

# INTERACTIONS BETWEEN FIRE AND INVASIVE PLANTS IN TEMPERATE GRASSLANDS OF NORTH AMERICA

James B. Grace

U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, LA 70506

Melinda D. Smith

Division of Biology, Kansas State University, 232 Ackert Hall, Manhattan, KS 66506

Susan L. Grace<sup>1</sup>

U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, LA 70506

Scott L. Collins

Division of Biology, Kansas State University, 232 Ackert Hall, Manhattan, KS 66506

Thomas J. Stohlgren

U.S. Geological Survey, Midcontinent Ecological Science Center, Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO 80523

## ABSTRACT

A substantial number of invasive grasses, forbs and woody plants have invaded temperate grasslands in North America. Among the invading species are winter annuals, biennials, cool-season perennials, warm-season perennials, vines, shrubs, and trees. Many of these species have been deliberately introduced and widely planted; some are still used for range improvement, pastures, lawns, and as ornamentals, though many are listed as state or federal noxious weeds. Others have been greatly facilitated by widespread land disturbance. Historically, fire has been a major selective force in the evolution of temperate grasslands. Further, prescribed fire is commonly used as a method of ecological management for native grassland communities as well as in conjunction with restoration efforts. Within this context, it is important to understand how invasive species will interact with natural and prescribed fire regimes.

In this paper, we consider what is known about how exotic species that invade temperate grasslands relate to fire. The primary issues addressed for each species are (1) Does fire appear to enhance colonization? (2) To what degree does fire affect the survival of plants? (3) Are plants that are burned able to regrow following fire and, if so, how rapidly can they recover? (4) How important is competition with native species to the response to fire? and (5) What effect does an invasive species have on the characteristics of the fire regime? For many species, results are preliminary, incomplete, or inconsistent among studies. For this reason, many of the conclusions drawn for individual species must be considered preliminary.

Based on analyses of individual species, a conceptual framework is presented for considering how invasive plants may interact with fire when they invade an ecosystem. The major categories of influences are the native community, the fire regime, growth conditions for both invasive and native species, and influences that disturbances, human impacts, and landscape characteristics have had in the past and will have in the future.

The examples considered in this paper provide support for a few, tentative generalizations. First, among our current worst invaders of temperate grasslands, adaptation to fire is quite variable. Some species are not well adapted to burning and can be easily eliminated; other species are better adapted but can still be eliminated if fire occurs during periods of particular vulnerability and/or at high frequency. There is a set of species that is extremely well adapted to fire and will not be eliminated through burning alone. Second, competitive interactions with native species play a crucial role in the success of nonnative invaders. In cases where differential burn responses between invasive and native species can be exploited, and adequate populations of native dominant species are present, fire can sometimes tip the competitive balance away from invasives. Third, there are a few invasive species that have exceptional attributes and for which there are no easy solutions. The ability of cheatgrass (*Bromus tectorum*) to enhance fire, the ability of Chinese tallow (*Triadica sebifera*) to suppress fire, and the ability of leafy spurge (*Euphorbia esula*) to resprout from repeated injury make these species exceptional threats to native diversity. Finally, the available information for many invasive species is very incomplete, particularly with regard to how fire affects competitive interactions with the native community. There is much more we need to know if we are to consistently predict how invasive species will respond to fire and how burning can best be used to manage for natural diversity.

*keywords:* alien plants, exotic species, invasive plants, grasslands, fire, prairie.

*Citation:* Grace, J.B., M.D. Smith, S.L. Grace, S.L. Collins, and T.J. Stohlgren. 2001. Interactions between fire and invasive plants in temperate grasslands of North America. Pages 40–65 in K.E.M. Galley and T.P. Wilson (eds.). 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. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

<sup>1</sup> Present address: U.S. Fish and Wildlife Service, Fire Management Field Office, 13093 Henry Beadel Drive, Tallahassee, FL 32312.

## INTRODUCTION

Temperate grasslands include some of the most threatened ecosystems in the world (Ricketts et al. 1999). In North America, the widespread use of grasslands for agriculture and livestock grazing, in addition to the effects of urbanization and other human activities, have led to dramatic losses in their extent and integrity. A major threat to conservation, rehabilitation, and restoration of temperate grasslands comes from invasive plants (Westbrooks 1998, Smith and Knapp 1999, Stohlgren et al. 1999a). Examples of invasions of temperate grasslands by nonnative plants indicate that the success and consequences of an invasion are strongly dependent on many factors, including fire. Because of the historic importance of fire in the development of these grassland systems, the interactions between invasive species and fire can be expected to be of particularly critical importance. A wide variety of types of interactions between invading species and fire regimes are possible. In some cases, fire may act as an environmental filter that eliminates or reduces nonnative invaders. In other cases, we can expect that fire-adapted invaders will be quite impervious to burning. Fire suppression may, in certain situations, provide a window of opportunity for the establishment of nonnative elements that may not be easily displaced once they have established. In other situations, fire may facilitate the invasion and spread of exotic plants. Species that successfully invade and become dominant may, themselves, radically change the fire regime and have detrimental effects on the native community thereby. Both the natural characteristics of a landscape and human modifications of that landscape can be expected to influence the interaction between invader and native communities profoundly in many ways. Further, the interaction between fire and invasives can be complicated by additional factors such as grazing and other disturbances (Collins et al. 1995, 1998, Stohlgren et al. 1999b). In this paper, we first present an overview of the major exotic invasive plant species that threaten temperate (as distinct from arid or tropical) grasslands in North America and then consider what is known about how some of these species interact with fire regimes. Finally, we place the available information in a framework that both summarizes the relationships between fire and invasives and suggests areas for future research. We recognize that various definitions exist for what constitutes an "invasive" species. In this paper, we focus on species that are not native to North America (i.e., exotic species) and that are capable of establishing populations outside of cultivation. Many of the principles discussed in this paper can also be applied to native species that are outside of their natural ranges or that have proliferated due to human activities; however, such species will not be emphasized in this paper.

## TEMPERATE GRASSLANDS OF NORTH AMERICA

In his overview of grasslands of North America, Coupland (1992) emphasized that the greatest expanse

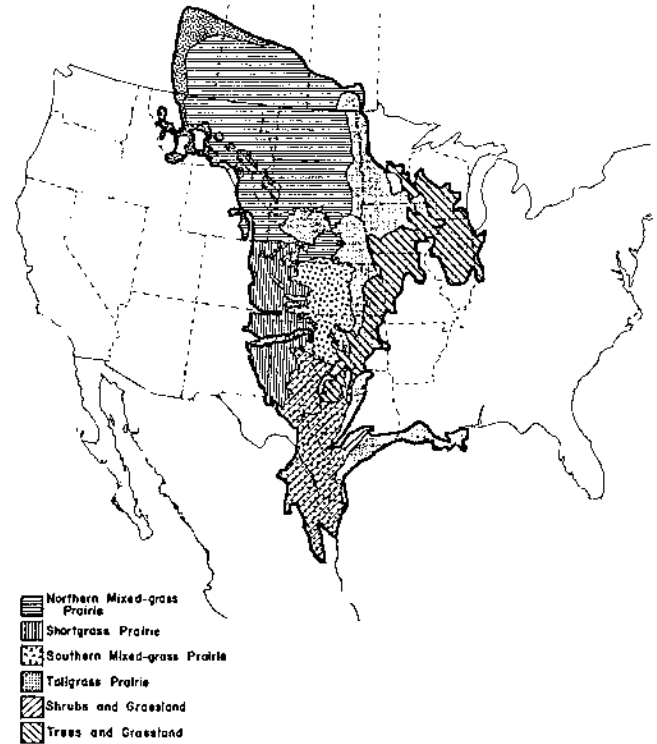


Fig. 1. Map of North America showing approximate distribution of temperate grasslands. Adapted from Risser et al. (1981).

of temperate grasslands occurs between the Rocky Mountains and the eastern deciduous forest (Figure 1). Included within this area are tallgrass prairie in the east, coastal prairie in the south, mixed prairie throughout much of the Great Plains, fescue prairie in the northwest, and shortgrass steppe in the westcentral to southwest. This area includes most of the temperate grassland types described by Kuchler (1964), though he recognized several additional, smaller types: the southern cordgrass marshes (along the Gulf of Mexico coast), the northern cordgrass marshes (along the Atlantic coast), the palmetto prairie (in central Florida), and the sea oats prairie (off the coast of south Texas).

In addition to these larger expanses of prairie that form distinct ecoregions (e.g., see Ricketts et al. 1999), temperate grasslands extend well into the Rocky Mountain region and also occur scattered throughout the eastern deciduous biome and the northern coniferous forest. As with all attempts to classify natural patterns of variation, we should recognize that temperate grasslands intergrade into arid grasslands and savannas of various types in many different geographic locations.

Within the region and areas occupied by temperate grasslands, there exists a great range of climate, topography, and soil conditions. Further, riparian and wetland habitats embedded within the temperate grassland region represent both additional variation in the ecological conditions and important areas of native biodiversity. Aside from major gradients in climate and soils, historic land-use practices also vary considerably among temperate grasslands. In the east, tillage agriculture eliminated huge fractions of the pre-

Columbian extent of tallgrass prairie. This generalization applies equally to the coastal prairie in the south. In many areas, less than 1% of the original prairie remains and this is broken into many small fragments scattered across the landscape. Many of the larger tallgrass remnant prairies are differentially representative of shallow and rocky soils that were less suitable for tillage agriculture. As one moves to the west, increasing use of grasslands for grazing is the trend, which means that much larger expanses of prairie remain, although a high percentage of these have been substantially altered. Further, in most situations, wetland and riparian habitats may differ in the magnitude and nature of historical anthropogenic impacts relative to the surrounding terrestrial landscape. In areas where wetlands were small and isolated, there was a tendency for many to be eliminated through drainage and tillage. In areas of extensive wetlands, such as those along the Gulf of Mexico coast, wetland communities are much less heavily impacted than adjacent terrestrial communities due to the physical difficulties of farming and grazing these habitats. Because of the great range of conditions included within temperate grasslands, we try to specify the ecosystem type to which various generalizations about invasive species and fire apply as much as possible.

### INVASIVE SPECIES THAT IMPACT OR THREATEN TEMPERATE GRASSLANDS

A substantial number of exotic plants currently occur in temperate grasslands of North America (Table 1). These species range from those with very broad current distributions and well-documented impacts—such as cheatgrass, smooth brome (*Bromus inermis*), tamarisk (*Tamarix* sp.), leafy spurge, spotted knapweed (*Centaurea biebersteinii* [= *C. maculosa*]), and Canada thistle (*Cirsium arvense*)—to others that are either of increasing concern (e.g., Caucasian bluestem [*Bothriochloa bladhii*], itchgrass [*Rottboellia cochinchinensis*], guineagrass [*Urochloa maxima*]), restricted to a limited portion of the range of grassland types (e.g., Angleton bluestem [*Dichanthium aristatum*]) or whose status is less well documented.

Invasive species of concern vary depending on geographic region. Of greater importance in the northern portion of the temperate grassland region are leafy spurge, cheatgrass, smooth brome, knapweeds (*Centaurea* spp.), Canada thistle, musk thistle (*Carduus nutans*), yellow starthistle (*Centaurea solstitialis*), sweetclovers (*Melilotus* spp.), Dalmation toadflax (*Linaria dalmatica*), and Kentucky bluegrass (*Poa pratensis*). In the southern portion of the Great Plains, guineagrass, Bermudagrass (*Cynodon dactylon*), sericea lespedeza (*Lespedeza cuneata*), Johnsongrass (*Sorghum halepense*), Chinese tallow, Macartney rose (*Rosa bracteata*), as well as Caucasian bluestem and several other escaped pasture grasses, are the most frequently mentioned species. Riparian and wetland habitats in many parts of the central United States have been invaded by tam-

Table 1. List of nonnative, invasive plants of major concern in the central grasslands of the United States. List based in part on Burkett et al. (2000). Scientific names are from the Integrated Taxonomic Information System (<http://www.itis.usda.gov/>).

Common name	Scientific name
<b>Grasses</b>	
Angleton bluestem	<i>Dichanthium aristatum</i>
Bahiagrass	<i>Paspalum notatum</i>
Bermudagrass	<i>Cynodon dactylon</i>
Buffelgrass	<i>Pennisetum ciliare</i> var. <i>ciliare</i>
Caucasian bluestem	<i>Bothriochloa bladhii</i>
Cheatgrass	<i>Bromus tectorum</i>
Cogongrass	<i>Imperata cylindrica</i>
Crested wheatgrass	<i>Agropyron cristatum</i>
Fountain grass	<i>Pennisetum glaucum</i>
Giant reed	<i>Arundo donax</i>
Giant sugarcane plumegrass	<i>Saccharum giganteum</i>
Guineagrass	<i>Urochloa maxima</i>
Itchgrass	<i>Rottboellia cochinchinensis</i>
Japanese brome	<i>Bromus japonicus</i>
Johnsongrass	<i>Sorghum halepense</i>
Kentucky bluegrass	<i>Poa pratensis</i>
King Ranch bluestem	<i>Bothriochloa ischaemum</i>
Kleberg bluestem	<i>Dichanthium annulatum</i>
Lehmann lovegrass	<i>Eragrostis lehmanniana</i>
Orchardgrass	<i>Dactylis glomerata</i>
Quackgrass	<i>Elymus repens</i>
Ryegrass	<i>Lolium</i> spp.
Smooth brome	<i>Bromus inermis</i>
Vaseygrass	<i>Paspalum urvillei</i>
<b>Forbs</b>	
Brazilian vervain	<i>Verbena brasiliensis</i>
Canada thistle	<i>Cirsium arvense</i>
Common mullein	<i>Verbascum thapsus</i>
Crown vetch	<i>Coronilla varia</i>
Dalmatian toadflax	<i>Linaria dalmatica</i>
Diffuse knapweed	<i>Centaurea diffusa</i>
Garlic mustard	<i>Alliaria petiolata</i>
Japanese climbing fern	<i>Lygodium japonicum</i>
Kochia	<i>Kochia prostrata</i>
Leafy spurge	<i>Euphorbia esula</i>
Missouri bladderpod	<i>Lesquerella filiformis</i>
Musk thistle	<i>Carduus nutans</i>
Ox-eye daisy	<i>Leucanthemum vulgare</i>
Purple loosestrife	<i>Lythrum salicaria</i>
Red-horned poppy	<i>Glaucium corniculatum</i>
Russian knapweed	<i>Acroptilon repens</i>
Scotch thistle	<i>Onopordum acanthium</i>
Sericea lespedeza	<i>Lespedeza cuneata</i>
Spotted knapweed	<i>Centaurea biebersteinii</i>
Squarose knapweed	<i>Centaurea triumfettii</i>
White sweetclover	<i>Melilotus alba</i>
Whitetop	<i>Cardaria draba</i>
Yellow sweetclover	<i>Melilotus officinalis</i>
Yellow starthistle	<i>Centaurea solstitialis</i>
Yellow toadflax	<i>Linaria vulgaris</i>
<b>Woody Species</b>	
Chinese privet	<i>Ligustrum sinense</i>
Chinese tallow	<i>Triadica sebifera</i>
European buckthorn	<i>Rhamnus cathartica</i>
Japanese honeysuckle	<i>Lonicera japonica</i>
Macartney rose	<i>Rosa bracteata</i>
Multiflora rose	<i>Rosa multiflora</i>
Russian olive	<i>Elaeagnus angustifolia</i>
Tamarisk	<i>Tamarix</i> spp.

arisk, Russian olive (*Elaeagnus angustifolia*), and purple loosestrife (*Lythrum salicaria*). In southern marshes and wetlands, additional invaders include giant reed (*Arundo donax*).



Ecological restoration is a topic of increasing importance related to invasive species and fire. Because restoration efforts often start with abandoned agricultural fields and must go through a fairly complete successional process, these sites are especially prone to invasion by a wide range of exotic species. For example, at the Walnut Creek National Wildlife Refuge in Iowa, where staff are currently restoring thousands of acres of former tallgrass prairie, one of the most problematic species is crown vetch (*Coronilla varia*). At present, prescribed fire does not seem to control this species on these restoration sites, though clearly more information is needed (C. Shutte, U.S. Fish and Wildlife Service, personal communication).

The species discussed in this paper, including those in Table 1, represent only a small fraction of the exotic species currently occurring in temperate grasslands. For example, a preliminary assessment of the flora of the coastal prairie (L.K. Allain, U.S. Geological Survey, unpublished) has identified over 150 non-native species in this type of prairie alone. Of the 304 grass species in Texas coastal prairies and marshes, 85 (26%) are introduced (Hatch et al. 1999). Our knowledge about the full suite of introduced species in grasslands and how they relate to fire is very incomplete. Similarly, potential threats posed by species that have not yet established substantial populations in temperate grasslands are unknown. Many questions remain unanswered: Will major invaders of arid grasslands gradually increase their effects on shortgrass steppe? How many of the recent invaders in Florida will be able to move along the Gulf of Mexico coast to south Texas? What will be the next major invader brought in from overseas? As these questions suggest, the bulk of the information summarized in this chapter represents a snapshot of our present knowledge about currently important invaders that have received significant scrutiny. While certain generalizations may apply to invaders, experience tells us that particular species-specific effects are often highly important and will be difficult to anticipate without a great deal more information than currently available.

## WHAT DO WE KNOW ABOUT THE INTERACTION OF INVASIVE SPECIES WITH FIRE IN TEMPERATE GRASSLANDS?

In this section, we briefly summarize what is known about how some of the more important invasive species relate to fire. To emphasize the dynamic nature of invasions, we also include examples from species that do not currently occupy a major place in grasslands of the central United States, but which appear to have the potential to have major impacts in the future. After examining species-specific interactions with fire, we will attempt to generalize across these examples and will present a framework for considering how invasive species interact with fire regimes.

### Grasses

#### *Cheatgrass*

Cheatgrass (*Bromus tectorum*) is reported to have been accidentally introduced from Mediterranean Europe into the northwestern United States during the 1880s (Mack 1981), though it was later introduced deliberately for forage trials (Carpenter and Murray 1999). Currently, cheatgrass occurs throughout the United States and southern Canada, though it is less common in the southern states. It now occupies grasslands in major parts of Washington, Idaho, Oregon, Nevada, and Utah (Morrow and Stahlman 1984). It is also a significant and increasing component of grasslands along the eastern front range of the Rocky Mountains (Carpenter and Murray 1999).

Cheatgrass is perhaps the single most important invader in major portions of western grasslands, shrublands, savanna, and desert (Knapp 1996). As a result, other papers in this volume deal extensively with this species and, for this reason, we will provide only a brief synopsis of its known relationship to fire. For more information, consult the papers by Brooks and Pyke, and Keeley.

Cheatgrass is an annual that is able to complete its life cycle in the spring before the dry summer weather begins. The phenology of this species is particularly important to both its desirability as an early season forage grass and to its ability to compete with native species, survive fire, and alter fire regimes. It can germinate from fall through spring whenever moisture conditions are suitable, and growth proceeds throughout the winter irrespective of cold temperatures. There is evidence that by-products of combustion during burning can enhance seedling growth (Blank and Young 1998). Rapid early growth allows it to set seed before most other species and once it begins to senesce, its persistent litter produces a highly flammable fuel that can greatly increase fire frequency in many, especially arid, habitats. Because it dries 4 to 6 weeks earlier than the native perennial species and also retains its dead leaf tissues for up to 2 months longer in the fall, it is capable of greatly increasing the opportunities for fire (Bradley 1986). Fire has been shown to negatively affect densities of cheatgrass the following year; however, the plants that do establish generally have especially high seed production (perhaps due to elevated soil resources and reduced intraspecific competition). Because of this, recovery after fire is very rapid for this species (Young and Evans 1978).

Cheatgrass is a strong competitor against other drought-adapted grasses (Francis and Pyke 1996). In addition to its ability to directly compete for resources, a key trait is its ability to intensify fire regimes, which promotes its ability to replace other species in arid habitats with low natural fire frequencies (Young and Evans 1978, Bradley 1986, Haidinger and Keeley 1993, Brooks 1999). In mesic grasslands, cheatgrass does not appear to be an especially successful competitor against native perennial grasses and it does not appear to pose as great of a threat to native communities.

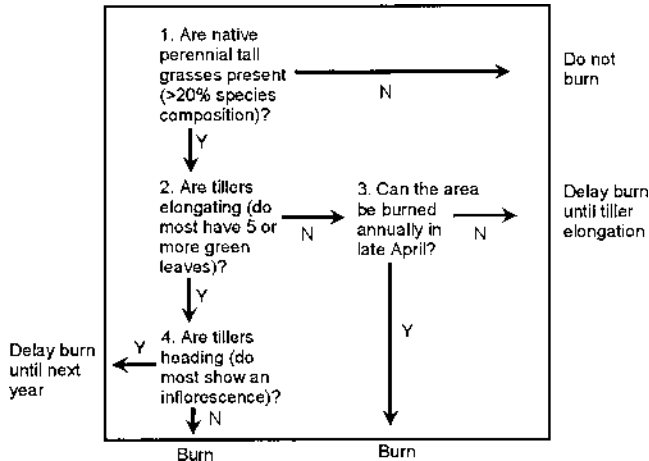


Fig. 2. Provisional model for managing smooth brome with prescribed burns. Y = yes and N = no. Redrawn from Willson and Stubbendieck (2000).

### Smooth Brome

Smooth brome (*Bromus inermis*) is one of the more widespread exotic grasses in the United States. Widely planted to increase forage or to reduce erosion following wildfires, this species readily escapes into prairies and pastures, particularly in the northern portion of its range (Sather 1987a). Smooth brome is classified as a cool-season, perennial grass and begins its growth early in the spring and continues growth late into the fall. It is a sod-forming species that sets seed from mid-summer through the fall and is a prolific seed producer. Studies indicate that it is quite drought resistant, though not terribly flood tolerant (Dibbern 1947). While most smooth brome cultivars are rhizomatous, some have a bunchgrass morphology. Because of the morphological variability among cultivars, Howard and Winkler (1996) have suggested that rates of post-fire recovery may differ between cultivars, although this has not been confirmed. Nonetheless, responses to fire are certainly variable, as discussed below, though this has been suggested to relate more to season of burn, available moisture, and the presence of competitors.

Smooth brome appears to be negatively affected by fire in some circumstances (Kirsch and Kruse 1973, Blankespoor and Larson 1994), but not in others (Grilz and Romo 1994). For example, early spring and late season burning have been reported to increase the productivity of smooth brome (Howard and Winkler 1996). Over a 15-year period, annual spring burning did not result in decreased frequency of this species in tallgrass prairie (Smith and Knapp 1999). Despite these variable results, Willson and Stubbendieck (2000) have proposed a provisional model for using prescribed burning to manage smooth brome (Figure 2). One fundamental aspect of this proposed control method relates to the species' phenology. There are generally reported to be 2 periods of tiller emergence in smooth brome, the first after flowering in early summer and the second in the fall (Lamp 1952). Fall tillers overwinter and begin to elongate in early May in the

central Great Plains and midwestern states. Willson (1991) found a 50% reduction in the density of tillers following prescribed burning in early May, presumably due to low carbohydrate reserves during tiller elongation. Kirsh and Kruse (1973) and Old (1969) have also reported that burns in April and May had substantial negative impacts on smooth brome. Further studies by Willson and Stubbendieck (1996, 1997) have involved burning smooth brome during (1) tiller emergence, (2) tiller elongation, (3) heading (initiation of morphological changes associated with sexual reproduction), and (4) flowering. Burning during any of the periods following emergence led to significant reductions in plant growth. A second fundamental aspect of successful control of smooth brome appears to relate to the presence of native competitors. Field observations suggest that spring burning during the time when smooth brome tillers are elongating shifts the competitive balance in favor of warm-season tallgrass species, such as big bluestem (*Andropogon gerardii*), which are less adversely affected by fire at that time (Willson and Stubbendieck 2000). In the absence of native warm-season perennials, Willson and Stubbendieck (2000) indicate that adverse effects of fire on smooth brome are insufficient to eliminate it from the system.

Unlike cheatgrass, there is no indication that smooth brome substantially alters the fire regime of systems it invades. In the absence of specific information, we might guess that part of this results from the fact that the grasslands smooth brome invades are typically high in herbaceous cover and naturally prone to high fire frequencies. Another factor that might contribute to a less conspicuous effect of smooth brome on fire regimes is its perennial nature and that, unlike cheatgrass, its aboveground tissues do not dry and become highly flammable early in the summer. Since the literature suggests that smooth brome can be burned almost any time of the year, it is unclear how important the difference in fuel drying may be.

### Japanese Brome

Japanese brome (*Bromus japonicus*) is a cool-season annual that has been widely planted for range-land improvement and which is highly palatable to deer and bison. Japanese brome is a prolific seed-producing species. Germination appears to be enhanced by a layer of litter that helps to retain moisture (Howard and Winkler 1994). Most successful seed germination occurs in the fall when sufficient rainfall occurs (Whisenant 1990) and because of dormancy mechanisms, fall germinants are typically from the seed crop in the previous year (Baskin and Baskin 1981).

In the West, Japanese brome can be found in prairie, sagebrush steppe, pinyon pine woodland, and arid grasslands. It is most common on disturbed sites and grazed areas (Stohlgren et al. 1999b) but also reported to invade native communities. It has been found to invade shortgrass prairie in eastern Wyoming (Fisser et al. 1989), mixed grass prairie in southwestern South Dakota (Cincotta et al. 1989), tallgrass prairie in cen-

tral Oklahoma (Ahshapanek 1962), mesquite savanna in Texas (Heitschmidt et al. 1988), and riparian zones in southcentral Oklahoma (Petranka and Holland 1980). This species is considered to be a threat to native diversity in rangelands and prairie because of its ability to outcompete many native perennials for water and nutrients. Compatible with its annual life cycle, disturbance appears to enhance Japanese brome populations. In 1 example, mowing in a Kansas tallgrass prairie during August resulted in a major increase in its abundance (Gibson 1989). Also consistent with its life cycle, the absence of disturbance may lead to its disappearance from a site when woody plants invade (Fitch and Kettle 1983), though it appears to persist even into very late successional conditions when woody plants do not dominate (Hulbert 1955, Fitch and Kettle 1983).

Our current view of the effects of fire on Japanese brome population dynamics is based on the need for this species to have sufficient moisture for successful establishment from seed and the role of plant litter in retaining soil moisture (Whisenant 1989). Fire not only kills the majority of Japanese brome plants (as well as much of the seed retained by the plant), but also removes the litter layer. Thus, populations of Japanese brome are substantially reduced following fire and the rate at which they recover depends on precipitation. When there is ample fall precipitation, litter is not required for successful establishment and populations can rebound immediately (Whisenant 1990). When moisture is less available, development of a litter layer is required before population recovery typically occurs. An example consistent with this hypothesis comes from Anderson (1965), who observed that annually burned, native prairie in the Flint Hills of Kansas remained free of Japanese brome while grazed prairie that was not burned was invaded by both this species and Kentucky bluegrass.

#### *Crested Wheatgrass*

Crested wheatgrass (*Agropyron cristatum*) is a cool-season, nonnative, perennial bunchgrass that was introduced into North America from Russia during the late 1800s. It has been widely planted for forage and erosion control in the western and central United States as well as in Canada (Holechek 1981). Zlatnik and Ahlenslager (1999) report that crested wheatgrass frequently hybridizes with desert wheatgrass (*Agropyron desertorum*), also a nonnative species, and produces fertile hybrids, creating taxonomic confusion. Its rapidly formed and extensive root system appears to promote establishment as well as tolerance of drought and cold conditions. Also important, crested wheatgrass develops green tissues 2 to 4 weeks earlier than most native grasses, which makes it highly valuable for spring forage. It tends to be dormant during the summer months, though it can exhibit fall growth if sufficient soil moisture is available. Marlette and Anderson (1986) have indicated that it may have substantial adverse effects on native plant diversity, limiting its value for erosion control.

In the northern Great Plains (particularly in North Dakota, South Dakota, eastern Montana, and eastern Wyoming) crested wheatgrass is reported to invade native grasslands. In contrast, it appears to have limited invasive potential in the shortgrass steppe of north-eastern Colorado (Coffin et al. 1996, Stohlgren et al. 1998b). Some evidence suggests that crested wheatgrass competes best under moderately arid conditions (Cook 1965) and does not compete well with other grasses on more moist sites (Hull 1974, Berube and Meyers 1982) or on very arid sites (Francis and Pyke 1996, Zlatnik and Ahlenslager 1999). There is also the possibility that crested wheatgrass is not as competitive in warmer climates (Zlatnik and Ahlenslager 1999), which may contribute to its greater success in the northern Great Plains. Aside from negatively affecting native diversity, crested wheatgrass may alter soil conditions. Studies indicate that this species produces less belowground organic matter than most native bunchgrasses, resulting in higher soil bulk densities, lower soil organic matter, and lower soil nutrient concentrations (Dormaar et al. 1995, Lesica and DeLuca 1996, Christian and Wilson 1999).

With regard to its relationship to fire, Lodge (1960) reported that crested wheatgrass suffered substantial reductions in biomass production as a result of spring fire during periods of active growth but was stimulated by fall burning. In contrast to these results, burning in either early spring or late fall had no significant effect on crested wheatgrass in studies conducted by Romo et al. (1994). One factor that could complicate the effects of burning is the effects on insect that attack crested wheatgrass. Haws and Bohart (1986) examined wheatgrass stands infested with black grass bugs (*Labops herperius*) and found that a fall burn destroyed most eggs of this bug species and depressed the bug population for several years. The generality of such an interaction between fire and insect herbivores is unknown, however. Thus, based on the limited available literature, it is unclear whether or not crested wheatgrass fits the model in Figure 2.

In contrast to most other grass species, which have been reported to either increase fire frequency or intensity, or to have no discernable effect, there is evidence that crested wheatgrass may reduce fire intensity or frequency under certain circumstances. In more arid regions, the sparse growth of crested wheatgrass can fail to propagate fire readily, reducing fire size and frequency. In certain cases, it has been observed to burn quickly and, as a result, to have less heat transfer downward, resulting in less nearground tissue damage compared with slower and/or hotter burning species (Zlatnik and Ahlenslager 1999). Because of its relatively high summer moisture content and low litter production, it appears that this species produces substantially cooler fires, especially compared with cheatgrass (Monsen 1994), though when senesced biomass is abundant, it is capable of producing intense fires.

#### *Kentucky Bluegrass*

Kentucky bluegrass (*Poa pratensis*), like smooth brome, is a perennial, cool-season, rhizomatous invad-



er of native grasslands that is widely planted, in this case primarily for lawns, as well as for pastures and erosion control. There appears to be some uncertainty as to whether it is native or nonnative to the United States (Sather 1987b), though it is usually treated as a nonnative invader. It is found throughout the United States as well as in much of southern Canada. Kentucky bluegrass is a significant invader in more mesic sites in the upper Great Plains as well as in eastern prairies, and it is considered to be a major problem in tallgrass and mixed grass prairies (Hensel 1923, Sather 1987b, Stohlgren et al. 1998b). Due to its strongly rhizomatous nature, Kentucky bluegrass is capable of rapid vegetative spread (Etter 1951) and populations persist for substantial periods.

In general, the model presented in Figure 2 for smooth brome may also apply to Kentucky bluegrass. Because it is a cool-season grass that elongates very early in the growing season (an attribute that helps to make it a desirable forage species), the opportunity to shift the competitive balance to native grasses exists in many situations, which is 1 reason that prescribed burning is widely used for combating this species. Many studies have shown that burning has negative effects on Kentucky bluegrass production, particularly when burning takes place during tiller elongation (Curtis and Partch 1948, Ehrenreich 1959). This effect is strongly influenced by available soil moisture, which may either enhance or nullify any detrimental impact of fire (Anderson 1965, Zedler and Loucks 1969). In addition to the importance of timing of fire and available moisture, native competitors make a critical difference in the impact of burning on Kentucky bluegrass (Schacht and Stubbendieck 1985). Where Kentucky bluegrass grows with warm-season native grasses, spring burning offers a substantial opportunity for shifting the competitive balance toward native species (Owensby and Smith 1973, Towne and Owensby 1984). Indeed, Kentucky bluegrass occurred less frequently in annually burned, mesic, tallgrass prairie sites over a 15-year period compared with unburned sites (Smith and Knapp 1999). In more arid regions of the western Great Plains where native cool-season species are more common, only a narrow window of opportunity exists for burning while Kentucky bluegrass is elongating, but before native species (*Agropyron smithii*, *Stipa* sp.) elongate (Sather 1987b). The use of early spring burning becomes somewhat more complex when both smooth brome and Kentucky bluegrass occur together because the optimum time for spring burning does not appear to be the same for both of these invaders. Certainly, Kentucky bluegrass is not always adversely affected by burning (Kirsch and Kruse 1973), leaving doubt as to its relation to fire.

#### Quackgrass

Quackgrass (*Elymus repens*) is considered to be one of the most harmful agricultural pests in the northern hemisphere (Holm et al. 1977). This cool-season, rhizomatous perennial is not native to North America and current evidence suggests that it is primarily an

invader of agricultural fields and sites subjected to substantial soil disturbance. Where quackgrass is likely to have the greatest impact on native diversity is in the context of habitat restoration. In this situation, it can represent a serious competitive obstacle to the establishment of native prairie species. For example, Choi and Pavlovic (1994, 1998) have reported that attempts to restore oak savanna in the Indiana dunes region of the Midwest have been hampered by several exotic grasses, including quackgrass (as well as Kentucky bluegrass). In their studies, burning during May was not found to reduce either quackgrass or Kentucky bluegrass substantially. These results were consistent with the findings of Curtis and Partch (1948), who found that repeated burning between 1941 and 1946 in a former agricultural field planted with prairie species had no overall effect on quackgrass. Kirsch and Kruse (1973) and Becker (1989) likewise found that repeated spring burns were not successful at eliminating quackgrass from an invaded prairie in Minnesota. However, the work by Howe (1995) suggests that quackgrass may fit the model in Figure 2 under some circumstances. In his study, Howe compared the effects of spring burning, summer burning, and no burning on prairie plantings that were 3–4 years old. Early flowering species, including quackgrass, were disfavored by spring burning (March) and by no burning, but retained their original share of the community when burned during the summer (mid-July). In contrast, late flowering species were disfavored by summer burns but represented an increasing component of the vegetation in spring-burned or unburned plots. While the available information is largely inadequate, it appears that the difference between success and failure in controlling quackgrass with fire might be a combination of precisely timed, early spring burning and the presence of native warm-season competitors.

#### Bermudagrass

Bermudagrass (*Cynodon dactylon*) is a warm-season, prostrate perennial that is considered to be one of the most serious invasive species in the world (Holm et al. 1977). In contrast to the species considered thus far, bermudagrass has its greatest prevalence in warmer climates and does not tolerate freezing conditions well (Gould 1951). It differs from cool-season grasses phenologically, with growth commencing later in the season and continuing through summer until the arrival of cold weather. It has been widely planted throughout the southern states from California to Florida, though its range extends as far north as Washington, Idaho, Iowa, Michigan, and New York. Bermudagrass is one of the principle lawn species in southern states and is also widely planted in pastures. It is commonly planted for erosion control and on mine spoil sites (Carey 1995). It is listed as a facultative wetland plant, which indicates considerable tolerance of wet soils. Most cultivars do not tolerate extreme drought well, and in arid regions it is largely restricted to riparian areas.

Bermudagrass is generally classified as an early-

successional species that persists in habitats subjected to frequent disturbances, including grazing, mowing, fire, or flooding (Vora and Messerly 1990, Dong and de Kroon 1994). In the southcentral and southwestern United States, bermudagrass has invaded many different community types, including pine-oak forest in eastern Texas, coastal prairie (L.K. Allain and J.B. Grace, unpublished), riparian areas, and mesquite (*Prosopis* sp.) savannas, as well as in woodlands in southern California (Carey 1995). It appears to be most successful in sites with soil disturbance, responds strongly to elevated soil nutrients, and tolerates grazing and mowing well. Its association with disturbed habitats suggests that one of its larger effects on native diversity will occur in restoration projects where it was previously established.

Bermudagrass is considered to be quite tolerant of dormant season burning (for an exception, see Odum et al. 1974), although there is some indication that the seeds at the soil surface do not always survive (Glennington and Pase 1964). Early spring burning while the plants are still dormant is typically recommended for management of bermudagrass (Carey 1995). It has been suggested that the enhancing effects of fire on this species result from removal of dead litter, reduction in insects and disease, and reduction of fire-intolerant competitors (Morris 1968, Monson et al. 1974). Available evidence indicates that the response to fire also depends on post-fire soil moisture conditions, as well as soil nutrient levels (Morris 1968, Monson et al. 1974), with the combination of burning and fertilization leading to substantial increases in bermudagrass. Experience with other warm-season grasses suggests that summer burns would be more likely to have detrimental effects than dormant season burns (Howe 1995), though there appear to be no specific studies of burn time on bermudagrass.

Since some bermudagrass cultivars are more strongly stoloniferous while others are more rhizomatous, tolerance to fire damage may be expected to vary. Pinkerton and Rice (1992) have shown that different cultivars do indeed vary in their responses to burning. After 3 years of annual burning, rhizomatous cultivars were unaffected by burning (compared with unburned controls) while more stoloniferous cultivars suffered reductions in yield.

### *Cogongrass*

Cogongrass (*Imperata cylindrica*) is an invasive, perennial, rhizomatous species that is widely distributed throughout tropical and subtropical regions of the world. It is described by Holm et al. (1977) as one of the worst perennial grass weeds in warm temperate and tropical regions of the world. In the United States, it is 1 of 72 terrestrial species listed as a noxious weed under the U.S. Federal Noxious Weed Act of 1974 and, as a result, its transport into and throughout the United States is restricted. This species is a relatively recent introduction in the United States, with the first entry occurring during 1911 through accidental inclusion in shipping material from Japan brought to Mo-

bile, Alabama. A second intentional introduction of material from the Philippines for forage trials took place before 1920 (King and Grace 2000a). Presently cogongrass has become established in Florida, Alabama, Mississippi, and Louisiana, with an outlying population recently discovered in eastern Texas (S.L. Grace, personal observations). This species is not yet known in coastal prairie, although we expect that this is simply a matter of time given its broad adaptability to various soil conditions, its adaptation to fire, and its current westward spread along the Gulf of Mexico coast. Because of the potentially devastating effects this species can have on biodiversity and ecosystem characteristics, we include it in this survey as a preview of things that may happen in the future.

Cogongrass typically flowers during late spring to early summer in the southeastern states and sexual reproduction is typically limited to a relatively brief period unless plants are damaged or disturbed. Seeds are very small, widely dispersed, germinate readily, and have a limited longevity of usually 1 year or less. It appears that outcrossing is required for the production of viable seed, which is currently helping to limit the rate of its range expansion. Experimental studies (King and Grace 2000a) have shown that it is readily capable of establishing from seed in pristine pine savanna dominated by heavy cover of native wiregrass (*Aristida* sp.). In these studies, the role of disturbance in facilitating establishment of this species was examined for germination and early seedling growth as well as for transplanted seedlings in the field using containment barriers. The effects of clipping, burning, complete vegetation removal (using herbicides), and soil disturbance were compared with untreated controls. Additionally, the importance of opening size was compared for gaps of 0, 10, 30, and 100 cm in diameter. Cogongrass was able to establish under all conditions, including in undisturbed vegetation. Burning prior to seed introduction caused a modest increase in seedling survival, but the main effect of disturbance was observed where soil was tilled; here, biomass production was 10 times greater than in any other treatment. Greenhouse experiments, in combination with field observations, indicate that standing water can inhibit the ability of cogongrass to establish from seed, but as seedlings increase in size, their tolerance of flooding increases (King and Grace 2000b).

When cogongrass invades a site, it rapidly excludes virtually all other herbaceous species, perhaps due to the persistence of its litter (see Grace 2001 for a discussion of this mechanism). The elevated production and heavy accumulation of litter suggests that fire behavior may be altered in communities it invades. Lippincott (2000) recently compared fine fuel attributes in sandhill pine savanna communities invaded by cogongrass with those in uninvaded areas. Cogongrass produced significantly greater amounts of persistent standing biomass, resulting in a greater fuel load than in the native vegetative association. She also found a higher degree of horizontal continuity of the vegetation (because of the spreading, rhizomatous nature of cogongrass), and a greater vertical distribution



to tissues. Fire-induced mortality of juvenile longleaf pine (*Pinus palustris*) was greater in the cogongrass-dominated community as was post-fire fuel accumulation. Preliminary results comparing invaded and uninvaded wet pine savannas in Mississippi suggest similar results (S.L. Grace, unpublished). Flame heights produced by cogongrass have been observed to be nearly twice as high as those produced by wiregrass. Rates of fire spread associated with cogongrass also tended to be greater and maximum temperatures were somewhat lower as a result.

#### Other Grasses

Johnsongrass (*Sorghum halepense*) is another warm-season rhizomatous grass that is a major invader of agricultural systems. Originally from the Mediterranean, it has spread throughout the world and now occupies habitats between latitudes 55°N and 45°S (Holm et al. 1977). In North America, it now occurs as far north as Ontario and is found in every U.S. state except Maine, Michigan, and Alaska. Generalizations about this species must be qualified because of the presence of numerous ecotypes (McWhorter 1971). It is generally associated with disturbed sites, such as abandoned crop fields, though it has been observed to invade tallgrass prairie, coastal prairie, riparian zones, and savannas (Snyder 1992). Because of its affinity for abandoned fields and disturbed sites, it is likely to be a major problem for restoration efforts. Because of its deeply placed rhizomes, it is well adapted to survive fire. In one of the few studies that have examined its response to burning, Odum et al. (1974) found that it was greatly enhanced in a fallow field subjected to a spring burn. Newman (1990) reported an unpublished study in Texas that found a substantial reduction in Johnsongrass resulting from a late April fire that promoted the growth of little bluestem (*Schizachyrium scoparium*). This finding suggests the possibility that precisely timed fires may negatively impact Johnsongrass, though it is premature to draw firm conclusions based on the data available at this time.

Orchardgrass (*Dactylis glomerata*) is a cool-season, perennial bunchgrass that is broadly distributed throughout North America, although less common in the southern states and in arid habitats (Sullivan 1992). It is widely planted as forage and for a variety of rehabilitation applications, including as a post-fire treatment for wildfires. Somewhat shade tolerant (relative to most grasses), it has a broader range of applications than some other grasses that tolerate little shade. It is highly palatable to both domestic and wild grazers, which is considered an additional benefit to its use in rehabilitation (Roppe and Hein 1978). In many areas it appears to be limited to early successional situations and is replaced by native vegetation (Sullivan 1992). In other parts of its range, particularly in the northcentral states, it is more of an invasive species. In areas of the West, it has been planted to suppress species perceived to be more of a threat, such as yellow starthistle and diffuse knapweed (*Centaurea diffusa*). One feature that reduces the invasive capa-

bility of orchardgrass is that its seeds generally lack innate dormancy and survive for only 2 to 3 years, resulting in a nonpersistent seedbank (Grime et al. 1988). While orchardgrass is widely planted in burned areas, few studies have examined its response to burning. Sullivan (1992) summarized a study on the effects of spring and fall burning on orchardgrass. This study was conducted near Missoula, Montana in a site recovering from a forest fire during 1945 and which was dominated by a mixture of woody and herbaceous species at the time of the prescribed burns. Neither the spring nor fall burn eliminated orchardgrass and biomass production in subsequent years was actually enhanced in the spring-burned area. It is not clear whether the difference in recovery from the 2 burns was due to phenological effects or the greater intensity of the fall burn. Thus, it seems that further work on the response of orchardgrass to burning is required before a clear picture of its threat as an invader will emerge.

Giant reed (*Arundo donax*) is an example of an extremely robust, exotic, ornamental species that has escaped into riparian and wetland areas throughout the southern U.S., from Maryland to California (Snyder 1991). Giant reed is a clump-forming perennial that develops shoots up to 6 m high. In deeper water, shoots of this species can be semi-floating. This species spreads locally by rhizomes and is reported to flower only once every few years (Snyder 1991), though in south Louisiana it appears that some plants are in flower every year (J.B. Grace, personal observations). This species aggressively colonizes riverbanks, marshes, and floodplains and has been observed to replace the common reed (*Phragmites communis*), a native species that is considered invasive by some. The aboveground material of giant reed is quite flammable once leaves have dried later in the year and because of its extensive rhizome system, it is quite capable of surviving fire (Snyder 1991). At present, there appears to be no information on its effects on fire regimes or succession, and no information about whether fire aids in its establishment.

A host of other invasive grasses occur in temperate grasslands, many of which have been introduced to improve rangelands or pastures, for erosion control, for ornamental purposes, or by accident. Species such as Caucasian bluestem, vaseygrass (*Paspalum urvillei*), bahiagrass (*Paspalum notatum*), King Ranch bluestem (*Bothriochloa ischaemum*), Kleberg bluestem (*Dichanthium annulatum*), Angleton bluestem, and buffelgrass pose threats of unknown degree, primarily to southern and central grasslands. In general, our observations suggest that all are reasonably tolerant of burning (see Mayeux and Hamilton 1983 for buffelgrass), though in most cases, it is unknown whether fire will tip the competitive balance in favor of the invasive species or towards native perennial species. One exception is Caucasian bluestem. At the Konza Prairie Biological Station, a tallgrass prairie preserve in the foothills of Kansas, cover of Caucasian bluestem was found to be lowest in plots that had been neither mowed nor burned during the period of invasion (Figure 3; M.D. Smith and S.L. Collins, unpublished data).

FIRE AND INVASIVE PLANTS IN TEMPERATE GRASSLANDS

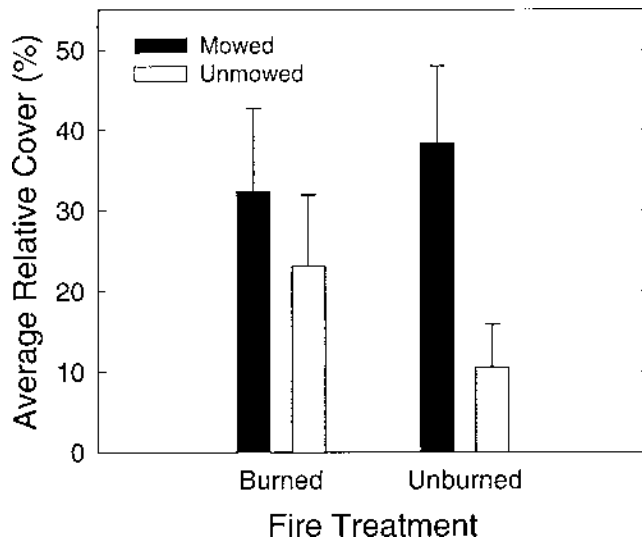


Fig. 3. Effects of fire and mowing on average relative cover (per 10 m<sup>2</sup>) of Caucasian bluestem (*Bothriochloa bladhii*) in tall-grass prairie plots located on Konza Prairie in the Flint Hills of northeastern Kansas (M. Smith and S. Collins, unpublished).

Both annually burned and mowed plots were found to have substantially greater cover of Caucasian bluestem. Based on these results, it appears that spread of Caucasian bluestem may be promoted by fire and grazing.

Forbs

*Leafy Spurge*

Leafy spurge (*Euphorbia esula*) is an erect, perennial forb that rapidly develops an extensive and deep root system that can reach depths of 4.5 m (Walkup 1991a). A key trait of this species is its capacity for vegetative spread and regrowth. A morphological feature that facilitates vegetative regrowth is the production of a basal crown of tissue just beneath the soil surface (Biesboer and Eckardt 1987). The crown develops a large number of buds which, in turn, produce aboveground shoots. The basal crown persists for many years and can also produce new roots. Leafy spurge also produces rhizomes and root buds that are capable of forming physiologically independent plants, especially when the original plant is disturbed (Selleck et al. 1962). A remarkable characteristic of leafy spurge is the rapidity with which it develops the capacity to resprout and, thereby, recover from damage (observed to be within 7–10 days from germination). Other important traits include its ability for prolific seed production and its explosive capsules, capable of dispersing seed up to 4.5 m from the parent. Seeds have been reported to remain viable for up to 8 years, although it has also been reported that the great majority germinate or perish within 2 years of production. Based on this information, it appears that leafy spurge relies on its bud bank perhaps as much as on its seed bank for regeneration.

In North America, leafy spurge occurs from Washington to California and east to Maine and New York,

as well as in adjacent Canadian provinces. Its highest concentrations in the United States are currently in Oregon, Idaho, Montana, Wyoming, Colorado, North Dakota, South Dakota, Nebraska, Minnesota, and Wisconsin. Leafy spurge occupies a broad range of ecological conditions from xeric to subhumid, though its most rapid growth is in more mesic sites. In particular, it invades disturbed areas with exposed mineral soil (Belcher and Wilson 1989, Wilson 1989), but also can establish and expand in pastures as well as in ungrazed native grasslands (Selleck et al. 1962). In addition to adverse effects on native diversity and restoration efforts (Belcher and Wilson 1989), it has been found to be toxic to cattle and humans, though goats and sheep are able to consume it without adverse effects (Landgraf et al. 1984, Stoneberg 1989).

One of the more frequently cited examples of adverse effects of fire on leafy spurge is attributed to Dix (1960). In this study, he compared 3 pairs of unburned and previously burned sites in North Dakota native grasslands to evaluate the effects of fire on community composition. Leafy spurge was found in only 1 of the 6 sites examined and this site happened to be one of the unburned grasslands. Dix drew no conclusions about the effects of fire on leafy spurge from this study, and given the absence of information about its distribution prior to the burns, we feel that no firm conclusions can be drawn from this example. Other studies have generally found prescribed fire to have limited effects on this species. Prosser et al. (1999) examined the effects of fall burning on leafy spurge and found no effects on stem densities the next year compared with unburned controls. Wolters et al. (1994) conducted studies of the effects of spring and fall burns on leafy spurge at the Little Missouri National Grassland in North Dakota. They found that both spring and fall burns reduced seed germination but increased the density of stems. Similarly, Masters (1994) found that stem densities increased with late spring burning. Fellows and Newton (1999) found that burning in late spring or early fall had immediate effects on leafy spurge densities, but these effects were not evident the following growing season. In all, these studies suggest that burning is ineffective in controlling leafy spurge.

Because of the currently active program to use biological control against leafy spurge, Fellows and Newton (1999) also examined the effects of prescribed burning on a flea beetle (*Aphthona nigriscutis*), a potential control agent. They found that burning enhanced the establishment of the beetle but that most beetle colonies did not survive past the first generation unless the habitat was otherwise suitable. They also found that established colonies were not adversely affected by May or October burns.

It appears that leafy spurge is especially well adapted to resprouting following fire. Even extensive control programs that attempt to eliminate leafy spurge using a combination of mechanical removal, chemical treatments, and prescribed fire, have found that this species must be treated repeatedly for many years due to its tremendous capacity to resprout. While there is

evidence that it can be impacted by competition with grass species (Lym and Tober 1997), there is no evidence yet that fire can be used to tip the competitive balance toward native species to a sufficient degree to negatively impact leafy spurge.

#### *Knapweeds and Yellow Starthistle*

Several species of knapweeds constitute major threats to native temperate grassland ecosystems. A partial list of the ones that are currently most important includes spotted knapweed, Russian knapweed (*Acroptilon repens*), diffuse knapweed, and yellow starthistle. All are nonnative, biennial, or perennial forbs in the Asteraceae that have spread across the northern United States and southern Canada. They are all relatively short-lived, produce taproots, form rosettes when vegetative prior to sexual reproduction, and reproduce primarily by seed.

Spotted knapweed is a short-lived perennial that forms a persistent seed bank and whose seeds germinate primarily in the fall or early spring (Spears et al. 1980, Schirman 1981). Established plants are reported to have an average lifespan of 3 to 5 years and a maximum lifespan of at least 9 years (Boggs and Story 1987). It has spread throughout most of the United States except for the southeastern states. The highest concentrations are in the Pacific Northwest states and western Canada, though it is also of major importance in the upper Great Plains and the northcentral states. As plants get older, they are capable of developing lateral shoots and multiple rosettes (Watson and Renney 1974). This species has some capacity to survive and resprout following low-intensity fires (Carey and Winkler 1995a). Aided by its persistent seedbank, the density of spotted knapweed plants frequently increases following fire. Carey and Winkler (1995a) report examples of immediate population increases following both spring and fall burns, as well as examples where spotted knapweed has invaded 3 to 5 years following severe wildfires. These and other examples suggest that prescribed burning may result in immediate reductions in spotted knapweed populations, but it is not likely to be an effective control measure (unless combined with an herbicide program) and may actually facilitate the spread of this species. Also, as with leafy spurge, there are numerous programs attempting to use biological control agents and the effects of fire on these agents has yet to be examined. There is some information that might suggest that spotted knapweed may reduce fire intensities. A fuel model has been developed for this species (Xanthopoulos 1986) and analyses, as well as field tests, indicate that in order for a stand of spotted knapweed to carry fire, burns should be conducted during early spring prior to grass and forb growth (because of the high moisture content of grasses and forbs in the spring). Moreover, the sparse foliage and discontinuous nature of spotted knapweed biomass suggests that under low wind-speeds (and flat or declining slopes), fires will be unlikely to spread.

Russian knapweed is a perennial herb that occurs

throughout the western and central United States, including the Great Plains, but is largely absent from eastern and southeastern areas (Watson 1980). Botanical descriptions indicate that this species has an extensive root system, is capable of rapid vegetative spread by root buds and rhizomes, and typically forms dense colonies (Watson 1980). It appears to be more long-lived than spotted knapweed and forms persistent populations lasting over 75 years. Russian knapweed frequently invades disturbed sites and pastures, as well as undisturbed rangelands and meadows, and is capable of developing largely monotypic stands (Maddox et al. 1985). It appears to be most competitive in arid circumstances and less competitive under more mesic conditions. This species is not palatable to livestock and causes a neurological disease in horses, though it is used by bighorn sheep and white-tailed deer (Esser 1994a). There appear to be no reported studies of the effects of fire on Russian knapweed or its effects on fire behavior. Carpenter and Murray (1998) have speculated based on available information that Russian knapweed readily survives most fires and that burning may even facilitate its spread. At present, management programs for this species rely on mechanical, chemical, and biological control methods.

Diffuse knapweed functions as a biennial or short-lived, semelparous perennial. It has a well-developed taproot, but is not capable of vegetative spread, relying solely on seed for population growth (Carey and Winkler 1995b). Reproductive success is highly dependent on plant size and strongly suppressed by intense competition (Powell 1990). Most of the germination takes place in the spring, and seedlings develop into rosettes that persist for 2 to several years before flowering and dying. Its current distribution is largely in the western United States and southwestern Canada. It is not widespread in the Great Plains or tallgrass prairie region (although it does occur in Iowa, Missouri, Minnesota, Indiana, Michigan, Kentucky, and Tennessee). We were unable to find published studies on its relationship to fire; however, its capacity to withstand repeated mowing along with its possession of a taproot suggests that it may be able to tolerate low intensity burns.

Yellow starthistle is a winter annual that develops a deep taproot but that does not spread vegetatively. As with diffuse knapweed, it reproduces exclusively by seed. Seedlings germinate in the fall, overwinter as rosettes, maintain root growth throughout the winter, bolt in late spring, and flower between June and August (Carey and Winkler 1995c). Yellow starthistle is distributed throughout most of the United States except for the Southeast. It generally requires habitats in which light reaches the soil surface for the growth of winter rosettes. As a result, open vegetative conditions are required during most of its life cycle and it is susceptible to competition from grasses, though clipping (and presumably grazing) reduces this disadvantage (Roche et al. 1994). Yellow starthistle occurs in grasslands, pastures, and disturbed areas but is in greatest abundance in the western states (Maddox et al. 1985). This species of *Centaurea* appears to be quite suscep-



tible to control by fire. Hastings and DiTomaso (1996) report results for 3 consecutive burns of an annual grassland in California. Burns were conducted during early summer to coincide with the time immediately prior to flowering by yellow starthistle (though following the production and dispersal of seeds by native annuals). Burns were highly effective in killing established yellow starthistle plants and also at preventing seed production. During the study, not only did the density of established plants drop to 4% of adjacent unburned controls but the seed bank appeared to have been almost completely depleted. This example represents one of the most successful cases reported for reducing the population of an exotic species using fire (see also DiTomaso et al. 1999).

#### *Canada Thistle*

Canada thistle (*Cirsium arvense*) is classified as one of the world's worst weeds (Holm et al. 1977). Despite its common name, it is native to Europe and not North America. It is an erect, dioecious perennial that is capable of spread up to 5 m or more via an extensive system of rhizomes and that produces an extensive and sometimes deep root system. Seed set is limited by pollen dispersal when male and female plants are more than 50 m apart. Canada thistle produces a large number of plumed, wind-dispersed seeds that form a very persistent seed bank (Heimann and Cussans 1996, Nuzzo 1997). The majority of seeds develop into female plants and germination, while opportunistic in actively disturbed sites, typically occurs in late spring to early summer. Plants generally overwinter as rosettes and flower the following summer. This species is widely distributed throughout North America except in the Southeast and is found in a vast range of habitat types (Walkup 1991b). It is invasive in tallgrass and mixed grass prairies as well as in shortgrass steppe and arid grasslands. Its spines and thorns make it generally unpalatable for both domestic livestock and wild grazers. Its establishment is enhanced by disturbance, but its strongly clonal nature allows it to spread in many vegetation types without further disturbance.

A variety of responses to fire have been reported for Canada thistle (Smith 1985, Becker 1989, Nuzzo 1997). Some dormant-season burns have had little effect, but in other cases, summer and fall burning have been associated with declines in Canada thistle (Kirsch and Kruse 1973), presumably due to both direct adverse effects and the stimulation of native competitors. Studies in mesic habitats by Hogenbirk and Wein (1991) found that spring burning had no effect on Canada thistle biomass while an August burn led to increases in biomass and shoot density as well as subsequent seedling density. Investigations by Thompson and Shay (1989) showed an increase in Canada thistle abundance following burning. Collectively, these studies do not give a clear picture of the effects of fire on this species. Despite this, Hutchison (1992) suggests that prescribed fire can be an effective control method for Canada thistle. He recommends repeated late

spring burns between May and June as most detrimental to this species. According to his prescription, early spring burns should be avoided because they increase shoot density.

#### *Other Forbs*

Information on the relationship of fire to other invasive herbaceous dicots, or forbs, is limited for most species. Available information suggests that a variety of patterns can be expected for this group. Fire has been observed to cause very little mortality in purple loosestrife, a long-lived perennial that has abundant buried buds (Welling and Becker 1990), and is not believed to be a likely control measure for this species, at least in the wetland circumstances where it typically occurs (Uchytel 1992a). *Sericea lespedeza*, a leguminous perennial widely planted throughout the eastern United States, appears to be promoted by fire, which stimulates germination and enhances establishment, while having little effect on adult survival (Coladonato 1992). Whitetop (*Cardaria draba*) and dalmatian toadflax appear to be well adapted to take advantage of recently burned areas where competition has been reduced, though their persistence against resumed competition is perhaps limited (Esser 1994b, Carpenter and Murray 1998). In contrast, another legume—white sweetclover (*Melilotus alba*), a widely planted biennial that has established in many grasslands and prairies—is killed when burned during the growing period, though it survives dormant-season fires (Uchytel 1992b). Evidence suggests that burning helps to break seed dormancy in this species and post-fire germination is enhanced (Kline 1986). The result of these 2 effects is that infrequent burning (especially in combination with grazing—see Hulbert 1986) actually promotes the expansion of this species while annual burning is recommended in order to decimate the population and deplete the seed bank. For some species, such as musk thistle, the effects of fire appear to be primarily related to the abundance of competitors. Hulbert's (1986) summary of fire effects on tallgrass prairie indicates that this species can be eliminated either with or without fire on ungrazed prairie, although spring burning was recommended to promote the vigor of native warm-season grasses.

#### *Woody Plants*

Most grasslands in the temperate region of North America are characterized by a natural succession to woody species that is interrupted by periodic drought as well as frequent fire. There is considerable interest in the apparent increases in native woody species in many grassland systems. To a significant degree, the issues associated with what appear to be unnaturally high levels of woody plants are similar to those involved with fire effects on nonnative woody species. Nonetheless, in this paper we will focus primarily on species that are exotic, though this issue will be revisited later in the paper.

### *Saltcedar*

Saltcedar (*Tamarix* sp.) here refers to a complex of taxa whose affinity is disputed. Some recent treatments have suggested that all species with flower parts divisible by 5 should be lumped under *Tamarix ramosissima* while those divisible by 4 should be lumped under *T. parviflora* (Carpenter 1999). In practice these entities are generally combined for ecological and management discussions, which we will do here. Saltcedar is a long-lived (50–100 years), deciduous shrub or tree that attains heights of up to 6 m, develops a deep taproot, and can spread clonally (Tesky 1992a). Saltcedar flowers are primarily insect pollinated and mature plants can produce hundreds of thousands of seeds annually. Saltcedar can flower as early as in its third year of growth. Seeds are very small and readily windborne. Seed viability lasts only a few weeks and seeds typically germinate immediately. Once wetted, seeds will germinate within 24 hours, regardless of light conditions.

Since its escape from cultivation, saltcedar has spread primarily in the southwestern United States and adjoining Mexico, although its distribution extends to many areas of the country. Most of its impact is currently in western riparian habitats, but it also invades marshes, wet pastures, and rangelands and is now spreading along the Gulf of Mexico into the coastal prairie. It has the ability to extend roots very deeply into the soil and to tap into the groundwater in some situations, which can allow it to escape from surface drought conditions. Its ability to withdraw large quantities of water from the soil has led some to propose that it can lower water tables and adversely affect water supplies (Loope et al. 1988). It is also extremely salt tolerant and by shedding its leaves, able to concentrate salt in the surrounding surface soils and, thereby, suppress establishment of other species (Brotherson and Field 1987).

Saltcedar is considered to be highly tolerant of burning (Tesky 1992a). The high moisture and salt contents of its foliage may make it difficult to ignite, but in most cases it burns readily. It greatly reduces fine fuels beneath its canopy (J.B. Grace, personal observations). However, litter accumulation beneath the tree contributes to fuel availability and in fire-prone areas, it burns frequently. (Tesky [1992a] estimates that fire return times are from 16 to 20 years.) It is capable of very vigorous resprouting, not only from roots and belowground structures but also from aboveground tissues (Brotherson and Field 1987). We have witnessed cut trees produce a profusion of new stems from the cambial layer of the stump and the plant appears to be able to withstand a great deal of damage without incurring death. There have been some reports of failure to resprout following hot fires, though in other cases, most individuals have survived fire through resprouting. Burned trees that are not killed often show an enhanced flowering response. Burning during the peak of summer appears to have the strongest adverse effect on saltcedar, presumably due to ensuing water stress. In cases where annual burning can

be achieved for several years, it appears that saltcedar can be controlled with fire alone (Duncan 1994). However, even when completely topkilled, it produces sprouts up to 2–3 m tall in the next year. As a result, saltcedar appears to be well adapted to fire and chemical applications are typically recommended to achieve control (Tesky 1992a, Carpenter 1999).

A factor that relates to the utility of fire as a control agent for saltcedar is that it is generally more fire tolerant than most native riparian woody species and fire is not considered to be a natural feature of these systems. Analyses of fire history by Busch (1995) indicate that the presence of saltcedar in riparian zones is increasing the frequency and intensity of fire in these habitats. In other habitats, such as the coastal prairie, the sites occupied by saltcedar are generally upland and part of the fire-dependent ecosystem. In this habitat, the use of fire appears to be appropriate, although preliminary observations do not suggest occasional fires will be sufficient to result in population control.

### *Chinese Tallow*

Chinese tallow (*Triadica sebifera* [= *Sapium biferum*]) is a rapidly growing exotic tree that has been imported from China, where it has been cultivated for the production of oils for 1,400 years. In general, Chinese tallow is considered to be an early successional tree (Bruce et al. 1995). However, in some circumstances trees can achieve heights as great as 20 m and diameters in excess of 1 m. The maximum life span is not known but generally after 50 years many trees begin to be somewhat senescent. This member of the Euphorbiaceae has exceptional growth rates and precocious sexual reproduction. In 1 experiment, an individual Chinese tallow seed germinated in the spring produced a tree over 1.5 m in height and flowering by the end of that growing season (T.C. Barrilleaux and J.B. Grace, unpublished). In addition to rapid growth, Chinese tallow is capable of vigorous resprouting if damaged and can reproduce by root sprouts produced at a distance of up to 5 m from the tree trunk. Most germination appears to take place during fall through the spring, although some germination can take place at any time of the year. Cameron et al. (2000) indicate that its seeds can survive for up to 8 years when stored in refrigerated conditions. In the field, it appears to develop at least a short-lived seed bank.

The current distribution of Chinese tallow extends from South Carolina in the east to south Texas and it has recently invaded areas of southern California. Studies indicate that it has a broad tolerance for soil and moisture conditions, though it can be limited by excess salinity (Barrilleaux and Grace 2000). The northern boundary of its range is maintained by plantings rather than natural reproduction; it appears to have limited tolerance to freezing conditions (though it can regrow after cold damage). Chinese tallow has invaded a number of habitats but the principal grasslands it occupies are coastal marsh and coastal prairie. It is likely that this species poses the greatest single threat to the conservation and restoration of the coastal

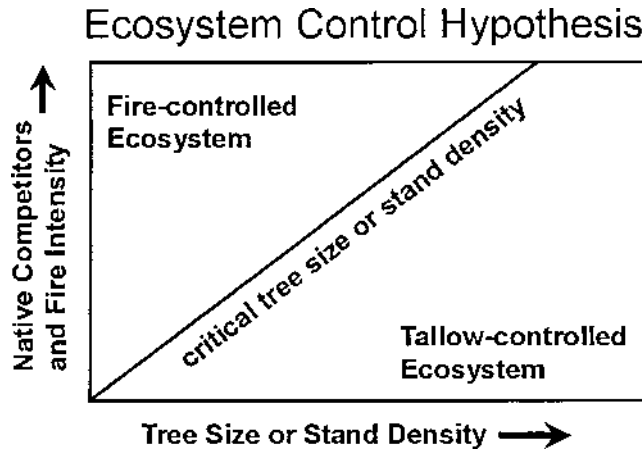


Fig. 4. Ecosystem control hypothesis for the impact of Chinese tallow on native grasslands (adapted from Grace 1998). According to this model, when trees exceed some critical minimum size or stand density, Chinese tallow will not be able to be controlled by fire and will not only dominate the community but will render it nonflammable. Below the critical boundary, herbaceous fuel is sufficient to substantially damage Chinese tallow and to maintain a pyrogenic community.

prairie ecosystem due to its rapid capacity for invasion (Bruce et al. 1995) and the dramatic changes it creates in this habitat (Grace 1998).

Because of its well-developed capacity for regrowth, it has been hypothesized that Chinese tallow is able to survive burning once it reaches a sufficient size (Figure 4). According to this hypothesis, once trees reach a critical size, which depends in part on the available fuel and related fire intensity, Chinese tallow escapes from fire control and comes to control the community composition and fire regime. Therefore, if burning can be conducted at sufficient frequencies and fuel conditions maintained, fire can be used to keep trees below the critical size and maintain the pyrogenicity of the system. Several experiments (J.B. Grace and L.K. Allain, unpublished) indicate that the relationship between fire effect and tree size is actually complex and depends on season of burn as well as other factors. Moreover, burns have been discovered to have long-term detrimental effects on Chinese tallow in even the largest trees. The result is that for isolated trees surrounded by a good layer of herbaceous fuels, even the largest individuals can be top-killed and repeated fires can lead to their death.

What makes Chinese tallow invasions more complex is the capacity of this species to suppress fire. When these trees grow in dense stands, which they often do, they rapidly suppress herbaceous species that provide the fuel to carry fire, since tallow itself will not propagate fire. Even before all fuel is eliminated by this species, herbaceous species composition shifts from grass to forb dominance and the effective fuel load is reduced. When Chinese tallow achieves canopy closure, regardless of the height of the trees, the habitat is quickly rendered nonflammable and fire can no longer be used to control this species. At this point, only widespread chemical applications are capable of re-

turning the system to a condition where there is sufficient grass cover for fire to occur.

#### European Buckthorn

European buckthorn (*Rhamnus cathartica*) is a dioecious, deciduous shrub or small tree that grows up to 6 m high (Converse 1984). Female plants produce numerous fruits (approximately 0.5 cm in diameter) that are eaten by birds and other wildlife. Although it has the ability to produce vegetative sprouts, apparently it reproduces primarily by seed. It appears that this species can successfully colonize undisturbed sites, though there is evidence that excess shading reduces seedling growth (Converse 1984).

European buckthorn has escaped from cultivation over a broad area and has established populations from Saskatchewan to Nova Scotia, and south to North Dakota, Minnesota, Iowa, Missouri, Illinois, and Virginia. It commonly invades oak savanna, pastures, fens, and prairies. European buckthorn is classified by the Minnesota Interagency Exotic Species Task Force as a severe threat to native communities (Minnesota Department of Natural Resources 2001). Boudreau and Willson (1992) report that it has invaded oak savanna habitat at Pipestone National Monument in Minnesota, where it has virtually eliminated native midstory and understory species. Godwin (1936) reported an example in Europe for a related species of *Rhamnus* where a mixed sedge marsh was colonized by seedlings that developed a continuous shrub thicket in 20 years. The most detailed description of stand development in European buckthorn yet presented is by Archibald et al. (1997). In this study, initial establishment of a site by a few individuals was followed by a localized increase in seedling recruitment once the initial trees began reproducing.

A limited amount of information suggests that mature European buckthorn trees are able to survive individual burns but that small trees and seedlings are killed. Boudreau and Willson (1992) report that spring burning in oak savanna killed European buckthorn seedlings, which were unable to resprout. However, mature trees were only topkilled and were able to resprout and survive. Converse (1984) suggests that prescribed fire treatments do not control *Rhamnus* species, in part because of their ability to suppress herbaceous fuel. Further work is needed to determine if repeated fires facilitate herbaceous growth and lead to eventual control of European buckthorn.

#### Other Woody Invaders

Russian olive is a deciduous shrub or small tree that forms a dense, spreading crown and has a well-developed taproot and lateral root system. The average age to first reproduction is 3–5 years and seeds are typically dispersed by birds and small mammals (Tesky 1992b). One attribute of this species that may give it an advantage over many native woody species in colonizing available habitats is its capacity to germinate and establish throughout the fall, winter, and spring months (Howe and Knopf 1991). Russian olive



is capable of sprouting from both aboveground and belowground structures. It has been planted throughout the United States, has escaped and spread primarily in western and central states, and is widely distributed from the West Coast to the Dakotas, Nebraska, Kansas, Oklahoma, and Texas (Knoff and Olson 1984). Russian olive readily colonizes disturbed floodplains, stream banks, and in some situations, marshy areas and wet grasslands (Olson and Knopf 1986). Once established, it appears to have a substantial capacity to withstand periodic drought, outcompete native woody species, and is considered to be the successional climax species in many cases (Howe and Knopf 1991). Observations indicate that Russian olive sprouts from the root crown following burning and is also capable of producing root sprouts whenever it is disturbed (Tesky 1992b). At present, there is little quantitative information about its response to fire.

Macartney rose (*Rosa bracteata*) is an evergreen, perennial, thorny vine or shrub (Vines 1960). Flowering begins in late spring and continues throughout much of the summer months. It was introduced from China primarily for erosion control and as a natural fence for pasture. Widely planted in the southern states, it has escaped in various habitats from Texas to Virginia. Macartney rose is a widespread invader in the coastal prairie and in south Texas and has been estimated to represent a problem on >250,000 hectares (Scifres and Hamilton 1993). Macartney rose is able to regenerate from shoot bases, root buds, or from decumbent shoots that touch the ground. It increases under grazing due to its unpalatable nature and forms dense, impenetrable mounds up to 6 m high. It is especially troublesome in pastures as well as in prairies that have been formerly overgrazed and that are now being rehabilitated. Scifres and Hamilton (1993) suggest that Macartney rose may possess volatile oils; during our studies (J.B. Grace and L.K. Allain, unpublished), it was observed to burn readily. Fires are generally effective at topkilling the plants regardless of the season of burn. Regrowth following winter burns is rapid and complete recovery may occur as early as the following late spring (Scifres and Hamilton 1993). Because of low mortality and the rapid rate with which Macartney rose can regrow following burning, repeated burning is required simply to prevent it from spreading further. We have observed substantial regrowth of Macartney rose following repeated growing-season burns that were followed by periods of extreme drought conditions. Available evidence suggests that Macartney rose is very well adapted to fire and that once it is established, prescribed burning alone will not result in its control.

## DISCUSSION

In the majority of cases examined in this paper, the available data permit only tentative conclusions to be drawn about species' relationships to fire. Much of the evidence summarized here for invasive grasses, forbs, and woody plants is observational, lacks ade-

quate controls, and fails to provide information on growing conditions during the period of study. Even the experimental studies, including our own, give only limited insight into the mechanisms behind responses in local areas and, more importantly, say little about the generality in space and time that can be attributed to the results. Despite this, some patterns have been observed frequently enough to convey some confidence in their general validity.

There are a number of caveats to any synthesis involving invasive plant species distributions. (1) Fire is only 1 type of disturbance that could effect the establishment and spread of invasive species. The plow, bulldozers, small mammals disturbing surface soils, floods, and droughts all likely play major roles in the invasion process. Since fire return intervals have been, and will continue to be, heavily influenced by land use, fire suppression, and grazing, these other disturbances can be expected to continue to play important roles in the future. (2) As previously alluded to for many species, disturbances are not absolutely necessary for the establishment and spread of many of the species reported here. Many exotic species are found in unburned and ungrazed areas. (3) Many other factors, such as soil fertility and water availability, influence the vulnerability of habitats to invasion (Stohlgren et al. 1997, 1998b, 1999a). (4) Even where environmental conditions may be ideal for the establishment of a given exotic species, there may be no seed source available (i.e., remote, uninvaded sites). (5) Even after fire, and following the establishment of invasive plant species, pests and pathogens can reduce their abundance and cover (Peterson 1998). Thus, the emphasis we place here on fire should not distract investigators from approaching exotic plant invasions as multifaceted problems.

Aside from the issue of the adequacy of information relied on in this paper, the great span of climatic and ecological conditions being considered means that many generalizations may apply to 1 portion of the range of an invader but not to another. In addition, generalizations that apply in 1 habitat may prove quite inapplicable to another habitat where growing conditions for the invasive species and competing native community are different. Typically, the most detailed studies are conducted where infestations are perceived to be the worst. Whether these results apply to other regions is questionable. Further, we should be very careful not to view the current status of an invader as the limit of its future range or distribution. It is likely for most of the species considered, including those introduced hundreds of years ago, that their populations are still expanding. For example, Chinese tallow was introduced during 1783, yet it only colonized southern California in the past decade. It was initially thought that Johnsongrass, a C<sub>4</sub> warm-season species, would be limited to southern U.S. states due to intolerance of cold conditions (McWhorter 1971). However, this species has since spread as far north as Canada. An additional factor that may change species interactions with fire is the gradual increase in seed output within a locale that occurs dur-

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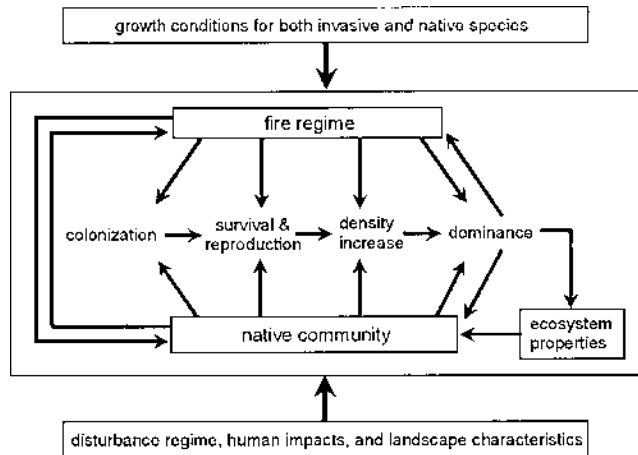


Fig. 5. Conceptual framework for considering the relationship between an invading species and the native community in the presence of fire.

ing establishment and which can increase colonization rates, seed banks, and the potential for local adaptation.

Despite these considerable obstacles, we feel there is merit in attempting to summarize the existing body of knowledge about invasive species and fire in temperate grasslands as it helps us to develop hypotheses and points to the most important information gaps. We ask, however, that the reader be aware that some of the generalizations presented in both the previous section and this section should be viewed as provisional until more extensive studies have been conducted.

Species' Relationships with Fire

Figure 5 presents a framework for summarizing and evaluating how an invading species may relate to the fire regime in a habitat. The major categories of influences are the native community characteristics, the fire regime, the growth conditions for both invasive and native species, and the influences that disturbances, human impacts, and landscape characteristics have had in the past and are projected to have in the future. Based on the information presented in the previous section, it is clear that several major relationships will determine whether an invasive species can successfully invade and grow in a habitat in the absence of fire. These include whether an invading species can survive and continue to increase when fires do occur, and the degree to which it will ultimately alter that system. In this framework, the process of invasion by a species into a native community is broken into 4 stages: (1) colonization, typically from seed (though cases of long-distance dispersal of vegetative propagules may occur in some cases); (2) survival and reproduction; (3) density increase within a site, which includes spread within a site (either through seed or vegetatively) as well as increases in abundance in colonized areas; and (4) dominance, which implies not only the establishment of substantial abundance but also the suppression of other species.

The framework in Figure 5 provides a basis for summarizing some of the main findings for individual

invasive species. Table 2 relies in part on this framework to provide comparative information for some of the species for which the available information appears to be most complete and reliable. In no case do we have all the information necessary to define all the relationships specified in Figure 5. For some species, only 1 or 2 key pieces of the puzzle are represented by published studies. Within these constraints, the information presented in Table 2 provides a provisional assessment for 5 main questions about how an invasive species relates to fire: (1) Does fire appear to enhance colonization? (2) To what degree does fire affect the survival of plants? (3) Are plants that are burned able to regrow following fire and, if so, how rapidly can they recover? (4) How important is competition with native species to the response to fire? (5) What effect does an invasive species have on the characteristics of the fire regime?

Patterns of Responses to Fire

Consideration of the information summarized in Table 2 about species' relationships to fire suggests that there are a finite number of patterns demonstrated by the species evaluated in this paper. Figure 6 presents a diagrammatic representation of 7 general patterns (based on Figure 5). It is important to keep in mind 2 main caveats when interpreting Figure 6: (1) the 7 patterns presented do not represent a complete set of possible relationships, only a range of examples suggested by the available data; and (2) the various pattern types describe situations rather than species. In some instances, a species tends to fit a particular pattern under a broad range of ecological circumstances while in other instances, a species may fit more than 1 pattern depending on circumstances. Even the particular conditions that affect the behavior of an individual fire may prove to be important. For virtually all species, current information is insufficient to permit a complete characterization of the range of patterns it exhibits.

Pattern I (Figure 6) depicts the case where species are strongly and adversely affected by fire and where that effect is sufficiently deleterious to prevent the invader from achieving dominant status. Many variations of pattern I are possible. In this idealized example, the native community promotes the pyrogenicity of the system. In turn, the fire regime does not have substantial negative effects on the native dominant species and, thus, promotes the long-term existence of the native, fire-adapted community. The invading species in this example is not well adapted to surviving the effects of fire and can be expected to be eliminated regardless of the direct competitive effects of the native community. One species that may exhibit this pattern under some circumstances is Japanese brome (Whisenant 1990). Two key attributes determine the fate of this winter annual in the presence of fire: (1) it often requires a litter layer to enable successful establishment from seed, and (2) both plants and seeds are killed by fire. It appears that the establishment of Japanese brome has been enhanced by widespread fire

Table 2. Summary of patterns observed for interrelations between invasive species and fire.

Species	Enhancement of colonization by fire	Effects of fire on survival	Ability to regrow following fire	Relation to competitors	Effects on fire regime
Cheatgrass	Likely	Killed by fire	Must reestablish by seed	Strong against annuals, weak against perennials	Increases fire frequency and size
Smooth brome	Likely	Direct mortality low	Burns during spring growth period more strongly reduce plant density	Strong against annuals, weak against perennials; timed burning can tip competitive balance	None reported
Japanese brome	Fire removes litter and inhibits colonization	Plants and seeds killed	Populations slow to recover	Strong in arid area, even against perennials	None reported
Crested wheatgrass	Likely	Various results reported	Various results reported	Competes best in arid sites, more poorly in mesic areas	Can reduce fire frequency and size
Kentucky bluegrass	Likely	Direct mortality low	Burns during spring growth period more strongly reduce plant density	Timed burning can tip competitive balance	None indicated
Quackgrass	Unknown	Direct mortality low	Plants can regrow quickly; may depend on burn time	May fit same pattern as for Kentucky bluegrass	None indicated
Bermudagrass	Unknown	Direct mortality unlikely	Dormant-season burns enhance growth	Perhaps outcompeted by taller grasses in absence of fire	None indicated
Cogongrass	Slight enhancement	Mortality unlikely	Very rapid recovery	Appears that fire will tip competitive balance further in its favor	Can alter fire characteristics
Leafy spurge	Unclear	Mortality unlikely	Extremely rapid recovery	May be outcompeted by heavy grass cover but, nonetheless, very competitive; fire not likely to tip competitive balance against it	May reduce fire frequency and intensity
Spotted knapweed	Enhanced	Substantial mortality	Population recovery aided by persistent seedbank	Undescribed	May reduce fire frequency and intensity
Russian knapweed	Unknown	Some survival likely	Unknown	Most competitive knapweed species	Unknown
Yellow starthistle	Enhanced	Adult plants killed	Must recover by seed	Timed annual burning can eliminate regardless of competitors	None reported
Purple loosestrife	Unknown	Most survive	Recovery rapid	Fire has no known effect	Unknown
Sericea lespedeza	Enhanced	Most survive	Recovery rapid	Unknown	Unknown
White sweetclover	Enhanced	Killed by growing-season burns	Rapid recovery by seed if burning infrequent	Appears to be strong competitor in restorations	Unknown
Musk thistle	Likely	Survival likely	Rapid recovery	Competition from native dominant grasses appears to be critical factor, with or without burning	Unknown
Saltcedar	Likely	Topkilled but most survive and resprout	Rapid recovery	Competition generally insufficient to make a difference	Intensify in riparian areas
Chinese tallow	Likely	Hot fires can topkill even large trees	Rapid recovery	Fire can tip balance towards native fuel species, thereby adversely affecting Chinese tallow	Major fire suppressor
European buckthorn	Unknown	Seedlings die; mature trees topkilled	Rapid recovery	Unknown	May be fire suppressor
Macartney rose	Not observed	No mortality for established plants	Very rapid recovery	Even frequent fire does not appear to tip balance once established	No observed effect



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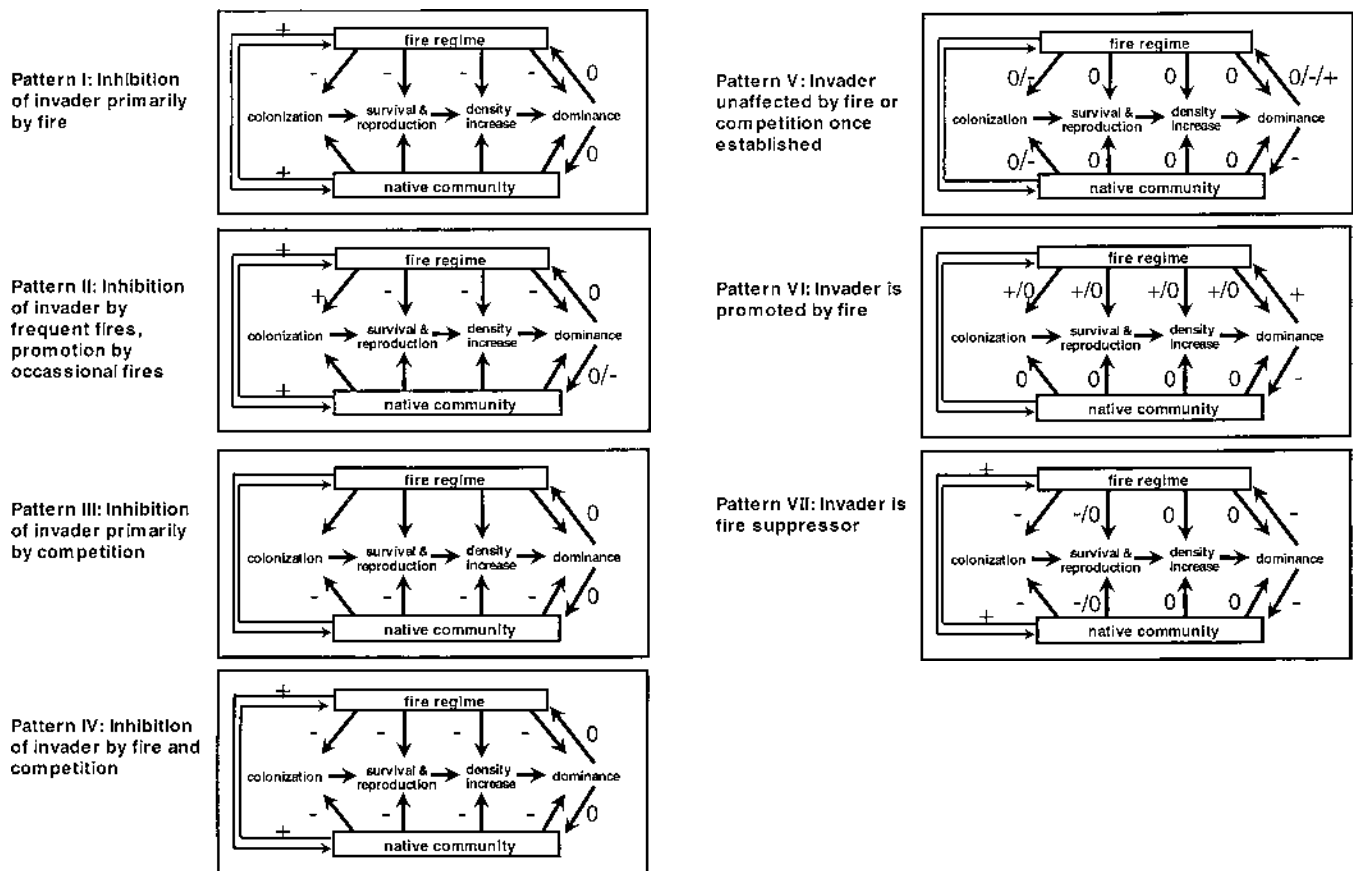


Fig. 6. Representation of specific patterns associated with the relationship between invasive species and fire. This figure presents the core relationships from Figure 5 and illustrates 7 different cases, which differ in the nature of relationships between invasive species and both the fire regime and the native community. Plus signs represent positive effects, minus signs indicate negative effects, and zeros indicate no effects. Arrows without a plus, minus, or zero represent the case where a relationship is not particularly important, regardless of its sign. As an example of how diagrams are to be interpreted, when an invader is inhibited primarily by fire (Pattern I), direct negative effects of fire on the invader are the main reason the invader fails to succeed while negative effects from the native community, even if they occur, are not terribly important (and are, therefore, not specified with a plus, minus, or zero). In this example, the native community supports the fire regime, which in turn favors the native community. Finally, since the invader does not come to dominate, it has no major effect on either the fire regime or the native community.

suppression, allowing regional populations to build up. Further, its ability to grow during the winter and initiate rapid growth earlier than most native, cool-season species makes it a good competitor in arid conditions. In the presence of occasional burns, it is able to recover from the resultant population reductions. However, a sequence of annual burns timed to kill the plants before seed set can deplete the seed bank and result in drastic reductions in population density.

Pattern II (Figure 6) represents the case where fire may promote the colonization process, but otherwise inhibits an invader. In this case, occasional fires promote an invader while frequent fires are inhibitory. Yellow starthistle and white sweetclover appear to fit this pattern under some circumstances. According to Hastings and DiTomaso (1996), germination in yellow starthistle is stimulated by fire but established plants are typically killed. As a result, individual fires can actually foster the process of colonization/recolonization and under most natural fire regimes, this species will not be controlled by fire. However, repeated, an-

nual fires timed to occur before yellow starthistle sets seed can deplete the seed bank and lead to its elimination from a site (Hastings and DiTomaso 1996). A similar relationship to fire has been reported for white sweetclover. Evidence suggests that its seedcoat is scarified by heat during burning and that, as a result, germination is stimulated by fire (Kline 1986). However, burns during the growing season appear to kill this biennial plant in its second year of growth and frequent burning is recommended as a means of controlling this species. Results presented by Collins (1987) suggest that frequent spring burns can actually inhibit establishment by many exotic invaders in tall-grass prairie.

Pattern III (Figure 6) represents the case where invaders may be tolerant of fire but are unable to persist over time due to competition from other vegetation. One species that has been reported to be sensitive to competitive effects is musk thistle. Hulbert (1986) has observed that in tallgrass prairie, musk thistle is unable to persist in ungrazed prairie regardless of the

fire regime due to competitive exclusion. To a lesser degree, this pattern may hold for bermudagrass in the absence of grazing or mowing. Pattern III certainly applies to many early successional species that are commonly found in abandoned agricultural fields or roadsides but that do not invade native grassland communities. Many of these species are turning out to be problems for restoration efforts, though it is hoped that over successional time they will be less problematic. Because of the large number of cases where exotic species invade following disturbance (either mechanical or associated with grazing), it is not always clear whether these species will turn out to be sensitive to competitive effects once disturbances are reduced. Also, because invaders may be quite competitive in 1 geographic region but weak competitors in another, many species may fit this pattern in various times and places. As an example, many of our worst invaders in arid regions, such as cheatgrass, Japanese brome, and spotted knapweed, may be poor competitors in more mesic parts of their ranges.

Pattern IV (Figure 6) represents the relatively common case where invaders are affected by both fire and the native community. Because so many herbaceous species are capable of surviving the direct effects of fire or rapidly recolonizing following fire, the competitive effects of native species and differential responses to burning are pivotal in determining the success of an invader. One species for which fire and competition commonly work in combination is smooth brome. It has been shown that in the absence of native warm-season competitors, even fire precisely timed to have maximum impact on smooth brome (a cool-season species) will not be sufficient to lead to sustained population reductions (Willson and Stubbendieck 2000). However, when smooth brome grows in conditions where there is an abundance of warm-season native grasses, fire can tip the balance of competition in favor of the native competitors. Several other examples of this pattern have been observed involving Kentucky bluegrass, quackgrass, and possibly crested wheatgrass and Canada thistle.

Pattern V (Figure 6) depicts the forces involved when an invader is relatively unaffected by fire or competition once it has established. Species that demonstrate this pattern are among those most difficult to control and for which herbicide and biological control programs are most widely used. One species that appears to commonly fit this situation is leafy spurge. Competitive effects by native species may be important in limiting its establishment; however, it also appears that under a broad range of conditions, including some cases of undisturbed tallgrass prairie, it is sufficiently competitive to become established and attain dominant status. Certainly its ability to withstand adverse effects from burning means that fire may have little capacity for tipping the competitive balance in favor of native species once leafy spurge has established. A number of other highly competitive species are very well adapted for recovering from burning and include Macartney rose, saltcedar, giant reed, purple loosestrife, sericea lespedeza, and Russian olive. For

these species, the key to their invasion success may be in the earliest stage of colonization when their competitive abilities are most weakly developed.

Pattern VI (Figure 6) represents the case where an invader is promoted by fire. Several processes can be involved in such a case. For example, if fire simply impacts native species more than the invader, this can tip the competitive balance in favor of the invading species. Several species are thought to be promoted by fire in this fashion under at least some circumstances (e.g., cheatgrass, smooth brome, yellow starthistle, several knapweed species). Further, if the invading species has the capacity to alter fuel characteristics and, as a result, increases fire frequency and/or intensity, this may further tip the balance in favor of the invader. The best publicized examples of this situation involve arid habitats with historically low fire frequencies; for example, where species such as cheatgrass increase fire probabilities and in Hawaii, where species such as broom sedge (*Andropogon virginicus*) have increased system flammability. In more mesic temperate grasslands, which are already well adapted to frequent fires in most cases, the effects of new species that create greater fuel loads and/or increase the probability of fire or the rate of fire spread will be expected to have less dramatic effects. Nonetheless, some species, such as cogongrass, may be able to change fire frequencies even in habitats with historically frequent fires.

Pattern VII (Figure 6) is indicative of the case where an invader is a fire suppressor. Fire-suppressing species pose a particular threat to ecosystems historically exposed to frequent wildfires, such as grasslands, because long-term persistence of the community depends on the ability of the dominant species to maintain the flammability of the system (Mutch 1970). Many species of forbs appear to have the potential to result in cooler fires and a narrower range of weather conditions under which a community will carry fire, especially when they replace native grasses. Some grasses, such as crested wheatgrass, may also retain higher moisture contents and produce less persistent litter, making the resulting fires lower in intensity. The most extreme example of fire suppression we have seen, however, involves the Chinese tallow tree. Once Chinese tallow invades a site, it can rapidly reduce the capacity of the system to burn. Several characteristics contribute to this effect. First, Chinese tallow itself rarely combusts and will not carry fire. Second, as trees begin to shade the herbaceous layer, shade-tolerant species, which are typically forbs, replace the shade-intolerant dominant species, which are typically grasses. The result is that the flammability of the system decreases before fuel loads are greatly reduced. Once canopy closure is achieved, virtually all herbaceous vegetation is eliminated and the system becomes nonflammable. There is some indication that European buckthorn may also suppress fuel species and reduce flammability, though to a lesser degree than Chinese tallow.

For many other species, their relationships to fire are not clear based on current information. For ex-

ample, little published information seems to exist on how Russian knapweed relates to fire. Many invasive grasses common to the southern states, such as Johnsongrass, bahiagrass, and Old World bluestems (species of *Andropogon*, *Bothriochloa*, and *Dichanthium*), are very productive, highly competitive, and resistant to direct effects of burning. Because the native grasses in these regions also tend to be highly competitive, these invaders are not necessarily successful in dominating undisturbed habitats, and we are not yet able to relate them to the patterns in Figure 6 with accuracy.

Woody invaders, as a group, appear to be resistant to the effects of fire, usually due to substantial capacities for resprouting. This generalization appears to apply to a large number of native woody species such as red cedar (*Juniperus virginiana*), Ashe juniper (*Juniperus ashei*), eastern baccharis (*Baccharis halimifolia*), honey mesquite (*Prosopis glandulosa*), huisache (*Acacia farnesiana*), wax myrtle (*Myrica cerifera*), yaupon (*Ilex vomitoria*), and numerous others that seem to have increased during periods of fire suppression and that are now proving difficult to control with fire (L.K. Allain and J.B. Grace, unpublished). While many of the nonnative and native woody species are capable of reducing herbaceous fuels to some degree, to our knowledge, these species are not capable of rendering the system nonflammable.

#### Community Perspectives

In addition to considering individual invasive species across the range of grasslands in which they occur, it is instructive to consider a few specific grasslands as a means of evaluating invasive species within the context of communities and landscapes.

#### Coastal Prairie—Brazoria National Wildlife Refuge

One landscape in which the relationship between invasive species and fire is being examined is in the coastal prairie at the Brazoria National Wildlife Refuge (NWR), Angleton, Texas (J.B. Grace and L.K. Allain, unpublished). This refuge acquired a 12,000-ha addition in 1990 that includes a mosaic of former rangeland (never plowed) and abandoned agricultural fields. Several rivers, streams, and canals, as well as freshwater marshes and tidal estuarine marshes, occur within this landscape. In addition to a series of experimental burns in areas being invaded by Chinese tallow, 27 sites across the range of terrestrial habitats have been monitored for changes in vegetation during the course of the prescribed burn program being conducted by the U.S. Fish and Wildlife Service. While the results are only preliminary at this time, there are several general observations that can be made about invasive species in this landscape.

First, the degree of previous disturbance to the soil has had a big impact on both the variety of invasive species and the abundance of native species. Abandoned rice fields are the primary invasion site for Chinese tallow and also have the lowest quantity of native competitors and the lowest quantity and quality of herbaceous fuel. Also, Macartney rose is well established

in areas that were previously overgrazed and once it becomes established, appears to be resistant to control by burning. One encouraging note for this system is that since fire has been reintroduced to this landscape, seed production from native species has greatly increased and recolonization of former agricultural fields by native species has been observed.

Second, individual invasive species have very different distributions and growth rates, depending on the edaphic conditions. Chinese tallow first invades riparian zones and fence lines and then spreads into the prairie. In part because of its large seeds, Chinese tallow appears to be able to establish in undisturbed sod at this site. Areas with more saline soils are not only free of Chinese tallow invasion, they are also generally free from most invasive species. The main exception to this is saltcedar, which is now invading the site as it spreads eastward along the Texas coast.

Third, there are many other invasive species on the roadsides and in disturbed areas on the refuge that have shown only limited capacity to invade the native communities thus far. This suggests that perhaps the majority of invaders may be inhibited at least to some degree by the competitive effects of native dominant species. Future observations, as well as off-site experiments, will be required in order to evaluate the threat some of these other species pose and the role that fire plays.

#### Tallgrass Prairie—Konza Prairie Biological Station

Konza Prairie, in part a National Science Foundation Long-Term Ecological Research site, is a 3,487-ha tallgrass prairie preserve located in the Flint Hills of northeastern Kansas, a region characterized by relatively steep topography. Grassland communities at Konza Prairie are dominated by several  $C_4$  warm-season tallgrass species, in particular big bluestem and Indiangrass (*Sorghastrum nutans*), with a number of subdominant forbs constituting a majority of the plant species diversity. Exotic species make up only a small percentage of the species found on these sites, and thus this mesic grassland is considered relatively resistant to invasion by exotic species (Smith and Knapp 1999).

Relationships between exotic species and fire in tallgrass prairie plant communities, in particular the effects of long-term annual burning and fire history, were examined using data collected from a 15-year experiment conducted at Konza Prairie (Smith and Knapp 1999). This experiment incorporated watershed-level fire frequency treatments, including spring burning at 1, 2, 4, 10, and 20-year intervals. Long-term annual burning resulted in 80–100% reductions in the number and abundance (cover) of exotic plant species compared with infrequently burned plots. Fire history also affected exotic species richness (Figure 7). Exotic species were absent from those sites that had been burned 26 of 27 years, whereas exotic species richness steadily increased as the number of times a site was burned decreased, with the highest richness for those sites burned fewer than 6 times over the 27-year period. Thus, the cumulative effects of fire appear



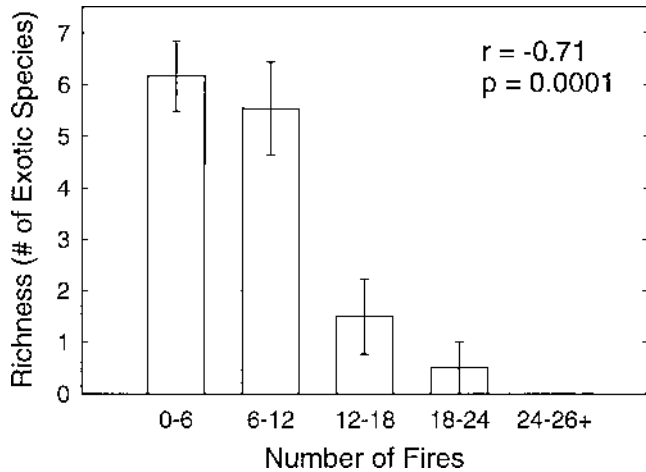


Fig. 7. Relationship between number of fires in the last 27 years and exotic plant species richness (per 200 m<sup>2</sup>) for ungrazed sites on Konza Prairie in the Flint Hills of northeastern Kansas. Error bars represent  $\pm 1$  SE of the mean. From Smith and Knapp (1999), with permission from *Oecologia*.

to be important in controlling invasion by exotic species in tallgrass prairie, with annual burning being most effective at preventing establishment or persistence by exotic species.

The effects of fire on exotics, and indeed, on total species richness (Collins et al. 1995), are not likely to be the result of the direct impacts of burning. Instead, by increasing the productivity of dominant C<sub>4</sub> tallgrasses, it appears that fire indirectly affects exotic species. Fire, by reducing nitrogen availability, homogenizing resources, and increasing dominance of C<sub>4</sub> grasses, also negatively affects native species richness (Collins and Steinauer 1998, Knapp et al. 1999). Thus, it appears that the same factors that influence native species in tallgrass prairie, such as fire and grazing, may affect exotic species as well (Figure 8; Collins et al. 1998, Knapp et al. 1999). Although annual burning appears to increase resistance of tallgrass prairie to invasion, there is evidence that exotic species richness increases 2-fold in annually burned sites that are grazed when compared with similar ungrazed sites. Again, the response by invasives mirrors that of native species richness. Collins et al. (1998) reported that total species richness on annually burned, nitrogen-enriched, mowed plots was significantly higher than on burned, nitrogen-rich plots that were not mowed. In addition, if there is a large pool of exotic species surrounding an annually burned site even these communities are susceptible to invasion by exotics (Smith and Knapp 2001). Further research is needed to determine the mechanisms controlling these relationships between fire and exotic species in tallgrass prairie.

#### Examples from Shortgrass Steppe, Northern Mixed Prairie, and Mixed Grasslands

Several recent multi-scale vegetation sampling studies in the Central Grasslands have found patterns of exotic plant distributions that may set the stage for future problems. Across the Central Grasslands, veg-

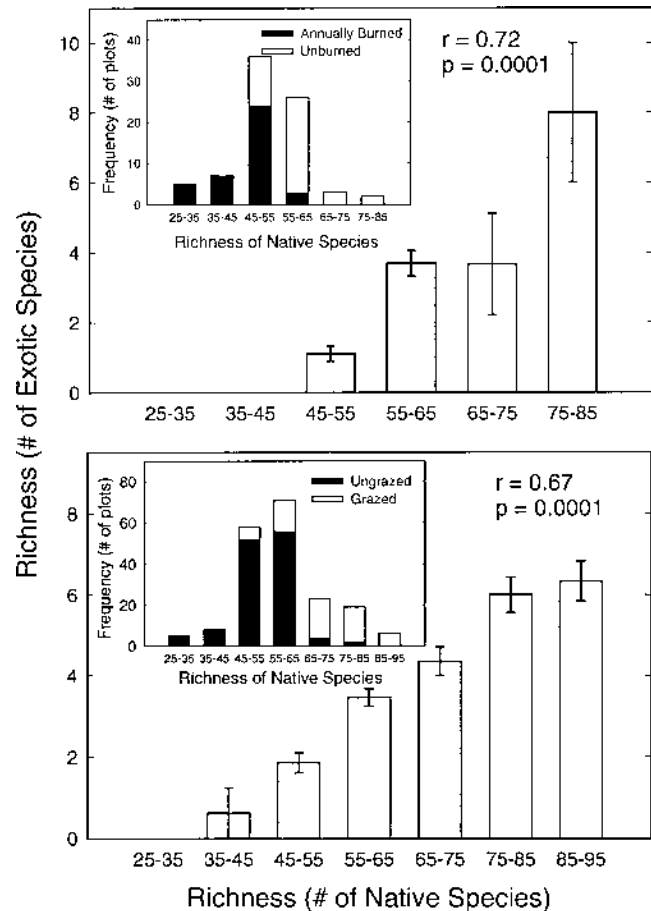


Fig. 8. Upper figure presents the relationship between native and exotic plant species richness (per 200 m<sup>2</sup>) for burned and unburned sites (all ungrazed) over a 15-year study at Konza Prairie in the Flint Hills of northeastern Kansas. Inset in upper figure: distribution of annually burned and unburned plots in different native species richness classes. The lower figure presents the relationship between native and exotic species richness (per 200 m<sup>2</sup>) for sites (both burned and unburned) that were or were not grazed. Inset in lower figure: distribution of grazed and ungrazed plots in different native species richness classes. Error bars represent  $\pm 1$  SE of the mean. From Smith and Knapp (1999), with permission from *Oecologia*.

etation types high in native plant diversity have been heavily invaded by exotic plant species (Stohlgren et al. 1998a, b, 1999a, b). Underlying this general pattern were significant positive correlations between native and exotic species cover, and between exotic species richness and cover. In general, native and exotic species richness and cover were also significantly positively correlated with soil nitrogen and carbon (soil fertility), and with soil clay and silt fraction (water holding capacity; Stohlgren et al. 1999a). Another study compared vegetation and soils in riparian zones and upland sites in shortgrass steppe (Central Plains Experimental Range, Nunn, Colorado) and northern mixed grass prairie (Wind Cave National Park and Badlands National Park, South Dakota; and Bighorn Mountains Natural Recreation Area, Wyoming). The study found significantly more exotic species in riparian zones compared with adjacent upland sites (Stohlgren et al. 1998b). The same patterns exhibited at large-

er scales were found within sites. Plots with greater native species richness and cover had more fertile soils and higher richness and cover of exotic species.

Grazing is thought to play a role in grassland fuel loads and in the spread of invasive plant species. However, 1 study evaluated vegetation and soils inside and outside of long-term grazing exclosures in temperate and montane grasslands in Colorado, Wyoming, South Dakota, and Montana and found no adverse effects of grazing (Stohlgren et al. 1999b). At 1-m<sup>2</sup> scales and 1,000-m<sup>2</sup> scales, exotic species richness and cover were no different in long-term grazed areas compared with long-term ungrazed areas. Rather, it may be that cessation of grazing would increase biomass and, thereby, increase fire frequency. For areas subject to invasion by species that are promoted by occasional fire, such as cheatgrass, yellow starthistle, and certain knapweeds, this may lead to an accelerated spread of invaders following fire.

#### *Understanding Site-to-Site Differences*

The site-specific examples presented above further emphasize the difficulty of drawing generalizations about invasive species that apply across a broad range of habitat conditions. At the Brazoria NWR (an example of coastal prairie), it appears that previous grazing activities may have permitted a number of invasive species to become established. Current prescribed burning appears to either support the recovery of the native community (e.g., through damage to small Chinese tallow trees) or have no effect (e.g., having little impact on established Macartney rose, saltcedar, or large-dense stands of Chinese tallow). Though information is somewhat limited, there is no indication at this time that burning is acting to promote the spread of invasive species in this landscape. At Konza Prairie (an example of Central Plains tallgrass prairie), it also seems that grazing has promoted the establishment of a number of exotic species while frequent burning has acted to impede invasion by many species. Some exotics, such as Caucasian bluestem, however, appear to be promoted by either fire or grazing and may escape control by frequent burning. At study sites within shortgrass steppe and mixed grasslands, which are typically more xeric than coastal or tallgrass prairie sites, several important exotic plants (e.g., cheatgrass, yellow starthistle, certain knapweed species), appear to be favored by occasional burning. Here, the interaction with grazing is more complex. While it again appears that grazing history may have allowed many exotic species to become established, reductions in grazing are expected to permit fuel buildups that will increase fire frequency, which in turn may actually promote the spread of some invasive species. Across the broad range of conditions and circumstances that occur in temperate grasslands, it is clear that the interplay of contemporary and historical factors will be ultimately important in how fire interrelates with invasive species.

#### MANAGEMENT IMPLICATIONS

Across all of the examples considered, there appear to be some common patterns for the relationships presented in Figure 5. First, some invasive species are not well adapted to fire and will be easily eliminated from grasslands if adequate effort is applied. Another set of invasive species is better adapted to burning, but their weaknesses can be exploited if burns are timed to coincide with physiologically vulnerable periods. Other species are extremely well adapted to fire and will not be eliminated through burning alone.

Second, the competitive environment plays a critical role in the ability of nonnative species to invade native communities. Systems with less human-induced disturbance seem to be able to resist invasion by many, though not necessarily all, exotic plant species. Konza Prairie, for example, is an area where the native vegetation appears to provide significant resistance to invasion. Brazoria NWR, in contrast, is a landscape in need of restoration, and it will take considerable effort to recover the abundance of native grasses that provide maximal protection against invaders. During this recovery period, significant effort will have to be dedicated to managing exotics, such as Chinese tallow, saltcedar, and Macartney rose. In shortgrass steppe and mixed grassland habitats, historic grazing, and what may be a naturally lower competitive resistance due to lower community productivity, combine to create a situation in which fire may actually favor the spread of exotic species.

Third, a few invasive species have traits entirely foreign to the communities they invade and which, as a result, pose extraordinary threats. The abilities of cheatgrass to enhance fire and Chinese tallow to suppress fire means that controlling populations of these 2 species will be difficult to achieve without intensive human intervention.

Finally, our base of knowledge about the relationship between invasive species and fire is quite inadequate. More research is needed on the prevention, early detection, and control of invasive species following fire. Research is also needed to evaluate appropriate restoration techniques. In addition to simply increased research effort, creative new approaches, as well as studies that involve more ecosystem components (such as other trophic levels), are needed if we are to acquire the information necessary to best utilize fire in conserving native diversity.

#### ACKNOWLEDGMENTS

We are indebted to Tracey McDonnell Wysor and Brian Fontenot for considerable effort in helping to locate much of the literature on which this review is based. Larry Allain, Heli Jutila, Tracey McDonnell Wysor, Bill Rogers, Beth Vairin, and 2 anonymous reviewers provided numerous helpful comments on the manuscript.

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