Effects of fire season and intensity on *Prosopis glandulosa* Torr. var. *glandulosa*

Paul B. Drewa

Jornada Experimental Range, USDA–Agricultural Research Service, Box 30003, MSC 3JER,
New Mexico State University, Las Cruces, NM 88003–0003, USA. Present address: Department of Biology,
Case Western Reserve University, 10900 Euclid Avenue, Cleveland, OH 44106–7080, USA.
Telephone: +1 216 368 4288; fax: +1 216 368 4672; email: pbd5@po.cwru.edu

Abstract. In pyrogenic ecosystems, responses of resprouting woody vegetation may depend more on fire season than on intensity. I explored this hypothesis by examining fire season and intensity effects on response of *Prosopis glandulosa*, a resprouting shrub in Chihuahuan desert grasslands of the south-western United States. Clipping as well as low and high intensity fires (natural and added fuels, respectively) were applied during the 1999 growing season and the 2000 dormant season. Both fire season and intensity affected shrub responses. Numbers of resprouts increased 16%, and heights increased 8% after dormant season versus growing season treatments of fire and clipping combined. Height and resprout number decreased with increased fire intensity. Fire season and intensity effects on canopy area and stem growth were generally not detected. My results do not support the above hypothesis. Instead, fire season and intensity influence shrub responses in different ways via different mechanisms. *Prosopis glandulosa* has the potential to respond more after dormant season than growing season fires, perhaps as determined by carbohydrate availability in underground organs at the time of fire. However, realization of this potential is contingent on fire intensity as influenced primarily by fuel amount. In turn, fire intensity will determine the amount and duration of heat penetration into soils and thus the amount of damage to growing points of underground organs.

Additional keywords: Chihuahuan desert grasslands; fire severity; fire temperature; honey mesquite; New Mexico; shrubs; south-western United States.

Introduction

In pyrogenic ecosystems, post-fire responses of resprouting woody vegetation are influenced by variation in fire regime characteristics, especially seasonal timing and intensity (Drewa *et al.* 2002). Post-fire recovery of resprouters may depend on their physiological status and location of plant carbohydrates at the time of fire (Wade and Johansen 1986a, 1986b; Glitzenstein *et al.* 1995). In particular, greater re-establishment of above-ground biomass may occur after dormant season than growing season fires. Though above-ground biomass is removed by dormant season fires, plants are physiologically inactive and carbohydrates, stored in underground organs (Pate *et al.* 1990), are available for resprouting. By contrast, growing season fires occur when plants are physiologically active. As a result, both above-ground biomass and carbohydrates are removed by fires that can delay or prevent recovery. Fire intensity may influence resprouting responses of woody vegetation also; recovery may depend on the extent to which fire directly damages

growing points (buds) through the transfer of heat (Matlack *et al.* 1993).

Intensity is well understood as a fire attribute, but its influence on vegetation is not well known. Fire intensity is the energy or heat output rate per unit length of fire front (Byram 1959). It is numerically expressed as the product of (1) heat yield, equivalent to the heat of combustion minus heat losses attributed to fuel moisture, incomplete combustion, and possibly radiation; (2) the quantity of fuel consumed by a fire's active combustion zone; and (3) the forward linear rate of fire spread (Byram 1959; Alexander 1982). Dynamics of woody species have been shown to be influenced by fire intensity (Williamson and Black 1981; Malanson and Trabaud 1988; Ansley and Jacoby 1998; Williams *et al.* 1999). However, its effects on woody vegetation responses are poorly understood for most pyrogenic ecosystems; improved understanding would be gained if the role of fire intensity was examined experimentally using fuel manipulations (Moreno and Oechel 1991a, 1991b). Despite a paucity of data, there

have been suggestions that resprouting responses of woody vegetation may be influenced more by fire season than fire intensity (Glitzenstein *et al.* 1995; Drewa *et al.* 2002). In these studies, effects of both fire characteristics were tested simultaneously in an experimental setting, but effects of fire intensity on woody vegetation were examined only indirectly and did not include any fuel manipulations.

Prosopis glandulosa (honey mesquite) is an ideal woody species to experimentally explore whether fire season is more influential than fire intensity on woody vegetation recovery. It occurs primarily in Chihuahuan and Sonoran desert grasslands of west Texas, New Mexico, and southeastern Arizona (Judd 1962; Isely 1973). Prior to European settlement in the late 1800s, fire frequency for these pyrogenic systems is not known. However, lightning-initiated fires occur in the late spring (June) and throughout the growing season (July–September) (Schmid and Rogers 1985; Gosz *et al.* 1995; McPherson 1995) and, prior to European settlement, may have burned from several hundred to several thousand hectares at a time (Schmid and Rogers 1985; Rogers and Vint 1987). Excessive livestock grazing of perennial grasses during the late 19th Century, periodic drought, and subsequent wind erosion of soils were largely responsible for altering natural fire regimes (McPherson 1995). Additionally, *P. glandulosa* has encroached from mostly bottomland water run-on areas into upland grasslands through the consumption and dissemination of seeds by livestock (Humphrey 1958; Buffington and Herbel 1965; Brown and Archer 1999). Following fire in desert grasslands, this deciduous arborescent legume can resprout rapidly from dormant buds located at the base of existing stems on adult plants where they are protected by bark just below ground level and thus are typically well insulated from fires (Cable 1972; McPherson 1995).

Little is known about the effects of fire on responses of *P. glandulosa* in Chihuahuan desert grasslands of New Mexico. Though changes in canopy cover and height of shrubs have been compared between burned and unburned areas (Drewa *et al.* 2001), no one has examined how differences in the fire regime affect these plant attributes. Also, resprouting patterns in terms of the number and growth of resprouts in response through fire regime manipulations have yet to be examined anywhere for *P. glandulosa*.

The main objective of my study was to explore the general hypothesis that woody vegetation responses are influenced more by fire season than fire intensity. Moreover, I posed the following questions in the context of *P. glandulosa*:

(1) Do either seasonal timing or intensity of fire affect shrub responses?
(2) Does fire intensity interact in any way with fire season to affect responses of shrubs?
(3) Are different attributes of *P. glandulosa* at the whole plant level (i.e. canopy cover, canopy height, resprout

number, and resprout growth) affected in similar ways by fire season and intensity?

Methods

Study site

My study was conducted on the Jornada Experimental Range (JER) located 37 km north-east of Las Cruces, Doña Ana Co., New Mexico ($32°37'$ N, $106°40'$ W). At an elevation of 1260 m (Gibbens *et al.* 1992), it represents an arid ecotone between grasslands and shrublands of the northern Chihuahuan Desert. The JER receives only 244 mm annual precipitation (85 year average, 1915–2000), 54% of which occurs from July through September as localized convective thunderstorms. From late fall to late spring, rainfall covers broader areas (Gibbens *et al.* 1992), occurs infrequently (Paulsen and Ares 1962), and may make up only 27% of the annual total (Drewa and Havstad 2001). On average, temperature is 24°C, and mean monthly maximum and minimum temperatures occur in June (36°C) and January (13°C), respectively (Paulsen and Ares 1962; Gibbens *et al.* 1986, 1992). The frost-free period averages 200 days/year, but the growing season for most vegetation, including shrubs, is mostly confined to a period of 90 days from July through September when soil moisture is more available, temperatures are higher, humidity is higher (40–50%), and evaporation is reduced (26 cm/month) (Paulsen and Ares 1962; Gibbens *et al.* 1986). However, annual net primary productivity on the JER ranges widely from 30 to 592 $g m^{-2}$ $year^{-1}$ (Ludwig 1987), coinciding with growing season precipitation that can be extremely variable from year to year (Nelson 1934; Miller and Donart 1979).

The study area was a 1252 ha pasture. Localized topography is characterized by gently undulating to moderately rolling fans (1–5% slopes), and soils are coarse-textured, well-drained, sandy loams (Typic Paleorthids) of the Simona-Harrisburg series (Bulloch and Neher 1980). These soils formed from wind-blown material derived from sandstone, volcanic ash, and shale and are underlain by a layer of calcium bicarbonate (caliche) at depths from 24 cm to >1 m (Bulloch and Neher 1980; Gibbens *et al.* 1986).

The study area has been grazed by livestock since the 1880s and has a recorded history of livestock grazing over the past 51 years. From 1949 to 2000, stocking rates have averaged 6.09 ha/Animal Unit Month with 8% of livestock forage demand from July through September. Animal Unit Month refers to the amount of vegetation required for 1 month to sustain a 454 kg cow aged >6 months (approximately 400 kg forage/month; Stoddart *et al.* 1975; Scarnecchia 1985). Similar to other south-western grasslands, shrub distributions of mostly *P. glandulosa* have expanded on the JER since the introduction of livestock in the late 19th Century (Fredrickson *et al.* 1998). Prior to that time, these sites were dominated by

perennial grasses such as *Bouteloua eriopoda* (black grama). While still dominant, its cover is discontinuous and has decreased at least 65% since the mid-1800s (Buffington and Herbel 1965).

Herbicide was once used on my study site to control shrub encroachment. In 1963, 3.28 g active ingredient/m canopy diameter of fenuron pellets (25%) were applied to individual shrubs of *P. glandulosa* covering 305 ha of the pasture on 19–28 June and another 94 ha on 29 July–1 August. These herbicide applications likely resulted in <20% complete kill of *P. glandulosa* (Norris *et al.* 1963).

Experimental design and data collection

I conducted a completely randomized multi-factorial field experiment where treatments of fire season and intensity were applied at two and three levels, respectively. A shrub served as my experimental unit, and each was multi-stemmed and may have been comprised of one or more genetic individuals. The 180 shrubs selected for study initially averaged 0.53 m (±0.01 m s.e.) in height and 1.11 m (±0.02 m s.e.) in canopy diameter; all stems were each <2 cm in diameter. Also, shrubs were individually tagged, mapped, and located at least 10 m apart. Each of six treatment combinations was administered randomly: (1) dormant season clipping; (2) dormant season low intensity fires; (3) dormant season high intensity fires; (4) growing season clipping; (5) growing season low intensity fires; and (6) growing season high intensity fires.

Fire intensity treatments were applied during the growing season (August) of 1999 and the dormant season (January) of 2000. During each season, low intensity head fires fueled by only natural vegetation were applied separately to 30 shrubs. Ground fuel cover of mostly herbaceous vegetation was at least 40% within the canopy area of these shrubs. High intensity fires were applied in the same way to another 30 shrubs during each of the two seasons. However, 8 kg/m² of alfalfa hay was added to each of these shrubs. Natural standing biomass estimates on the JER range from 0.05 to 0.81 kg/m² (L. Huenneke, New Mexico State University, unpublished data). Thus, the added fuel represented an approximate 10-fold increase in biomass and ensured that fires were of greater intensity than those fueled by only natural vegetation. Each of the 120 fires was initiated 2 m from the south-western side of a shrub, and each burned an area of approximately 16 m². Clipping was administered by cutting stems at the ground surface of another 30 shrubs during each of the growing and dormant seasons, including any vegetation ground cover within the canopy area of these shrubs. Clipping was intended to simulate fires of no intensity. Fires tend to completely burn ground cover fuels, but top-killed stems of *P. glandulosa* are present after fire. Thus, I removed ground cover fuels after clipping, but not shrub stems. On a cautionary note, effects of possible fire-induced inputs of nutrients and ash/char were not accounted for in this treatment (see Moreno and Oechel 1991*a*, 1991*b*); clipping may more

accurately represent above-ground biomass removal without the possible influence of heating.

Treatments of clipping and high intensity fire were used to improve understanding of the mechanism underlying intensity effects on shrubs through direct heat damage to root crowns. These treatments rarely if ever occur in Chihuahuan desert grasslands. However, they represented two extreme scenarios: clipping represented the absence of such a mechanism; high intensity fires represented a scenario where the presence of such a mechanism was highly likely. Also, they provided the means of comparing their effects with more natural fires fueled by only natural vegetation.

Each of the 120 experimental fires was measured for maximum temperature. Prior to each fire, a set of Tempil heat sensitive tablets (Big Three Industries, Inc., Tempil° Division, South Plainfield, NJ, USA), individually wrapped in one, 6.3 cm × 6.3 cm piece of heavy duty aluminum foil and strung on wires, was placed in the center area of each shrub at ground level. Each set comprised a series of tablets designed to melt at 48°C, 132°C, 212°C, 302°C, 371°C, 454°C, 538°C, 621°C, 704°C, 732°C, 843°C, 954°C, 1038°C, 1149°C, and 1232°C. Tablet sets were collected immediately after the fires. Tablets were scored as melted if any portion was melted or heavily charred. Wrapping tablets raises the ambient temperature at which they melt. Thus, I determined actual melting temperatures of wrapped tablets by using an existing regression equation,

$$Y = 1.24X + 25.63,$$

where Y = actual melting temperature (°C) and X = Tempil temperature rating (°C) ($P < 0.001, r^2 = 0.999$; Drewa *et al.* 2002). Melting temperatures were adjusted for the aluminum foil wrapping (85°C, 189°C, 289°C, 400°C, 486°C, 589°C, 693°C, 796°C, 899°C, 933°C, 1071°C, 1209°C, 1313°C, 1450°C, and 1553°C, respectively).

Fire intensity was estimated using maximum flame length data. Before each fire, a 1 m aluminum pole was positioned vertically beside a shrub. Attached to the pole was a 15 cm × 15 cm aluminum sign where I wrote the shrub's tag number. When the fire front began to enter the center of a shrub, flames were typically at their maximum length at that location. It was then that I took two photographs at 5 s intervals of the fire, the aluminum pole, and the sign. Based on two photographs of each fire, I identified the shrub with its tag number and measured average maximum flame length to scale using the 1 m pole. For each fire, intensity was calculated using the equation

$$I = 259.83(L^{2.174}),$$

where I = fireline intensity (kW/m) and L = average flame length (m) (Byram 1959). This equation has been shown to yield reliable estimates of fire intensity for a wide variety of ecosystems ranging from coniferous forests to grasslands (see Albini 1976).

My method of measuring flame lengths yielded very approximate estimates of maximum fire intensity. However, this study is more concerned with fire effects on the ecology of shrubs rather than a thorough examination of fire intensity as a physical attribute in Chihuahuan desert grasslands. Moreover, my method was sufficient to show quantitatively that experimental fires fueled by natural vegetation were not as intense as those fueled by hay additions. More accurate estimates of fire intensity could have involved the collection of fuel consumption (Glitzenstein et al. 1995) and spread rate data (see Alexander 1982). Estimates of fire intensity based on flame length can be inaccurate since the equation assumes no 'pulsating' or wide fluctuation in the length of the fire front (Byram 1959). In my study, this source of error was likely reduced or at least consistent between experimental fires given the uniformly distributed nature of 'flash' fuels comprising exclusively non-woody vegetation.

All 180 shrubs were either clipped or burned. I was interested in comparing responses to fires of different intensities conducted in different seasons, not to conditions of fire versus no fire. Significant differences thus represent deviations from a null hypothesis of no differences in response to treatments that involved different seasons and intensities of fire. Similar to other fire studies, there were no true controls that involved no changes to shrubs within this general experimental framework (see Platt et al. 1988; Glitzenstein et al. 1995; Drewa et al. 2002). However, my experimental treatments involving growing season fires fueled by natural vegetation served as a 'reference condition' since only these fires likely occurred in Chihuahuan desert grasslands prior to European settlement and thus represented normal or natural conditions.

All shrubs may have been affected by non-fire-related changes during the time I conducted this study and might be confounded with the experimental treatments. Thus, 30 additional shrubs were selected just prior to treatments during each of the growing and dormant seasons. These supplemental shrubs were not treated and were not used to address questions related to fire season and intensity effects on P. glandulosa. Instead, they were used to ensure that post-treatment shrub responses of the 180 treated shrubs could not be attributed to unforeseen extraneous environmental conditions. These 60 untreated shrubs were individually tagged, mapped, and represented multi-stemmed (each < 2 cm in diameter) shrubs during conditions of no fire. They averaged 0.57 m ($\pm$0.02 m s.e.) in height and 1.11 m ($\pm$0.04 m s.e.) in canopy diameter. Responses of the 180 treated shrubs were compared with those of the 60 untreated shrubs. This latter group served as a control because they were not manipulated, and I did not expect any changes in their attributes over the course of the study.

Data were collected before and after treatments. Immediately prior to applying experimental treatments, the 180 shrubs of P. glandulosa were individually measured for height, stem number, and canopy area that was assumed to be ellipsoidal in shape and estimated using two perpendicular measurements of canopy diameter. Similar to other fire studies (e.g. Martin 1983; Abrahamson et al.1984; Olson and Platt 1995; Drewa et al. 2002), resprouting occurred rapidly, within 1 year after treatments. Thus, the same measurements were taken 1 year after dormant season treatments and 1 year after growing season treatments where all stems were resprouts. In this way, all shrubs had the same length of time to recover (i.e. same number of growing season months) before post-treatment data were collected. Resprout growth for each shrub was also determined after treatments by averaging the lengths of the five longest stems.

The 60 untreated shrubs were measured in the same way before and 1 year after treatments. However, stem growth was determined differently. Since these shrubs were not top-killed, the five longest stems for each of the shrubs were tagged and measured for length at the onset of the study. During a final sample, tagged stems were remeasured for length. Stem growth for each of the untreated shrubs was then determined by subtracting pre-treatment from corresponding post-treatment data and then averaging across the five stems. Thus, in contrast to the 180 shrubs that comprised entirely resprouts following treatments, the 60 untreated shrubs possessed the same stems throughout the study.

Statistical analyses

Fire characteristics

Effects of fuel amount and seasonal timing on fire intensity were examined using ANOVA. Similarly, I examined effects of these treatments on maximum fire temperature. However, these latter data were analysed using a χ^2 test of homogeneity given the discrete nature of these data and the approximate estimates provided by the use of heat-sensitive tablets as opposed to thermocouples and dataloggers. Prior to this analysis each of the 120 experimental fires was assigned to a temperature category of 'low,' 'medium' or 'high', designating their maximum temperature in one of three classes: (1) <589°C; (2) 589°C–<1071°C; and (3) 1071°C–<1553°C, respectively. Thus, a χ^2 test of homogeneity was performed on these categorical data and examined how the proportion of high, medium, and low fire temperatures differed between dormant and growing season fires fueled by either natural vegetation or additions of hay.

Fire season and intensity effects

I examined the overall effect of fire/clipping season, intensity, and their interaction on P. glandulosa by performing an ANCOVA on post-treatment height data. Pre-treatment height data served as a covariate. Two additional ANCOVAs were performed on post-treatment canopy area data and then on post-treatment resprout number data. Pre-treatment canopy area and initial resprout number data served as a covariate,

respectively. ANCOVA was also used to determine fire treatment effects on resprout growth. However, shrub volume at the onset of the study was used as a covariate since overall shrub size may influence resprout growth following aboveground biomass removal (Wenger 1953). Shrub volume was assumed to resemble that of a cone and was estimated using both initial height and canopy area data. Where intensity had a significant effect in each of the four analyses, a first set of contrasts tested whether each of the four response variables differed between (1) clipping and low intensity fires; (2) clipping and high intensity fires; and (3) low and high intensity fires. A second set of contrasts tested whether seasonal timing at each level of intensity had an effect on each of the four response variables.

For each of the response variables that included only height, canopy area, and resprout number, I employed a third set of contrasts to examine if pre- and post-treatment samples were different for ₂ach combination of fire season a.ıd intensity. To do this, I re-analysed the same data for each of the three response variables, but used ANOVA since pre-treatment data were not used as a covariate. Instead, both pre- and post-treatment data were analysed as two samples collected over time. Thus, 'time' was incorporated into each analysis as a split-plot factor. These contrasts were not performed on resprout growth data since they were not collected at the onset of the study.

Season (alone) and treatment effects

I compared collective responses of treated shrubs with those of untreated shrubs. For each of the four shrub attributes, collective responses of treated shrubs were prepared by combining data across the three levels of fire intensity, but not across the two seasons or time (i.e. across pre- and post-treatment samples). ANCOVA was then used to examine the overall effect of season alone, removal of aboveground biomass (i.e. fire and clipping collectively), and their interaction on *P. glandulosa* using height, canopy area and then stem number data. For each of these three analyses, initial height, canopy area, and then stem number data served as a covariate, respectively. ANCOVA was used also to compare stem/resprout growth between treatments, but initial shrub volume was used as a covariate. A fourth set of contrasts examined whether season had an effect on each of the four shrub responses that were (1) treated and (2) untreated.

For each of the response variables that included height, canopy area, and stem number, a fifth set of contrasts was used in the same way as the third set to examine if pre- and post-treatment samples were different for each combination of season and aboveground biomass removal. This fifth set of contrasts was not performed on stem/resprout growth data since they were not collected over time.

Statistical analyses were conducted using PROC MIXED in SAS (SAS Institute 1994) that provided the flexibility of modeling means as well as the variance–covariance structure. In analyses where time was used as a split-plot factor, I consistently selected a compound symmetry variance–covariance structure based on Akaike's Information Criterion and Schwarz's Bayesian Criterion. The level of significance for all ANCOVA and contrast tests was $\alpha = 0.05$. However, a Bonferroni adjustment was performed on P values for the first set of contrasts. The total number of degrees of freedom of this first set was three, which exceeded that of fire intensity (i.e. two degrees of freedom) contained in the ANCOVA test. Thus, the level of significance for the first set of contrasts was $\alpha = 0.05/3$ or 0.017 (Sokal and Rohlf 1995). The four remaining sets of contrasts were unrelated to the factorial structure of my experiment and thus did not constitute true subhypotheses of the ANCOVA and ANOVA tests. Thus, for each set, I constructed a global contrast test that analysed all contrasts simultaneously using ANOVA. All global contrast tests were significant ($P < 0.001$) and provided justification for performing these contrasts separately. To meet model assumptions, data were square-root transformed except resprout/stem growth.

Results

Fire characteristics

Seasonal timing had no effect on fire intensity ($P = 0.219$). Overall, intensity of growing season fires was only 6% greater than that of dormant season fires. However, fuel amount had an overall effect on fire intensity ($P < 0.001$). High intensity fires averaged 732 kW/m more than low intensity fires. Interaction between these treatments had no effect on fire intensity ($P = 0.534$); seasonal differences were too variable for low as well as high intensity fires (Table 1a).

A χ^2 test of homogeneity revealed that maximum fire temperatures were affected by treatments ($P < 0.001$). Low intensity, dormant season fires were only 92°C hotter than those during the growing season (Table 1b). Also, 80% of these dormant season fires and 93% of these growing

Table 1. Mean intensity (a) and maximum temperature (b) of experimental fires
Dormant: dormant season fires; Growing: growing season fires;
Low intensity fires: fires fueled by only natural vegetation;
High intensity fires: fires each fueled by natural vegetation and
8 kg/m² of alfalfa hay

	Low intensity fires		High intensity fires	
	Mean	s.e.	Mean	s.e.
(a) Intensity (kW/m)				
Dormant	26	5	762	70
Growing	54	14	782	59
(b) Maximum temperature (°C)				
Dormant	678	74	1392	22
Growing	586	39	1375	24

Table 2. *P*-values for ANCOVA and three sets of contrasts that were used to examine fire season and intensity effects on four characteristics of *P. glandulosa*

C: clipping; L: low intensity fire; H: high intensity fire; D: dormant season; G: growing season; Pre: pre-treatment; Post: post-treatment

Source	*P*-value for			
	Height	Canopy area	Resprout number	Resprout growth
ANCOVA				
Covariate	<0.001	<0.001	<0.001	<0.001
Fire season	0.010	0.800	0.023	0.899
Fire intensity	0.001	<0.001	<0.001	0.002
Season × intensity	0.553	0.470	0.031	0.963
Contrasts (1st set)				
C vs. L	0.376	0.801	0.002	0.116
C vs. H	<0.001	<0.001	<0.001	<0.001
L vs. H	0.008	<0.001	0.004	0.051
Contrasts (2nd set)				
DCPost vs. GCPost	0.039	0.792	0.002	0.781
DLPost vs. GLPost	0.072	0.259	0.127	0.958
DHPost vs. GHPost	0.525	0.664	0.505	0.914
Contrasts (3rd set)				
DCPre vs. DCPost	0.413	0.647	<0.001	
GCPre vs. GCPost	0.471	0.489	<0.001	
DLPre vs. DLPost	0.893	0.102	<0.001	
GLPre vs. GLPost	0.007	0.097	0.002	
DHPre vs. DHPost	0.005	0.002	0.470	
GHPre vs. GHPost	<0.001	<0.001	0.272	

Fig. 1. Mean height (cm) of *P. glandulosa* shrubs before (Pre-treatment) and 1 year after (Post-treatment) (*a*) clipping (Clipping); (*b*) fires fueled by solely natural vegetation (Low intensity); and (*c*) fires each fueled by natural vegetation and 8 kg/m^2 of alfalfa hay (High intensity) that were conducted during the dormant and growing seasons.

season fires did not exceed 1071°C. Conversely, temperatures of high intensity fires were twice that of low intensity fires regardless of season. High intensity fires were only 17°C hotter during the dormant season than the growing season, and 98% of all high intensity fires reached temperatures >1071°C.

Fire season and intensity effects

Shrub height

Fire season had an overall effect on shrub height ($P = 0.010$; Table 2). Shrubs were 8% taller after dormant season than growing season treatments. Intensity had an overall effect on height also ($P = 0.001$). Though shrubs were of similar height after clipping and low intensity fires ($P = 0.376$), they were 12% ($P < 0.001$) and 10% ($P = 0.008$) taller than shrubs after high intensity fires, respectively.

Shrubs were 13% taller after dormant season than growing season clipping ($P = 0.039$; Table 2, Fig. 1*a*). However, regardless of seasonal timing, these shrubs returned to their initial height within 1 year ($P > 0.413$). After low intensity fires, seasonal timing had a similar effect on shrub height, but approached significance ($P = 0.072$; Fig. 1*b*). Nonetheless, when low intensity fires were conducted during the growing season, height decreased 14% over time ($P = 0.007$)
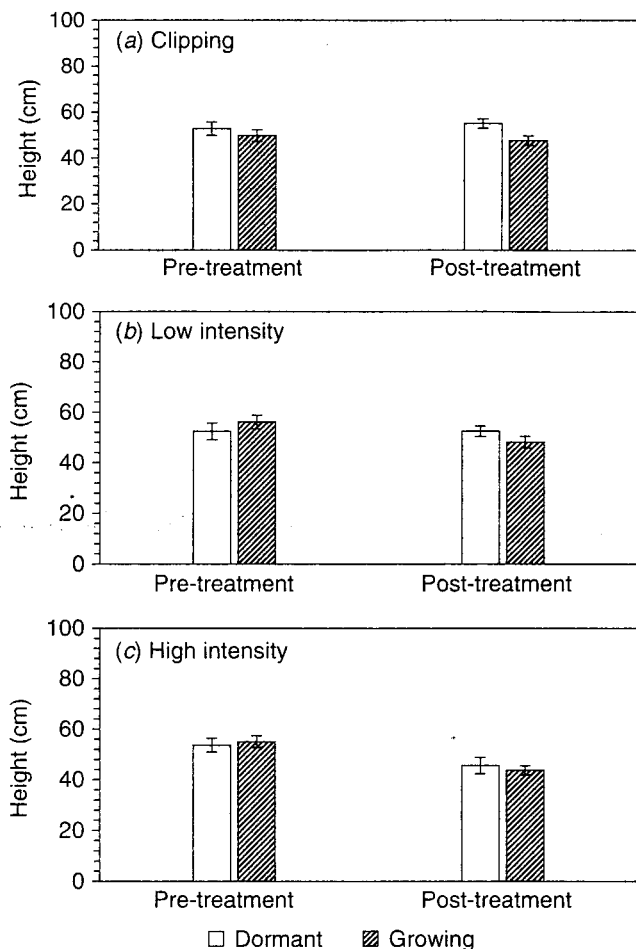
while temporal changes in shrub height were negligible after low intensity fires during the dormant season ($P = 0.893$). Following high intensity fires, seasonal timing had no effect on shrub height ($P = 0.525$; Fig. 1*c*). Compared with initial levels, shrub height decreased 15% after dormant season ($P = 0.005$) and 21% after growing season fires of high intensity ($P < 0.001$).

Canopy area

Only fire intensity had an effect on canopy area ($P < 0.001$; Table 2). Canopy area was similar after clipping and low intensity fires ($P = 0.801$). However, after high intensity fires, it was 34% less than that following clipping ($P < 0.001$) and low intensity fires ($P < 0.001$).

Canopy area was similar after dormant and growing season treatments of clipping and low intensity fires ($P > 0.259$; Table 2; Figs 2*a* and 2*b*). Following these treatments, canopy
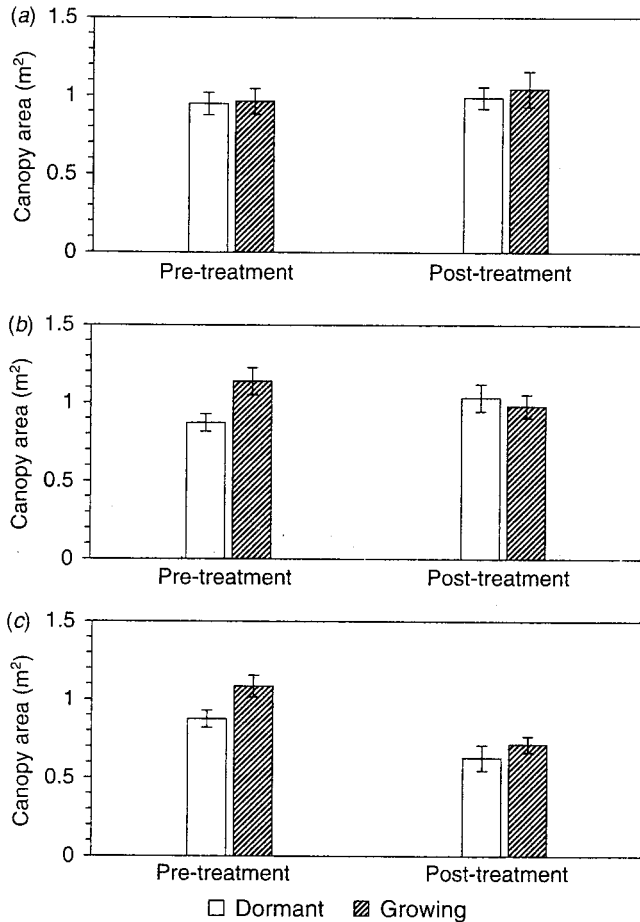
Fig. 2. Mean canopy area (m²) of *P. glandulosa* shrubs before (Pre-treatment) and 1 year after (Post-treatment) (*a*) clipping; (*b*) low intensity; and (*c*) high intensity fires that were conducted during the dormant and growing seasons. Explanation of intensity treatments follows Fig. 1.

Fig. 3. Mean number of stems of *P. glandulosa* shrubs before (Pre-treatment) and 1 year after (Post-treatment) (*a*) clipping; (*b*) low intensity; and (*c*) high intensity fires that were conducted during the dormant and growing seasons. Explanation of intensity treatments follows Fig. 1.

area was equivalent to that initially ($P > 0.097$). Seasonal timing had no differential effect on canopy area after high intensity fires also ($P = 0.664$; Fig. 2*c*). Over time, however, canopy area decreased 28% after dormant season ($P = 0.002$) and 35% after growing season high intensity fires ($P < 0.001$).

Stem number

Fire season had an overall effect on the number of stems ($P = 0.023$; Table 2). Stem numbers were 16% greater after dormant season than growing season treatments. Intensity affected stem numbers too ($P < 0.001$). After clipping, resprouting was 35% greater ($P = 0.002$) and 60% greater ($P < 0.001$) than that following low and high intensity fires, respectively. Compared with low intensity fires, high intensity fires resulted in 15% fewer stems ($P = 0.004$)

Dormant season clipping resulted in 1 1/2 times more stems than clipping during the growing season ($P = 0.002$; Table 2; Fig. 3*a*). Compared with initial levels, stem numbers
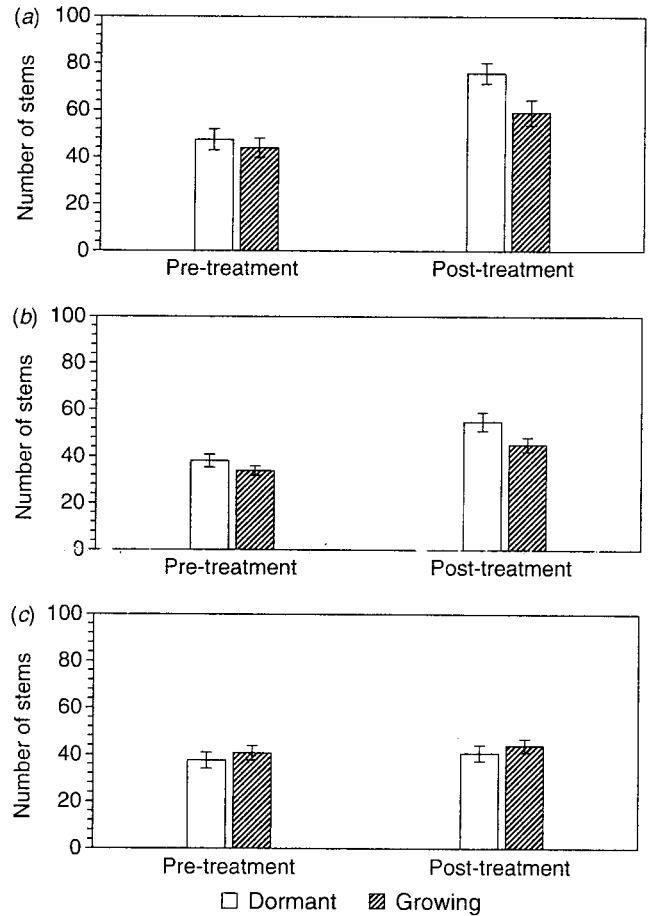
increased 60% after dormant season ($P < 0.001$) and 35% after growing season clipping ($P < 0.001$). Though numbers of stems were 13% greater after dormant season than growing season fires of low intensity, these responses were too variable to detect differences ($P = 0.127$; Fig. 3*b*). However, stem numbers increased 44% ($P < 0.001$) and 33% ($P = 0.002$) after these dormant and growing season fires over time. Dormant and growing season fires of high intensity yielded similar numbers of stems ($P = 0.505$) that were also equivalent to pre-treatment numbers ($P > 0.272$; Fig. 3*c*).

Resprout growth

Only fire intensity affected resprout growth ($P = 0.002$; Table 2). Resprouts grew 61 cm (±2 cm s.e.) after clipping and 58 cm (±2 cm s.e.) after low intensity fires ($P = 0.116$; data not shown). After high intensity fires, regrowth was 14% ($P < 0.001$) but only 9% ($P = 0.051$) less than that following clipping and low intensity fires, respectively.

Season (alone) and treatment effects

Season had an overall effect on shrub height ($P = 0.014$), but not canopy area, number, or growth of stems/resprouts ($P > 0.379$; Table 3). However, treatments of fire and clipping combined had an overall effect on all these response variables ($P < 0.001$).

Table 3. *P*-values for ANCOVA and two additional sets of contrasts that were used to examine effects of season alone and fire and clipping (combined) on four characteristics of *P. glandulosa*

Treatments, T: treatments of fire and clipping collectively; U: untreated; D: dormant season; G: growing season; Pre: pre-treatment; Post: post-treatment

Source	*P*-value for			
	Height	Canopy area	Stem number	Stem growth
ANCOVA				
Covariate	<0.001	<0.001	<0.001	<0.001
Season alone	0.014	0.741	0.379	0.778
Treatments	<0.001	<0.001	<0.001	<0.001
Season × treatments	0.820	0.804	0.204	0.876
Contrasts (4th set)				
DT vs. GT	0.007	0.564	0.031	0.899
DU vs. GU	0.196	0.959	0.820	0.800
Contrasts (5th set)				
DTPre vs. DTPost	0.238	0.566	<0.001	
GTPre vs. GTPost	<0.001	0.004	<0.001	
DUPre vs. DUPost	0.127	<0.001	0.255	
GUPre vs. GUPost	0.995	<0.001	0.503	

Height of treated shrubs was affected by season ($P = 0.007$; Fig. 4a). Over time, it decreased 13% after growing season ($P < 0.001$), but only 4% after dormant season ($P = 0.238$) fire and clipping combined. By contrast, season alone had no effect on height of untreated shrubs ($P = 0.196$) that changed little over time, regardless of season ($P > 0.127$; Fig. 4b).

Canopy area of treated and untreated shrubs changed in different ways. Season had no effect on canopy area of either treated or untreated shrubs ($P > 0.564$; Table 3; Figs 4c and 4d). When treatments were applied during the dormant season, canopy area changed little over time ($P = 0.566$). When conducted during the growing season, however, canopy area decreased 14% from that initially ($P = 0.004$). By contrast, canopy area of dormant season and growing season untreated shrubs increased 43% and 25% over time, respectively ($P < 0.001$).

Season had an effect on stem numbers of treated shrubs ($P = 0.031$; Fig. 4e), but season alone had no differential effect on those that were untreated ($P = 0.820$; Fig. 4f). Compared with initial levels, stem numbers increased 39% and 25% after dormant season and growing season treatments, respectively ($P < 0.001$). Conversely, untreated shrubs changed little over time, regardless of season ($P > 0.255$).

Season had no effect on growth of either treated or untreated shrubs ($P > 0.800$; data not shown). Stems of untreated shrubs senesced or decreased 1.5 cm on average
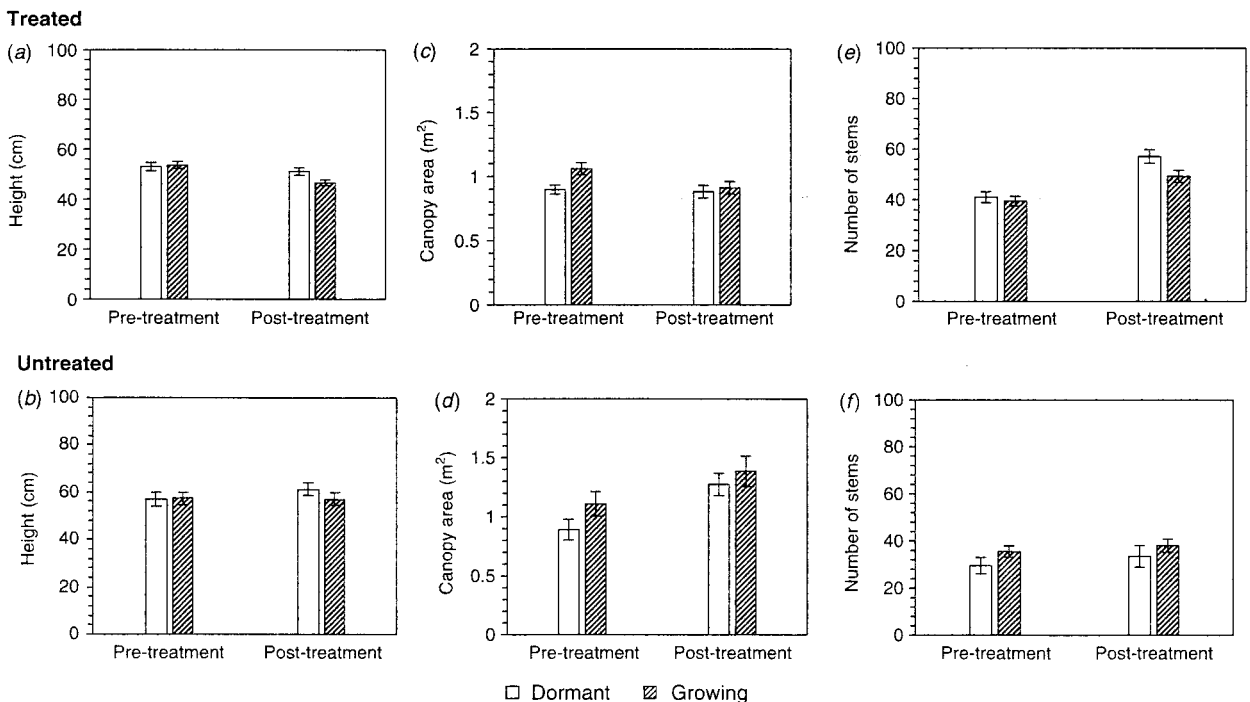
Treated

Untreated

□ Dormant   ▨ Growing

Fig. 4. Mean height (cm) (*a, b*), canopy area (m²) (*c, d*), and stem number (*e, f*) of *P. glandulosa* shrubs that were burned and clipped collectively (Treated) and not manipulated in any way (Untreated) before (Pre-treatment) and 1 year after (Post-treatment) experimental treatments during the dormant and growing seasons.

(±1 cm s.e.), regardless of season. By comparison, resprouts grew 38% more following both dormant and growing season treatments.

Discussion

Both fire season and intensity influenced height of *P. glandulosa* in my study. Shrub height was greater after dormant season than growing season clipping. A similar seasonal timing effect was detected with the addition of heat using low intensity fires. However, responses were variable and approached significance, suggesting that height was not determined by seasonal timing and the availability of carbohydrates alone. Variable responses may have been attributed to shrubs that were damaged or stressed differently by fire intensity. This intensity-induced damage or stress was illustrated using fires fueled by hay additions. Regardless of seasonal timing, shrubs were always shorter after high intensity fires than after clipping or fires of low intensity. The influence of both fire season and intensity may explain why heights of two *Prosopis* species in semi-arid grasslands of Argentina were greater after dormant season than growing season fires, yet were too variable to infer significance (Boo *et al.* 1997). Heights of shrub species have responded in a similar fashion following single dormant season and growing season fires in other pyrogenic ecosystems including south-eastern pine savannas (Hughes and Knox 1964; Drewa *et al.* 2002) and conifer forests of the Sierra Nevada (Kauffman and Martin 1990).

Resprout number was also influenced by a combination of fire season and intensity. In general, post-treatment numbers of resprouts varied inversely with fire intensity. In addition, resprouting increased after dormant season versus growing season clipping. This was also the case following seasonal timing treatments involving low intensity fires, but this difference approached significance. Nonetheless, compared with pre-treatment levels, dormant season clipping and low intensity fires always resulted in greater numbers of stems than when conducted during the growing season. Similarly, incidence of shrub resprouting is usually greater following dormant season than growing season fires in south-western desert grasslands (Blydenstein 1957; McPherson 1995 and references therein). However, these responses can be variable, depending on fire intensity (Cable 1965, 1972). In turn, intensity is determined by different loadings of fuel and thus will determine a fire's effectiveness in stressing or damaging growing points used for resprouting (Wright and Bailey 1982). Fire intensity has similarly influenced resprouting responses in south-eastern pine savannas (Hughes and Knox 1964; Glitzenstein *et al.* 1995; Drewa *et al.* 2002), California chaparral (Moreno and Oechel 1991a, 1991b; Beyers and Wakeman 2000; Odion and Davis 2000), dry sclerophyll forests of Australia (Morrison and Renwick 2000), and in the garrigue of France (Malanson and Trabaud 1988).

Fire intensity was directly related to fire severity in this study, regardless of seasonal timing. Fire severity refers to the impact of fire intensity on vegetation responses (White and Pickett 1985). This relationship is often contingent on seasonal dryness of soil organic matter or duff (Ryan 2002). For example, during a fire in boreal forests, duff can act as an insulator especially when wet, and thus can minimize heat penetration into the soil and damage to underground organs (Ryan 2002). By contrast, Chihuahuan desert grassland soils are devoid of duff and contain <1% organic matter (Gile and Grossman 1979); intensity of my experimental fires never differed by season. Instead, fire severity was determined more by fuel amount. Compared with low intensity fires, my high intensity fires were more effective in reducing shrub height and resprout number. Given the additions of hay, they produced more heat that was likely to have penetrated deeper into soils for a longer period of time and thus resulted in greater damage or stress to growing points of underground organs.

Effects of fire season and intensity on other attributes of *P. glandulosa* were not always detected. Specifically, canopy area was similar after clipping and low intensity fires compared with initial levels, regardless of seasonal timing. Similarly, changes in canopy cover of *P. velutina* were not detected after dormant season fires using natural fuels in Arizona desert grasslands (Martin 1983). In Idaho ponderosa pine forests, shrub cover was equivalent after dormant season fires of widely varying intensity (Armour *et al.* 1984). Shrub cover in south-eastern pine savannas also remained equivalent even after three annual, dormant and growing season fires (Hughes and Knox 1964). Another example in my study included resprout growth that diminished only after high intensity fires. By contrast, following high intensity fires in California chaparral, where fuel loadings were equivalent to my fuel additions, resprout growth of shrubs was equivalent to that after fires fueled by natural vegetation (Moreno and Oechel 1991b).

Shrub responses in my study were attributable to fire and clipping treatments and not extraneous, environmental conditions. Changes in height, stem number, and stem growth of untreated shrubs were negligible. However, their canopy area increased as much as 43% over the course of the study. These untreated shrubs may have responded to an inordinate amount of growing season precipitation during 2000 that was 133% of the average. Conversely, a combination of fire and clipping resulted in canopy area that was less than that initially, but only when conducted during the growing season.

I did not observe any complete kill of shrubs even after high intensity fires. Similarly, after growing season fires in desert grasslands of south-central New Mexico, only 1% of 210 *P. glandulosa* shrubs were completely killed (Drewa *et al.* 2001). Complete kill was <5% based on >3450 *P. glandulosa* shrubs/trees in Texas grasslands following 23 different treatments of fire season, frequency, and intensity (Ansley and Jacoby 1998). In south-eastern Arizona grasslands, by contrast, mortality of *P. velutina* shrubs that were similar in size to those in my study, was as much as 54% after single

fires (Glendening and Paulsen 1955). In the same study, complete kill of larger shrubs (i.e. 2.5–5 cm in basal diameter) was 20% and as much as 10% after growing season and dormant season fires, respectively. Even after high intensity June fires where fuel loadings were 6% of that used to fuel my high intensity fires, complete kill of *P. velutina* shrubs was 25%, many of which were >5 cm in basal stem diameter. In agreement with Wright and Bailey (1982), *P. velutina* may be more susceptible to complete kill than *P. glandulosa*.

Despite the addition of fuels, my high intensity fires burned at much lower intensities than those reported in other ecosystems. For example, in *P. glandulosa* savannas of Texas, fire intensities were as much as five times greater, and herbaceous fuel loadings were only 6% of that in my study (Ansley and Jacoby 1998). Compared with my high intensity fires, intensity was as much as 12 times greater in tropical savannas of Australia (Williams and Cook 1998; Williams *et al.* 1999) and south-eastern pine savannas (Glitzenstein *et al.* 1995). Additionally, my fuel loads were up to eight times greater than those used in these studies. Thus, too much moisture may have been trapped in bales of hay that were used to fuel the high intensity fires in this study. This would explain why flame lengths of these fires rarely exceeded 2 m. Nonetheless, hay additions provided intensities that exceeded those of fires fueled by only natural fuels. Also, excessive moisture within hay additions may have been responsible for similar intensities between dormant season and growing season high intensity fires. At the same time, however, seasonal timing had no effect on fire intensities fueled by only natural vegetation.

My results suggest that responses of *P. glandulosa* are not influenced more by fire season than fire intensity. Instead, both fire attributes affect shrub responses, but in different ways. Fire season determines shrub response potential. In the context of *P. glandulosa*, greater height and number of resprouts can result when fires are conducted during the dormant season than the growing season as determined by carbohydrate availability in underground organs at the time of fire. However, whether this response potential is fully realized will depend on fire intensity. In grasslands of the Chihuahuan Desert, fire intensity is likely to be determined primarily by the amount of flash fuels. In turn, the intensity of fires will determine the amount and duration of heat penetration into soils and thus the amount of damage or stress to growing points of underground organs. On a cautionary note, careful selection of response variables is required to detect the influence of both fire season and intensity as not all shrub attributes will be affected by fire regime manipulations.

References

Abrahamson WG, Johnson AF, Layne JN, Peroni PA (1984) Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Florida Scientist* **47**, 209–250.

Albini FA (1976) Estimating wildfire behavior and effects. USDA Forest Service, Intermountain Forest and Range Experiment Station General Technical Report INT-30. Ogden, Utah. 92 pp.

Alexander ME (1982) Calculating and interpreting forest fire intensities. *Canadian Journal of Botany* **60**, 349–357.

Ansley RJ, Jacoby PW (1998) Manipulation of fire intensity to achieve mesquite management goals in north Texas. *Proceedings of the Tall Timbers Fire Ecology Conference* **20**, 195–204.

Armour CD, Bunting SC, Neuenschwander LF (1984) Fire intensity effects on the understory in ponderosa pine forests. *Journal of Range Management* **37**, 44–49.

Beyers JL, Wakeman CD (2000) Season of burn effects in southern California chaparral. In 'Interface between ecology and land development in California'. 2nd edn. (Eds JE Keeley, M Baer-Keeley and CJ Fotheringham) pp. 45–55. (United States Geological Survey, Open-File Report 00–62: Sacramento, CA)

Blydenstein J (1957) The survival of velvet mesquite (*Prosopis juliflora* var. *velutina*) after fire. *Journal of Range Management* **10**, 221–223.

Boo RM, Pelaez DV, Bunting SC, Mayor MD, Elias OR (1997) Effect of fire on woody species in central semi-arid Argentina. *Journal of Arid Environments* **35**, 87–94.

Brown JR, Archer SR (1999) Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* **80**, 2385–2396.

Buffington LC, Herbel CH (1965) Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* **35**, 139–164.

Bulloch Jr. HE, Neher RE (1980) 'Soil survey of Doña Ana County area New Mexico.' (USDA, Soil Conservation Service: Las Cruces, NM). 177 pp.

Byram GM (1959) Combustion of forest fuels. In 'Forest fire: control and use'. (Ed. KP Davis) pp. 61–89. (McGraw-Hill: New York)

Cable DR (1965) Damage to mesquite, Lehmann lovegrass and black grama by a hot June fire. *Journal of Range Management* **18**, 326–329.

Cable DR (1972) Fire effects on southwestern semidesert grass-shrub communities. *Proceedings of the Tall Timbers Fire Ecology Conference* **12**, 109–127.

Drewa PB, Havstad KM (2001) Effects of fire, grazing, and the presence of shrubs in Chihuahuan desert grasslands. *Journal of Arid Environments* **48**, 429–443.

Drewa PB, Peters DPC, Havstad KM (2001) Fire, grazing, and honey mesquite invasion in black grama-dominated grasslands of the Chihuahuan Desert: a synthesis. In 'Proceedings of the invasive species workshop: the role of fire in the control and spread of

invasive species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management'. (Eds TP Wilson and KEM Galley) pp. 31–39. (Tall Timbers Research Station Miscellaneous Publication No. 11: Tallahassee, FL)

Drewa PB, Platt WJ, Moser EB (2002) Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. *Ecology* **83**, 755–767.

Fredrickson E, Havstad KM, Estell R, Hyder P (1998) Perspectives on desertification: south-western United States. *Journal of Arid Environments* **39**, 191–207.

Gibbens RP, Herbel CH, Morton HL, Lindemann WC, Ryder-White JA, Richman DB, Huddleston EW, Conley WH, Davis CA, Reitzel JA, Anderson DM, Guiao A (1986) Some impacts of 2,4,5-T on a mesquite duneland ecosystem in southern New Mexico: a synthesis. *Journal of Range Management* **39**, 320–326.

Gibbens RP, Beck RF, McNeely RP, Herbel CH (1992) Recent rates of mesquite establishment in the northern Chihuahuan Desert. *Journal of Range Management* **45**, 585–588.

Gile, LH, Grossman RB (1979) 'The desert project soil monograph.' (USDA, Natural Resources Conservation Service, National Soil Survey Center: Lincoln, Nebraska) 984 pp.

Glendening GE, Paulsen Jr. HA (1955) Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. USDA, Technical Bulletin Number 1127. Washington, D.C. 50 pp.

Glitzenstein JS, Platt WJ, Streng DR (1995) Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. *Ecological Monographs* **65**, 441–476.

Gosz JR, Moore DI, Shore GA, Grover HD (1995) Lightning estimates of precipitation location and quantity on the Sevilleta LTER, New Mexico. *Ecological Applications* **5**, 1141–1150.

Hughes RH, Knox FE (1964) Response of gallberry to seasonal burning. USDA Forest Service, Southeastern Forest Experiment Station Research Note SE–21. Asheville, NC. 2 pp.

Humphrey HH (1958) The desert grassland. *Botanical Review* **24**, 193–253.

Isely D (1973) *Prosopis. New York Botanical Garden* **25**, 116–122.

Judd BI (1962) Principal forage plants of southwestern ranges. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Station Paper Number 69. Fort Collins, CO. 93 pp.

Kauffman JB, Martin RE (1990) Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. *Forest Science* **36**, 748–764.

Ludwig JA (1987) Primary productivity in arid lands: myths and realities. *Journal of Arid Environments* **13**, 1–7.

Malanson GP, Trabaud L (1988) Vigour of post-fire resprouting by *Quercus coccifera*. *Journal of Ecology* **76**, 351–365.

Martin SC (1983) Responses of semidesert grasses and shrubs to fall burning. *Journal of Range Management* **36**, 604–610.

Matlack GR, Gibson DJ, Good RE (1993) Regeneration of the shrub *Gaylussacia baccata* and associated species after low-intensity fire in an Atlantic coastal plain forest. *American Journal of Botany* **80**, 119–126.

McPherson GR (1995) The role of fire in the desert grasslands. In 'The desert grassland'. (Eds MP McClaran and T.R. van Devender) pp. 130–151. (The University of Arizona Press: Tucson)

Miller RF, Donart GB (1979) Response of *Bouteloua eriopoda* (Torr.) Torr. and *Sporobolus flexuosus* (Thurb.) Rybd. to season of defoliation. *Journal of Range Management* **32**, 63–67.

Moreno JM, Oechel WC (1991*a*) Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* **72**, 1993–2004.

Moreno JM, Oechel WC (1991*b*) Fire intensity and herbivory effects on postfire resprouting of *Adenostoma fasciculatum* in southern California chaparral. *Oecologia* **85**, 429–433.

Morrison DA, Renwick JA (2000) Effects of variation in fire intensity on regeneration of co-occurring species of small trees in the Sydney region. *Australian Journal of Botany* **48**, 71–79.

Nelson EW (1934) The influence of precipitation and grazing upon black grama grass range. USDA, Technical Bulletin Number 409. Washington, D.C. 32 pp.

Norris JJ, Valentine KA, Gerard JB (1963) Mesquite control with monuron, fenuron, diuron. Agricultural Experiment Station, New Mexico State University, University Park, New Mexico. 14 pp.

Odion DC, Davis FW (2000) Fire, soil, heating, and the formation of vegetation patterns in chaparral. *Ecological Monographs* **70**, 149–169.

Olson MS, Platt WJ (1995) Effects of growing season fires on resprouting of shrubs in longleaf pine savannas. *Vegetatio* **119**, 101–118.

Pate JS, Froend RH, Bowen BJ, Hansen A, Kuo J (1990) Seedling growth and storage characteristics of seeder and resprouter species of mediterranean-type ecosystems of s. w. Australia. *Annals of Botany* **65**, 585–601.

Platt WJ, Evans GW, Davis MM (1988) Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. *Oecologia* **76**, 353–363.

Paulsen HA, Ares FN (1962) Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the Southwest. USDA Forest Service, Technical Bulletin Number 1270. Washington, D.C. 56 pp.

Rogers GF, Vint MK (1987) Winter precipitation and fire in the Sonoran Desert. *Journal of Arid Environments* **13**, 47–52.

Ryan KC (2002) Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica* **36**, 13–39.

SAS Institute Inc. (1994) 'SAS/STAT user's guide, version 6, 4th edition.' (SAS: Cary, NC)

Scarnecchia DL (1985) The animal-unit and animal-unit-equivalent concepts in range science. *Journal of Range Management* **38**, 346–349.

Schmid MK, Rogers GF (1985) Trends in fire occurrence in the Arizona upland subdivision of the Sonoran Desert, 1955 to 1983. *The Southwestern Naturalist* **33**, 437–444.

Sokal RR, Rohlf FJ (1995) 'Biometry: the principles and practice of statistics in biological research.' (WH Freeman: New York) 887 pp.

Stoddart LA, Smith AD, Box TW (1975) 'Range management.' 3rd edn. (McGraw-Hill: New York) 532 pp.

Wade DD, Johansen RW (1986*a*) Relating wildland fire to defoliation and mortality in pine. In 'Proceedings of the fourth biennial southern silvicultural research conference (4–6 November 1986. Atlanta, Georgia, USA).' USDA Forest Service, General Technical Report SE–42. Washington, D.C. pp. 107–110.

Wade DD, Johansen RW (1986*b*) Effects of fire on southern pine: observations and recommendations. USDA Forest Service, Southeastern Forest Experiment Station General Technical Report SE–41. Asheville, NC. 14 pp.

Wenger KF (1953) The sprouting of sweetgum in relation to season of cutting and carbohydrate content. *Plant Physiology* **28**, 35–49.

White PS, Pickett STA (1985) Natural disturbance and patch dynamics: an introduction. In 'The ecology of natural disturbance and patch dynamics'. (Eds STA Pickett and PS White) pp. 3–13. (Academic Press: San Francisco)

Williams RJ, Cook GD (1998) Fire and trees in the savannas of the World Heritage Kakadu National Park, northern Australia. *Proceedings of the Tall Timbers Fire Ecology Conference* **20**, 404–412.

Williams RJ, Cook GD, Gill AM, Moore PHR (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**, 50–59.

Williamson GB, Black EM (1981) High temperatures of forest fires under pines as a selective advantage over oaks. *Nature* **293**, 643–644.

Wright HA, Bailey AW (1982) 'Fire ecology.' (John Wiley and Sons: New York) 501 pp.