by squirrels and germinated in the areas monitored surrounding the sowing plots. All acorns that were not removed from plots became inviable within nine months of sowing. The maximum
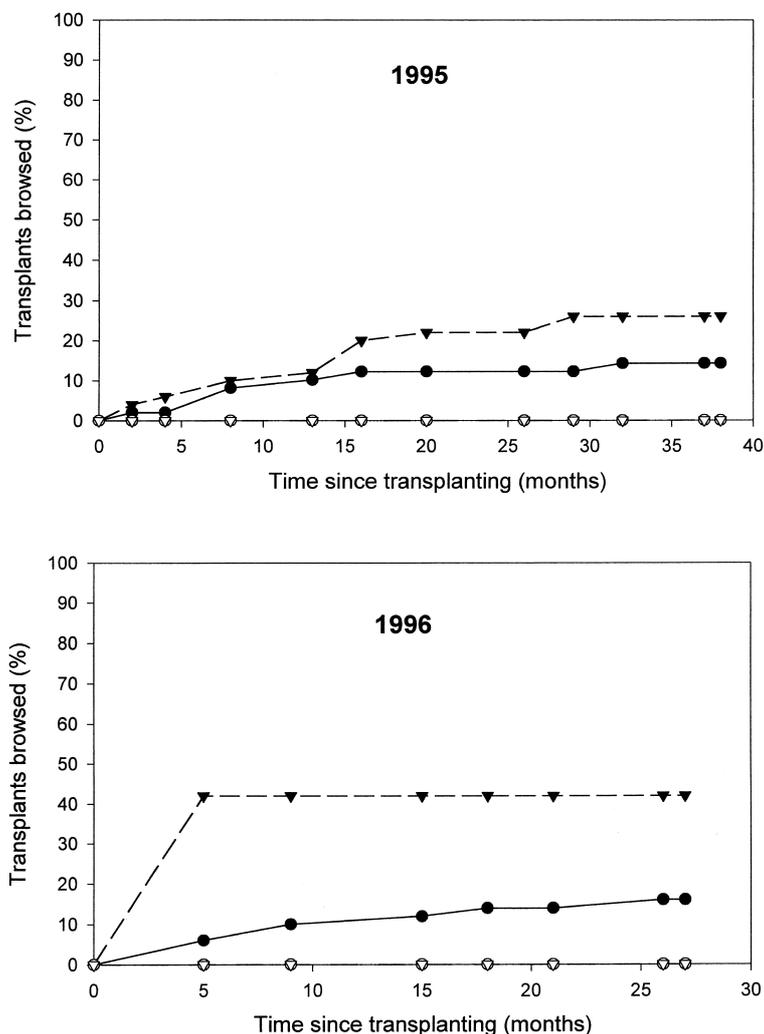
Figure 1. Cumulative proportion of *Quercus buckleyi* transplants in the 1995 cohort and the 1996 cohort that were browsed before each census date. Shaded circles are +juniper/+deer plots; open circles are +juniper/ − deer plots; shaded triangles are − juniper/+deer plots; open triangles are − juniper/ − deer plots.

distance at which a seedling that had sprouted from a sown acorn was discovered was 10.1 m in 1996 and 8.1 m in 1997.

Experimental study of seedlings and saplings

Junipers significantly reduced the number of *Q. buckleyi* transplants that were browsed where deer were present (p < 0.001; Figure 1). As planned, fencing eliminated browsing by deer. A few transplants in fenced plots suffered damage by stem-boring insects that removed their apical meristems and leaves.

Deer significantly increased the mortality rate of *Q. buckleyi* transplants in both the 1995 and 1996 cohorts (Table 1). In addition, deer significantly reduced the number of transplants in the 1995 cohort that survived until May 1998 (p = 0.002; Figure 2). The interaction of deer and junipers significantly affected the number of transplants in the 1996 cohort that survived until May 1998 (p = 0.007): where deer were present, more transplants survived under junipers, but where deer were excluded, more transplants survived away from junipers.

Deer and junipers had a significant interaction effect on the total proportional change in height of *Q. buckleyi* transplants in the 1995 cohort (p < 0.001;

Table 1. Results of Cox regression analysis to determine the effects of deer and junipers on the mortality risk of *Q. buckleyi* transplants. Cox regression estimates parameters for the proportional hazards model; $h_i(t) = \lambda_0(t)\exp\{\beta_{jun}x_{i,jun} + \beta_{deer}x_{i,deer} + \beta_{junxdeer}x_{i,junxdeer}\}$

Variable	DF	Parameter estimate	Standard error	Wald Chi square	P-value	Risk ratio (e^β)
1995 Cohort						
Juniper	1	0.281	0.261	1.152	0.283	1.324
Deer	1	0.661	0.254	6.772	0.009	1.937
Jun×Deer	1	−0.259	0.347	0.557	0.456	0.771
1996 Cohort						
Juniper	1	0.193	0.224	0.742	0.389	1.213
Deer	1	0.597	0.226	6.959	0.008	1.816
Jun×Deer	1	−0.335	0.313	1.148	0.284	0.715

Figure 3A). Where deer were present, juniper saplings had a positive effect on the mean total proportional change in height of transplants, but where deer were excluded the effect of junipers was negative. Neither deer nor junipers significantly affected the total proportional change in height of transplants in the 1996 cohort. In both cohorts, absolute changes in height between planting and harvest were much smaller than the increases in height required to grow above the browseline (~150 cm). The largest increases in height of transplants in the 1995 and 1996 cohorts were 10.9 cm and 10.5 cm, respectively. Deer significantly reduced the total proportional change in aboveground biomass of transplants in the 1995 cohort (p < 0.05; Figure 3B). Effects on these variables in the 1996 cohort were not significant, partly because sample sizes were smaller.

The presence of junipers in the plot significantly (p < 0.039) reduced the monthly rate of proportional change in height of *Q. buckleyi* transplants of the 1995 cohort. In the analysis of the 1996 cohort, date, juniper×date, deer×date, and juniper×deer×date all reached significance (p < 0.001, p < 0.002, p < 0.040, and p < 0.010, respectively). Contrasts revealed significant negative effects of the presence of junipers on transplant height growth between the May and August 1997 censuses (p < 0.001) and between the April and May 1998 censuses (p = 0.003). Because the three-way interaction was significant, the two-way juniper×deer interaction was tested at the two census dates that had significant deer or juniper effects. The juniper×deer interaction, however, did not reach the Bonferroni-adjusted significance threshold during either interval. The monthly rate of proportional change in aboveground biomass in the 1995 cohort was significantly affected by date (p < 0.001). The juniper×date interaction effect was mar-

ginally significant (p = 0.055), but contrasts did not reveal a significant effect of junipers during any census interval. The monthly rate of proportional change in aboveground biomass in the 1996 cohort was significantly affected by date and by the juniper×date and deer×date interaction effects (p < 0.001, p < 0.024, and p < 0.040, respectively). The effect of deer did not reach significance during any of the four separate census intervals, despite the significant deer×date interaction effect, but junipers significantly reduced the rate of biomass accumulation of transplants between the May and November 1997 censuses (p = 0.004). During this interval the juniper×deer interaction effect was also significant (p = 0.004): transplant growth rate was on average greatest in the +deer, −juniper plots.

Neither deer nor junipers significantly affected the estimated final taproot mass of young saplings in either cohort.

Additional analyses of transplants in the +deer/−juniper plots

The greater the initial size of a transplant of the 1996 cohort in the +deer, −juniper plots, the greater its chance of being browsed (p = 0.040). There was a similar trend in the 1995 cohort that did not reach statistical significance (p = 0.135). Larger initial aboveground biomass was significantly associated with a higher probability of transplant survival in the transplants of the 1995 cohort in the +deer, −juniper plots (p = 0.023).

As expected, browsing reduced the proportional rate of change in height during the interval in which the plant was browsed (p = 0.052; Fig 4A). At the end of the experiment, the only significant difference between browsed and unbrowsed plants in these plots
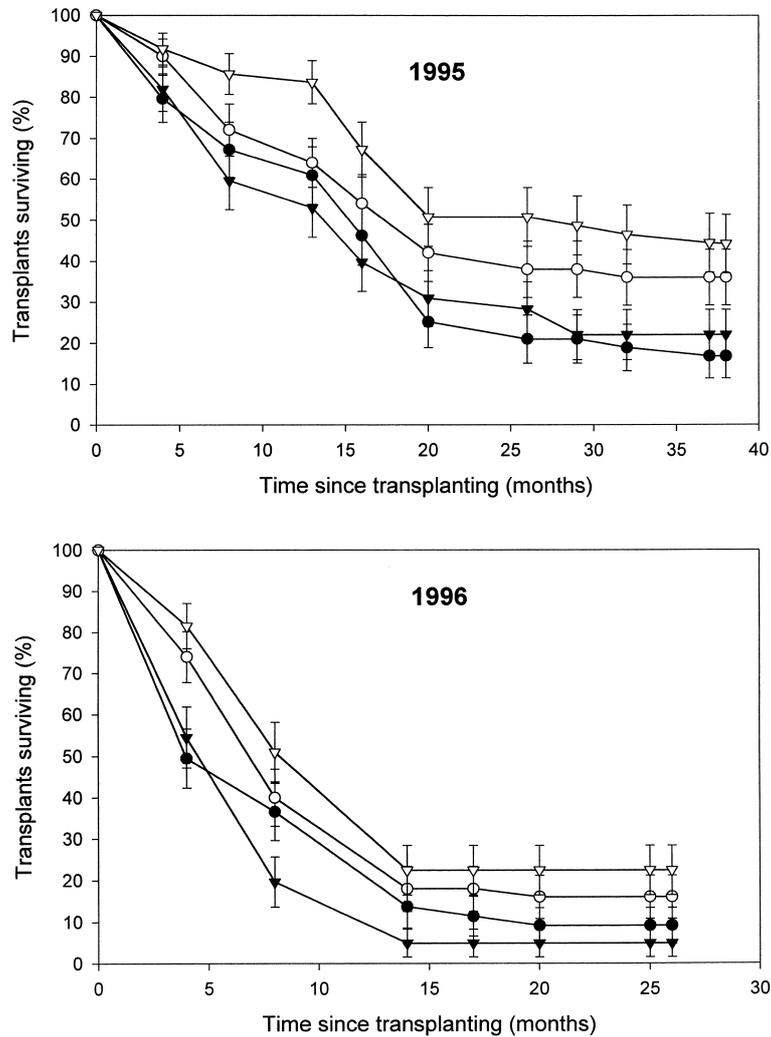
Figure 2. Proportion (s.d.) of *Quercus buckleyi* transplants in the 1995 cohort and the 1996 cohort that survived until each census date (n = 50). Treatment combinations indicated by symbols as in Figure 1.

was in survival: browsed plants of the 1995 cohort were more likely to have survived to the end of the experiment than were unbrowsed plants of this cohort in these plots (p = 0.008; Figure 4B). Small sample sizes (< 10) limited the power of these analyses, however.

Discussion

Direct effects of deer on Quercus buckleyi

The results of this study support the hypothesis that white-tailed deer are responsible for the observed scarcity of *Quercus buckleyi* saplings taller than 20

cm in mixed woodlands on the Edwards Plateau (Russell and Fowler 1999). Only *Q. buckleyi* transplants outside the deer exclosures were browsed. Protection from deer browsing significantly increased rates of survival, height growth, and biomass accumulation in these transplants.

Although white-tailed deer also eat acorns of this and most other oak species, the results of this study indicate that this form of granivory is not an important cause of the scarcity of *Q. buckleyi* saplings in this region. Deer exclosures had no detectable effect upon the survival and germination rates of acorns. Although mast is a large component of deer diets during autumn and winter on the Edwards Plateau (McMahan 1964), any acorns not eaten by deer are
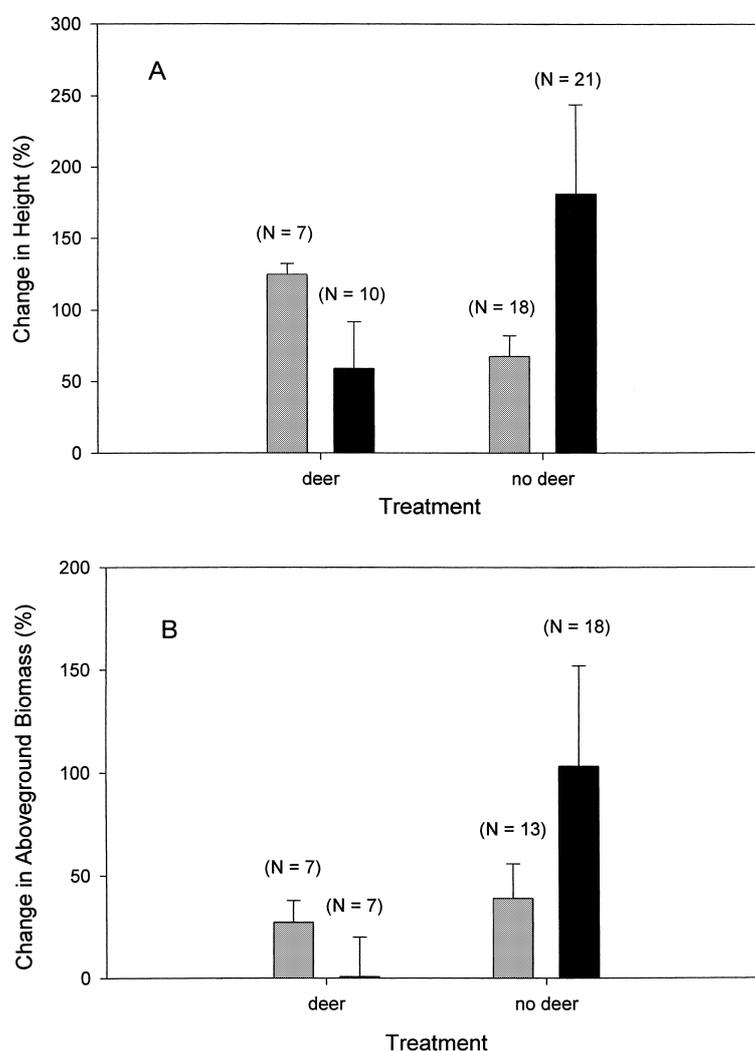
Figure 3. Treatment effects on growth of *Quercus buckleyi* transplants. A) Mean (s.e.) total proportional change in height. B) Mean (s.e.) total proportional change in aboveground biomass. Darkly shaded bars represent plots away from *Juniperus ashei* saplings; lightly shaded bars represent plots amid *Juniperus ashei* saplings.

probably consumed by other granivores, especially rodents or insects, unless they are cached and forgotten at depths or in locations where germination is impossible. Similarly, in California woodlands, *Quercus douglasii* acorns are subject to granivory by many species and deer do not affect their germination rate (Borchert et al. 1989).

No cause other than deer browsing of seedlings and small saplings seems likely to be responsible for the failure of adult recruitment of *Q. buckleyi* in this region. In a previous study, we documented successful adult recruitment during the past two decades at a site where deer densities are kept low through hunting and

fencing (Russell and Fowler 2002). Outside of this one site, the few naturally occurring *Q. buckleyi* saplings between 20 cm and 150 cm tall evidently escape deer browsing because they occur on cliff edges and steep slopes (Russell 1999). These plants have high survival rates and grow rapidly, indicating that the present climate is not unfavorable to *Q. buckleyi*.

The effect of deer on transplant survival observed in this study was larger than has been found in comparable studies. In other studies of deer herbivory, negative effects on survival have been found to be weaker than negative effects on growth. Alverson and Waller (1997) found no significant reduction in the
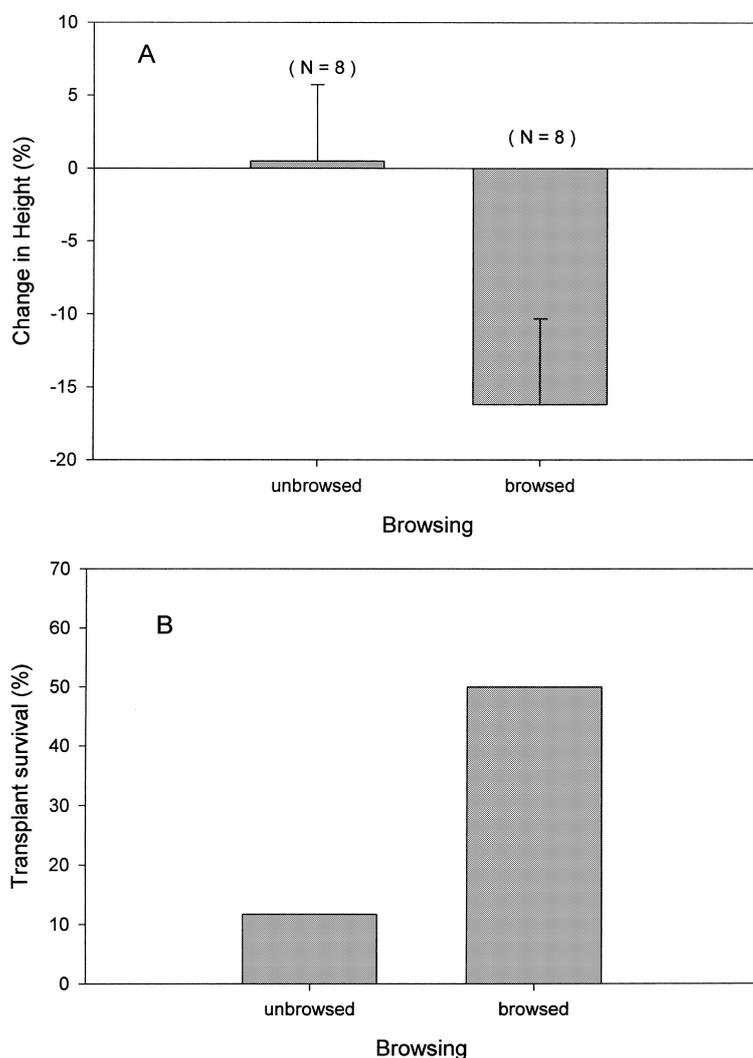
Figure 4. Effects of browsing on *Quercus buckleyi* transplants of the 1995 cohort in the −juniper/+deer treatment combination. A) Mean (s.e.) change in height between pre-browse and post-browse censuses. B) Survival until harvest.

survival rate of transplanted *Tsuga canadensis* (L.) Carr. saplings that were exposed to deer for two years. Similarly, Griffin (1971) found that *Q. douglasii* juveniles could survive repeated browsing for decades, although they did not increase in height. It may be that the small size (< 15 cm tall) and youth of *Q. buckleyi* juveniles in our experiment made them less able to tolerate browsing than saplings in other studies. Alternatively, the intensity of browsing on such small plants may have been particularly high in this study; the intensity of deer browsing on seedlings and small saplings appears to be higher in mixed woodlands than in other communities (Inouye et al. 1994; Rooney et al. 2000).

The comparisons between experimental manipulations (between transplants inside and outside of the deer exclosures) make the negative effects of deer on *Q. buckleyi* juveniles clear. Had we done a purely observational study, however, the effects of deer would have been partly masked by the correlations between plant size, plant survival, plant growth rate, and probability of being browsed, as is shown by the analyses of the transplants in the '+deer/−juniper' plots. In these 'control' plots, larger transplants were more likely to survive, as one would expect, but larger plants were also more likely to be browsed. In addition, the longer a plant lived, the more likely it was to be browsed; most of the deaths occurred before

much of the browsing did. These relationships produced the superficially paradoxical result that browsed plants were more likely to survive in these plots. The correlation between a plant's lifespan and likelihood of its being browsed is merely a mathematical artifact, but the correlation between a plant's size and the likelihood of its being browsed may have important biological consequences. Deer herbivory may be more effective than other kinds of herbivory at reducing plant population growth rates because deer preferentially eat the largest individuals, which would otherwise be the most likely to survive to adulthood.

This study, in combination with other information about the relationship of white-tailed deer and *Q. buckleyi* in central Texas, provides an example of a native herbivore greatly reducing growth rates of populations of a native plant by virtually preventing the recruitment of individuals into adult size classes. Deer not only reduce *Q. buckleyi* population growth rates, but also cause a dramatic shift in the stage structures of these populations (Russell and Fowler 1999). The resulting structure is unstable because no population can persist indefinitely without recruitment of new individuals into reproductive size classes. It is not rare for tree populations to be missing cohorts due to episodic recruitment; it is the likelihood that the failure of individuals to achieve reproductive size in this species will continue indefinitely into the future, as it has for the past 60 years, that sets *Q. buckleyi* apart.

Worldwide few other native herbivores have been shown to have sustained direct effects of this magnitude on tree populations. McInnes et al. (1992) showed that on Isle Royale, Michigan USA, moose (*Alces alces*) browsing can prevent recruitment to adult size classes of preferred species, such as *Abies balsamea*. However, moose populations appear to fluctuate cyclically, which may allow adult recruitment during times of low population sizes (McInnes et al. 1992). Perhaps an example of an herbivore having an effect of similar magnitude on tree populations would be the effects of dense elephant populations on preferred browse species in African national parks and preserves (Barnes 1983; Ben-Shahar 1996). However, there is still considerable debate as to whether elephant actually have caused woodland decline (Dublin et al. 1990; Ben-Shahar 1998).

Facilitation of Quercus buckleyi by Juniperus ashei

The results of this study indicate that the direction, as well as the magnitude, of the effects of junipers on *Q. buckleyi* juveniles is determined by the presence or absence of deer. Juniper saplings increased the rates of *Q. buckleyi* survival and height growth where deer were present, but reduced them where deer were absent. Evidently the positive effects of a juniper neighbor outweighed its negative effects on a transplant unless deer were excluded. The most likely explanation is that junipers prevent browsing deer from reaching *Q. buckleyi* juveniles, and this protection outweighed the effects of competition for water, light, and nutrients. We cannot, however, determine from the results of this study whether the net effect of junipers is positive or negative throughout the life of *Q. buckleyi* individuals, or even during the entire portion of their lives that they are short enough to be accessible to browsing deer.

Although there is no doubt that competition between neighboring plants is very important and common in plant communities, facilitation is now recognized as also important (Bertness and Callaway 1994; Callaway 1995). The role of facilitation in structuring plant communities was first recognized in low productivity communities where facilitative interactions largely result from amelioration of abiotic stresses (Callaway and King 1996; Pugnaire et al. 1996). However, it is becoming increasingly apparent that physical protection from herbivory, of the sort we document here, is an important mechanism of facilitation in many communities, especially where humans have introduced high densities of non-native herbivores, frequently domestic livestock (Callaway et al. 2000; Rousset and Lepart 2000), or have caused inflated populations of native herbivores (Borgmann et al. 1999). For example, Borgmann et al. (1999) showed that the density and mean height of *Tsuga canadensis* saplings, a preferred browse species of white-tailed deer in northern hardwoods forests in the Upper Great Lakes region USA, were significantly greater where a dense understory of *Abies balsamea* was present than where such an understory was absent.

Community composition, landscape patterns, and conservation

What is the future of the mixed woodlands of the Edwards Plateau likely to be? The negative effects of

deer on survival and growth of *Q. buckleyi* juveniles demonstrated here, together with the fact that deer appear to have inhibited recruitment of *Q. buckleyi* for sixty years (Russell and Fowler 2002), lead us to predict the gradual loss of *Q. buckleyi* from these woodlands as existing trees age and die. Stump-sprouting will slow, but not reverse, the process. Deer probably are reducing or preventing adult recruitment of most deciduous species in these woodlands, not just *Q. buckleyi*. Saplings of *Prunus serotina* and *Fraxinus texensis*, both preferred browse species (Armstrong et al. 1991), are rare or absent in most of these mixed woodlands (Van Auken 1988). In fact, *Q. buckleyi* may better withstand intense browsing than either *P. serotina* or *F. texensis* because its stump sprouts can occasionally grow rapidly enough to escape browsing. It is possible that these mixed woodlands will become savannas or grasslands if deer populations remain high. However, populations of the unpalatable *Juniperus ashei* are increasing in numbers and spatial extent in most sites (J. Noel, pers. comm., C. Sexton, pers. comm.). These mixed woodlands may therefore become nearly pure stands of *J. ashei*.

In either case the conservation implications may be substantial. These mixed woodlands are the primary habitat of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). It is not known how many other species might be endangered, or at least might become much rarer, if these woodlands were to disappear. Nor is it known how many other plant species are being directly threatened by deer browsing in this region. Deer are known to be one of the major causes of the extreme rarity of the endangered bracted twist-flower (*Streptanthus bracteatus*; Zippin 1997).

If the conclusions of this study are general, browsers that consume early life-stages of trees may be an important factor in determining spatial and temporal patterns of other landscapes that are also a mosaic of woodlands, savannas and grasslands. The effects of browsing herbivores, especially those whose populations have been greatly affected by human activities, on woodlands may often be substantial. In semi-arid woodland communities worldwide, humans have altered the sizes of populations of browsing herbivores through predator eradication (Hahn 1945), introduction of non-native browsers (both as livestock and for hunting) (Lange and Willcocks 1980; Lange and Graham 1983), and introduction of novel diseases (Prins and van der Jeugd 1993). While effects of herbivores that browse juvenile trees are not as immediately ob-

vious as are effects of herbivores, such as elephants, that affect the survival, growth and reproduction of adult trees, the browsing of juvenile trees may greatly affect woodland tree populations.

Acknowledgments

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