EFFECTS OF SUMMER FIRES ON WOODY, SUCCULENT, AND GRAMINOID VEGETATION IN SOUTHERN MIXED-PRAIRIE ECOSYSTEMS: A REVIEW

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ABSTRACT

Interest in the use of summer fires to restore southern Great Plains prairie ecosystems infested with woody plants and cactus is increasing, but information regarding effects on target and nontarget plant species is needed before this practice can be recommended. We review effects of summer and winter fires on mortality and growth of honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia phaeacantha*), and grasses common to the southern mixed prairie, including C_4 midgrass sideoats grama (*Bouteloua curtipendula*), C_4 shortgrass buffalograss (*Buchloe dactyloides*), and C_3 midgrass Texas wintergrass (*Nassella leucotricha*). Summer fires were more effective than winter fires at top-killing mature mesquite, but plant mortality was $<$4% in all fire treatments. Prickly pear plant mortality was much greater following summer than winter fires. Sideoats grama, buffalograss, and Texas wintergrass were all tolerant of summer fire, although post-fire recovery rate was slower in sideoats grama than in the other species. Clipping once each spring reduced sideoats grama and Texas wintergrass standing crop in all treatments when measured 1 y after clipping, but effects of clipping + summer fire were not negatively additive. The only time fire negatively affected Texas wintergrass was when spring clipping followed winter fire. In contrast, buffalograss standing crop was not reduced by clipping or clipping + summer fire at 1 y after treatment. Results suggest that summer fire will not eradicate mesquite and that frequent fires either in summer or winter are necessary to maintain suppression. Grasses studied thus far have demonstrated a tolerance to fire in either season.

keywords: cactus, grassland, herbaceous production, mesquite, prescribed fire, southern Great Plains, species composition, summer fire, woody plants.

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INTRODUCTION

Prescribed fires in the southern Great Plains prairie have historically been conducted during the dormant season (January–March) because they are safer and more manageable than growing-season, or ‘‘summer,’’ fires (Wright and Bailey 1982, Scifres and Hamilton 1993). However, there has been increasing interest in the use of summer-season fires because of their greater ability to suppress or even kill noxious woody plants and cacti species (Ansley and Jacoby 1998, Taylor 2001, Ansley and Taylor 2004). While the potential controlling effects of summer fires on target noxious species holds promise, there is concern that summer fires may damage economically and/or ecologically important nontarget herbaceous species (Bailey 1988) or drastically reduce grass production (Engle and Bultsma 1984, Engle and Bidwell 2001). Very few data are available that document responses of target or nontarget species in replicated studies that compare summer fires, winter fires, and an unburned control. Our purpose is to provide a historical context for and to summarize the effects of summer fires on Great Plains vegetation, with particular emphasis on plant species in the southern Great Plains.

Historically, Great Plains vegetation was most probably maintained as grassland because of the frequent occurrence of fires (Archer 1989, Collins and Wallace 1990, Van Auken 2000). This conclusion is not new, and it is surprising how many early observers realized that the vast grasslands of the Great Plains were maintained by fire and would experience woody plant encroachment if fire was removed from these ecosystems. As early as 160 y ago, Josiah Gregg, probably writing about western Oklahoma (Stewart et al. 2002), commented on how fires (called ‘‘conflagrations’’) maintained the southern prairie grasslands (Gregg 1844:202):

> It is unquestionably the prairie conflagrations that keep down the woody growth upon most of the western uplands. The occasional skirts and fringes which have escaped their rage have been protected by the streams they border. Yet, may not the time come when these vast plains will be covered with timber? . . . Indeed there are parts of the southwest now thickly set with trees of good size that within the remembrance of the oldest inhabitants were as naked as the prairie plains and the appearance of the timber in many other sections indicates that it has grown up within less than a century. In fact, we are now witnessing the encroachment of the timber upon the prairie wherever the devastating conflagrations have ceased their ravages.

Bray (1901:209) in western Texas, even acknowledging then that this was not a new idea, stated:

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> Apparently under the open prairie regime the equilibrium was maintained by more or less regular recurrence of prairie fires. This, of course, is by no means a new idea, but the strength of it lies in the fact that the grass vegetation was tolerant of fires and the woody vegetation was not. It was only after weakening the grass floor by heavy pasturing and ceasing to ward off the encroaching species by fire that the latter invaded the grass lands.

Cook (1908:1–16) wrote about fire and woody encroachment in South Texas prairies:

> That such fires were evidently the cause of the former treeless condition of the southwestern prairies is also shown by the fact that trees are found in all situations which afford protection against fires.

Foster (1917:442–445) wrote, concerning central Texas:

> The causes which have resulted in the spread of timbered areas are traceable directly to the interference of man. Before the white man established his ranch home in these hills the Indians burned over the country repeatedly and thus prevented an extension of forest areas. With the settlement of the country grazing became the only important industry. . . .
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> . . . Overgrazing has greatly reduced the density of grass vegetation. . . . Almost unquestionably the spread of timbered areas received its impetus with the gradual disappearance of grassland fires and has been hastened by the reduction of the grass cover itself.

Recent review articles by Daubenmire (1968), Axelrod (1985), Anderson (1990), Bock and Bock (1995), Van Auken (2000) and Briggs et al. (2005) have all reaffirmed that fires were common and necessary to maintain Great Plains grasslands. Sauer (1950) and Bock and Bock (1995) concluded that there is no climatic condition that favors grassland over woodland. In other words, there is no combination of precipitation and temperature that is sufficient to allow grassland to replace desert, but that is insufficient for woodland to replace grassland. Thus, without fire, the soils and climate that support grasslands could, in most cases, support a shrubland or woodland as well.

Frost (1998) suggested the fire return interval in most of the Great Plains was <6 y, and in certain regions, <3 y. It is thought that most fires were caused by lightning strikes of dry vegetation. However, fires in some areas were ignited by Native Americans, either to assist hunting large game by surrounding them with a ring of fire, or kill small mammals and reptiles for food, or use as a means to stimulate lush herbaceous growth the following year to either attract game, such as bison (*Bison bison*), or to increase yields of seeds and berries (Axelrod 1985, Stewart et al. 2002). In some instances, they may have used fire to clear areas of brush or fires occurred accidentally (Foster 1917, Stewart et al. 2002).

Because lightning strikes are more frequent during summer thunderstorms, many fire ecologists believe that summer wildfires were more common than dormant-season (i.e., winter or spring) fires (Higgins 1986, Ewing and Engle 1988, Taylor 2001). The timing of the ignition of fires by Native Americans on southern Great Plains grasslands is largely unknown. Higgins (1986) indicated that, in the northern mixed-grass prairie of the Dakotas, most fires were ignited by Native Americans during fall (October) or early spring (April). Stewart et al. (2002) quoted several early explorers near St. Louis who witnessed late autumn burning by Native Americans. Jared Smith, referring to central Texas, wrote in 1899 that, ‘‘Weeds and brush were kept in check by the fires set by the Indians in early spring to improve pasturages. In this manner the encroaching of thorny shrubs, cactus and mesquite was prevented. . . .’’ (Smith 1899:7–8). While traveling in Oklahoma in October 1832, Washington Irving reported that he observed daily ‘‘haziness’’ from fires being ignited by Native Americans (Stewart et al. 2002:150). In contrast, Frost (1998) suggested that burning by Native Americans in the southern mixed-prairie regions of Oklahoma and North Texas coincided with lightning strike peaks in midsummer.

It is our opinion that it was more likely for Native Americans in the southern prairie to conduct dormant-season rather than summer fires, especially if the goal was to provide green growth in spring to attract bison and other game. Thus, if we make a very simplistic generalization and imagine that most lightning-strike fires occurred in summer and most Native American–ignited fires occurred during the dormant months (late fall, winter, or early spring), it is conceivable that fire could potentially have occurred most months of the year in the southern prairie. Thus, the long-term result prior to European settlement may have been a continually changing mosaic of summer-burned, dormant season–burned, and unburned patches of widely ranging and often overlapping sizes.

For this paper, we assumed that summer fires were common to the southern Great Plains prior to European settlement (Engle and Bidwell 2001). We review some of the research that has been conducted regarding responses of certain plant species to summer fires. In particular, we focus on our research in North Texas that has emphasized direct contrasts between summer fire and dormant-season (i.e., ‘‘winter’’) fire effects within the same experimental framework on the woody legume honey mesquite (*Prosopis glandulosa*), brown-spined prickly pear cactus (*Opuntia phaeacantha*), the C_4 midgrass sideoats grama (*Bouteloua curtipendula*), the C_4 shortgrass buffalograss (*Buchloe dactyloides*), and the C_3 midgrass Texas wintergrass (*Nassella leucotricha*). Research from other locations is also reviewed where it most strongly relates to our studies, but this is by no means a comprehensive review.

MESQUITE RESPONSE TO SUMMER FIRES

Most of the early research on fire effects on honey mesquite focused on effects of late-winter or early spring fires (Wright and Bailey 1982). This research provided little evidence that single winter fires will kill adult mesquite trees. Wright et al. (1976) and Britton and Wright (1971) found moderate adult honey mesquite mortality (50% and 32%, respectively) following single late-winter (March) fires in West Texas. However, the reason for even this level of mortality was that the mesquite had been sprayed with a top-killing herbicide (2,4,5-T) 2–5 y prior to burning, and when fire was applied, the standing dead stems from the herbicide treatment ignited and burned into live root crowns, killing the buds that would have developed basal sprouts. Because these fires occurred so soon after a herbicide treatment, we view these results as responses to a combined herbicide–fire treatment, rather than to effects of fire alone.

In contrast, Ansley and Jacoby (1998) found that no adult mesquite trees were killed following single high-intensity winter fires (average 2,435 kW/m intensity, 2.4 m flame height, 2,800 kg/ha fine fuel) in North Texas. In this study, mesquite had also been sprayed with top-killing herbicides, but fire treatments were not implemented until 11–26 y after the herbicide treatments. Because of this delay, most of the standing dead stems from the herbicide treatments had decayed and disappeared. This may explain why root-kill response to fire was so low. On another site in North Texas, Ansley and Castellano (2006) found that high-intensity winter fires (flame heights 2–5 m, fine fuel 3,150 kg/ha) killed only 3% of 2- to 3-m-tall honey mesquite.

The literature indicates that honey mesquite is not susceptible to summer fires, with respect to plant mortality, although few studies have quantified this. Less than 3% of adult mesquite trees were completely killed by intense summer fires (average 4,042 kW/m intensity), even after 2 summer fires in 3 y or consecutive summer fires and under moderate herbaceous fine fuel loads (2,800 kg/ha) (Ansley and Jacoby 1998). Recent studies in southern New Mexico found similar results for 10-y-old honey mesquite (height 0.8 m) (Drewa et al. 2001) or 0.5-m-tall honey mesquite (Drewa 2003). In South Texas, late-summer fires caused 10% honey mesquite mortality (Box et al. 1967). However, this evaluation was conducted <1 y post-fire and possibly overestimated mortalities because basal sprouting following top-kill is often delayed the first growing season post-fire.

Aboveground mortality (i.e., top-kill) of adult multistemmed honey mesquite has been found to be greater following summer fires than winter fires, but this may depend on composition of the herbaceous fine fuel vegetation. On a site that had a mixture of C_3 and C_4 grasses, top-kill was greater following summer (93%) than winter (33%) fire (Ansley and Jacoby 1998). However, on a site dominated by C_4 grasses, there was little difference in top-kill between summer (86%) and winter (70%) fires. The C_3 grasses on the mixed site (mainly Texas wintergrass) were somewhat green during winter fires, and this lowered fire intensity and reduced fire impact on mesquite canopies.

Research in Arizona during the last 60 y has investigated the effects of annual or biennial summer fires (mostly in June) on velvet mesquite (*Prosopis glandulosa* var. *velutina*). Humphrey (1949) found that summer fires caused 50% velvet mesquite mortality. Glendening and Paulson (1955) found only 15% mortality in adult velvet mesquite, but 52% mortality in mesquite seedlings following summer fire. Cable (1965) reported that a June fire killed 25% of mesquite on a high herbaceous fuel area (5,000 kg/ha), but only 8% on a lower fuel area (2,400 kg/ha). However, this evaluation was conducted at 1 y post-fire and possibly overestimated mortalities. Cable (1967) reported that a June fire reduced velvet mesquite density by 26% at 3 y post-fire. Reynolds and Bohning (1956) found 28% velvet mesquite mortality 2 growing seasons after June fires.

In studies that directly contrasted effects of summer and winter fires, Glendening and Paulson (1955) found that summer fires in June killed 29% of velvet mesquite, while winter fires killed only 4%. Blydenstein (1957) found that summer fires killed 5% of velvet mesquite, while winter fires yielded only 1% mortality. Thus, in these studies in Arizona, mortality of mature velvet mesquite from summer fires ranged from 5 to 50%, and averaged 23%.

In summary, these results indicate that one or two fire events, either in winter or summer, will not kill many adult honey mesquite trees. On sites with a high percentage of C_3 grasses, summer fire has a greater potential than winter fire for top-killing mesquite. Summer fire has caused greater mortality on adult velvet mesquite in Arizona than on honey mesquite in Texas and New Mexico.

It remains unknown as to whether or not a historical pattern of frequent fire was successful in killing the majority of honey mesquite plants that encroached into the southern Great Plains, although this is widely assumed (Gregg 1844, Van Auken 2000, Stewart et al. 2002). Wright et al. (1976) found that nearly 100% of honey mesquite seedlings that were 1.5 y old or younger were killed by fire, but mortality ranged from 20 to 72% in 2.5-y-old seedlings, depending on fire temperature, and was only 8% in 3-y-old seedlings. Thus, mesquite developmental resistance to fire may occur more rapidly than what is believed to be the historical fire regime for the southern Great Plains (Frost 1998).

PRICKLY PEAR RESPONSE TO SEASONAL FIRES

Little research has been published that has contrasted effects of summer and winter fires on prickly pear cactus. In a recent study, we (Ansley and Castellano 2007*a*) compared brown-spined prickly pear response to summer fires (7,446 kW/m intensity), high-intensity winter fires (4,314 kW/m), low-intensity winter fires (791 kW/m), and unburned controls. At 3 y post-treatment, mortality of individual prickly pear mottes (size ranging from 10 to 500 pads per motte) was 86% in summer fire and <16% in all other treatments. Similarly, Taylor (2001), in the Edwards Plateau of south-central Texas, found that summer and winter fires reduced prickly pear density by 97% and

47%, respectively. Thus, while winter fires may have some effect on reducing prickly pear, summer fires are clearly superior in reducing density of this species when it has become dominant.

These results differ from the findings of Bunting et al. (1980), who demonstrated that winter fires effectively killed brown-spined prickly pear in West Texas. For reasons explained earlier with honey mesquite, the region where the study of Bunting et al. (1980) occurred is dominated by C_4 grasses instead of C_3 grasses, and one might expect fewer differences in responses to summer and winter fires. However, effects of summer and winter fires were not directly compared in the study (Bunting et al. 1980).

Much anecdotal evidence suggests that most ranchers in the southern Great Plains are not satisfied with the level of prickly pear control winter fires yield. This is especially true in areas where C_3 grasses, such as Texas wintergrass and annual bromegrasses (*Bromus* spp.), dominate. For these areas, it appears that summer fire may be necessary to gain effective control over pastures dominated by prickly pear cactus.

HERBACEOUS RESPONSES TO SUMMER FIRES

The literature is quite varied on assessment of individual grass species responses to summer-season fires. Part of the problem in interpretation arises from the differences in variables used to assess herbaceous responses. Many studies have taken an autecological approach and measured post-fire production of individual grass species over time (Reynolds and Bohning 1956, Cable 1967, Engle and Bultsma 1984, Whisenant et al. 1984). Those species that recover more slowly, usually in comparison to an unburned control, are generally viewed as fire intolerant. However, as mentioned earlier, this may be misleading because of the short-term nature of many fire studies. Other studies have measured ecosystem-level changes in species composition following fire (Steuter 1987, Biondini et al. 1989, Engle et al. 2000). Common variables used are species frequency of occurrence, richness, and/or percent basal cover. Those species that decreased relative to other species within the community matrix were viewed as less fire tolerant.

Sideoats Grama (C_4 Midgrass)

Ansley et al. (2006*b*) found in North Texas that sideoats grama end-of-growing-season total weight (live + dead) in the absence of grazing or clipping fully recovered from winter fires in 2 y, while it took 3 growing seasons to recover from summer fires (Figure 1). Fine fuel and peak fire temperature averaged 4,340 kg/ha and 718°C in winter and 4,205 kg/ha and 679°C in summer fire, respectively. Live yields recovered more rapidly than did total yields, and there was no difference in live yields between summer fire, winter fire, and the no-fire control by 2 y post-fire (data not shown). Annual spring clipping in addition to the fire treatments reduced total yields to a greater degree

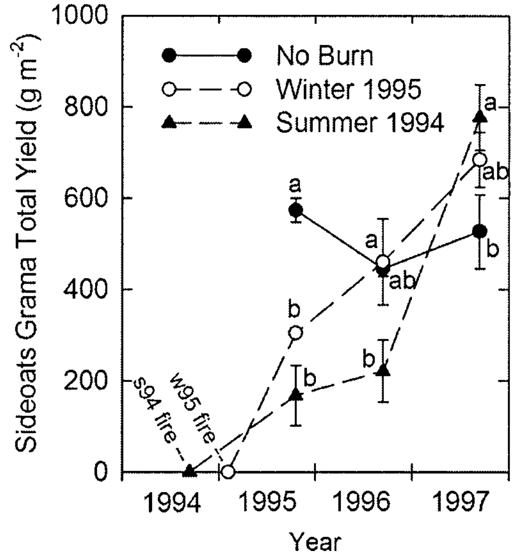

Fig. 1. Sideoats grama end-of-growing-season total standing crop following fires in summer 1994 (s94) or winter 1995 (w95) in North Texas. Means with similar letters within years are not significant ($P < 0.05$). Vertical bars are ±1 SE. (Figure adapted from Ansley et al. 2006*b*.) Copyright © 2006 Society for Range Management. From *Rangeland Ecology and Management,* by R.J. Ansley, M.J. Castellano, and W.E. Pinchak. Reprinted by permission of Alliance Communications Group, a division of Allen Press, Inc.

in the no-fire and winter fire treatments than in the summer fire treatment when measured 1 y after clipping (Figure 2). At 5 y post-fire, a severe drought greatly reduced growth in the no-fire treatment, but high yields in both summer and winter fire treatments were maintained.

Wright (1974) found in West Texas that sideoats grama yields were reduced by 40–45% for the first 2 y after winter fires. These studies measured responses of the rhizomatous growth form of sideoats grama to fire, and Wright (1974:418) concluded that this form ‘‘never benefits from fire,’’ even if fires occur in the dormant season. Wright’s conclusions regarding sideoats grama responses to fire were based on 1–2 y of post-fire data. However, as stated previously, duration of post-fire measurements can affect interpretation of species tolerance to fire. Our study revealed that sideoats grama needed 3 y to recover fully and exceeded the no-fire control by 5 y post-fire (Ansley et al. 2006*b*). Taylor (2001) found in central Texas that sideoats grama frequency of occurrence increased to a greater degree 6 y after a summer fire than after either a winter fire or no fire. In New Mexico, summer fires increased sideoats grama cover by >100% (Brockway et al. 2002).

Several studies in the tallgrass prairie of the central Great Plains show a marked decline in C_4 midgrass and tallgrass production the first year after a summer fire but a recovery to pre-burn or unburned levels by the second or third year (Engle and Bultsma 1984; Ewing and Engle 1988; Engle et al. 1993, 1998; Engle and Bidwell 2001). In contrast, some C_4 bunchgrasses, such as threeawn (*Aristida* spp.), have elevated growing points and are killed by fire, especially summer

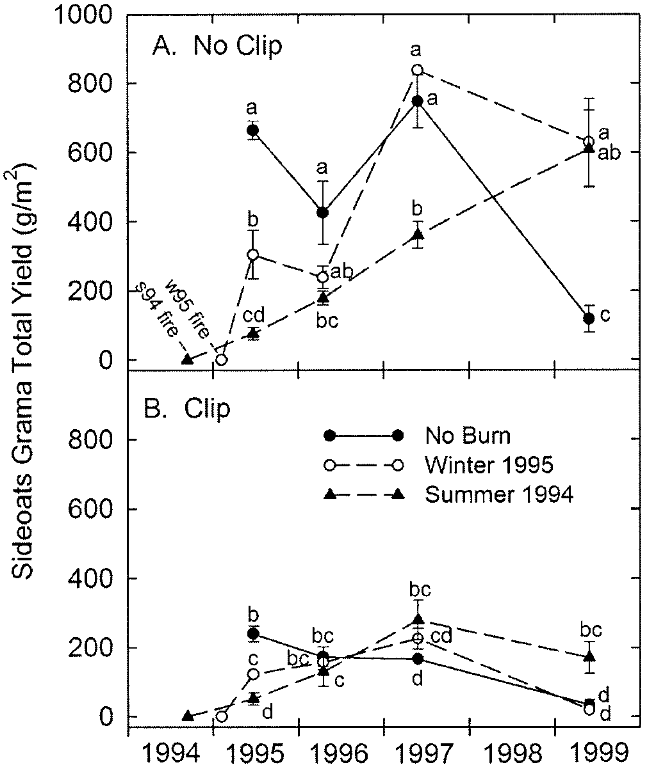

Fig. 2. Sideoats grama spring-season total standing crop following fires in summer 1994 (s94) or winter 1995 (w95) when unclipped (A) or clipped once each spring (B) in North Texas. Means with similar letters within years and across both panels are not significant ($P < 0.05$). (Figure adapted from Ansley et al. 2006*b*.) Copyright © 2006 Society for Range Management. From *Rangeland Ecology and Management,* by R.J. Ansley, M.J. Castellano, and W.E. Pinchak. Reprinted by permission of Alliance Communications Group, a division of Allen Press, Inc.

fires (Owensby and Launchbaugh 1977). In South Africa, Everson et al. (1985) and Trollope (1987) indicated that recovery of C_4 red grass (*Themeda triandra*) was significantly delayed by summer fire.

In summary, several studies have documented that C_4 midgrass and tallgrass species can survive summer fires and eventually fully recover from the disturbance. Recovery rates may be slower than what would occur following winter fires, although empirical evidence for this is not abundant.

Buffalograss (C_4 Shortgrass)

In a recent study in North Texas (Ansley and Castellano 2007*b*), buffalograss end-of-growing-season total weight in the absence of grazing or clipping recovered from both summer and winter fires the first growing season post-fire and exceeded the no-fire control by 3 y post-fire. Annual clipping once each spring in addition to either the summer or winter fire treatments did not have a negative effect on buffalograss yields when measured 1 y after clipping. The only time we have observed buffalograss to be negatively affected by summer fire was when it was exposed to 2 summer fires in consecutive years (with no clipping treatment). In this case, a community that was approximately 60% buffalograss and 40% Texas wintergrass shifted to >90% Texas wintergrass (R.J. Ansley, unpublished data).

Other studies have found variable responses of buffalograss to summer fires. Buffalograss increased significantly following late-summer (September) fires on the Welder Wildlife Refuge in South Texas (Box et al. 1967). However, in New Mexico shortgrass prairie, summer fires reduced buffalograss cover from 5.7 to 0.5% (Brockway et al. 2002).

Other C_4 shortgrass species, such as blue grama (*Bouteloua gracilis*) and common curly-mesquite (*Hilaria belangeri*), appear tolerant of summer fires (Trlica and Schuster 1969, Mayeux and Hamilton 1988, Brockway et al. 2002). In contrast, in Southwest desert grasslands of New Mexico and Arizona, black grama (*Bouteloua eriopoda*) has been severely damaged by summer fire and may take up to 50 y to recover (Reynolds and Bohning 1956, Cable 1965, Drewa and Havstad 2001).

In summary, few studies have examined the effect of summer fire on buffalograss or other C_4 shortgrass species. However, the literature suggests that, with the exception of black grama, C_4 shortgrass species in general appear to be tolerant of summer fires and recovery rates are often more rapid than for C_4 midgrass species. However, it must be emphasized that very few studies have clearly documented this.

Texas Wintergrass (C_3 Midgrass)

In a recent study in North Texas, there were no negative long-term effects of winter or summer fires on Texas wintergrass total standing crop in the absence of grazing or clipping (Ansley and Castellano 2007*b*). The additional stress of annual spring clipping reduced total weights in the winter fire treatment, but not the summer fire or no-fire treatments when measured 1 y later. Thus, clipping (to simulate grazing) in spring exacerbated the negative effects of winter fire, but not summer fire.

Whisenant et al. (1984) found on one site in central Texas that Texas wintergrass standing crop was significantly reduced the first June following either a late-summer (September), winter (January), or late-winter (March) fire. By the second growing season post-fire, there was no difference in standing crop between fire and no-fire treatments. On a second site, Whisenant et al. (1984) found no differences in Texas wintergrass standing crop between the no-fire and the same 3 fire treatments either the first June or second growing season post-fire. In South Texas chaparral, Box and White (1969) found that Texas wintergrass herbage production was reduced to a greater degree by late-summer fires than by winter fires. Engle et al. (1998) found that two late-summer fires in tallgrass prairie increased Texas wintergrass production by 40% compared with no-fire controls on both a shallow and a deep soil site in Oklahoma.

In summary, with the exception of the study by Box and White (1969), Texas wintergrass appeared to be tolerant of summer fire with or without clipping to simulate grazing. The only time fire negatively affected Texas wintergrass was when spring clipping followed winter fire. Anecdotal observations often report an increase in dominance of Texas wintergrass following summer fires, and some studies support this observation. However, more research is needed to adequately document this response.

Herbaceous Composition Responses to Summer Fire

There is limited information on effects of summer fires on Great Plains herbaceous composition. Negative response to fire is hypothesized to increase if grass species are physiologically active at the time of burning (Daubenmire 1968, Howe 1994, Engle and Bidwell 2001). Thus, with respect to herbaceous species composition, in mixed stands of C_3 and C_4 herbaceous species, we might expect to see a shift toward C_4 species and away from C_3 species following winter or early spring fires, and the opposite following summer or early fall fires.

There is evidence that in northern and central Great Plains communities, spring fires will shift a mixed C_3–C_4 grass community toward a greater C_4 presence (Anderson et al. 1970; Engle and Bultsma 1984; Steuter 1987; Howe 1994, 1995, 2000). There is less evidence that summer fires will shift mixed C_3–C_4 communities toward a greater C_3 dominance. Steuter (1987) found in northern mixed prairie of South Dakota that summer fires shifted composition toward C_3 species, and Howe (1995) found in anthropogenically seeded C_3–C_4 mixed-grass plots in Wisconsin that summer fires retarded C_4 grasses and favored C_3 species. However, in other studies in Wisconsin, Howe (1994, 2000) found that summer fires maintained a mix of C_3 and C_4 grasses, and thus increased diversity, but did not strongly favor C_3 grasses.

In the tallgrass prairie regions of Oklahoma, Engle et al. (2000) found that edaphic features and time since the last fire were the most important factors determining species composition on two Oklahoma prairie sites, but that summer fire did not necessarily cause long-term shifts in species composition. Ewing and Engle (1988) found in Oklahoma that a summer fire increased C_3 annual grass and decreased C_4 perennial grass production the first year post-fire, but long-term responses were not available. Coppedge and Shaw (1998) found in Oklahoma tallgrass prairie that summer fires increased C_3 sedges (*Carex* spp.), annual bromegrasses and forbs, and decreased C_4 tallgrasses and little bluestem (*Schizachyrium scoparium*) when compared with winter fires. These measurements were only made the first growing season post-fire, and long-term shifts in composition are not known. However, Engle and Bidwell (2001) concluded that summer fires do not cause long-term changes in species composition.

In South Texas, Owens et al. (2002) found no major shifts in species composition following summer fires. In North Texas, Texas wintergrass basal cover increased following summer fires but did not displace cover of C_4 grasses (R.J. Ansley, unpublished data). Texas wintergrass usually increased into areas that were either bare ground or undefined litter prior to the fire. As indicated earlier, we found only one situation in North Texas, when summer fires were applied in two consecutive years, where Texas wintergrass actually replaced the dominant pre-fire grass, C_4 buffalograss (R.J. Ansley, unpublished data).

Numerous studies report increases in forb populations following fires. This appears to be true following repeated spring fires in northern mixed prairie (Biondini et al. 1989; Howe 1994, 1995), and in tallgrass prairie of eastern Kansas (Knapp et al. 1998), Oklahoma (Engle et al. 1993, 1998), and South Texas (Owens et al. 2002). Summer fires may drastically reduce grass production for several years (Engle and Bultsma 1984), but also can greatly increase subdominant species diversity, largely through increases in C_3 forbs (Biondini et al. 1989, Howe 1994, Drewa and Havstad 2001, Copeland et al. 2002). Summer fires appear to increase forbs to an even greater extent than do dormant-season fires (Biondini et al. 1989). For example, in North Texas, Tunnell and Ansley (1995) found much greater cover of common broomweed (*Amphiachyris dracunculoides*) the first growing season following summer (35%) than winter fires (3%). However, Box et al. (1967) found just the opposite result in South Texas: late-summer fires decreased forbs, while dormant-season fires increased forbs. The increase or decrease in forbs in response to summer fires may be viewed as a positive or negative response, depending on the desired land-use objective (Engle et al. 1993). Generally those with a wildlife management perspective would view an increase in forbs and species diversity as a positive response.

We are thus left with a mixed interpretation of summer fire effects on herbaceous composition but, in general, it appears that dormant-season fires are better able to shift C_3–C_4 communities to C_4 dominance than are summer fires in shifting such communities toward C_3 dominance. Of those studies that document summer fires shifting species composition toward C_3 dominance, most have been located in the northern Great Plains (Steuter 1987; Howe 1994, 1995). This may simply mean that there are more studies of this nature in the northern Great Plains, or it may indicate that such a response occurs more readily in the northern Great Plains than in the southern Great Plains.

MANAGEMENT IMPLICATIONS

In all the research we have reviewed, most grass species appear to be tolerant of summer fire. An important exception is black grama in Southwest desert grasslands that appears to be very sensitive to fire, and some *Aristida* species. Prickly pear cactus is more susceptible to summer fires, and it is not difficult to imagine how the loss of summer fires in southern prairie ecosystems facilitated an increase in this species. Some woody species like honey mesquite may not be killed by fire, even after repeated summer fires of moderate to high intensity (flame heights 2–5 m) and burned with moderate herbaceous fine fuel loads (2,000–3,000 kg/ha). These fires successfully top-kill most mesquite, but basal regrowth is stimulated. Fire must thus be applied repeatedly for sustained suppression of this species (Ansley and Jacoby 1998). Frequency of fire application depends on rate of woody regrowth but, typically, a fire every 7 to 10 y is considered adequate across most of the southern Great Plains (Scifres and Hamilton 1993). An important concept in fire application in mesquite-dominated systems is the necessity of managing livestock grazing to allow for an accumulation of an adequate herbaceous fine fuel amounts to facilitate the frequent use of fire (Scifres and Hamilton 1993, Teague et al. 1997).

Stewart et al. (2002:149) commented on how the loss of fire caused woody encroachment in Texas grasslands and how repeated prescribed fire was needed to restore such grasslands:

> . . . grasslands were burned by Indians, and under the grazing by wild game such burning kept woody growth from becoming important. The early ranchers continued the Indian practice with the same results. With ever increasing herds of cattle and sheep, grasses were so reduced that the fires could no longer check the expansion of shrubs and trees. Without a thick stand of grass to carry the flames and produce sufficiently destructive heat, fires could no longer destroy brush. A very careful control of burning and grazing would be required to restore the grasslands to their presettlement condition and such control would have to be continued if fire were to serve the purpose it did for the Indians.

We would add that additional summer fires from lightning may have played a significant role in maintaining grasslands in the southern prairie and that, because of this, prescriptions for summer fires are necessary to aid in the grassland restoration process (Ansley and Taylor 2004). Further research is needed to identify safe and effective summer fire prescriptions and responses of other plant species as well as other components of the ecosystem, such as soil nutrients (Ansley et al. 2006*a*), before broad-scale recommendations for summer fire as a management practice can be made.

In addition, because no research to date has documented that fire in any season can kill a very high percentage of adult honey mesquite, it is our opinion that a few fire events alone cannot return heavily wooded stands of mesquite to grassland (Ansley and Castellano 2006). Thus, a repeated fire regime to maintain suppression of regrowth may be the best option unless an additional treatment, such as a herbicide or mechanical extraction, is employed. Because summer fires are inherently a greater risk to apply safely than are dormant-season fires (Ansley and Taylor 2004), one possible management scenario would be to initially apply a summer fire to top-kill a majority of the mesquite trees, assuming mesquite encroachment is not so high that it would prevent growth of an adequate herbaceous fine fuel, then follow up with a repeated fire regime that includes mostly dormant-season fires.

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