

WILDFIRE-INDUCED MORTALITY OF WOODY PLANTS IN A CENTRAL
TEXAS SAVANNA

THESIS

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By

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ABSTRACT

WILDFIRE-INDUCED MORTALITY OF WOODY PLANTS IN A CENTRAL
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by

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Historically, the vegetation of the Edwards Plateau was probably a mosaic of grassland, savanna parkland and woodland. Over the last two centuries, woody plants have expanded into areas that were previously grassland, in part because of over grazing and fire suppression. Prescribed fires during the cool season have been used to restore grasslands in this region, but less is known about impacts of warm season fires on these savannas. I examined effects of a warm season wildfire on the mortality of woody species in four habitats (savanna parklands, woodlands, and north and south facing slopes) in an eastern Edwards Plateau savanna. I addressed the following questions: 1) How did the population structure of the woody species in each habitat change

because of the fire? 2) Was woody plant mortality size and species dependent? Overall, fire-induced mortality was greatest in the open parkland (40.0%, $p = 0.004$) and lowest on the densely wooded south facing slopes (10.6%). Across all species, mortality was negatively related to plant height ($p = 0.016$, $r^2 = 0.836$), and basal diameter ($p = 0.003$, $r^2 = 0.596$). Out of the 23 species inventoried, mortality was greatest for *Juniperus ashei* ($p < 0.05$). Results indicate that warm season fires have the potential to significantly decrease woody abundance in these savannas, however effects vary with habitat, plant size and species. Thresholds may exist that limit the efficacy of hot, summer fires in restoring these savannas to pre-settlement conditions.

INTRODUCTION

Savanna ecosystems are typically defined as areas with scattered trees and a continuous understory of grasses (Van Langevelde et al. 2003; Rebertus and Burns 1997). However, within savannas, specific habitats vary from open parklands to near closed canopy woodlands. The Edwards Plateau in central Texas exhibits a blend of these vegetative types (Weniger 1988). In savanna parklands, the woody plants are often clumped into discrete clusters consisting of central live oaks (*Quercus fusiformis*) and a variety of woody understory species (Phillips and Barnes, 2003; Gass and Barnes 1998). Evergreen species (*Q. fusiformis* and *Juniperus ashei*) dominate woodland canopies with various evergreen and deciduous shrubs in the understory. Historically, savannas of the southeastern portion of the Edwards Plateau were more open (i.e., more grassland) than today (Barnes et al. 2000; Fonteyn et al. 1988; Van Auken 1988; Weniger 1988).

A complex network of biotic and abiotic interactions, such as water availability, soil texture, soil nutrients, herbivory and fire, influence the spatial and temporal balance between grasses and woody

species in a savanna (Van Langevelde et al. 2003; Higgins et al. 2000). Higgins et al. (2000) suggested that an understanding of grass-tree coexistence requires consideration of long-term effects of life history-disturbance interactions on demography rather than a concentration on fine-scale effects of resource competition. Rebertus and Burns (1997) proposed that savannas arise primarily as a result of fire rather than climatic or edaphic factors. In many studies, fire frequency was instrumental in determining the relative abundance of both grass and woody growth forms in grasslands (Heisler et al. 2003; Anderson 1990; Hartnett and Fay 1998; Knapp and Seastedt 1998; Gibson and Hulbert 1987).

Fires can and do change the characteristics of vegetated landscapes. They affect savannas directly by causing an immediate decline in woody vegetation. Fire intensity is positively and linearly related to the amount of grass biomass. The impact of fire on woody biomass is also positively and linearly related to fire intensity (Van Langevelde et al. 2003). Fires in grasslands, where the biomass is largely composed of grasses and forbs, characteristically have a uniform continuity because of the large volume of live and dead fine fuels. Consequently, grassland fires consume most of the fuel, including woody plant seedlings. Woodlands, on the other hand, possess coarse, moisture-rich fuels, such as twigs, woody debris and leaf litter, and support sporadic ground fires to severe crown fires. Because fire

intensity is primarily determined by grass biomass on the ground, crown fires are difficult to ignite and eliminate woody plants in only the most severe cases (Van Langevelde et al. 2003).

Roques et al. (2001) documented woody plant encroachment in savanna systems in North America, South America, Australia, India and Africa. Hoffmann (1999) and Archer (1995) attributed this encroachment in some savannas to reduced fire frequencies. Before Anglo-European settlement, fires ignited by lightning and Native Americans kept grasslands relatively free of woody plants. Many woody individuals were therefore restricted to sites protected from fire, such as sloped, rocky drainages (Leopold 1924; Foster 1917). The historical frequency of these fires in savannas is uncertain (Hoffmann 1999). A chronology of natural fires in Missouri revealed that fire frequency was greatest before 1850, however, return intervals increased in the following years, in association with increased settlement by Anglo-Americans (Cutter and Guyette 1994). Likewise, in the last two centuries, settlement of central Texas led to an increase in grazing and fire suppression.

As a result of these widespread changes in land management, isolated clusters of woody plants have coalesced and formed larger areas of continuous canopy cover (Archer 1989). For example, woody species, such as *J. ashei*, increased in areas historically considered open savannas. Some have proposed that *J. ashei* was historically restricted to limestone outcroppings, ridges, ravines and slopes protected from fire

(Jessup et al. 2003; Smeins 1980; Bray 1904). However, the recent lack of fire may have promoted the increase of *J. ashei* into grasslands and, in some cases Ashe junipers may form dense-canopy woodlands within 75 years (Fuhlendorf et al. 1996). Similarly, in the absence of fire in African savanna systems tree density doubled in six years (Hochberg et al. 1994) and shrub cover increased from 2% to 31% in 43 years (Roques et al. 2001).

Savanna related increases in *J. ashei* densities have also been associated with decreases in light dry grass fuels (Van Auken 1988). Consequently landscapes have changed from fine-fueled grassland savannas to coarse fueled Ashe juniper-dominated woodlands. The increase of dense-canopy woodlands has also resulted in decreased production and quality of forage and browse for wildlife, decreased grazing distribution, accessibility and quality for livestock, decreased diversity of the plant community and increased erosion (White and Hanselka 1989; Burkhardt and Tisdale 1976). Russell and Fowler (1999) stated that these changes could have large effects on species compositions and physiognomies of savannas and woodlands, specifically the eastern Edwards Plateau.

In some ecosystems, prescribed burning is used to regenerate vegetation and create mosaics of habitats, which then increases biological diversity (Woods 1995). After a single fire in a central Illinois

sand forest, a significant increase in richness and cover of herbaceous species accompanied a decrease in woody cover (Nuzzo et al. 1996).

The seasonal timing of a burn can be critical in influencing the response of a plant community to fire. For example, cool season fires with a maximum return interval of 25 years can maintain an open savanna community. By comparison, warm season fires can maintain the same landscapes with return intervals longer than 25 years (Fuhlendorf et al. 1996). Additionally, fires conducted during the extreme warm season have the capability to kill large trees and this can then open up virtually closed canopy woody vegetation (Fuhlendorf et al. 1996).

Historically, the natural fire regime in some subtropical areas likely included warm season wildfires (Boo et al. 1997; Glitzenstein et al. 1995). Summer wildfires are extremely hot and can cause extensive damage to vegetation already drought stressed and highly flammable at that time of year (White and Hanselka 1989). Fires conducted with dry herbaceous ground cover vegetation are considered severe (Hopkins 1965). Fully cured grassy fuels under dry season conditions cause intense savanna fires (Russell-Smith et al. 1998). The vulnerability of woody species to fire increases from the dormant, cool season with low air temperatures, to mid warm season (June to September) when air temperatures reach their maxima. In Australia, fire combustion energy intensities differed by 36-fold, with a low of 341 kW/m in a winter burn

compared to a high of 12,300 kW/m in a summer burn with climatic conditions highly conducive to rapid combustion (Hodgkinson 1991). Large oak mottes in central Texas only received extensive damage under conditions of high ambient temperatures and low fuel moisture (O'Neal et al. 1996).

Evergreens are especially susceptible to late summer or autumn fires (Glitzenstein et al. 1995). For example, *J. ashei* individuals of all size classes have suffered mortality from the intensity of a summer fire (Fonteyn et al. 1984) while seedling-size individuals showed the greatest mortality during summer months (Jackson and Van Auken 1997).

The changes in land management in the recent past could have long-term effects on the species compositions and physiognomies of savannas and woodlands (Russell and Fowler 1999). Understanding these changes will require comprehension of the effects of fire on woody plants (Hoffmann 1999). Although fire studies addressing this problem in savanna ecosystems are common, they typically discuss prescribed cool season fires (Fonteyn et al. 1988). The effects of severe warm season, i.e. summer, fires are infrequently documented.

In this study I examined the effects of a warm season wildfire on woody plant mortality and population structure in four different habitats (savanna parklands, woodlands, north facing slopes and south facing slopes) in a central Texas savanna. This research specifically addressed the following questions: 1) How did the community change in regard to

the abundance and density of woody plants, the species richness, and diversity and dominance indices? 2) Did the size structure of the woody species in each habitat change due to the fire? 3) Was mortality of woody plant species habitat dependent, size dependent and/or species dependent? Because of contrasts in the fuel complex of savanna parkland versus woodland habitats, I hypothesized that woody plant mortality would be highest in the open parklands and lowest in the woodland habitat. Relevant literature indicated that evergreens are more vulnerable to summer fires than deciduous species. Based on these studies, I hypothesized that evergreen species, such as, *J. ashei* would suffer greater mortality than the deciduous species in all habitats. And last, I hypothesized that mortality of woody species within each habitat would be inversely related to size such that smaller individuals would suffer greater mortality than larger individuals.

METHODS

Study Site

The study was conducted at the Texas State University Freeman Ranch (29° 56' N, 98° W; max elevation 274 m) (Barnes et al. 2000), located 8 km west of San Marcos in the southeastern Edwards Plateau physiographic region (Fig. 1). Topographic features of the ranch include flat to undulating plains, hilly regions and deeply dissected drainages with north and south facing slopes. The underlying parent material is limestone and limestone embedded with clay and marl (Carson, 2000). Thus, soils of Freeman Ranch are stony, clay-rich soils that developed over this sedimentary limestone layer. Six soil series have been identified on the ranch: Comfort, Eckrant, Medlin, Orif, Rumble and Tarpley (Carson, 2000). Combinations of these series have formed five soil types: the Rumble-Comfort, Comfort-Rock, and Medlin-Eckrant associations, Orif soils, and Tarpley clays (Barnes et al. 2000). The Comfort-Rock association and the Rumble-Comfort soil association underlie the upland terrain, while slopes along drainages are composed of Orif soils, Eckrant and Comfort-Rock associations (Barnes et al. 2000; Carson, 2000).

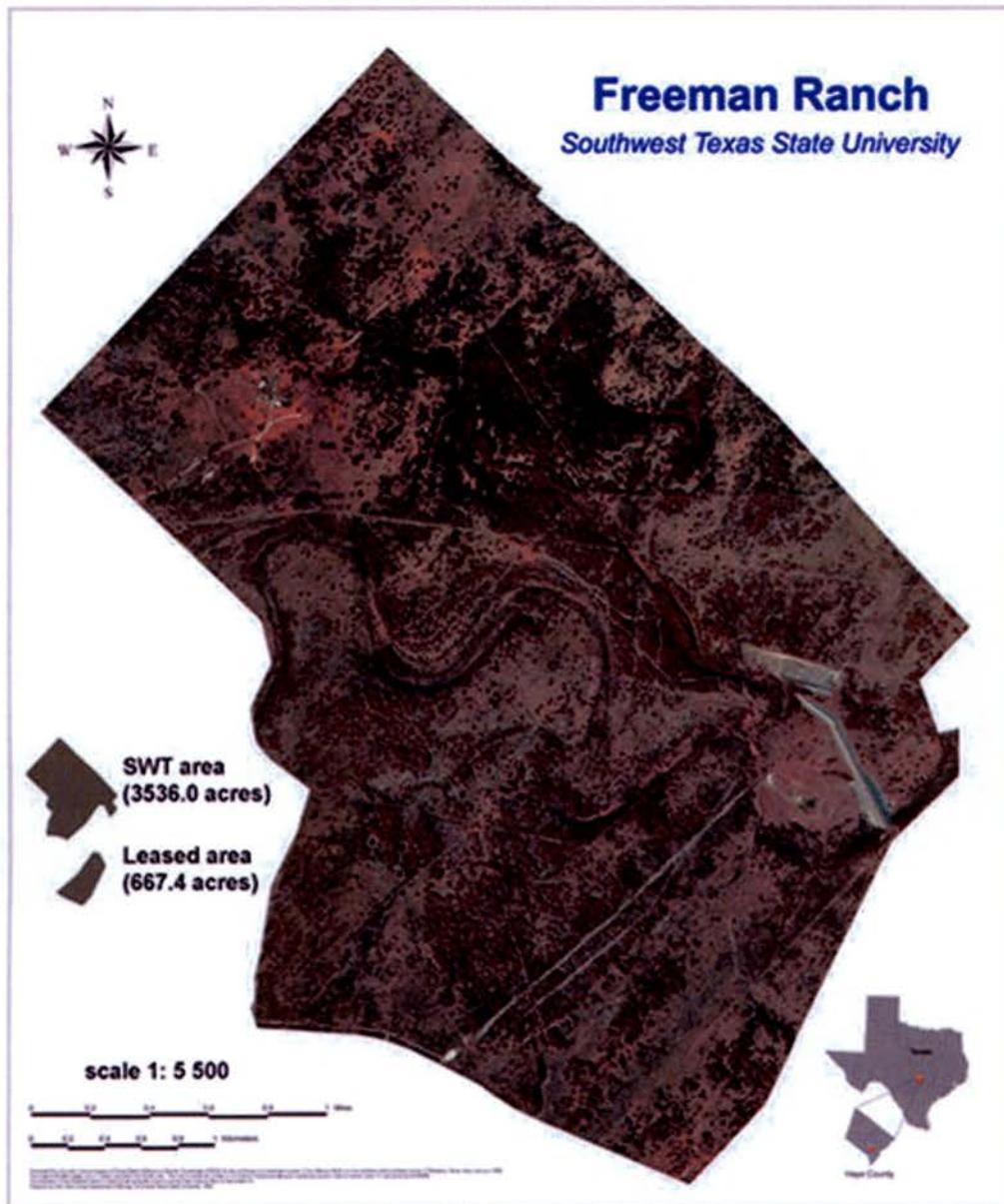


Figure 1. Color infrared aerial Digital Orthophoto Quarter Quadrangle (DOQQ) of the Texas State University - San Marcos (formerly Southwest Texas State University) Freeman Ranch, Hays County, TX. Image created in 1995.

The climate of the Edwards Plateau is generally subtropical to subhumid with periodic droughts leading to occasional semi-arid conditions (Dixon, 2000; Riskind and Diamond 1988). The mean annual temperature of Freeman Ranch is 15.6 °C. Maximum daytime temperatures exceed 32.2 °C, 119 days of the year; however July and August have daily maximum temperatures well above 35 °C. The average annual relative humidity (RH) is 67%, and the average RH for August is 63.8%. Mean annual precipitation is 87 cm, spread almost evenly throughout the year, with only a slight peak in September. On average, precipitation falls four days a month (Dixon, 2000).

The particular wildfire that formed the basis for the present study spread throughout the eastern and southeastern areas of Freeman Ranch, August 6-7, 2001. The fire originated from a campsite located north east of the ranch on private property. This two-day fire burned approximately 260 ha (Fig. 2). Based on data collected from the closest NOAA weather station in San Marcos, TX (29° 52' N, 97° 55' W, elevation 186.5 m), the maximum/minimum air temperatures were 37.8/23.9 °C and 38.3/21.1 °C on Aug. 6 and 7, respectively. The closest area weather station equipped to record wind and evaporation measurements was Canyon Dam (about 32 km from San Marcos, 29° 52' N, 98° 12' W, elevation 304.8 m). The maximum wind speeds recorded at Canyon Dam were 45.1 km/hr and 70.8 km/hr on Aug. 6 and 7.

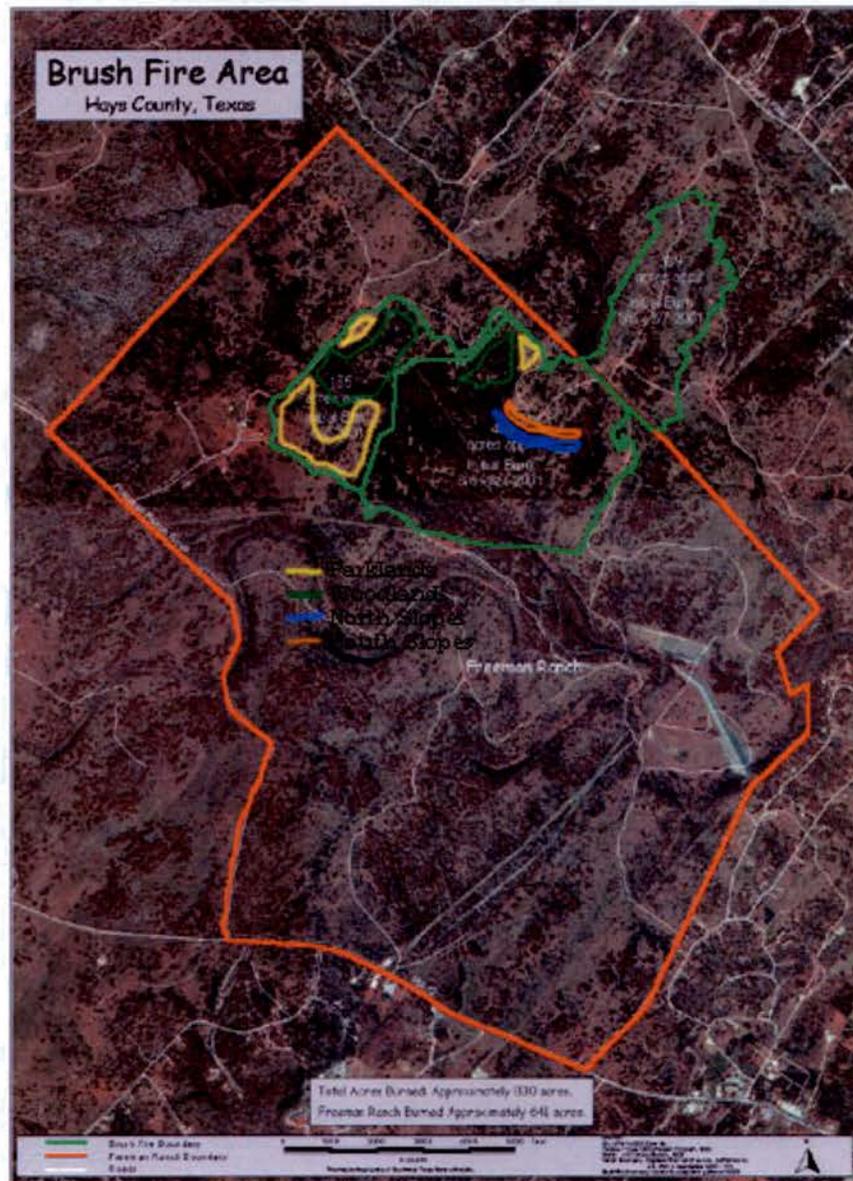


Figure 2. Color infrared aerial Digital Orthophoto Quarter Quadrangle (DOQQ) (created in 1995) of Texas State's Freeman Ranch, Hays County, TX, with boundaries of the August 2001 wildfire, and habitat areas overlaid. Source: Created by Robert Stafford, Texas State University's Physical Plant.

The evaporation value for both days was 0.7 mg H₂O/cm³ at Canyon Dam. There was no precipitation recorded on either day of the fire.

Sampling Methods

Sampling was conducted during June-August, 2003, which was about two years after the August 2001 fire. Within the burned area, four habitats were selected for sampling: upland savanna parklands and juniper/oak woodlands (hereafter referred to as “parkland” and “woodland”, respectively), and north facing slopes and south facing slopes (hereafter referred to as north slopes and south slopes)(Figs. 3-6). The north and south slopes are lowland habitats, situated adjacent to drainages and rocky escarpments. The parkland habitats are characterized by woody plant clusters interspersed in perennial grasslands dominated by *Nasella leucotricha* (Texas wintergrass) and *Bouteloua rigidiseta* (Texas grama). The woodland habitats are characterized by continuous canopy cover dominated or co-dominated by *J. ashei*, in addition to a variety of other woody species. The north slopes support mesic deciduous forest vegetation whereas the exposed south slopes support more xeric evergreen woodland vegetation.

In each habitat, I established twenty 10 m x 10 m quadrats were established. Quadrats were arbitrarily placed within each habitat type. An Etrex GPS unit was used to record the UTM coordinates for mapping purposes and to ensure that quadrats did not overlap (Appendix A).

Quadrats were measured with a meter tape and delineated with surveyor flags. Within each quadrat I recorded the woody species present, diameter (m) at ground level of each individual (i.e., basal diameter), maximum height (m) of each individual, maximum canopy diameter (m) of each individual and general condition of each individual (i.e., alive or dead). For some individuals, the only measurable remains were charred boles. In these cases, only the basal diameter was recorded. In other cases, the fire may have been carried into the canopy, loosing area as a result. This prevented measurement of the maximum canopy diameter. For these individuals, only height and basal diameter were measured. Because of this, some data sets referring to the same habitat or species had differing sample sizes within the size class categories (For example, see Fig. 7).

The woody species were identified by sight, or if unknown, were keyed to species. Plant identification and nomenclature follows Diggs et al. (1999). If woody plant remains were charred beyond species recognition, they were recorded as “unidentifiable” and any size category data possible was recorded. The diameter of each woody individual was measured with a diameter tape, the maximum height was measured with a telescoping range pole and the canopy diameter was measured with a meter tape. Because two growing seasons had passed before sampling occurred, it was assumed that woody plant plants had sufficient time to form new growth, thus survive, or to completely perish from the fire.

Individuals were considered alive if green sprouts were observed from any part of the exposed individual. Individuals showing signs of charring from the ground level to the top of the canopy and lacking green growth were considered dead.

To compare the community prior to and after the fire, importance values (IV) for each species were calculated as follows:

$$IV = RD + RC + RF, \text{ where}$$

RD = relative density (number of individuals of a species/total number of individuals of all species) $\times 100$,

RC = relative cover (cover/total cover for all species) $\times 100$,

where Cover = Density \times mean basal area for the species, and

RF = relative frequency (frequency/total frequency values for all species) $\times 100$.

Shannon-Weiner indices (H') were calculated using the following equation:

$$H' = -\sum (p_i \times \ln p_i), \text{ where}$$

p_i = IV for each species/total IV for all species

\ln = logarithm to base e.

Simpson's Dominance index (D) was calculated as follows:

$$D = \sum (p_i)^2.$$

All calculations follow Krebs (1999).

Statistical Analyses

Single factor analyses of variance (ANOVAs) were used to statistically analyze mortality data in the four habitats. For these analyses individual quadrats were considered the sampling unit. ANOVAs were also conducted on data pooled across species and also for individual species. Mean comparisons were made using Tukey's multiple comparison tests with differences considered significant at $p < 0.05$. Simple linear regression analysis was used to explore relationships between mortality, density and the three size variables.



Figure 3. Example of a parkland habitat at the Texas State University - San Marcos Freeman Ranch. Note the continuous grassy understory with interspersed woody individuals. Photo taken August 2003.



Figure 4. Example of a woodland habitat at the Texas State University - San Marcos Freeman Ranch. Note the numerous *Juniperus ashei* individuals and the crowded overstory canopy. Photo taken August 2003.



Figure 5. Example of a north slope habitat at the Texas State University - San Marcos Freeman Ranch. Note the deciduous woody vegetation and rock outcrops. Photo taken August 2003.



Figure 6. Example of a south slope habitat at the Texas State University - San Marcos Freeman Ranch. Note the various sizes of evergreen trees and shrubs, as well as the partially burned individual in the right foreground. Photo taken August 2003.

RESULTS

Pre-Fire Community Composition

The pre-fire community composition described here is inferred from the data collected on both live and dead individuals. Based on these data, a total of 23 woody species representing 14 different families were inventoried. Eight of these species (*Berberis trifoliolata*, *Celtis laevigata*, *Diospyros texana*, *J. ashei*, *Ptelea trifoliata*, *Q. fusiformis*, *Quercus buckleyi*, and *Ulmus crassifolia*) were present in all four habitats (i.e. parklands, woodlands, north slopes and south slopes). A number of species were unique to a specific habitat. These included *Zanthoxylum hirsutum* (parkland), *Eysenhardtia texana* (woodland), *Cercis canadensis*, *Garrya ovata*, and *Morus microphylla* (north slopes), and *Condalia hookeri* and *Sophora affinis* (south slopes). In all four habitats, the dominant species was *J. ashei*, and the two co-dominants were *D. texana* and *U. crassifolia* (Table 1). Within each particular habitat a third, virtually unique, co-dominant was determined. These were: *Forestiera pubescens* (parkland), *Q. fusiformis* (woodlands and south slopes), and *Sophora secundiflora* (north slopes).

Species composition varied in richness (10-18 species) and density ($890 \pm 1.0 - 4580 \pm 3.0$ plants/ha, prior) between habitats (Table 2). Pre-fire woody plant densities were 4-5 times greater in the woodland and sloped habitats than in the parklands (Table 2). Species richness (18) was greatest in the north slopes habitats and lowest in the parkland habitats (10). Despite the low species richness of the parklands, dominance was more evenly spread between the species present ($D_s = 0.23$) and diversity was greatest ($H' = 1.8$). Dominance values were higher for the woodland and south slope habitats compared to the parklands and north slopes. Diversity values for the woodlands and south slopes were the lowest (0.8 for both habitats) (Table 2).

The size structure of the community (all habitats and species combined) was skewed toward smaller size classes for all measures of size (height, basal diameter and, although less apparent, canopy diameter). All size classes were represented (Fig. 7). By comparison, the parkland habitat had an extremely skewed distribution with few to no individuals present in the largest size classes (Fig. 8). Although the size class structures of the three remaining habitats were similar to that of all habitats combined, there were fewer large woody plants (those within and greater than the size classes of 5.25 m in height, 0.25 m basal diameter, and 5.25 m canopy diameter) in the north slopes (161 plants) than the woodlands (233 plants) and south slopes (362 plants) habitats (Figs.9-11).

Table 1. Importance values (IV = RD + RC + RF) calculated for each species present (alive and dead) per habitat prior to the August 2001 wildfire, the growth form (deciduous=D, evergreen=E), and the family of each species.

Species	IV per Habitat				Growth	
	Parkland	Woodland	North Slopes	South Slopes	Form	Family
<i>Berberis trifoliolata</i> Moric.	3.7	2.8	0.5	3.0	Shrub (E)	Berberidaceae
<i>Celtis laevigata</i> var. <i>reticulata</i> Torr.	5.6	3.9	10.6	1.9	Tree (D)	Ulmaceae
<i>Cercis canadensis</i> L.			0.4		Tree (D)	Fabaceae
<i>Condalia hookeri</i> M.C. Johnst.				0.4	Shrub (E)	Rhamnaceae
<i>Diospyros texana</i> Scheele	30.4	14.2	18.2	15.1	Tree (D)	Ebenaceae
<i>Eysenhardtia texana</i> Scheele		1.1			Shrub (D)	Fabaceae
<i>Forestiera pubescens</i> Nutt.	25.5	0.3	0.9	0.4	Shrub (D)	Oleaceae
<i>Garrya ovata</i> subsp. <i>lindheimeri</i> (Torr.) Dahling			1.7		Shrub (E)	Garryaceae
<i>Ilex decidua</i> Walter		0.6	0.4	0.9	Shrub (D)	Aquifoliaceae
<i>Ilex vomitoria</i> Sol. in Aiton		0.1	3.9	3.2	Shrub (E)	Aquifoliaceae
<i>Juniperus ashei</i> J. Buchholz	82.4	162.0	125.5	157.5	Tree (E)	Cupressaceae
<i>Morus microphylla</i> Buckley			0.5		Shrub (D)	Moraceae
<i>Prosopis glandulosa</i> Torr	0.6		0.2	0.3	Tree (D)	Fabaceae
<i>Ptelea trifoliata</i> L.	21.8	0.1	1.4	1.2	Tree (D)	Rutaceae
<i>Quercus buckleyi</i> Nixon & Dorr		0.6	2.9	1.3	Tree (D)	Fagaceae
<i>Quercus fusiformis</i> Small	1.7	5.3	4.7	7.1	Tree (E)	Fagaceae
<i>Sideroxylon lanuginosum</i> Michx.		0.7	2.3	0.7	Shrub (D)	Sapotaceae
<i>Sophora affinis</i> Torr. & A. Gray				0.1	Tree (D)	Fabaceae
<i>Sophora secundiflora</i> (Ortega) Lag.ex DC.		0.2	11.3	0.5	Tree (E)	Fabaceae
<i>Ulmus crassifolia</i> Nutt.	8.3	7.3	13.9	6.3	Tree (D)	Ulmaceae
<i>Viburnum rufidulum</i> Raf.			0.4	0.1	Tree (D)	Caprifoliaceae
<i>Zanthoxylum hirsutum</i> Buckley	0.5				Shrub (E)	Rutaceae

Table 2. Species richness (number of species), density (number of plants per hectare (ha) \pm standard error, Shannon-Weiner diversity index (H') and Simpson dominance index (D_s) for each habitat comparing all individuals (dead and alive = prior) to surviving individuals only (post).

		Parkland	Woodland	North Slopes	South Slopes
Species Richness	Prior	10	14	18	17
	Post	10	14	18	17
Density (#/ha)	Prior	890 \pm 1.0	3070 \pm 3.0	4170 \pm 3.0	4580 \pm 3.0
	Post	540 \pm 1.0	2440 \pm 2.0	3700 \pm 3.0	4100 \pm 2.0
Diversity Index (H')	Prior	1.8	0.8	1.5	0.8
	Post	1.7	0.7	1.5	0.8
Dominance Index (D_s)	Prior	0.23	0.66	0.41	0.63
	Post	0.23	0.70	0.40	0.66

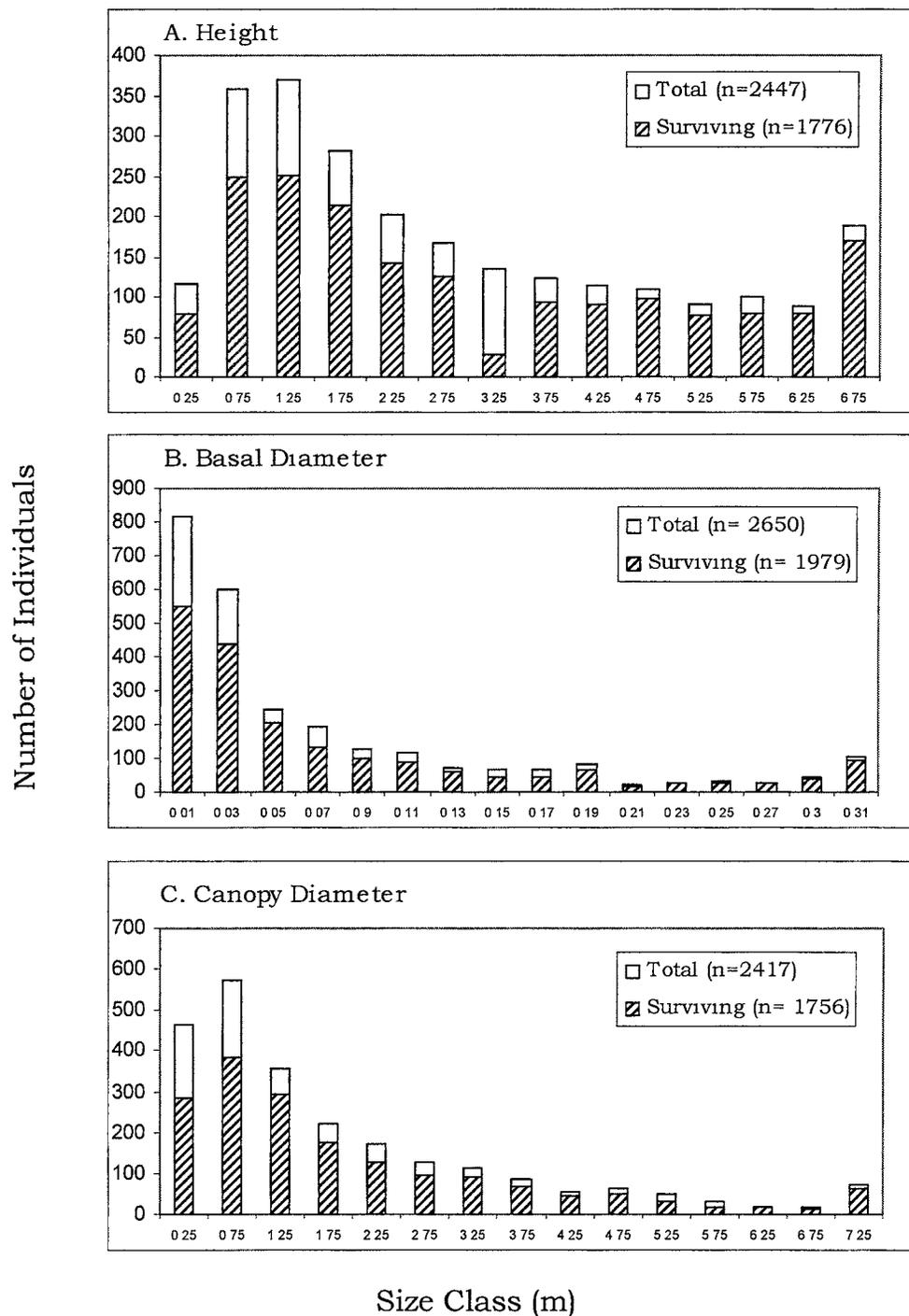


Figure 7. Number of individuals across all habitats, alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

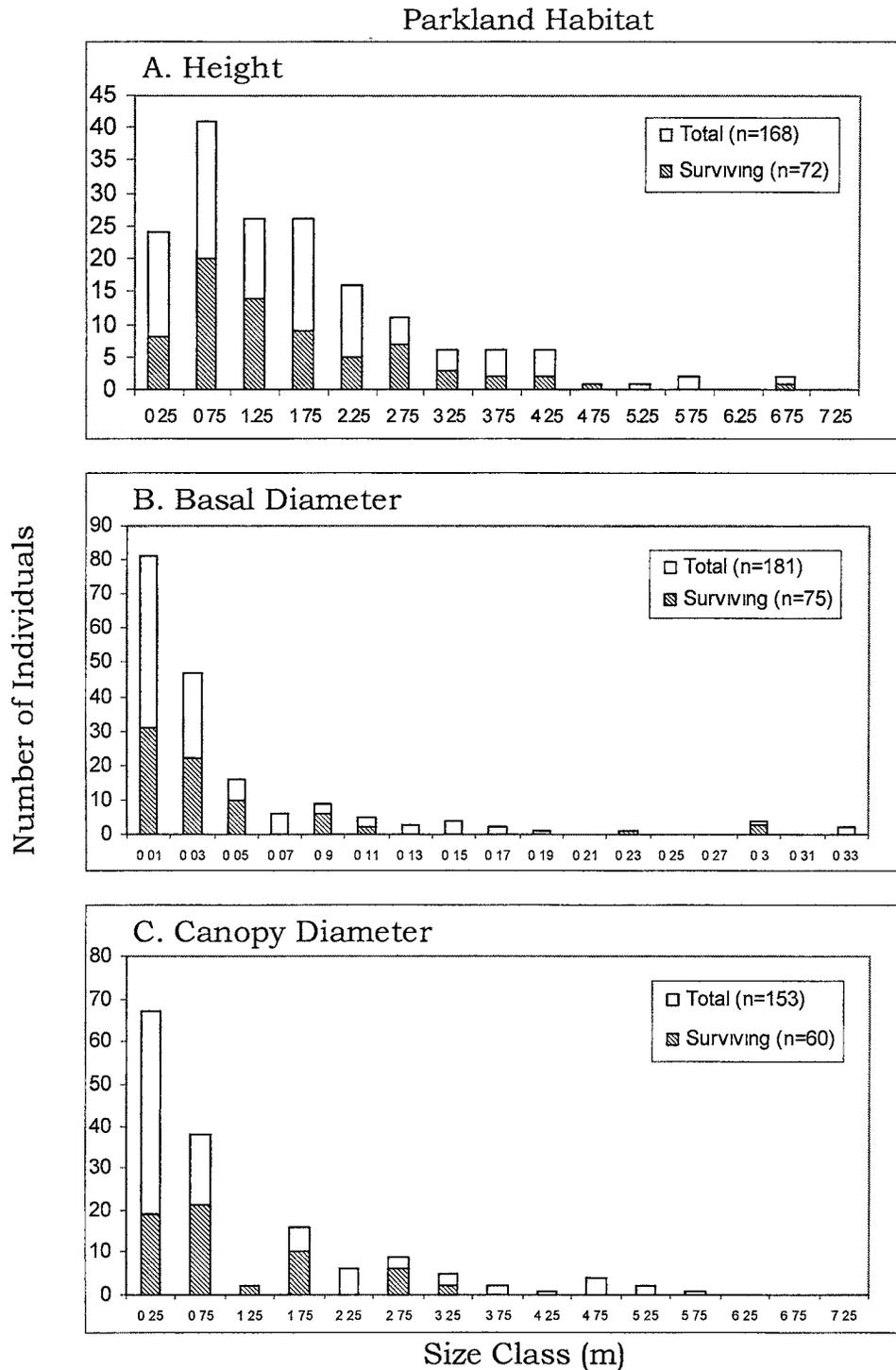


Figure 8. Number of individuals in the parkland habitat, alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

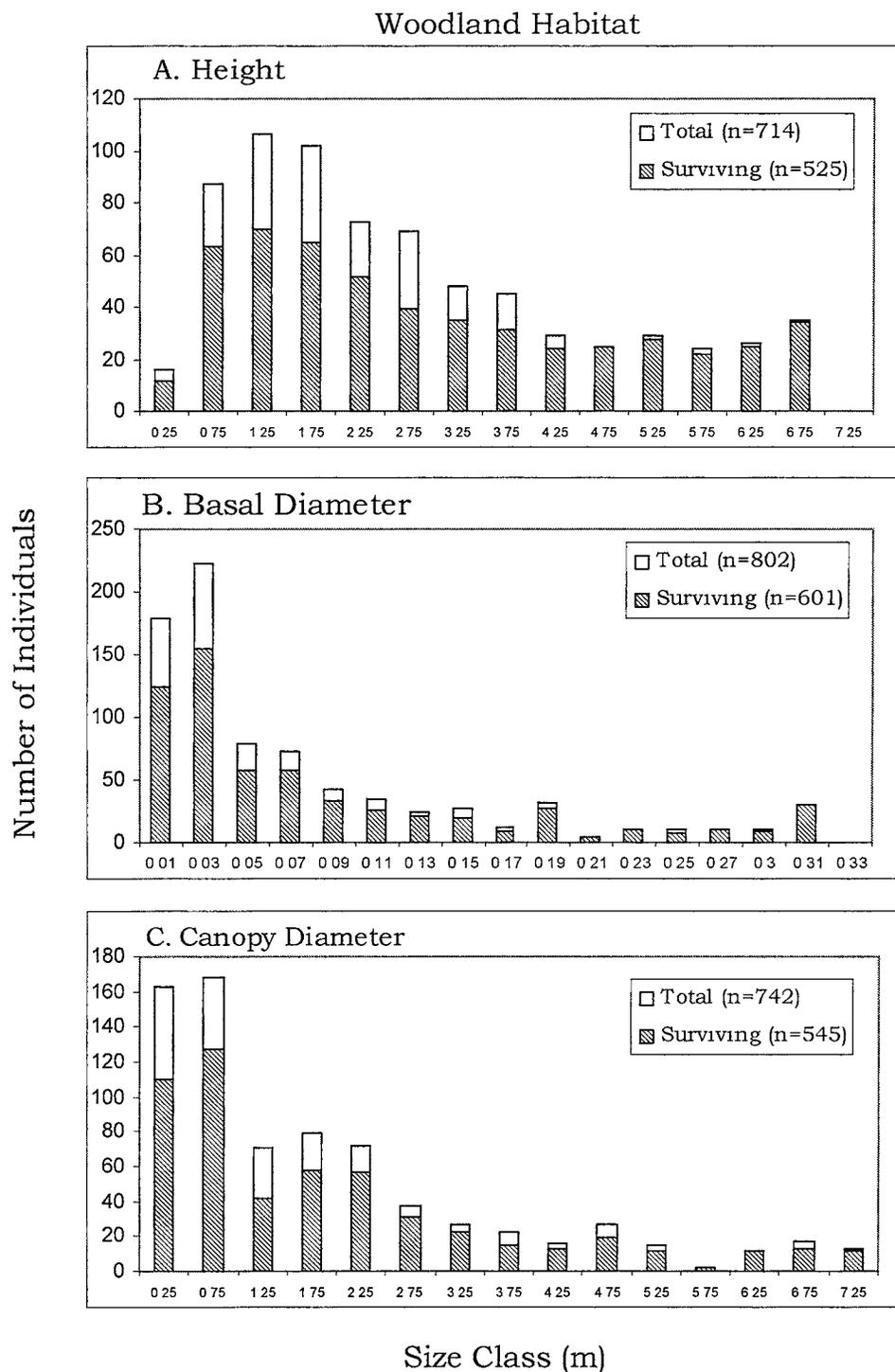


Figure 9. Number of individuals in the woodland habitat, alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

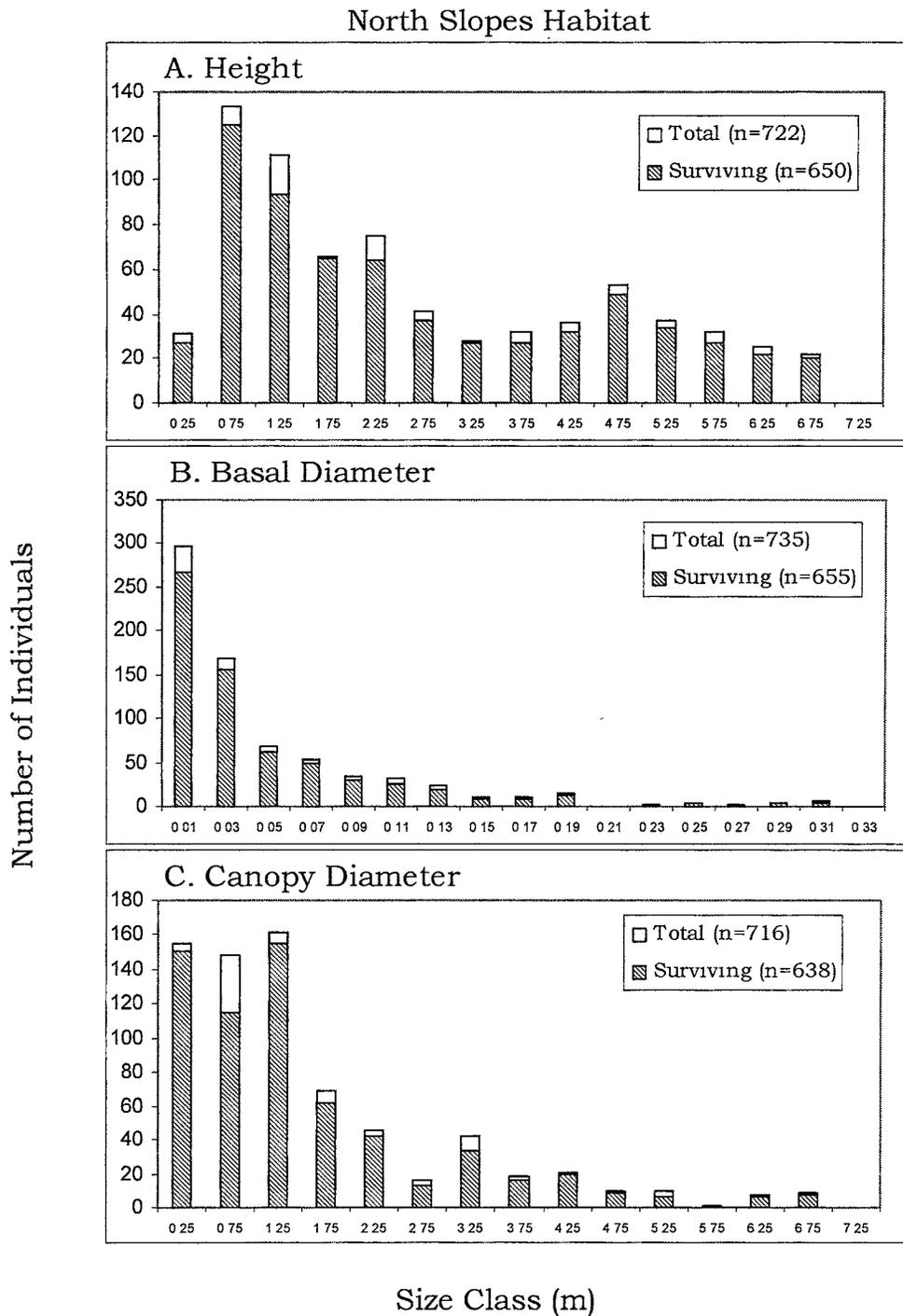


Figure 10. Number of individuals in the north slopes habitat, alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

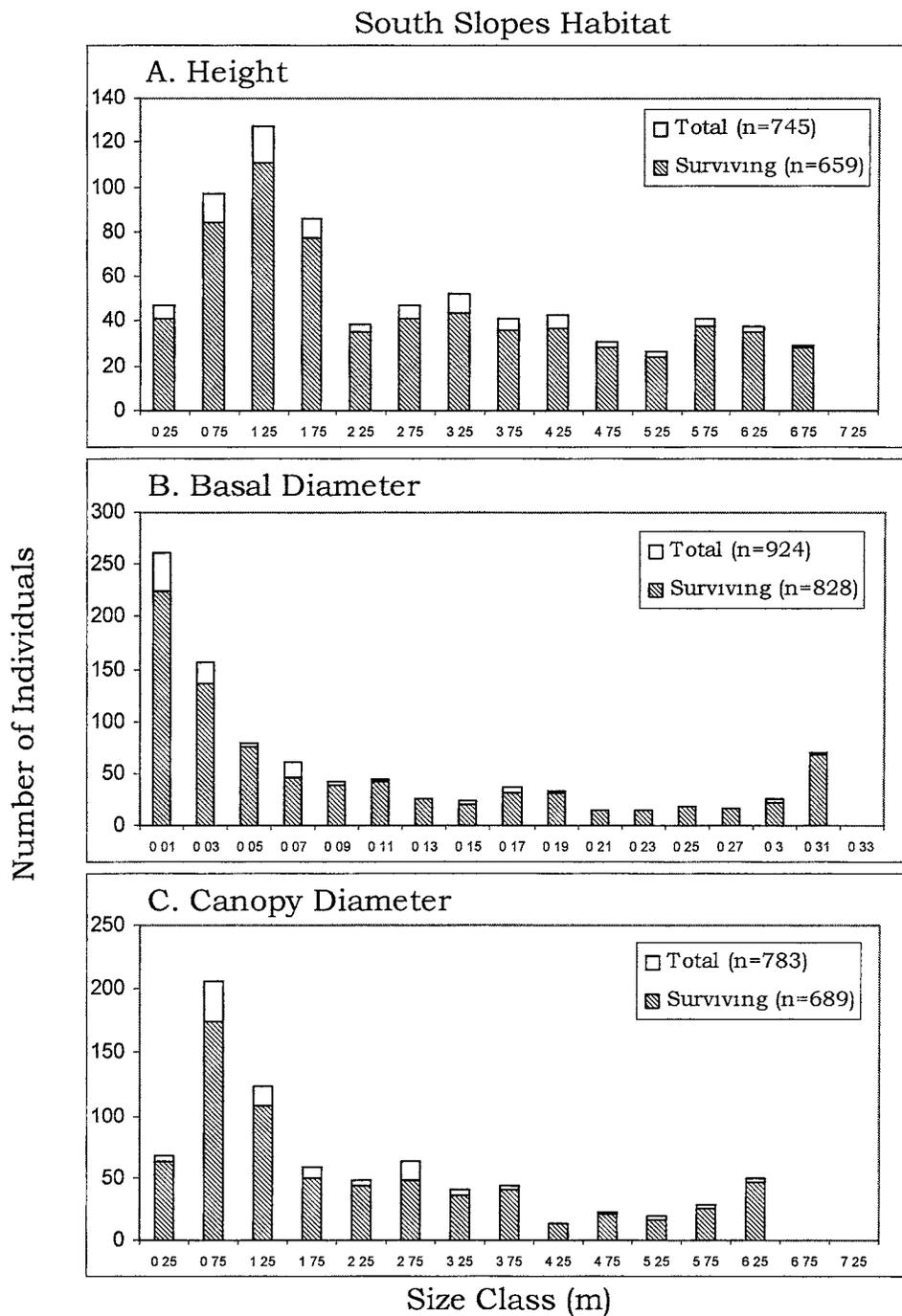


Figure 11. Number of individuals in the south slopes habitat, alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, (C) canopy diameter. X-axes indicate size class mid points.

Habitat Effects

Analysis of variance (ANOVA) indicated a significant effect ($p = 0.004$, $df = 3, 78$) of habitat on woody plant fire-induced mortality (Fig.12). When averaged over species, mean (\pm SE) percent mortality was highest in the parkland habitat ($40.0 \pm 7.9\%$), and lowest in the south slopes habitat ($10.6 \pm 1.6\%$) (Fig.12). Mortality in the parklands was at least twice that of both sloped lowland habitats, while mortality in the woodlands was intermediate. Plant density differed between the habitats (Table 2), but regression analysis showed that percent mortality per quadrat and overall stand density were only weakly correlated (Fig. 13).

Species Effects

ANOVAs performed on the mean (\pm SE) percent mortalities of the eight species common to all habitats resulted in a significant species effect on mortality ($p < 0.001$). Tukey's HSD Tests indicated that mortality for *J. ashei* ($32.3 \pm 3.9\%$) was significantly greater than *B. trifoliolata* ($7.3 \pm 4.4\%$; $p = 0.002$), *D. texana* ($15.4 \pm 3.5\%$; $p = 0.021$), *Q. fusiformis* ($13.2 \pm 4.4\%$; $p = 0.035$), and *U. crassifolia* ($8.2 \pm 3.0\%$; $p < 0.001$) (Fig. 14).

Individual ANOVAs were also used to compare the percent mortalities for the eight species per habitat. Within the parkland habitat, species effects were significant ($p = 0.001$). Tukey's HSD tests showed that mortality for *J. ashei* (76.3%) was significantly greater than

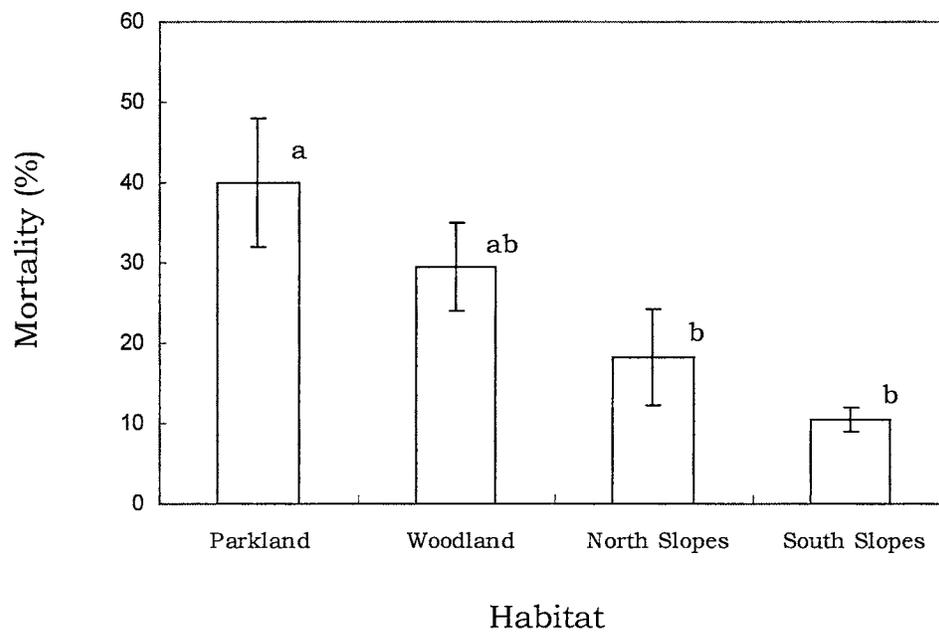


Figure 12. Mean (\pm SE, $n = 80$) fire-induced percent mortality among all woody species present in each of the four habitats at Freeman Ranch, Hays County, TX. Columns with different letters indicate significant differences as determined by Tukey's HSD test ($p < 0.05$).

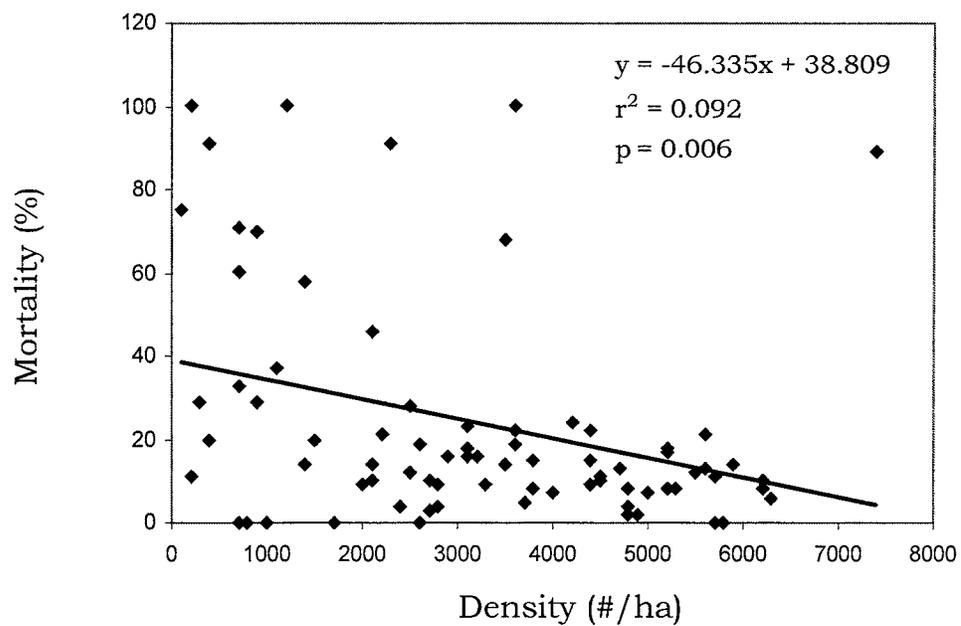


Figure 13. Regression relationship between the percent mortality per quadrat sampled ($n = 80$) and the plant density (# plants/ha). Line indicates best-fit simple linear regression.

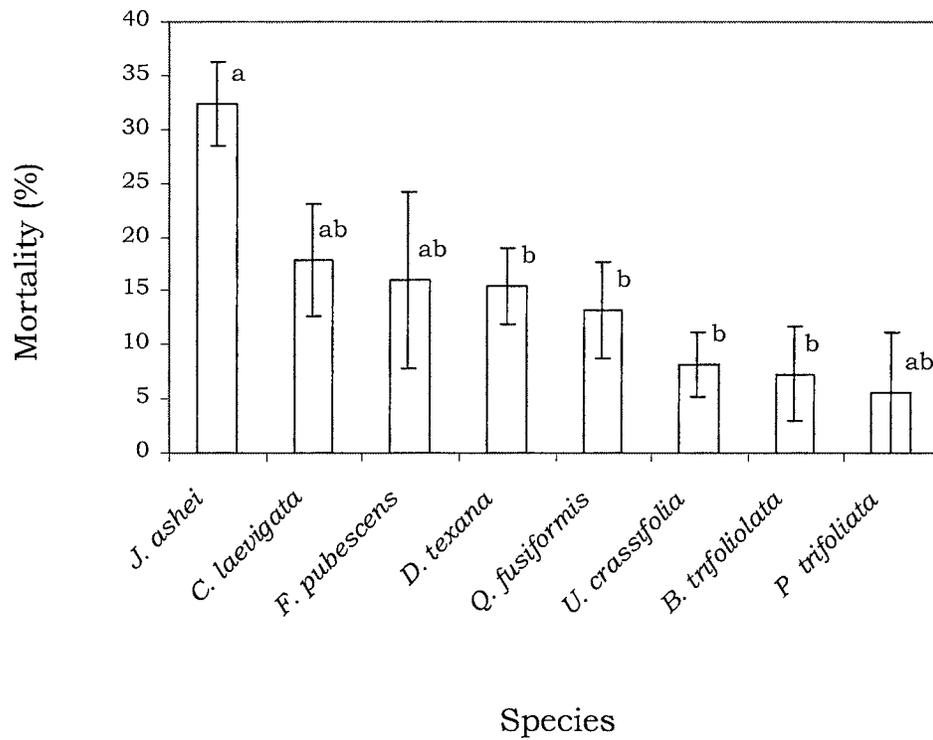


Figure 14. Mean (\pm SE) percent mortality per each species present in all four habitats. Columns with different letters indicate significant differences as determined by Tukey's HSD test ($p < 0.05$). Arranged in descending order by percent mortality.

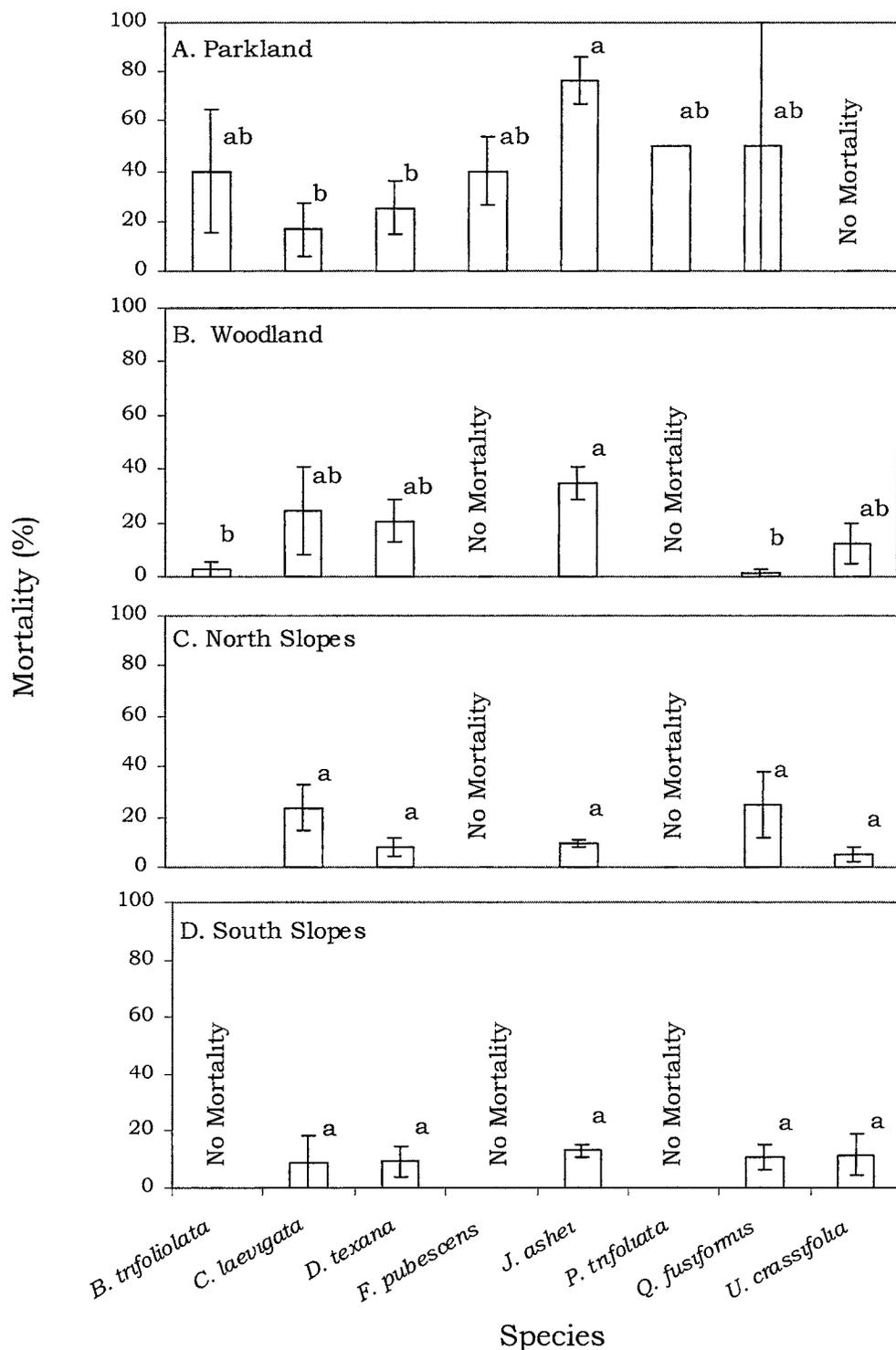


Figure 15. Percent mortalities for the species present in all four habitats separated by (A) parkland, (B) woodland, (C) north slopes, and (D) south slopes. Columns with different letters indicate significant differences as determined by Tukey's HSD test ($p < 0.05$).

C. laevigata (16.7% mortality; $p = 0.029$) and *D. texana* (25.3% mortality; $p = 0.011$)(Fig. 15A).

Significant species effects were also found within the woodland habitat ($p = 0.004$). *Juniperus ashei* had the greatest percent mortality (34.8%), which was significantly greater than that of several species. Unlike the parkland habitat, the differences were between *J. ashei* and *B. trifoliolata* (2.8% mortality; $p = 0.017$) and *Q. fusiformis* (1.5% mortality; $p = 0.008$) (Fig. 15B).

Although the lowland sloped habitats (north and south) showed lesser mortality overall than the two upland habitats, no differences were found between the species' percent mortalities within the north and south slopes (Fig. 15C,D).

Size Effects

Simple linear regression analyses of mortality data for all individuals pooled across habitats indicated that fire-induced mortality was inversely related to plant size. These regressions were significant for height and basal diameter (Fig. 16 A, B), but not canopy diameter (Fig. 16C).

Among habitats, there was variation in these size-mortality relationships. The parkland habitat showed a positive relationship between percent mortality and canopy diameter (Fig. 17C). However, mortality was consistently high with means of 100% for most size

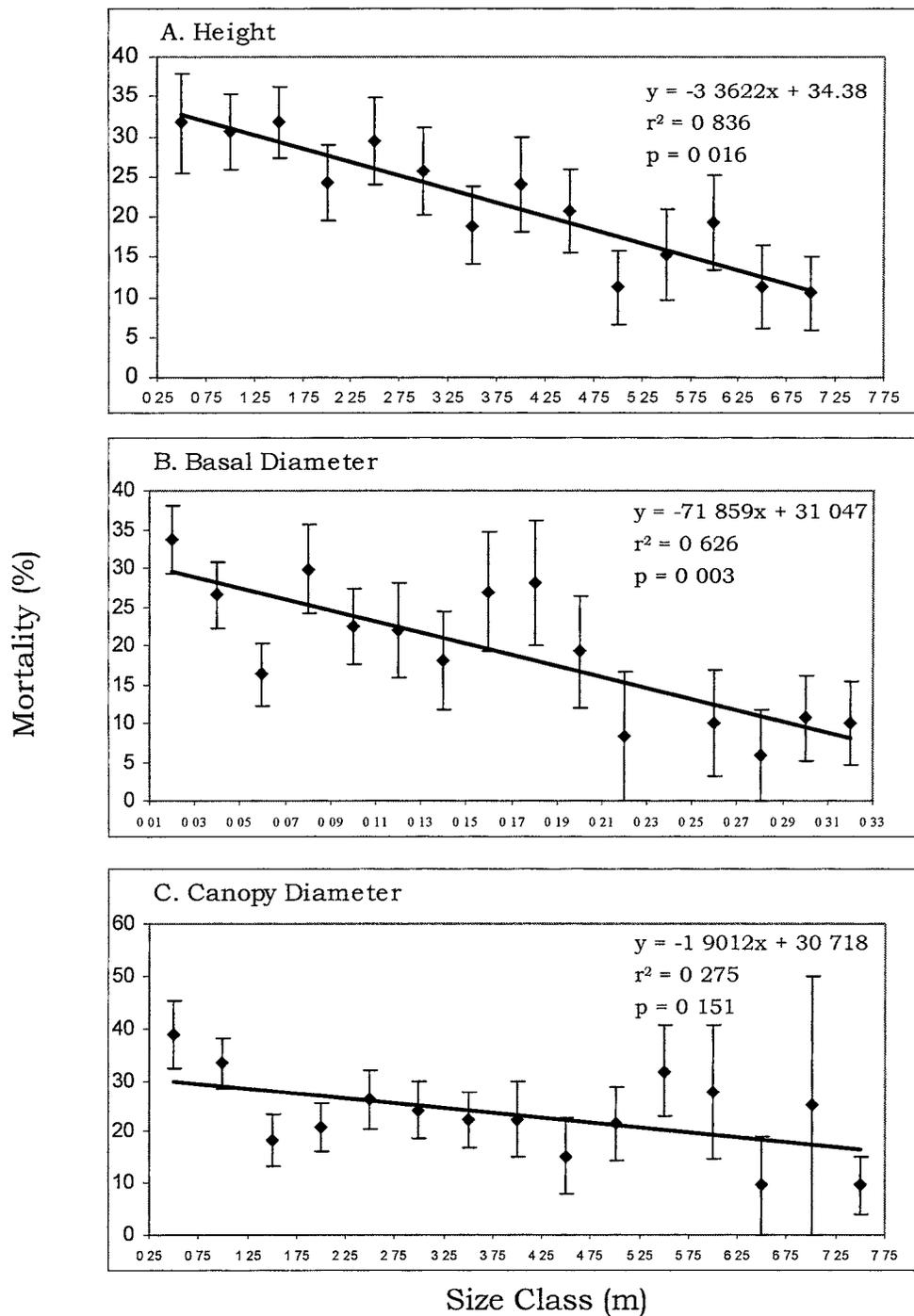


Figure 16. Regression relationships between percent mortalities for all individuals in all four habitats and (A) height, (B) basal diameter, and (C) canopy diameter. Lines indicate best-fit simple linear regression. X-axes indicate size class mid points.

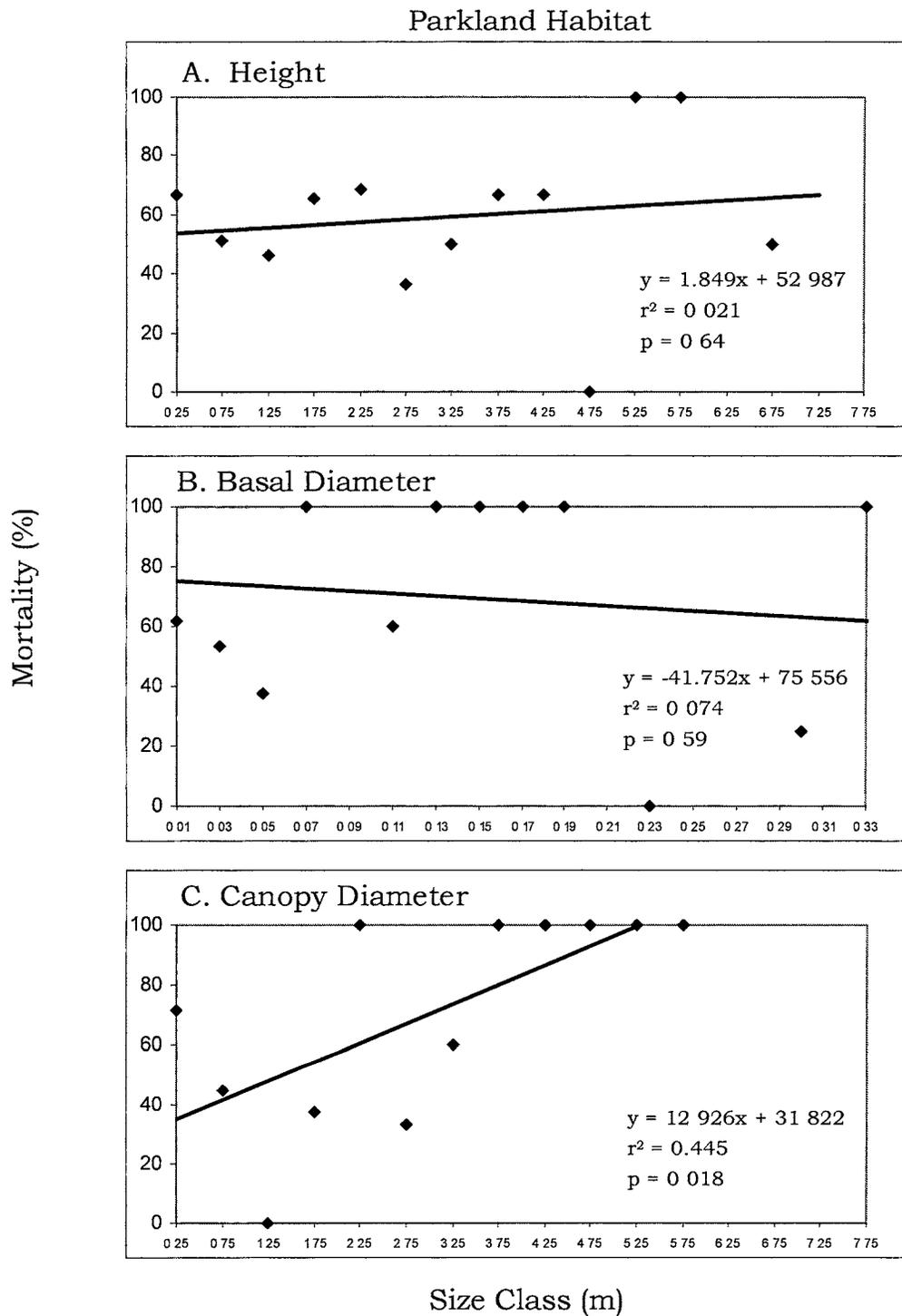


Figure 17. Regression relationships between percent mortalities for all individuals in the parkland habitat and (A) height, (B) basal diameter, and (C) canopy diameter. Lines represent the best-fit simple linear regression. X-axes indicate size class mid points.

classes. Unlike the data pooled across all habitats, significant linear relationships did not occur between percent mortality and height size classes or basal diameter size classes in the parkland habitat (Fig. 17A, B). Within the woodland habitat, percent mortality decreased with increasing size for all size variables (Fig. 18). By comparison, percent mortality showed no significant relationships with any size variables within the north slopes habitat (Fig. 19). The south slopes habitat showed significant inverse relationships between percent mortality and height and basal diameter, but not canopy diameter (Fig. 20).

With the exception of *J. ashei*, the majority of woody species showed no significant relationships between fire-induced mortality and plant size (Table 3). Regression analysis revealed significant linear relationships between all three size class variables and percent mortalities for *J. ashei* (Fig. 21). However, the relationship between basal diameter and mortality was stronger ($r^2 = 0.83$) than for height ($r^2 = 0.74$) or canopy diameter ($r^2 = 0.26$). To further elucidate these relationships, regressions were performed on a habitat basis. Mortality was significantly related to height in the woodland habitat (Fig. 22B), but not related in other habitats (Fig. 22A,C,D). Note, however, that mortality was uniformly high in the parkland habitat. Size specific mortality was also significant for the basal diameter size classes in the woodland

Woodland Habitat

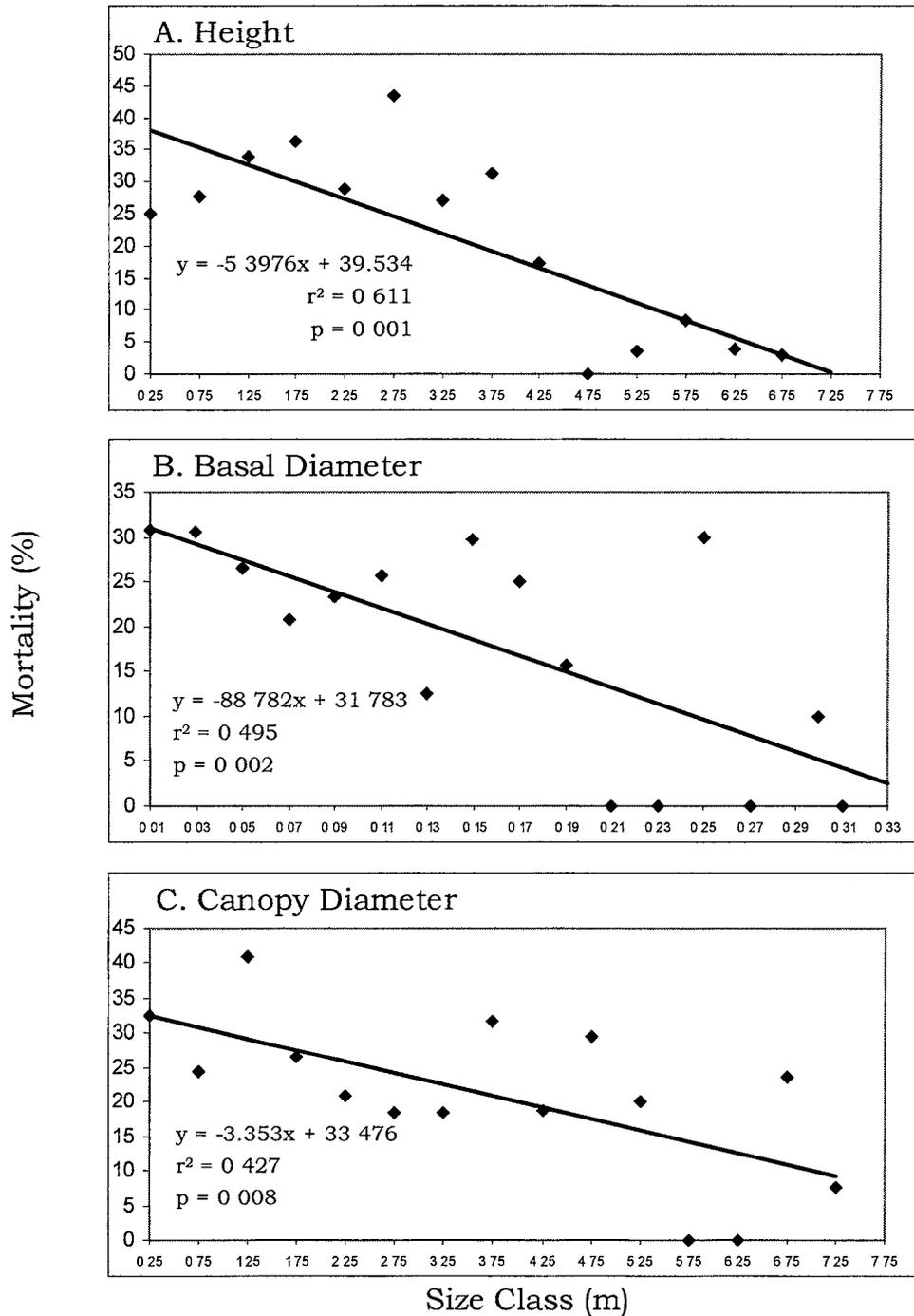


Figure 18. Regression relationships between percent mortalities for all individuals in the woodland habitat and (A) height, (B) basal diameter and (C) canopy diameter. Lines indicate the best-fit simple linear regression. X-axes indicate size class mid points.

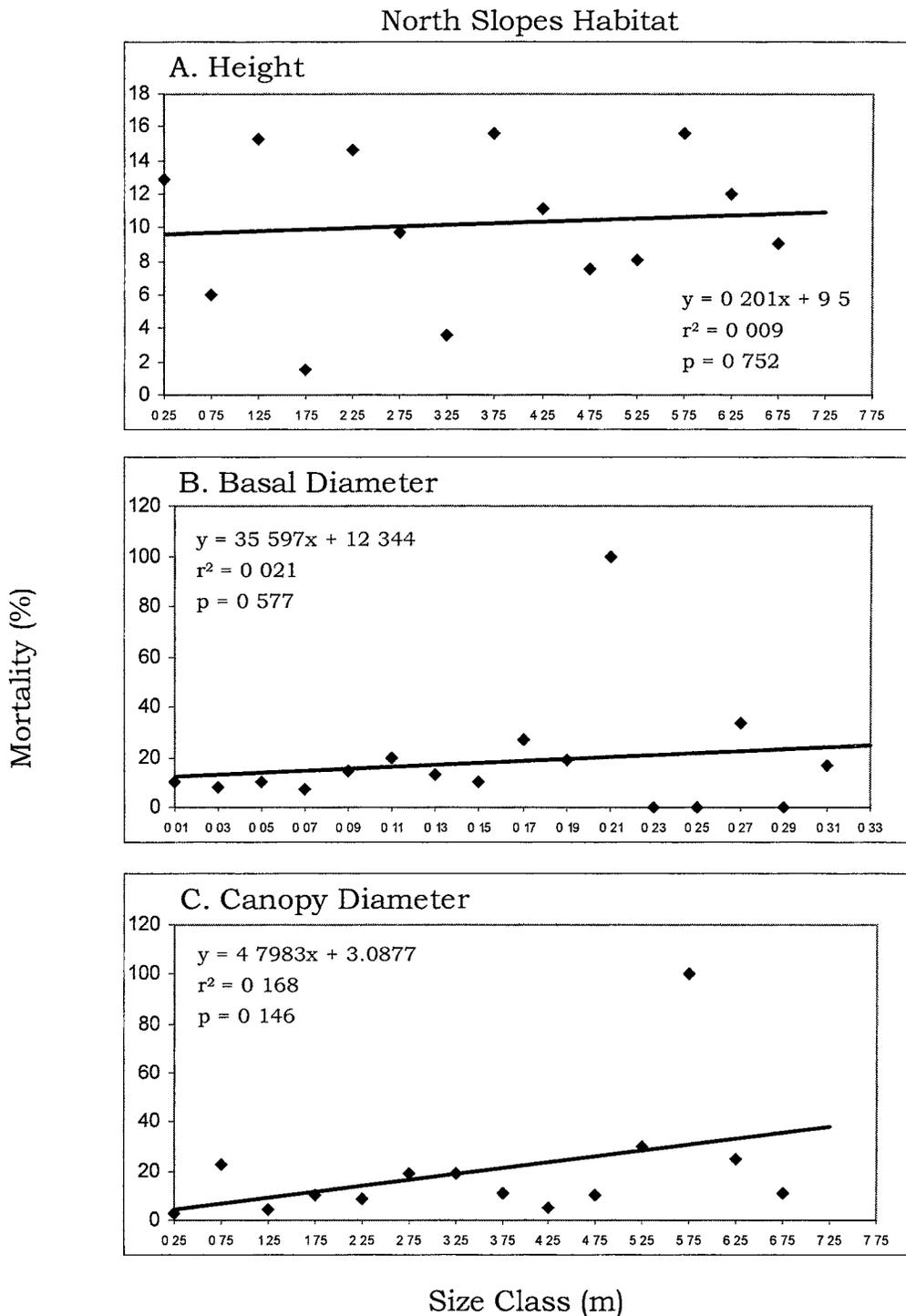


Figure 19. Regression relationships between percent mortalities for individuals in the north slopes habitat and (A) height, (B) basal diameter, and (C) canopy diameter. Lines indicate best-fit simple linear regression. X-axes indicate size class mid points.

South Slopes Habitat

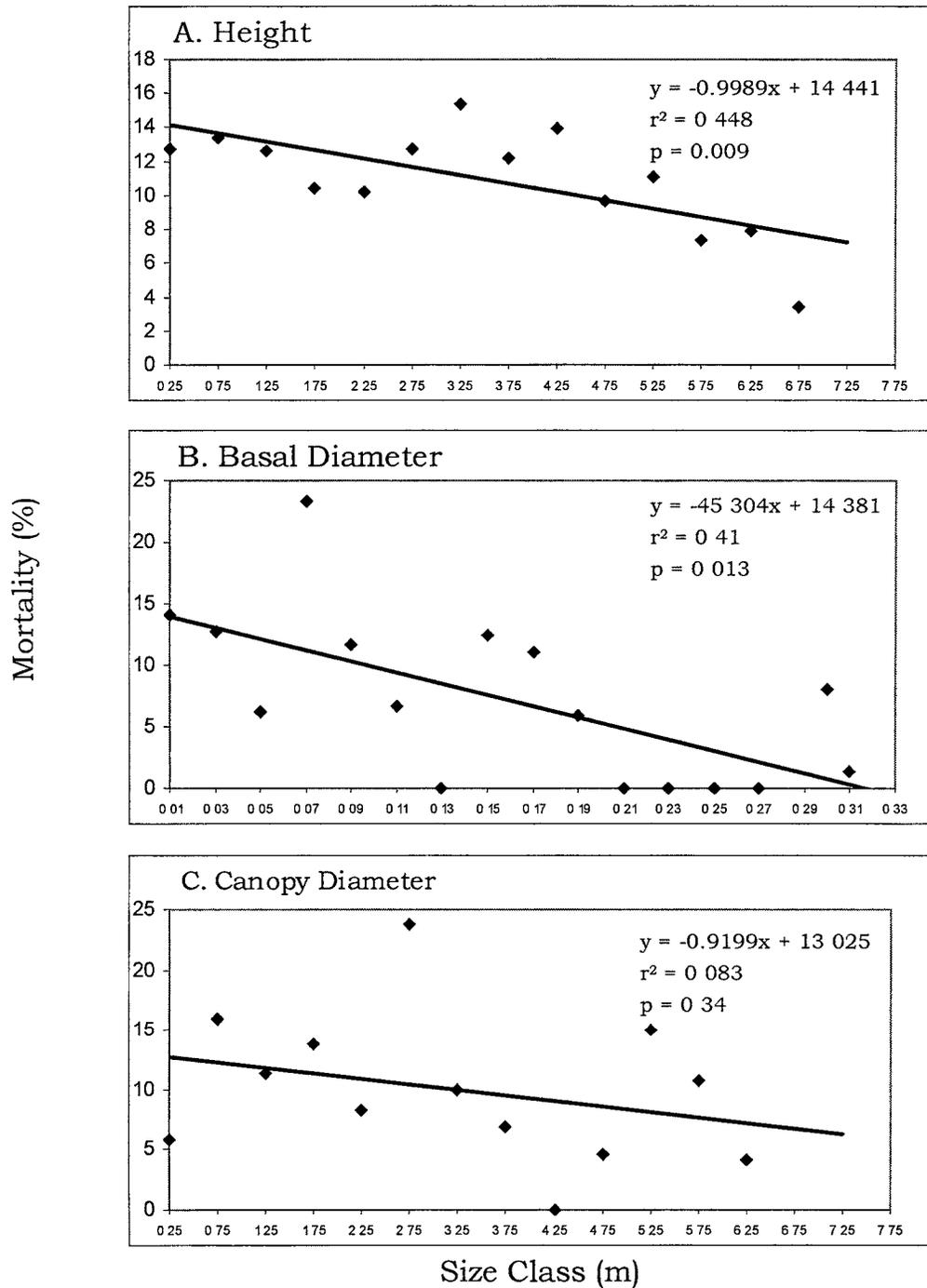


Figure 20. Regression relationships between percent mortalities for individuals in the south slopes habitat and (A) height, (B) basal diameter and (C) canopy diameter. Lines indicate best-fit simple linear regression. X-axes indicate size class mid points.

Table 3. Summary of linear regression relationships between percent mortality and size class categories for each species. “Other species” include combined sub-dominant species (*Cercis canadensis*, *Condalia hookeri*, *Eysenhardtia texana*, *Garrya ovata*, *Ilex decidua*, *Ilex vomitoria*, *Morus microphylla*, *Prosopis glandulosa*, *Ptelea trifoliata*, *Sophora affinis*, *Sophora secundiflora*, *Sideroxylon lanuginosum*, *Viburnum rufidulum*, and *Zanthoxylum hirsutum*).

Species	Height	Basal Diameter	Canopy Diameter
<i>Berbers trifoliolata</i>	NS	NS	NS
<i>Celtis laevigata var. reticulata</i>	NS	NS	NS
<i>Diospyros texana</i>	**	NS	NS
<i>Forestiera pubescens</i>	NS	NS	NS
<i>Quercus buckleyi</i>	NS	NS	NS
<i>Quercus fusiformis</i>	NS	NS	NS
Other species	NS	NS	NS
<i>Ulmus crassifolia</i>	NS	NS	NS

NS = not significant, ** $p < 0.01$

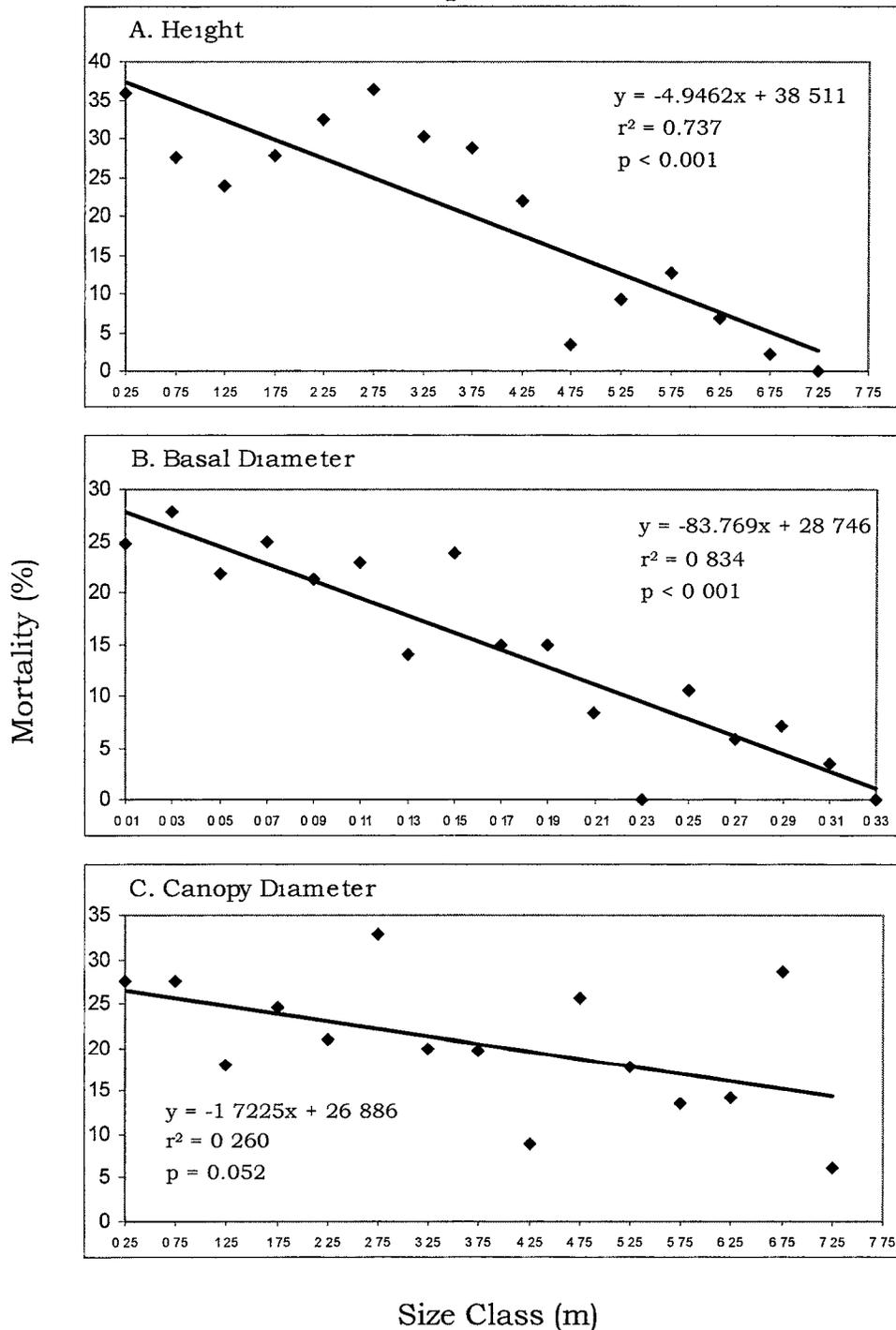
Juniperus ashei

Figure 21. Regression relationships between percent mortalities for *Juniperus ashei* and (A) height, (B) basal diameter, and (C) canopy diameter. Lines indicate best-fit simple linear regression. X-axes indicate size class mid points.

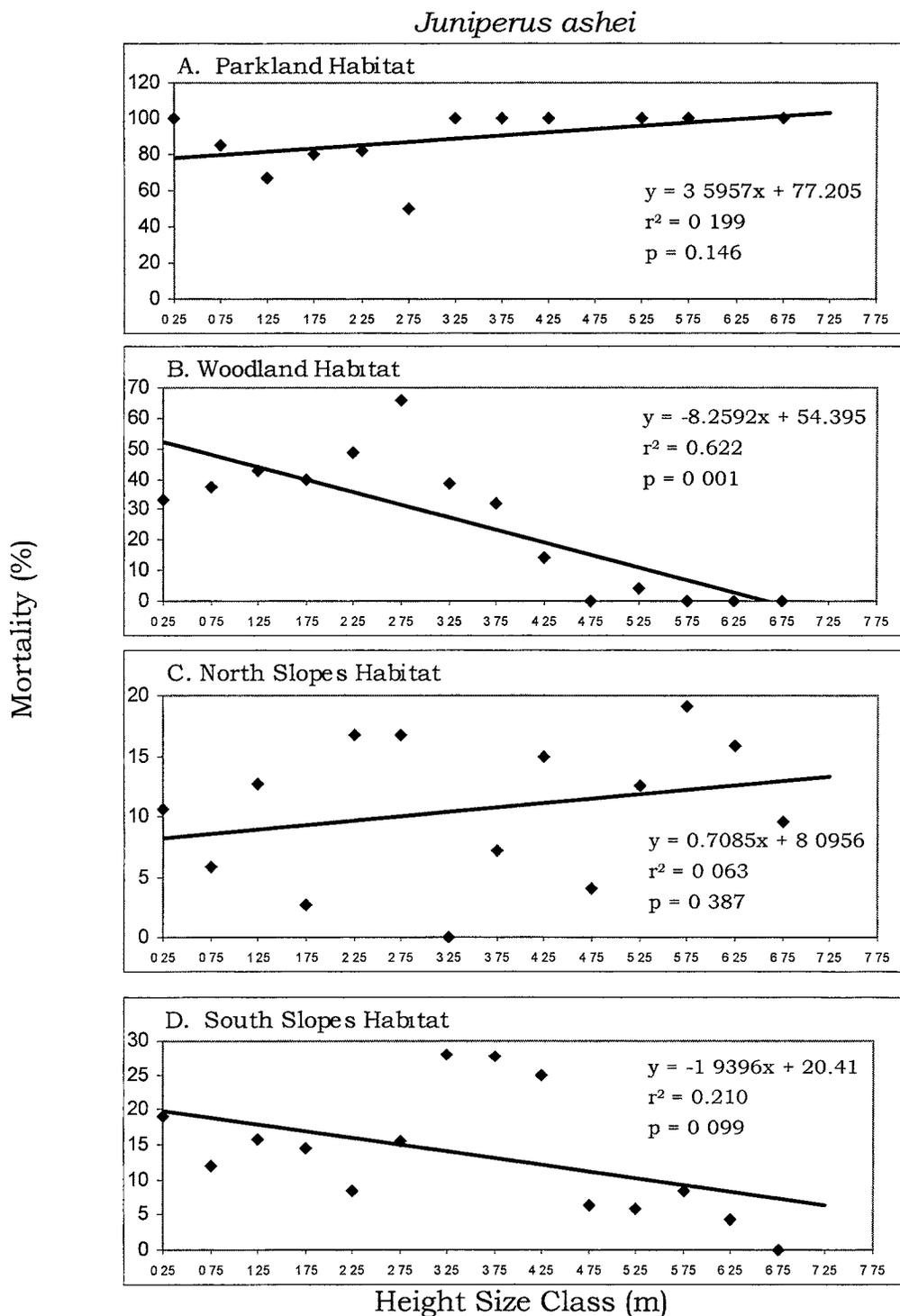


Figure 22. Regression relationships between percent mortalities of *Juniperus ashei* and height size classes for the (A) parkland habitat, (B) woodland habitat, (C) north slopes habitat, and (D) south slopes habitat. Lines represent best-fit linear regression. X-axes indicate size class mid points.

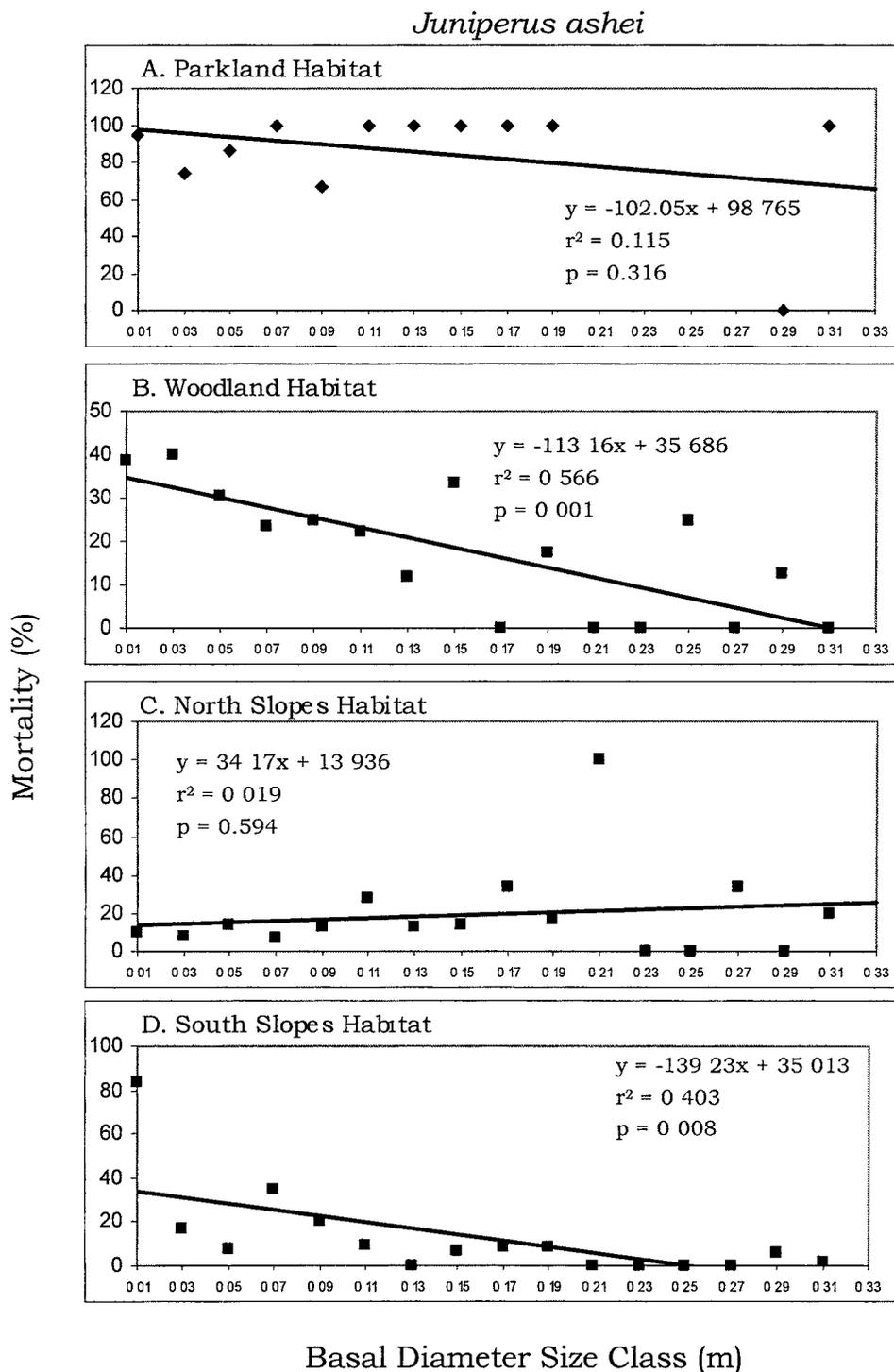


Figure 23. Regression relationships between percent mortalities of *Juniperus ashei* and basal diameter size classes for the (A) parkland habitat, (B) woodland habitat, (C) north slopes habitat, and (D) south slopes habitat. Lines represent best-fit linear regression. X-axes indicate size class mid points.

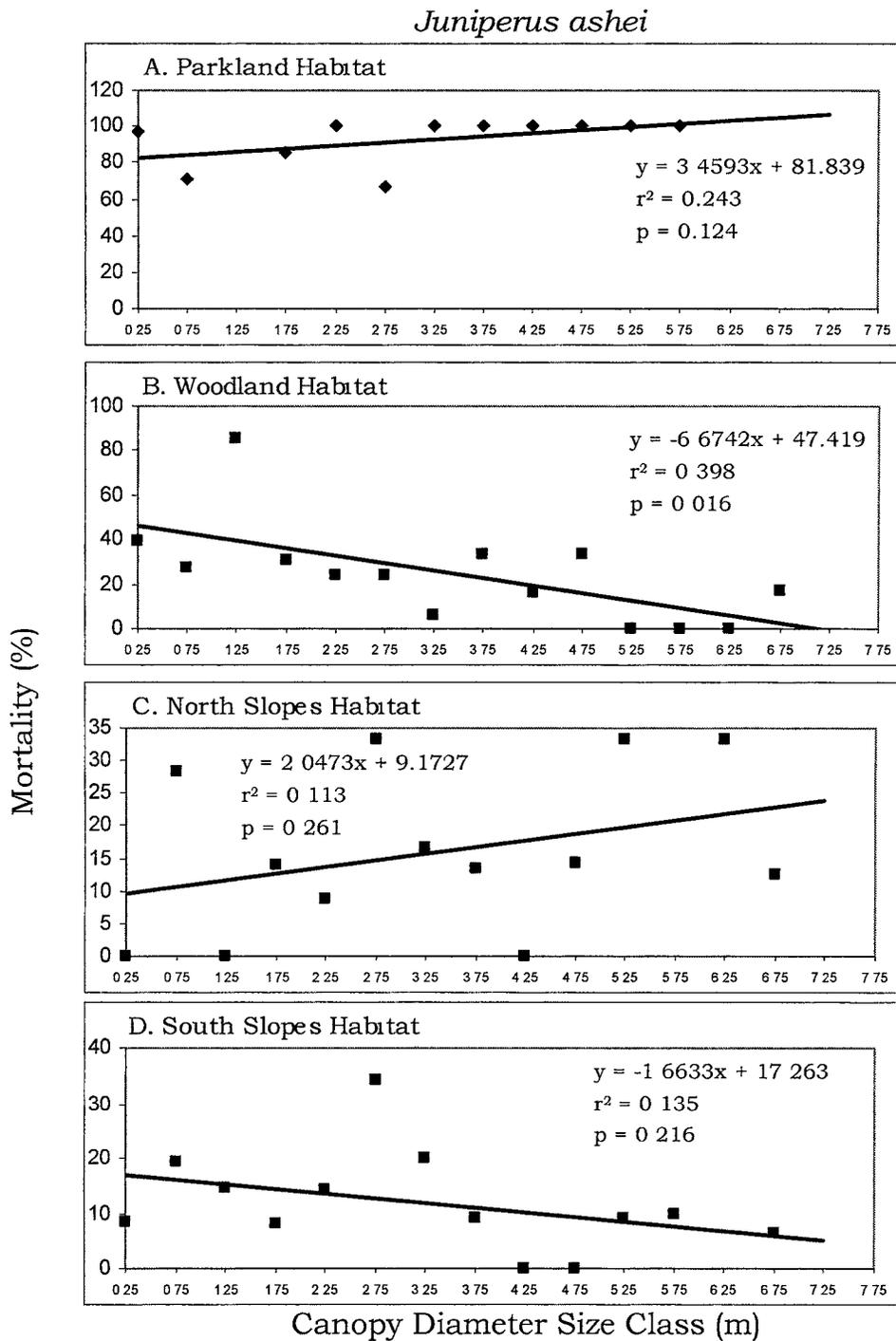


Figure 24. Regression relationships between percent mortalities of *Juniperus ashei* and canopy diameter size classes for the (A) parkland habitat, (B) woodland habitat, (C) north slopes habitat, and (D) south slopes habitat. Lines represent best-fit linear regression. X-axes indicate size class mid points.

habitat (Fig. 23B) and in the south slopes habitat (Fig.23D). A significant linear relationship also existed for canopy diameter and percent mortality within the woodland habitat (Fig. 24B). Trends were not significant for the remaining habitats, however (Fig. 24A,C,D).

Because of the general lack of size-dependent mortality for most species, the wildfire had minimal effects on size distributions (Figs. 25-28, 30) with only one exception, *J. ashei* (Fig. 29).

Noteworthy though are those size structures in regard to community structure. Two shrub species, *B. trifoliolata* and *D. texana*, had similar size class structures. For both species, few individuals were recorded in larger size classes of the three size categories (Figs. 25 and 27). Interestingly, many *C. laevigata* individuals were classified in the mid-height classes (Fig. 26A). These same individuals however, corresponded to a large number of individuals occupying the small basal and canopy diameter size classes (Fig. 26B,C). In contrast to all other species, *F. pubescens* was sparsely represented in all size class categories and suffered mortality in only the smallest size classes (Fig. 28).

Juniperus. ashei individuals were more evenly dispersed throughout height size classes than most other species (Fig. 29A). Despite their height structure, most were still within the smallest basal and canopy diameter size classes (Fig. 29B,C). Many species with low sample sizes (*C. canadensis*, *C. hookeri*, *E. texana*, *G. ovata*, *I. decidua*, *I. vomitoria*,

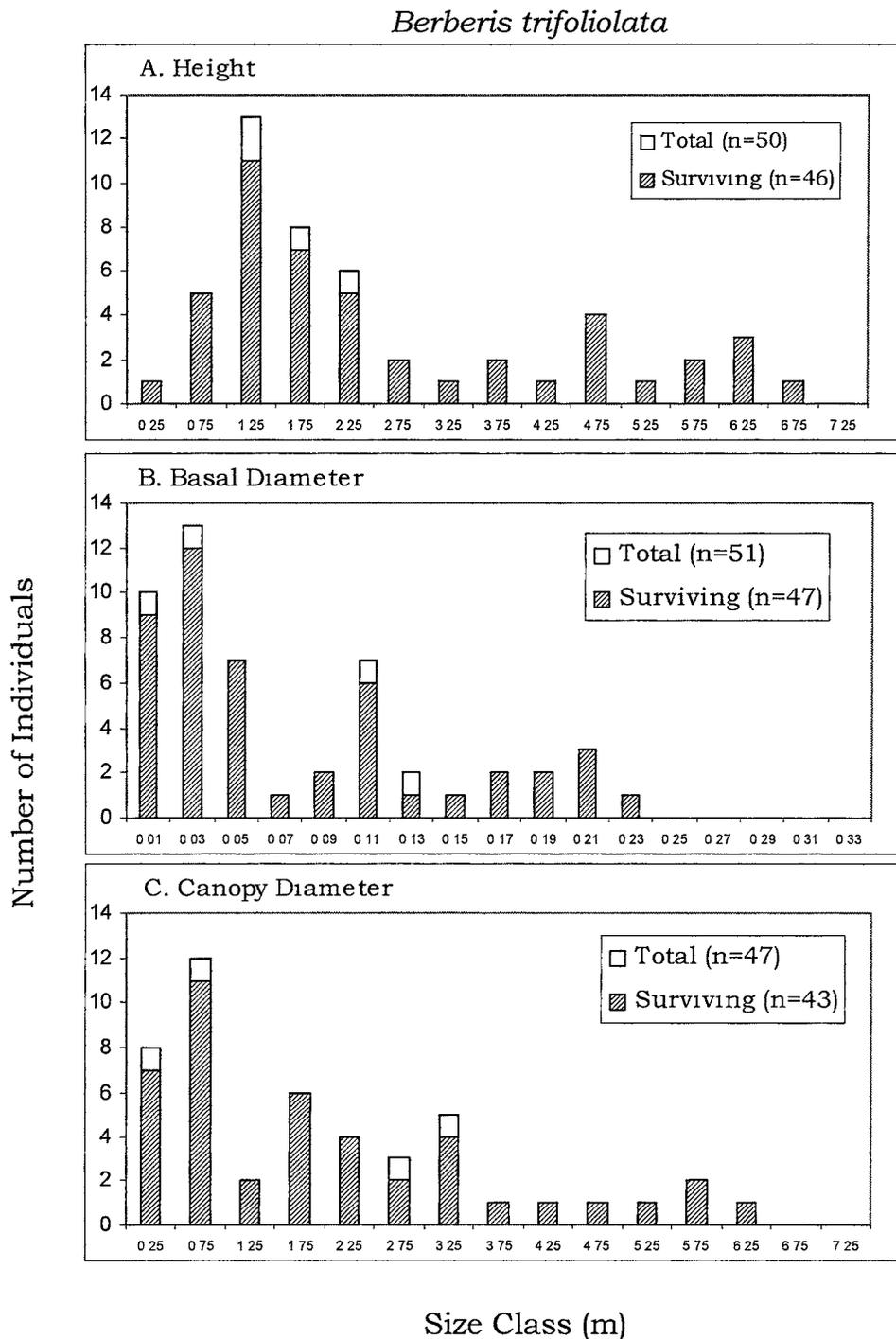


Figure 25. Number of *Berberis trifoliolata* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

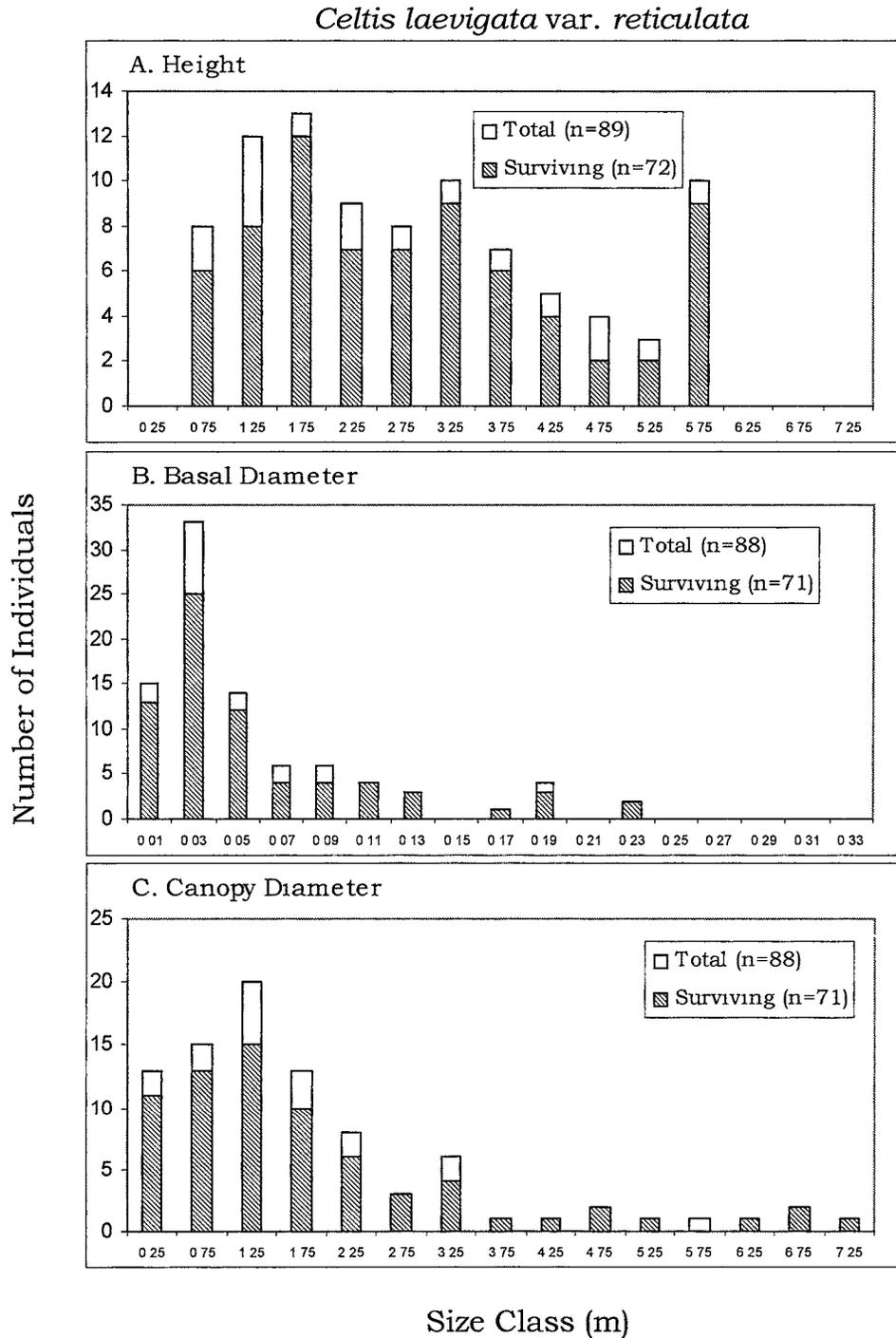


Figure 26. Number of *Celtis laevigata* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

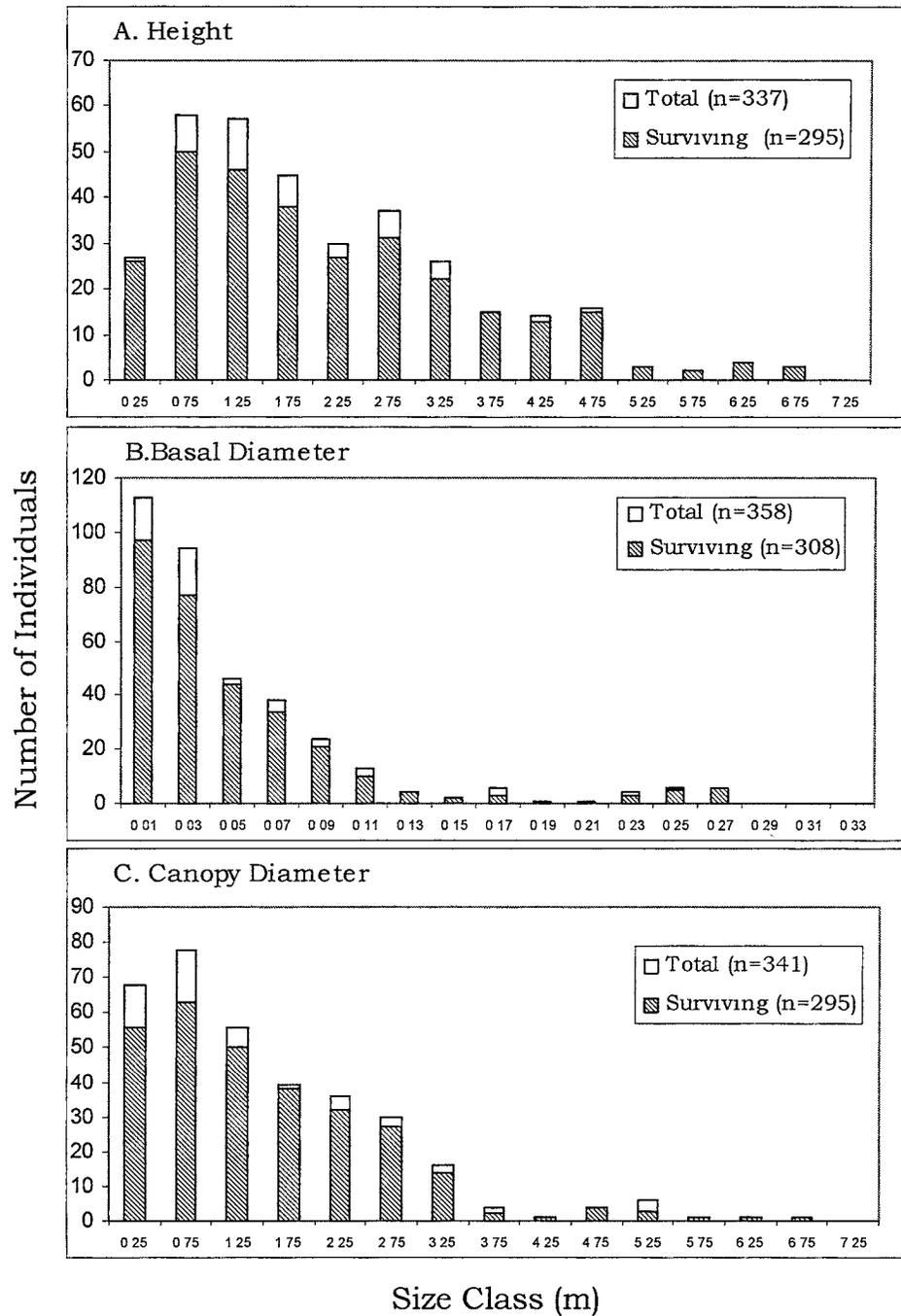
Diospyros texana

Figure 27. Number of *Diospyros texana* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

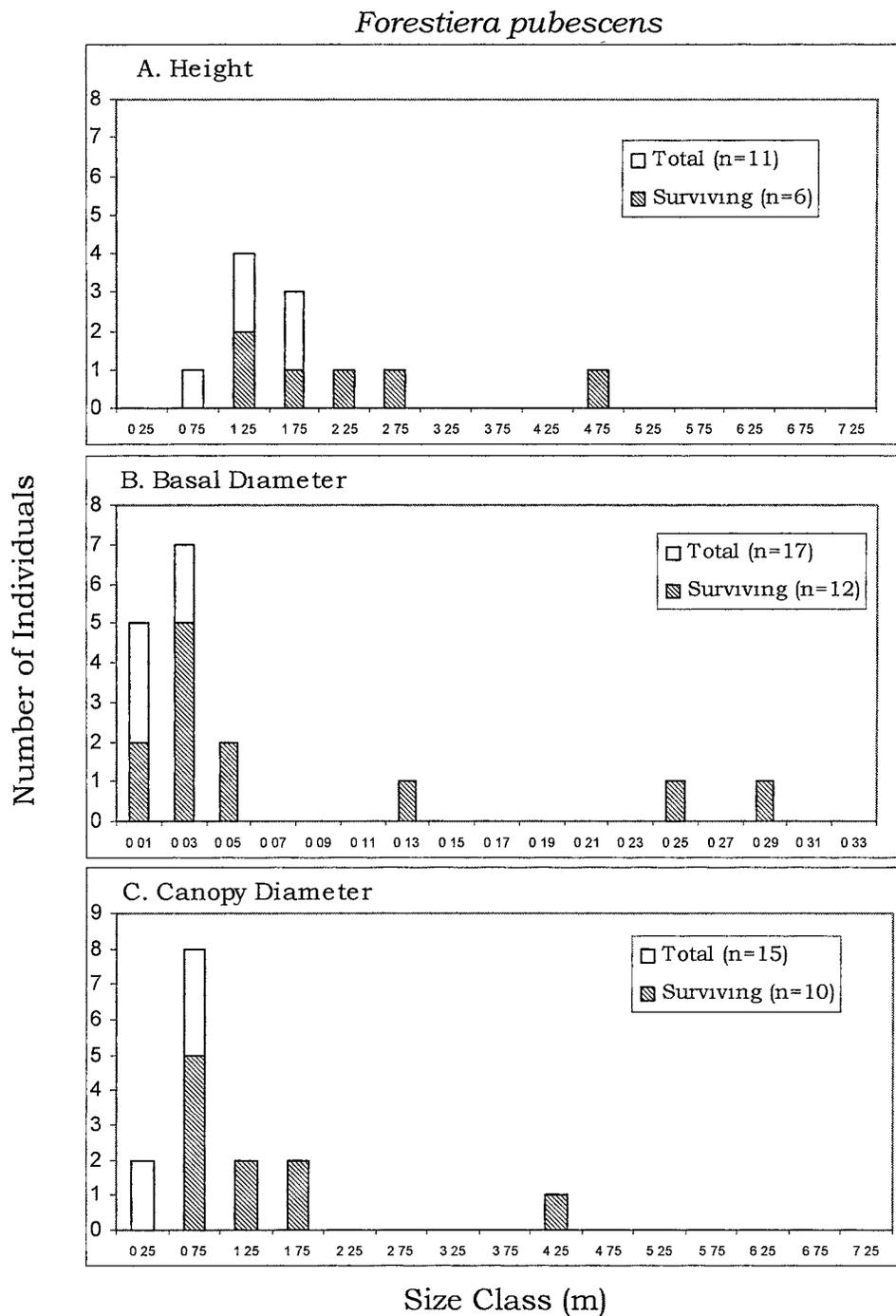


Figure 28. Number of *Forestiera pubescens* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

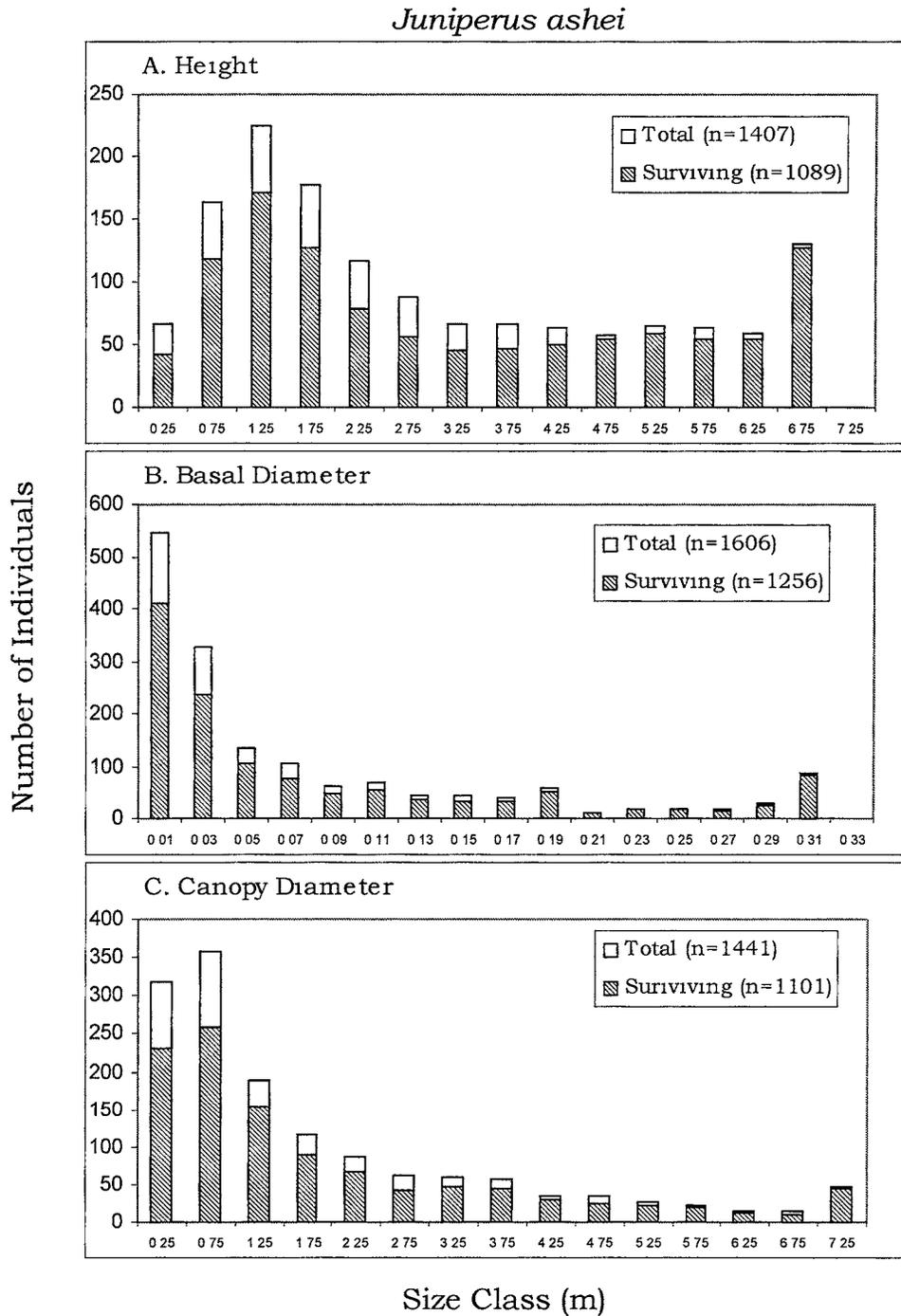


Figure 29. Number of *Juniperus ashei* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

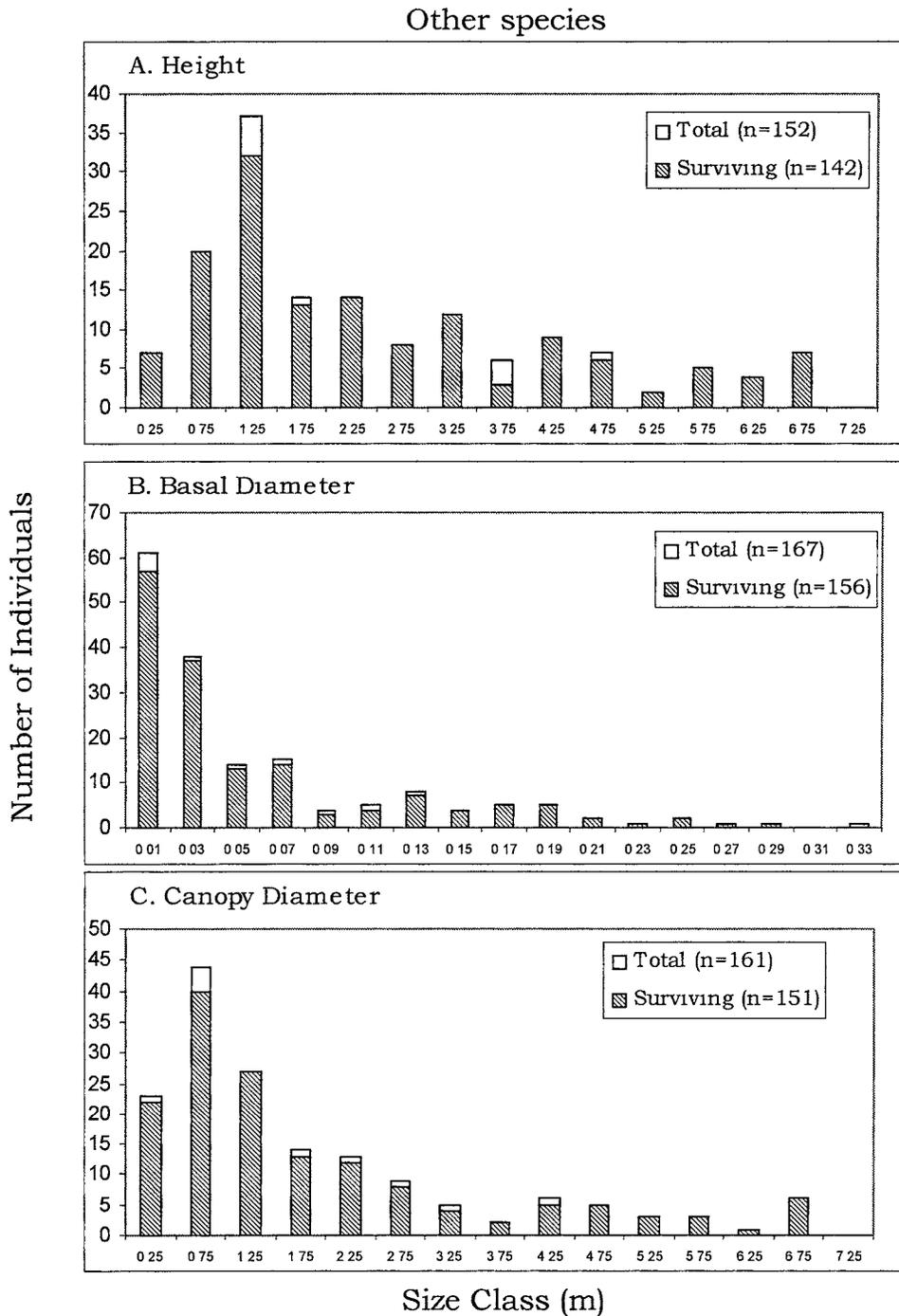


Figure 30. Number of other species (*Cercis canadensis*, *Condalia hookeri*, *Eysenhardtia texana*, *Garrya ovata*, *Ilex decidua*, *Ilex vomitoria*, *Morus microphylla*, *Prosopis glandulosa*, *Ptelea trifoliata*, *Sophora affinis*, *Sophora secundiflora*, *Sideroxylon lanuginosum*, *Viburnum rufidulum*, and *Zanthoxylum hirsutum*) alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

M. microphylla, *P. glandulosa*, *P. trifoliata*, *S. affinis*, *S. secundiflora*, *S. lanuginosum*, *V. rufidulum*, and *Z. hirsutum*) were pooled and designated, “Other Species”. Data from this combined group represented all but the largest height and canopy diameter classes, but were still disproportionately skewed toward smaller sizes (Fig. 30).

The two *Quercus* species had very dissimilar size structures. *Quercus buckleyi* had few to no individuals in larger classes while at least 30% of trees sampled were in the two smallest size classes represented for all size categories (Fig. 31). Data for *Q. fusiformis*, on the other hand, had a peak in the largest height size class (Fig. 32A) and were more evenly dispersed throughout the remaining two size classes (Fig. 32B,C). More *U. crassifolia* individuals were in mid-height classes than in the extremes of the size category (Fig. 29A). The structures of the basal and canopy diameter size profiles were, however, skewed toward the smallest classes (Fig. 33B,C).

Fire-Induced Community Consequences

Two species, *D. texana* and *J. ashei*, had the greatest relative abundances in all four habitats prior to the burn (Tables 4-7). In the parkland habitats, *J. ashei* suffered very high mortality. Consequently, this species decreased almost 73.3% in relative abundance and 82.9% in IV and thus was relegated to subdominant status after the fire (Table 4).

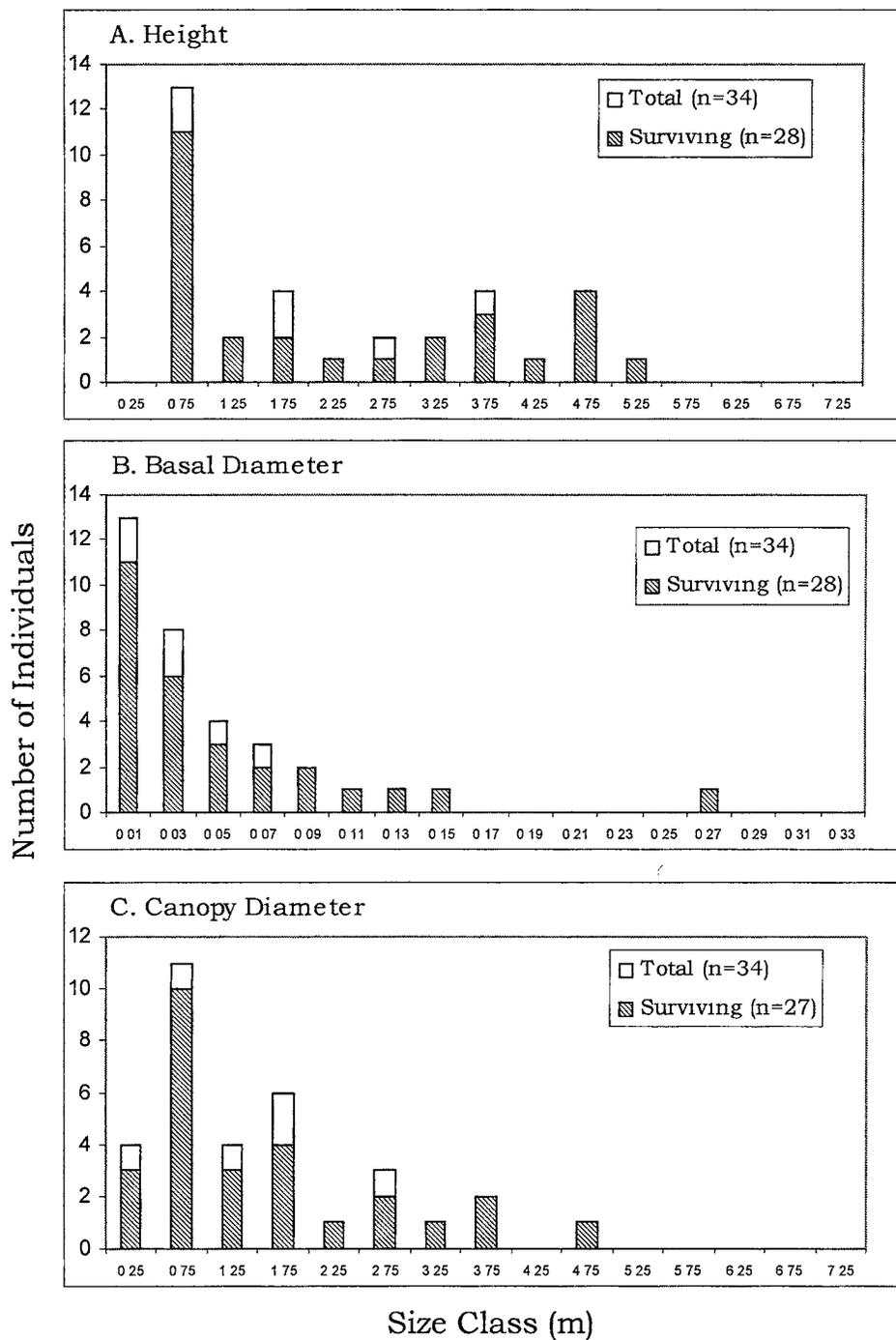
Quercus buckleyi

Figure 31. Number of *Quercus buckleyi* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

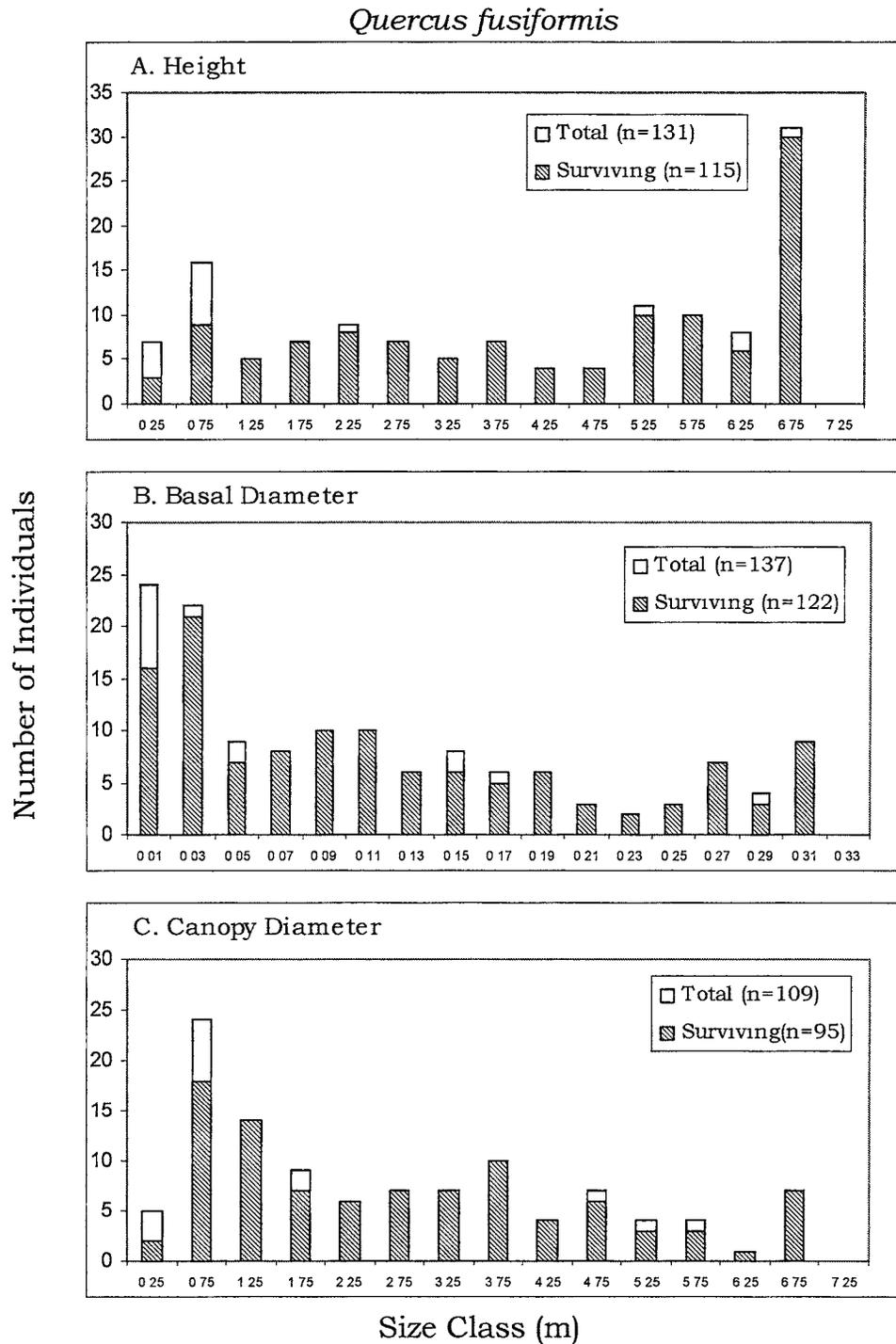


Figure 32. Number of *Quercus fusiformis* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

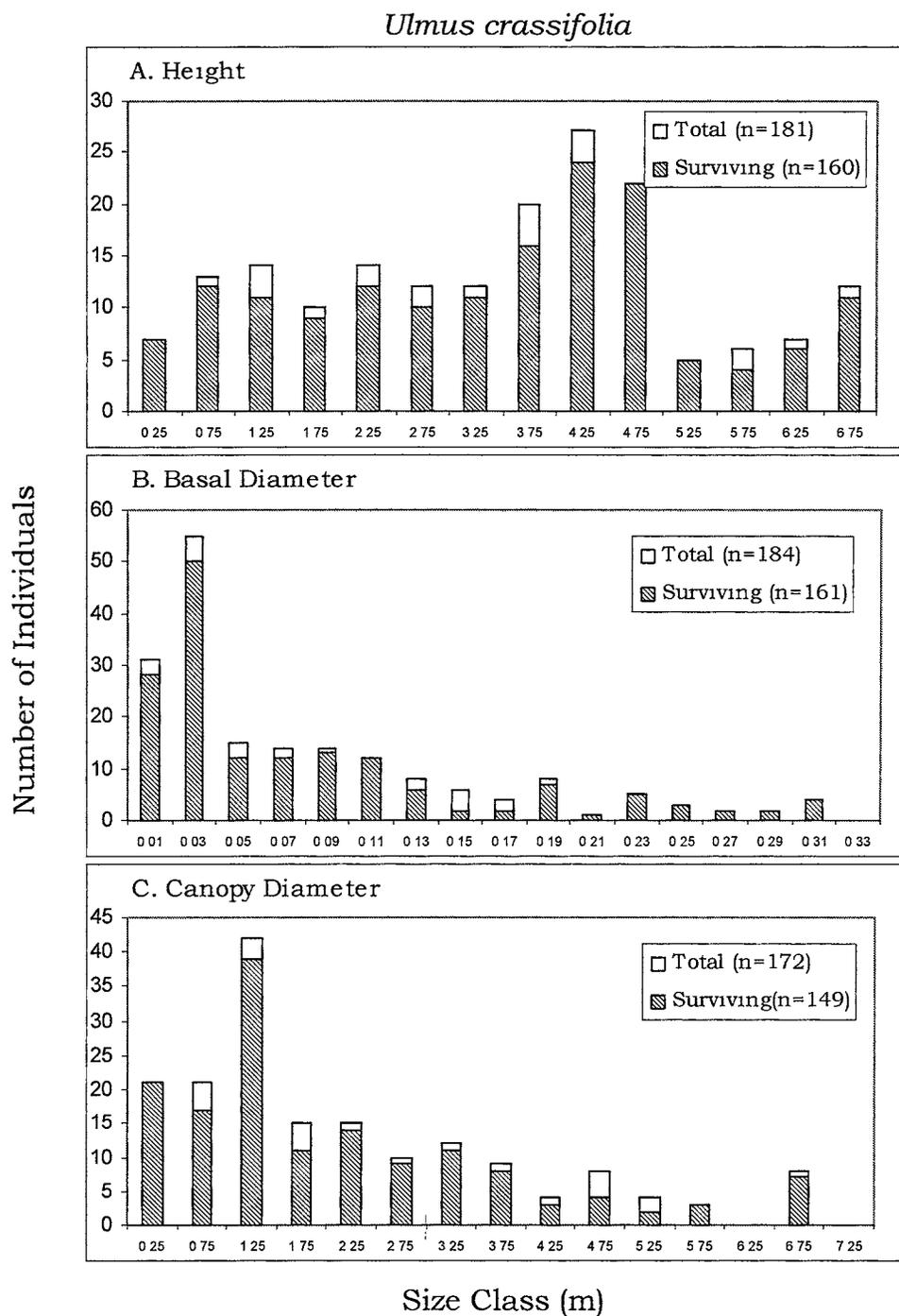


Figure 33. Number of *Ulmus crassifolia* individuals alive and dead (total) and surviving in relation to (A) height, (B) basal diameter, and (C) canopy diameter. X-axes indicate size class mid points.

Table 4. Woody species of the parkland habitat: the relative abundance (RA, %) of alive and dead individuals (prior), surviving individuals only (post), the loss/gain in RA per species, IV per species prior and post-fire, and the loss/gain IV per species. (Most to least abundant)

Species	Parkland Habitat					
	RA Prior	RA Post	% Loss/Gain	IV Prior	IV Post	% Loss/Gain
<i>Juniperus ashei</i>	46.0	12.3	-73.3	82.4	14.1	-82.9
<i>Diospyros texana</i>	25.1	43.8	74.5	30.5	46.6	52.8
<i>Ulmus crassifolia</i>	6.6	16.4	148.5	8.3	22.2	167.5
<i>Forestiera pubescens</i>	5.5	6.9	25.5	25.5	73.4	187.8
<i>Celtis laevigata</i> var. <i>reticulata</i>	4.9	8.2	67.3	5.6	9.8	75.0
Unidentifiable species	3.8	0.0	-100.0	19.4	0.0	-100.0
<i>Berberis trifoliolata</i>	3.3	5.5	66.7	3.7	6.0	62.2
<i>Ptelea trifoliata</i>	2.2	2.7	22.7	21.8	19.6	-10.1
<i>Quercus fusiformis</i>	1.6	1.4	-12.5	1.7	1.3	-23.5
<i>Prosopis glandulosa</i>	0.5	1.4	180.0	0.6	1.5	150.0
<i>Zanthoxylum hirsutum</i>	0.5	1.4	180.0	0.5	1.3	160.0

By comparison, after the fire *D. texana* and *U. crassifolia* had the greatest relative abundances (43.8% and 16.4%). Also, based on IVs, dominance drastically changed from *J. ashei* prior to the burn to *F. pubescens* (73.4 IV) after the burn (Table 4).

The most abundant species after the fire in the woodland habitat were *J. ashei* and *U. crassifolia* (68.7% RA and 7.8% RA) (Table 5). They were also the most dominant (159.3 IV and 8.4 IV). Unlike the parkland habitat, *J. ashei* increased slightly in relative abundance, while decreasing minimally in importance values. *Diospyros texana* decreased more than any other species, losing almost 68.1% in relative abundance and 61.1% IV (Table 5).

In the north slopes, *J. ashei* decreased slightly in IV (-4.4%), but still remained the most abundant (gaining 3.4%) and important species after the fire (Table 6). Although *C. laevigata* was not very abundant or dominant prior to the fire, it decreased the most in both relative abundance (-75%) and importance (-60.4%) compared to all other species recorded on the north slopes.

Similar to that for the woodlands and north slopes, *J. ashei* remained by far the most abundant (57.8% RA) and dominant (156.4 IV) species after the fire in the south slopes habitat with only a slight decrease in both relative abundance and importance values (Table 7). The only other species to decline were the two *Quercus* species. *Quercus fusiformis* and *Q. buckleyi* decreased in relative abundance (-2.9% and

Table 5. Woody species of the woodland habitat: the relative abundance (RA, %) of alive and dead individuals (prior), surviving individuals only (post), the loss/gain in RA per species, IV per species prior and post-fire, and the loss/gain IV per species. (Most to least abundant)

Species	Woodland Habitat					
	RA Prior	RA Post	% Loss/Gain	IV Prior	IV Post	% Loss/Gain
<i>Juniperus ashei</i>	65.0	68.7	5.7	162.0	159.3	-1.7
<i>Diospyros texana</i>	14.1	4.5	-68.1	14.2	4.1	-71.1
<i>Ulmus crassifolia</i>	6.0	7.8	30.0	7.3	8.4	15.1
<i>Quercus fusiformis</i>	5.1	7.3	43.1	5.3	6.8	28.3
<i>Berberis trifoliolata</i>	2.8	3.5	25.0	2.8	3.1	10.7
<i>Celtis laevigata</i> var. <i>reticulata</i>	2.6	3.1	19.2	3.9	4.1	5.1
<i>Eysenhardtia texana</i>	1.1	1.3	18.2	1.1	1.2	9.1
<i>Sideroxylon lanuginosum</i>	0.7	1.0	42.9	0.7	1.0	42.9
Unidentifiable species	0.7	0.0	-100.0	0.7	0.0	-100.0
<i>Ilex decidua</i>	0.6	0.9	50.0	0.6	0.8	36.7
<i>Quercus buckleyi</i>	0.6	0.7	16.7	0.6	0.7	16.7
<i>Forestiera pubescens</i>	0.3	0.4	33.3	0.3	0.3	0.0
<i>Sophora secundiflora</i>	0.2	0.4	100.0	0.2	0.3	65.0
<i>Ilex vomitoria</i>	0.1	0.2	100.0	0.1	0.2	100.0
<i>Ptelea trifoliata</i>	0.1	0.2	100.0	0.1	0.1	0.0

Table 6. Woody species of the north slopes habitat: the relative abundance (RA, %) of alive and dead individuals (prior), surviving individuals only (post), the loss/gain in RA per species, IV per species prior and post-fire, and the loss/gain IV per species. (Most to least abundant)

Species	North Slopes					
	RA Prior	RA Post	% Loss/Gain	IV Prior	IV Post	% Loss/Gain
<i>Juniperus ashei</i>	61.0	63.1	3.4	125.5	120.0	-4.4
<i>Diospyros texana</i>	9.0	9.1	1.1	18.2	20.4	12.1
<i>Ulmus crassifolia</i>	8.1	8.9	9.9	13.9	16.0	15.1
<i>Celtis laevigata</i> var. <i>reticulata</i>	5.6	1.4	-75.0	10.6	4.2	-60.4
<i>Quercus fusiformis</i>	4.2	4.2	0.0	4.7	4.5	-4.3
<i>Ilex vomitoria</i>	2.3	2.6	13.0	3.9	4.5	15.4
<i>Quercus buckleyi</i>	2.3	2.7	17.4	2.9	3.3	13.8
<i>Sideroxylon lanuginosum</i>	2.0	2.4	20.0	2.3	2.6	13.0
<i>Garrya ovata</i> subsp. <i>lindheimeri</i>	1.1	0.6	-45.5	1.7	0.6	-64.7
<i>Ptelea trifoliata</i>	1.1	1.3	18.2	1.4	1.5	7.1
<i>Sophora secundiflora</i>	1.1	1.3	18.2	11.3	14.2	25.7
<i>Berberis trifoliolata</i>	0.5	0.6	13.0	0.5	0.6	20.0
<i>Cercis canadensis</i>	0.4	0.5	15.0	0.4	0.5	25.0
<i>Ilex decidua</i>	0.4	0.4	0.0	0.4	0.5	25.0
<i>Morus microphylla</i>	0.3	0.3	3.3	0.5	0.5	0.0
<i>Viburnum rufidulum</i>	0.3	0.3	11.1	0.4	0.4	0.0
<i>Forestiera pubescens</i>	0.1	0.2	7.1	0.9	1.4	55.6
<i>Prosopis glandulosa</i>	0.1	0.2	42.9	0.2	0.2	0.0

Table 7. Woody species of the south slopes habitat: the relative abundance (RA, %) of alive and dead individuals (prior), surviving individuals only (post), the loss/gain in RA per species, IV per species prior and post-fire, and the loss/gain IV per species. (Most to least abundant)

Species	South Slopes					
	RA Prior	RA Post	% Loss/Gain	IV Prior	IV Post	% Loss/Gain
<i>Juniperus ashei</i>	59.8	57.8	-3.3	157.5	156.4	-0.7
<i>Diospyros texana</i>	14.3	15.4	7.7	15.1	15.3	1.3
<i>Quercus fusiformis</i>	6.8	6.6	-2.9	7.1	6.9	-2.8
<i>Ulmus crassifolia</i>	6.3	6.5	3.2	6.3	6.3	0.0
<i>Ilex vomitoria</i>	3.2	3.5	9.4	3.2	3.5	9.4
<i>Celtis laevigata</i> var. <i>reticulata</i>	1.9	2.1	10.5	1.9	2.1	10.5
<i>Berberis trifoliolata</i>	1.8	2.1	16.7	2.9	3.2	10.3
<i>Quercus buckleyi</i>	1.3	0.8	-35.4	1.3	0.8	-38.5
<i>Ptelea trifoliata</i>	1.2	1.3	8.3	1.2	1.3	8.3
<i>Ilex decidua</i>	0.9	1.0	6.7	0.9	1.0	11.1
<i>Sideroxylon lanuginosum</i>	0.6	0.7	20.0	0.7	0.7	0.0
<i>Sophora secundiflora</i>	0.5	0.6	11.1	0.5	0.6	20.0
<i>Condalia hookeri</i>	0.4	0.5	25.0	0.4	3.5	775.0
<i>Diospyros texana</i>	0.4	0.5	25.0	0.4	0.5	25.0
<i>Prosopis glandulosa</i>	0.3	0.4	20.0	0.3	0.4	33.3
<i>Sophora affinis</i>	0.1	0.1	9.1	0.1	0.1	0.0
<i>Viburnum rufidulum</i>	0.1	0.1	20.0	0.1	0.1	0.0

-35.4%, respectively) and by similar magnitudes in importance values (-2.9% and -38.5%)(Table 7). All other species, as in the north slopes, gained minimally in both relative abundance and importance values.

Woody plant densities decreased in each habitat after the fire (4.0-42.0 plants/ha post). This change was most severe for the parkland habitat wherein the density decreased by more than 50% (from 0.9 to 0.4 plants/ha) (Table 2). Plant density in the woodlands decreased by more than 10% and in both lowland habitats by five or less percent.

Diversity indices changed only slightly after the fire in the upland parklands and woodlands (1.8 to 1.7, parklands; 0.8 to 0.7, woodlands), and remained the same prior to and after the fire in each respective sloped habitat (Table 2). Interestingly, the diversity index values were very similar for the woodland and south slopes habitats both prior to and after the fire. And, although approximately twice as diverse as the other two habitats, the parklands and north slopes had similar indices before and after the fire, as well (Table 2).

Dominance indices remained similar to pre-fire levels in all four habitats (Table 2). The parklands continued to have the lowest dominance index, while the woodlands and south slopes had similar and highly concentrated dominance values after the fire. The woodlands remained at an intermediate dominance level, changing very little after the fire (Table 2).

DISCUSSION

Changes in Community Structure

Species composition of the woody plant communities varied among habitat types prior to the summer fire, presumably because of characteristics of each habitat contributing to the success of certain species. Moisture availability gradients are important influences on density, dominance and woody species composition within different habitats (Adams and Anderson 1980). On the Edwards Plateau, evergreen species tend to be more abundant in more xeric uplands or on exposed south facing slopes (Van Auken et al. 1981). Carson (2000) stated that the moisture storage capacity of the Comfort soil complex, found in sloping areas, rock outcrops and drainageways of Freeman Ranch, is limited by the lack of depth and stony content. Numbers of deciduous species (species richness) should be greater in areas of high soil moisture, such as lowlands and north facing slopes (Barnes et al. 2000). Since evergreen species dominated the upland woodlands, dry south slopes and moist north slopes, I concur with Van Auken et al. (1981), and propose that the microclimate of north slopes is conducive to both evergreen and deciduous species. Van Auken et al. (1981) further

stated that the species composition of deciduous communities is changing and may eventually be completely dominated by the evergreen species *J. ashei* and *D. texana* (facultative).

Size class structures across all habitats and including all individuals, thus representing pre-fire conditions, suggest that steady recruitment of most species was occurring and that populations were expanding in all habitats. Size classes were more evenly distributed within the woodland, north slopes and south slopes habitats, while the parkland habitat had a higher ratio of small to large individuals. This may be indicative of a more recent increase in woody species in this habitat.

In all habitats, fire moderately altered size class structures. The parkland and, to a lesser extent, woodland lost more small sized individuals, and thus, the community became less skewed toward smaller individuals. Proportionately the sloped habitats did not lose a greater ratio of small to large individuals. This could result from habitat characteristics. The community structure that develops after a fire may be related to microhabitat variations in fire temperatures (Fonteyn et al. 1988). In this study, mortality was greater, although not significantly, in the upland woodlands than in the north slopes. Moisture availability is greater on north slope, deciduous forests than in evergreen woodlands (Van Auken 1988) because of reduced solar radiation and lower

temperatures. These microclimate differences may have contributed to decreased fire intensity and therefore reduced mortality in the north slope habitats.

In general, woody plants are more likely to perish from fire if large volumes of dry grass fuels surround them (i.e., in grasslands) (Hochberg et al. 1994). By comparison, tree-dominated habitats that suppress grasses tend to be more fire resistant due to the reduction in fire intensity. Hochberg et al. (1994) also stated that fire will maintain clusters of trees by preferentially burning young plants isolated from the clusters, consequently reinforcing clusters and halting the spread of trees. The differences in fuel load and moisture that occur from grasslands to woody clusters will cause declines in fire energy, and thus, fire temperatures. For example, Fonteyn et al. (1984) demonstrated that as fire burns from areas of grassland into overstory canopies, fire temperatures and intensities decline. These variations in fire characteristics could have facilitated woody plant mortality in the parkland habitat, which did suffer the highest mortality.

A reduction in the abundance and density of woody species was expected, since extreme summer fires cause extensive damage to woody individuals (Fuhlendorf et al. 1996). However, with increasing woody plant density, there was a significant, although weak ($r^2 = 0.092$) decrease in mortality, possibly directly related to the decrease in grassy

fuels accompanying the transition between grassland to wooded areas (Hopkins 1965). Likewise, Hochberg et al. (1994) found that fire had a halting effect on the spread of trees in systems with low density. In cases of high densities, it may be necessary to conduct follow-up high intensity fires to ensure that fire is carried throughout these wooded areas (Hodgkinson 1991).

Influences of Habitat, Size and Species on the Effects of Fire

Results showed that mortality, when pooled across all species and habitats, was related to size of the individual, specifically height and basal diameter. Shifts in size distributions may have large effects on the physical structure of vegetation (Hoffmann 1999). Greater mortality in smaller size classes of woody species has been documented in many studies (Fonteyn et al. 1988; Hochberg et al. 1994; Crow et al. 1994; Barton 1999; Hoffmann 1999). The effects of burning in Florida pine savannas varied with tree size, as smaller trees were more vulnerable to fire than larger individuals (Glitzenstein et al. 1995). Jameson (1962) showed an exponential decrease in mortality with increasing size, while this study showed a linear decrease in tree mortality with increasing height. Two explanations may support this common result. First, smaller individuals' apical buds may be within zones of high flame temperatures and therefore damaged, and second, their thinner bark

may provide less protection to the underlying cambium tissues (Hopkins 1965). Hodgkinson (1998) reported that survival and bark thickness increased with height, and diminished damage has been attributed to growth in stem diameter and bark thickness (Cutter and Guyette 1994).

The effects of fires on Ashe junipers depend to a large extent on the size of the trees, with younger individuals more severely affected than older, larger trees. Burkhardt and Tisdale (1976) found that mortality from fire was higher among Ashe juniper seedlings and saplings. Jackson and Van Auken (1997) also reported significant strong linear trends ($r^2 = 0.95$) between basal diameter and Ashe juniper mortality. Likewise, observed mortalities of Ashe junipers in this study were significantly inversely related to height ($r^2 = 0.74$) and basal diameter ($r^2 = 0.83$). McPherson et al. (1988) found that Ashe juniper age was correlated with height. If so, this wildfire effectively eliminated younger Ashe junipers that had recently become established. Consequently, hot summer fires could be used to manage Ashe juniper and restrict their distribution to canyons and ravines, where most individuals are older and have grown into more fire-resistant size classes.

Although detrimental to the dominant Ashe juniper, fire may grant less invasive savanna species, such as plateau live oak (*Q. fusiformis*), an advantage. Because of extended periods without fire, overstory and understory canopies have become crowded, thus influencing seedling

germination to the advantage or detriment of woody species competing for growth space and resources. Higher seedling densities of Ashe juniper found under mature *J. ashei* and *Q. fusiformis* canopies suggest that seedlings have acclimated to low light levels and low temperatures (Jackson and Van Auken 1997). These microclimate characteristics, specifically attenuation of light from above canopy levels to the ground surface, may contribute to the poor recruitment of *Q. fusiformis* into adult size classes. A shortage of *Quercus* species saplings and small adults and a lack of recruitment into the population seem common in the eastern Edwards Plateau (Van Auken 1993; Russell and Fowler 1999). In this study, as well, few *Q. fusiformis* individuals were noted in the smaller size classes, suggesting a lack of recently established juveniles. With a decrease in smaller understory Ashe junipers, opportunities may arise for juvenile oak trees to succeed into larger size classes.

There are differential effects of fire on species structure and composition for savanna vegetation (Russell-Smith et al. 1998). For instance, deciduous hardwoods, such as *Q. buckleyi* and *Q. fusiformis* (usually considered an evergreen) are most vulnerable to spring fires, occurring shortly after leaf expansion, while true evergreens (those whose leaves do not abscise) are susceptible to late summer or early autumn fires (Glitzenstein et al. 1995). Thus, depending upon the fire regime, some woody plant growth forms may decline while others may become

more abundant (Hoffmann 1999). The results of this study showed that the percent mortalities of many of the deciduous species inventoried (*C. laevigata* var. *reticulata*, *D. texana* (facultative), *F. pubescens*, *I. decidua*, *Q. buckleyi*, and *U. crassifolia*) were significantly less than that of the dominant evergreen species, *J. ashei*. Although *G. ovata*, an evergreen shrub, actually suffered the highest mortality (72.0 ± 29.0), it was not significantly greater than any other species inventoried due to small sample size ($n = 8$) and inflated standard errors. In congruence with this particular study, Fonteyn et al. (1988) found that the effect of fire on community structure is indeed determined by the species-specific responses of the vegetation. Dwyer and Pieper (1969) hypothesized that Ashe junipers were more susceptible to fire due to the architecture of the canopy. This study, however, showed only a weak relationship between canopy diameter and Ashe juniper mortality and no relationship between any other species' mortality and canopy diameter.

Conclusions

Changes in the plant community can be predicted with knowledge of the fire regime (Hodgkinson 1998). In communities modified by cool season fires, woody plant clusters coalesce and become more prevalent in grasslands (Archer 1989), while severe warm season fire regimes cause even larger arborescent species to die (Fonteyn et al. 1988). From a

restorative point of view, it may be possible to restore parklands to their historic low abundances and densities of woody species. Areas in South Africa returned to a dominant grassland growth form under frequent and intense fire regimes (Russell-Smith 1998). Previously, it was hypothesized that a summer fire would burn uniformly, thus eliminating safe sites for woody individuals (Fonteyn et al. 1988). Results of this study, however show that thresholds seem to exist that limit the efficacy of hot summer fires in restoring savannas to pre-settlement conditions. Smeins et al. (1976) concluded that woody species of the Edwards Plateau, upon establishing, increase to a point of stabilization under protection from disturbance. Similar results have been found stating that annual fires can constrain but not eliminate shrub expansion (Heisler et al. 2003). Therefore, further study may be necessary to elucidate whether fire intensity or frequency is the more important factor in reducing woody plant encroachment. After a single fire, communities have persisted with only minimal variation in the abundance of principal woody species (Boo et al. 1997). Roques et al. (2001), found that an inverse relationship existed between shrub encroachment and fire frequency, and increased shrub density was associated with augmented fire return intervals in African savannas. Fire severity, however was acknowledged as the most significant ecologically modifying force of a fire regime (Wang 2002). This was supported by the assumption that

summer fire intensities have the capability to effectively reduce woody plant abundance regardless of size (Fonteyn et al. 1988). Cutter and Guyette (1994) combined both theories and stated that understanding the frequency and intensity of fire was vital in efforts to reconstruct pre-settlement vegetative mosaics. Thus, a combination of frequent fire and high fire intensity may be the key to long-term reduction of woody plants in savannas of central Texas.

APPENDIX A

Table of UTM (Universal Transmercator) Coordinates recorded at the northeast corner of each quadrat sampled per habitat.

Habitat	Easting	Northing
North Slope	596768	3312334
North Slope	597576	3312755
North Slope	597622	3312433
North Slope	597634	3312431
North Slope	597655	3312419
North Slope	597760	3312415
North Slope	597783	3312408
North Slope	597820	3312405
North Slope	597854	3312411
North Slope	597847	3312408
North Slope	597868	3312397
North Slope	597916	3312386
North Slope	597935	3312397
North Slope	597957	3312389
North Slope	597960	3312390
North Slope	597980	3312381
North Slope	598027	3312352
North Slope	598027	3312317
North Slope	596500	3313087
North Slope	596452	3312934
Parkland	596420	3312977
Parkland	596194	3312506
Parkland	596185	3312543
Parkland	596181	3312576
Parkland	596184	3312633
Parkland	596152	3312708
Parkland	596475	3313098
Parkland	596308	3312903

Appendix A cont.

Parkland	596422	3312225
Parkland	596533	3312342
Parkland	596551	3312413
Parkland	596611	3312532
Parkland	596638	3312527
Parkland	596633	3311973
Parkland	596670	3311958
Parkland	597445	3313151
Parkland	597742	3312561
Parkland	597706	3312575
Parkland	597665	3312592
Parkland	596260	3312711
South Slope	597555	3312830
South Slope	597535	3312786
South Slope	597813	3312448
South Slope	597766	3312443
South Slope	597712	3312453
South Slope	597858	3312429
South Slope	597870	3312429
South Slope	597887	3312433
South Slope	597918	3312435
South Slope	597947	3312441
South Slope	597964	3312438
South Slope	597984	3312426
South Slope	598019	3312419
South Slope	598026	3312413
South Slope	598044	3312546
South Slope	598017	3312525
South Slope	597581	3312493
South Slope	598110	3312593
South Slope	598094	3312586
South Slope	598071	3312571
Woodland	596718	3312595
Woodland	596744	3312522
Woodland	596681	3312444
Woodland	596705	3312495
Woodland	596736	3312634
Woodland	596638	3312527

Appendix A cont.

Woodland	596756	3312323
Woodland	596669	3312027
Woodland	596745	3312002
Woodland	596598	3311992
Woodland	596982	3311875
Woodland	597531	3312715
Woodland	597513	3312706
Woodland	597893	3312398
Woodland	597908	3312397
Woodland	596202	3312659
Woodland	596269	3312694
Woodland	596098	3312706
Woodland	597598	3312952
Woodland	597619	3312831

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VITA

Kristine Elliott nee Biermann, was born on a blustery 4th of March 1978 in Fredericksburg, Texas, and grew up in the charming town of Comfort, Texas. In 1996 she graduated with her 51 fellow classmates from Comfort High School. The following autumn of that year she made her way to Southwest Texas State University, where four...and a half... years later she graduated with a Bachelor's Degree of Science in Biology. After a whirlwind year, including an April wedding to sweetheart, Bryan Elliott, purchasing a home in Canyon Lake and moving with 5 dogs, she began graduate school. During her graduate career she was employed as an instructional assistant for Human Anatomy and Physiology and Plant Ecology labs, as well as a graduate research assistant for her advisor, Dr. Paul Barnes. From this experience, specifically, she learned there was no limit to her tolerance of the oppressive south Texas heat, ticks, or thorny shrub species. After graduating her plan is simple, get a job and to give birth to the healthiest, happiest baby possible this coming November.

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