

# Invasive Species in a Changing World



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A Project of SCOPE,  
the Scientific Committee on Problems of the Environment

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## Chapter 4



# Fire, Plant Invasions, and Global Changes

*Carla M. D'Antonio*

Fire has played an important role in human history and in the ability of humans to control the natural world. Nonetheless, in the last century, our ability to control plant growth with fire has begun to change as unwanted exotic species spread across the landscape and interact with fire in a way that may be both unpredictable and undesirable. Generalizations regarding the relationship between fire and the dynamics of invasive, exotic species have been elusive because of the diversity of ecosystems being invaded by introduced species and the variation in the frequency and importance of natural fire. Yet clarification of this relationship is essential if we are to predict how climate, land use, and other global-scale changes will influence the occurrence and outcome of wildfire. Because well-established invaders can themselves influence fire regimes (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998), it is also important to begin identifying invader traits that might promote or suppress fire under current and changing climate.

There is clear evidence that many invasive nonnative species can be promoted by fire, but there is also evidence that many introduced species can be controlled by fire. For example, in the Hawaiian islands, fire in seasonally dry

ecosystems appears to promote exotic grasses to the detriment of native species (Smith and Tunison 1992; Hughes et al. 1991). Yet in the California coast and interior valleys, fire is used as a management tool to reduce exotic and promote native species (e.g., Parsons and Stohlgren 1989; Hastings and DiTomaso 1996). In addition, in some areas of the western United States, introduced European annual grasses increase fire frequency and respond positively to it (e.g., Whisenant 1990a; Young 1992; Brooks 1998) while in other parts of the western United States, fire is being used to control some of these same invaders. Clearly then, it is important to try to clarify the conditions under which fire suppresses versus promotes introduced species. In addition, many of the fire-promoted and fire-promoting invasive exotic species are grasses that were purposefully brought to or planted into the region where they are now naturalized. If these species promote fire to the potential detriment of native species, then we need the tools with which to evaluate the ecological versus cultural or socioeconomic trade-offs that arise from the grass-fire interaction.

In this chapter I will discuss recent literature examining the impacts of fire on introduced species and the impacts of introduced plants on fire regimes with the goal of finding generalizations that might be useful in a management framework. I will also briefly explore potential interactions between fire, invasion, and other elements of global environmental change. I used BIOSIS, an abstract service, and references cited in D'Antonio and Vitousek 1992 and D'Antonio et al. (1999) to survey for recent (past thirteen years) literature on the subject. I did not attempt to survey the extensive gray literature or older literature on use of fire as a management tool. Several caveats should be noted a priori regarding our ability to draw firm conclusions in this area: (1) Fire intensity and behavior is extremely variable even within a site, so variation in impacts should be expected at all scales. (2) Quantification of fire frequency and intensity is rarely done because it is difficult. Thus few data are available to look for numerical correlation between fire regime parameters and invasion intensity, and much of the information available is anecdotal. (3) There is no general consensus on what constitutes an invasion or what level of population increase or decrease after fire represents a biologically important change. In spite of these caveats, there is ample information available to begin to make reasonable predictions about the relationship between fire and invasions now and into the near future.

## Role of Fire in Promoting Invasion of Native Ecosystems

Understanding the role of fire in promoting the invasion of native ecosystems is important because human contact with ecosystems often promotes accidental fire as well as provides a means for propagules of exotic species to enter

an ecosystem. In addition, many societies use fire to manage ecosystems both to promote or to discourage particular species. Lastly, several investigators (e.g., Torn and Fried 1992) have suggested that natural fire frequency and/or intensity should increase in many regions of the world as a result of climate changes predicted by recent global circulation models. Such changes may affect the abundance of invasive exotic species, which in turn might affect native biological diversity and the functioning of ecosystems.

### *Fire Often Promotes Invasion*

Over the past two decades many studies have documented an increase, decrease, or no change in the abundance of an exotic species in response to fire. A sampling of these are detailed in Tables 4.1 and 4.2. In the vast majority of cases, fire resulted in an increase in introduced species; only in 20 percent of the cases did fire reduce or eliminate an invader. In very few cases did fire have no effect on the abundance of an invader. Ecosystems where fire had a positive effect on native species include (1) desert shrublands and woodlands of western North America, including the Great Basin and the Mojave and Sonoran Desert regions; (2) semiarid shrublands including heathland and shrublands of Australia, the fynbos of South Africa, and California chaparral; (3) grassland/savanna ecosystems from eastern Australia, Venezuela, France, and California; and (4) more mesic but seasonally dry woodland including Hawaii, western Australia, and parts of eastern Australia.

Despite a sizable literature on the role of recurrent "natural" fire in many ecosystems throughout the world, such as California mixed-conifer forest and interior chaparral, the garigue of Spain, monsoonal forests and savannas in northern Australia, and dry savannas of Africa (e.g., MacDonald and Frampton 1988), there is very little mention of the occurrence of invasive exotic species in these systems. In the case of California chaparral, we know that the propagules of introduced species are sometimes close by, yet communities experiencing a more or less "natural" fire regime appear to be somewhat resistant to invasion (at least right now!). By contrast, South African shrublands, which have a long history of recurrent fire, are becoming heavily invaded by a few fire-tolerant woody species (e.g., Richardson et al. 1990, 1996). Although native species there can respond positively to fire, the introduced species appear to have more prolific seed production and more rapid regeneration and fire provides a "window of opportunity" for the invaders. After successive fire cycles, invaders increase and native species richness declines (Holmes and Cowling 1997). This instructive example demonstrates that even communities where fire has been an historic occurrence can be invaded by fire-resistant or -responsive species.

In many studies, investigators conducted controlled burns specifically to try to reduce the abundance of an exotic pest plant (Table 4.2). The effective-

an ecosystem. In addition, many societies use fire to manage ecosystems both to promote or to discourage particular species. Lastly, several investigators (e.g., Torn and Fried 1992) have suggested that natural fire frequency and/or intensity should increase in many regions of the world as a result of climate changes predicted by recent global circulation models. Such changes may affect the abundance of invasive exotic species, which in turn might affect native biological diversity and the functioning of ecosystems.

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Table 4.1. Examples showing increase in exotic species after accidental or natural fire. Most studies are observational or correlative. Controlled burn studies are described in Table 4.2.

Study region (habitat)	Invader (common name)	Role of fire	Reference	Study region (habitat)	Invader (common name)
California (riparian)	<i>Arundo donax</i> (giant reed)	Invasion occurs without fire but fire promotes thickening	Bell 1997	Hawaii (seasonal sub-montane woodland)	<i>Schizachyrium condensatum</i> (beard grass), <i>Melinis minutiflora</i> (mole grass)
(maritime chaparral)	<i>Carpobrotus edulis</i> (highway iceplant)	Invades slowly without fire; germination reduced by fire but invasion enhanced by it	Zedler and Schiedt 1988; Hickson 1988; D'Antonio et al. 1991	NW Territories Canada (boreal forest)	European annuals and biennials
(chaparral)	<i>Bromus</i> spp., <i>Schismus barbatus</i> , <i>Brassica nigra</i> (black mustard)	Enhanced by repeated burning	Haidinger and Kee 1993	Venezuela (llanos)	<i>Hyparrhenia rufa</i> (thatching grass/jaragua)
(Sierra foothills)	<i>Cytisus scoparius</i> (Scotch broom)	Germination promoted by fire	Bossard 1991	Brazil (cerrado)	<i>M. minutiflora</i> (molasses grass)
(Mojave Desert)	<i>Bromus rubens</i> (red brome), <i>S. barbatus</i>	Invade without fire; dominance promoted by fire	Brown and Minnie 1986; Brooks 1998	France (grassland)	Exotic annual grasses
Western U.S.A. (Great Basin Desert)	<i>Bromus tectorum</i> (cheatgrass)	Slow invasion without fire; thickening and dominance promoted by fire	Klemmedson and Smith 1955; Sparks et al. 1990; Whisenand 1990a; Svejcar and Tausch 1991	W. Australia ( <i>Eucalyptus</i> woodland) (open woodland, shrubland)	Annual forbs and grasses Perennial grasses, primarily <i>Ehrharta calycina</i> (veldt grass)
	<i>Taeniatherum asperum</i> (medusahead)	Needs fire to invade some areas but not others	Young and Evans 1992	SW Australia (roadsides adjacent to sclerophyll woodland)	<i>Eragrostis curvula</i> (weeping lovegrass) <i>E. calycina</i>
(desert riparian floodplain)	<i>Tamarix ramosissima</i> (salt cedar)	Invades without fire, increases with fire	Busch 1995	South Africa (proteoid fynbos) (mountain fynbos)	<i>Acacia</i> spp. <i>Pinus radiata</i> (Montana pine), <i>P. halepensis</i> , <i>Banksia</i> (3 spp.)
Nevada (Great Basin Desert)	<i>Bromus rubens</i> (red brome)	Invades without fire; enhanced by fire	Beatley 1966; Hunter 1991; Svejcar and Tausch 1991		
Arizona (Sonora Desert grassland)	<i>Eragrostis lehmaniana</i> (Lehman's lovegrass)	Can spread without fire but may be enhanced by fire	Cable 1971; Anable et al. 1992		
Sonora, Mexico (Sonoran Desert/thornscrub)	<i>Pennisetum ciliare</i> (buffel grass)	Invades slowly without fire in several habitats; thickening enhanced by fire	Búrquez and Quintana 1994; A. Burquez, UNAM Hermosillo, personal communication		

<i>Study region (habitat)</i>	<i>Invader (common name)</i>	<i>Role of fire</i>	<i>Reference</i>
Hawaii (seasonal sub- montane woodland)	<i>Schizachyrium condensatum</i> (beard grass), <i>Melinis minutiflora</i> (molasses grass)	Invade without fire, but some, particularly <i>M. minutiflora</i> , are promoted by fire	Hughes et al. 1991
NW Territories Canada (boreal forest)	European annuals/ biennials	Temporary invasion occurred after large natural fire	Wein et al. 1992
Venezuela (llanos)	<i>Hyparrhenia rufa</i> (thatching grass/ jaragua)	Invades without fire but is promoted by fire	Bilbao 1995
Brazil (cerrado)	<i>M. minutiflora</i> (molasses grass)	Can invade without fire but also promoted by fire	J. Augusto Santos, R. Oliviera, personal communication
France (grassland)	Exotic annual grasses	Temporary invasion occurs after fire	Trabaud 1990
W. Australia ( <i>Eucalyptus</i> woodland)	Annual forbs and grasses	Enhanced by fire	Bridgewater and Backshall 1991
(open woodland, shrubland)	Perennial grasses, primarily <i>Ehrhardta calycina</i> (veldt grass)	Enhanced by fire	See MacDonald and Frame 1988
SW Australia (roadsides adjacent to sclerophyll wood- land)	<i>Eragrostis curvula</i> (weeping lovegrass), <i>E. calycina</i>	Invasion enhanced by fire	Milberg and Lamont 1995
South Africa (proteoid fynbos)	<i>Acacia</i> spp.	Invasion enhanced by fire	Holmes et al. 1987
(mountain fynbos)	<i>Pinus radiata</i> (Monterey pine), <i>P. halepensis</i> , <i>Banksia</i> (3 spp.)	Invasion slow with- out fire but enhanced by fire	Richardson and Brown 1986; Rich- ardson 1988; Rich- ardson et al. 1990



Table 4.2. Examples where invaders responded either positively or negatively to experimental burning. Examples organized by geographic proximity. Common names presented if available.

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Location (habitat)	Invader (common name)	Invader life-form	Burn treatments	Species responses	Reference
California (Sierra foothill woodland)	Exotic grasses and forbs	Annuals	Season of burn	Grasses declined; forbs increased regardless of season	Parsons and Stohlgren 1989
(coast range grassland)	<i>Centaurea solstitialis</i> (yellow star thistle)	Thistle	Season of burn	<i>Centaurea</i> declined	Hastings and Di Tomaso 1996
(Central Valley prairie)	Eurasian annual grasses	Grasses	Season of burn	Grasses decline with spring burning but exotic forbs increase	Meyer and Schiffman in press
(coastal grassland)	<i>Genista monspessulana</i> (French broom)	Shrub	Repeated late-summer fire	Shrubs decline only with recurrent fire	D. Boyd, Calif. State Parks, D. Odion, Marin Water District, personal communication
Arizona (high Sonoran Desert)	<i>Eragrostis lehmanniana</i> (Lehmann's love grass)	Grass	Season of burn	All treatments favored love grass germination	Ruyle et al. 1988
South Dakota (short-grass prairie)	<i>Bromus japonicus</i> (Japanese brome grass)	Grass	Spring burning	Reduced by fire	Whisenant 1990b Whisenant and Uresk 1990
Nebraska (tall-grass prairie)	<i>Bromus inermis</i> (smooth brome)	Grass	Season of burn	Target declines when fire occurs at tiller elongation	Willson and Stubbendieck 1997
Wisconsin (tall-grass prairie)	<i>Agropyron repens</i> (quack grass), <i>Phalaris arundinacea</i> (canary reed grass)	Perennial grasses	Season of burn	Both species increase with summer burning	Howe 1995
Illinois (woodland)	<i>Alfilaria petiolata</i> (garlic mustard)	Perennial forb	Intensity	No decline with low-intensity fire, some with midintensity	Nuzzo 1991
Florida (woodlands)	<i>Schinus terebinthifolia</i> (pepper tree)	Small tree	Repeat burning; intensity	Very little reduction in any treatment	Doren and Whiteaker 1990
NE Alberta, Canada (wetland w/in boreal forest)	<i>Sonchus arvensis</i> (sow thistle), <i>Cirsium arvensis</i> (Canada thistle)	Forbs	Light versus "deep" versus no burning	No change in abundance with any fire intensity	Hogenbirk and Wein 1991
Victoria, Australia (temperate grassland)	Exotic grasses and forbs	Annual and perennial	One burn only	Most exotics increased	Lunt 1990
Western Australia (sand plain heath)	Exotic annuals	Grasses and forbs	One burn period	No effect	Hobbs and Atkins 1991
(shrubland)	Exotic annuals	Grasses and forbs	One burn period	No effect	Hester and Hobbs 1992
( <i>Eucalyptus</i> woodland)	Exotic annuals	Grasses and forbs	One burn period	Reduced exotics	Hester and Hobbs 1992
( <i>Banksia</i> woodland)	Exotic annuals	Grasses and forbs	Sept. low intensity, March higher intensity	Short-lived increase in exotics	Hobbs and Atkins 1990
NSW, Australia (dry rainforest)	<i>Lantana camara</i> (lantana)	Shrub	Propane torch; 2 intensities	All methods promoted invasion	Gentle and Duggin 1997; Duggin and Gentle 1998
Queensland, Australia (open sclerophyll forest)	<i>Lantana camara</i> (lantana)	Shrub	Repeated winter burning	Little effect—maybe slowed invasion small amount	Russell and Roberts 1996
(dry tropical forest)	<i>Cryptostegia grandiflora</i> (rubber vine), <i>Zizyphus mauritiana</i> (jube)	Shrubs	One fire at end of dry season	<i>C. grandiflora</i> reduced by fire; no effect on <i>Z. mauritiana</i>	Grice 1997

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ness of fire in killing nonnative species or reducing their population growth will depend on fire intensity, time of burning and prior and subsequent weather conditions. While fire intensity is likely to directly affect control, very few studies estimated it (but see Nuzzo 1991; Gentle and Duggin 1997). Several investigators found that timing of burning had a strong influence on the degree to which control was achieved (e.g., Parsons and Stohlgren 1989; Hastings and DiTomaso 1996; Willson and Stubbendieck 1997; Meyer and Schiffman, in press). While simulating the timing of "natural" fire seems like an intuitive thing to do (see Parsons and Stohlgren 1989; Howe 1995; Hastings and DiTomaso 1996), it is not always effective at reducing exotics. Howe (1995) measured substantial increases in abundance of two exotic perennial prairie grasses after midsummer (the lightning season) burns in a Wisconsin prairie. In two studies where the response of the entire community to fire was measured (Parsons and Stohlgren 1989; Meyer and Schiffman, in press), fire was used successfully to reduce exotic annual grasses but exotic forbs increased. The relative impact of the forbs compared to the grasses on native diversity or ecosystem function was not evaluated. Nonetheless, the results of these studies imply that if fire is to be used as a management tool, the benefits (reduction of one invader) must be weighed carefully against the costs (increase in another invader or decline of native species). In addition, past land-use history and availability of seed have a strong effect on the outcome of controlled burns even in vegetation types thought to have evolved with fire (see Lunt 1990). If the seedbank is full of exotic species and natives are depleted (e.g., Parsons and Stohlgren 1989; Lunt 1990), or if individuals of exotic species are resistant to fire (Johnson and Purdie 1981; Doren and Whitaker 1990; Grice 1997), then fire has little effect on their control.

I found numerous studies where invasion of a native-dominated habitat could occur without fire but where subsequent fire promoted thickening or spread of the invader. These studies were largely in arid or semiarid ecosystems where introduced grasses invade the understory or intershrub spaces in largely woody vegetation. In many of these cases, disturbances such as cattle grazing and/or gopher activity may have preceded invasion, but Whisenant (1990a) and Svejcar and Tausch (1991) provide clear cases where invasion occurred without fire or livestock grazing. Also, in South Africa woody exotics can invade without fire but are promoted by it (e.g., Richardson 1988; Richardson et al. 1990).

I also attempted to assess whether the invaders that were promoted by fire were a long-term part of the community or whether they rapidly gave way to native species. In many cases, studies were very short term, so it was not possible to make this assessment. In the majority of cases, however, invaders appeared to be a persistent part of the community. These included

annual and perennial grasses, shrubs, trees, and succulents. The cases where exotics persisted for only a short time (<5 years) were all instances where invaders were annuals or biennials (Hobbs and Atkins 1990; Traubad 1990; Wein et al. 1992) and fire was a part of the recent (<10,000 years) history of the sites.

Lastly, invasion due to fire suppression in an otherwise fire-prone ecosystem does not yet appear to be a common phenomenon, yet a few examples exist. In dry woodland fragments within an urban boundary near Sydney, Australia, fire suppression is practiced for the protection of houses and buildings. There, invasion by an introduced woody species appeared to increase with increasing time since previous fire (Rose and Fairweather 1997). Likewise, Putz (1998) suggests that fire suppression is leading to the replacement of native oaks by the exotic laurel oak in Florida woodlands. Fire is well known to control the invasion of grasslands by woody species, and in Texas prairies, fire suppression is partly responsible for widespread invasion by *Sapindus sebiferum*, Chinese tallow tree (Bruce et al. 1995; Whisenant, personal communication).

### Conclusions

Johnson and Purdie (1981) suggest that fire is rarely effective at controlling woody invaders in grassland and that fire alone may even encourage many troublesome invaders. Recent literature on fire and exotic species also suggests that fire in most ecosystems tends to promote rather than discourage introduced species. The exceptions to this are some ecosystems where fire has a long evolutionary history (e.g., California chaparral and mixed-conifer forest, Australia monsoonal forests, African savannas). Yet fire can favor exotics in many ecosystems where fire has been an important force prior to European colonization, including South African fynbos ecosystems and northcentral U.S. prairies (Howe 1995).

No two fires are alike, and the outcome of fire depends on its timing, intensity, recurrence interval, and subsequent weather. Thus, specifically predicting fire impacts is difficult. Nonetheless, examples accumulating from throughout the world suggest that, more often than not, fire promotes nonnative species, and that if fire is to be used for their control, it must be carefully applied and factors such as seed availability (of both natives and exotics), plant phenology, and fire intensity must be critically evaluated.

### Impact of Invaders on Fire Regimes

One of the most potentially damaging impacts that an invading species can have on native biological diversity and ecosystem functioning is to alter the

disturbance regime (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998). Introduced species can alter the rate of spread of fire, the probability of occurrence of fire, and the intensity of fire in an ecosystem. The nature of the evidence provided varies considerably among studies and is indicated in Table 4.3. I also include unpublished information from systems where invasions are well documented in published literature but impacts on fire regime are speculative but based on a firm understanding of the biology of the system (see *Myrica faya*).

### *Invasers Affect Frequency and Intensity of Fires*

I found very few published studies where an introduced species had the potential to, or clearly did, decrease the spread of fire in the invaded systems. Nonetheless, I believe that this may become a more broadly recognized phenomenon as our awareness of the role of fire and invaders increases. Potential examples include (1) invasion of maritime chaparral in coastal California by the South African succulent *Carpobrotus edulis* (invasion documented by Zedler and Schied 1988; D'Antonio et al. 1993; impacts on fire = personal observation of author); (2) invasion of the nitrogen-fixing tree *Myrica faya* in Hawaii Volcanoes National Park (invasion documented by Vitousek and Walker 1989 and others; effects on fire = personal observation, T. Tunison, Hawaii Volcanoes National Park, Resources Management); (3) *Mimosa pigra* (nitrogen-fixing shrub) invasion in western Australia (Gill et al. 1990; Lonsdale and Miller 1993); (4) invasion by the tree *Schinus terebinthifolius* in Florida (Wade et al. 1980; Doren et al. 1991); (5) invasion by vines that blanket trees in Florida (Gordon 1998); and (6) invasion by leguminous shrubs such as French and Scotch brooms in California grasslands (personal observation). In the case of *Myrica faya* invasion into Hawaii, *Myrica*'s low flammability and lack of litter layer is expected to suppress the spread of fire in woodland ecosystems invaded by introduced grasses. *Myrica* is not necessarily suppressing an historic fire regime, but it could suppress the recent regime created by grass invasion of the forest understory. In four of the remaining examples, recurrent fire plays a role in stimulating native species regeneration in the ecosystems the invaders are entering. Hence fire suppression by the invaders could reduce regeneration of native species.

In contrast to the relatively small number of cases cited above, I found numerous cases where invaders had a significant effect on fire regime, enhancing some aspect of it (Table 4.3). In the majority of cases, invaders were suspected of increasing fire frequency while in a few cases (e.g., van Wilgen and Richardson 1985; Bilbao 1995; Lippincott, in press), invaders were suspected of increasing fire intensity. These latter cases were largely from the Americas and the fynbos of South Africa in places where fire has been a

Table 4.3. Examples of invaders that alter fire regimes in invaded ecosystem by increasing frequency and/or intensity of fire. Most examples are observational. Very few numbers are available on fire frequency or intensity changes. Examples organized by geographic proximity. Common name given if available.

Region (habitat)	Invader (common name)	Growth form	Invader = new life-form? *	Effect on fire	Reference
Hawaii (submontane dry forest & woodland)	<i>Andropogon virginicus</i> (broom sedge), <i>Schizachyrium condensatum</i> (beard grass), <i>Melinis minutiflora</i> (molasses grass)	Perennial grasses	Yes	Increase frequency size, intensity	Smith and Tunison 1992; Tunison et al. 1995
(coastal lowlands, shrubland)	<i>A. virginicus</i> , <i>S. condensatum</i> , <i>M. minutiflora</i> , <i>Hyparrhenia rufa</i> (thatching grass or jaragua)	Perennial grasses	Not always	Increase frequency and intensity	Smith and Tunison 1992; Tunison et al. 1994
(subalpine woodland)	<i>Holcus lanatus</i> (velvet grass), <i>Anthoxanthum odoratum</i> (sweet vernal grass)	Perennial grasses	No	Increase fire intensity	Smith and Tunison 1992
Western U.S.A. (Great Basin Desert)	<i>Bromus tectorum</i> (cheatgrass)	Annual grass	Yes	Increase frequency	Steward and Hull 1949; Whisenant 1990a
	<i>Taeniatherum caput-medusae</i> (medusahead)	Annual grass	Yes	Increase frequency	Menke 1989; Young 1992
(Mojave Desert)	<i>Bromus rubens</i> (red brome), <i>B. tectorum</i> , <i>Schismus</i> spp.	Annual grasses	Yes	Increase frequency	Beatley 1966; Brown and Minnich 1986; Brooks 1998

(continues)

Table 4.3. Continued

Region (habitat)	Invader (common name)	Growth form	Invader = new life-form? *	Effect on fire	Reference
California (riparian)	<i>Arundo donax</i> (giant reed)	Perennial grass	Yes	Increase frequency and intensity	Bell 1997
(coastal chaparral)	<i>Lolium perenne</i> (perennial rye)	Perennial grass	Yes	Increase frequency	Zedler 1983
(chaparral)	Various annual grasses, forbs		Yes	Increase frequency	Haidinger and Keeley 1993
NW Mexico (Sonoran Desert)	<i>Pennisetum ciliare</i> (buffel grass)	Perennial grass	Yes	Increase frequency	Búrquez and Quintana 1994
Florida (pine sandhills)	<i>Imperata cylindrica</i> (cogongrass)	Perennial grass	No	Increase fire intensity	Lippincott, in press
(prairie)	<i>Melaleuca quinquinervia</i> (punk tree)	Tree	Yes	Increase fire intensity	Gordon 1998
Costa Rica (dry forest)	<i>Hyparrhenia rufa</i> (jaragua/thatching grass)	Perennial grass	Yes	Increase fire frequency	Janzen 1988
Venezuela (llanos)	<i>Hyparrhenia rufa</i> (thatching grass)	Perennial grass	No	Increase fire intensity	Bilbao 1995
South America (savannas)	<i>Hyparrhenia rufa</i> , <i>Melinis minutiflora</i> , <i>Panicum maximum</i> (guinea grass), <i>Brachiaria</i> spp. (Para)	Perennial grasses	No	Increase fire frequency and intensity	Blydenstein 1967; Medina 1987
Australia (riparian)	<i>Cenchrus</i> (= <i>Pennisetum</i> ) <i>ciliare</i> (buffel)	Perennial grass	Yes	Increase fire frequency and area	Latz 1991
(woodland)	<i>Ehrhardta calycina</i> (veldt grass)	Perennial grass	Yes	Increase fire frequency	Baird 1977
(mesic forest)	<i>Melinis minutiflora</i> (molasses grass), <i>Pennisetum polystachum</i> (feathery pennisetum)	Perennial grasses	Yes	Increase fire frequency	Gill et al. 1990
South Africa (mountain fynbos)	<i>Pinus</i> spp.	Tree	Yes	Increase fire intensity; decrease fire frequency	van Wilgen and van Hensbergen 1992
(fynbos)	<i>Acacia saligna</i> , <i>Hakea sericea</i> (silky wattle)	Shrubs	No	Increase fire intensity; decrease frequency	van Wilgen and Richardson 1985; van Wilgen and van Hensbergen 1992

\* Decision based either on investigators' comments or opinion of this author.



part of the recent (pre-invasion) disturbance regime and invaders more or less resemble natives in terms of life form. The former cases come largely from woodland ecosystems including desert and semiarid shrublands and dry or seasonally dry tropical forests.

### *Characteristics of Invaders That Alter Fire Regime*

Can we predict on the basis of species characteristics, which invaders should lead to alterations in fire regime? Models of fire behavior such as BEHAVE, REFIRE (Davis and Burrows 1994), and others rely heavily on fuel characteristics such as live and dead fuel moisture, fuel packing density, biomass and vertical distribution of fine versus medium and coarse fuels, horizontal fuel distribution, and fuel energy content to predict rates of fire spread and intensity. When measured in the field, these parameters are based on community-wide or plotwide values. Yet they are strongly influenced by the species composition within the sample unit and thus by individual species traits. Invaders can have a strong influence on any of these parameters. In addition, fire behavior is also strongly influenced by wind and weather conditions. While these are ultimately controlled by regional climate, wind speed can be strongly affected by plant species composition. For example, when comparing wind speeds over two adjacent pieces of land, a fire-induced exotic grassland and a remnant patch of unburned woodland, Freifelder et al. (1998) found that wind speeds were consistently higher over the grassland regardless of season.

Several authors have attempted to sort out which fuel characteristics or species parameters will have the largest effect on fire spread rates and/or intensity. Using simulation models where one or more fuel parameters was manipulated while the others were held constant, van Wilgen et al. (1990) found that the variability in fuel energy content among vegetation patch types had little influence on fire spread rates. Likewise, van Wilgen and van Hensbergen (1992) found that fuel energy content was not responsible for observed variation in fire intensity in South African fynbos. Lippincott (in press) found that the variability in fuel energy content between native and exotic fuels in a Florida pineland was not large and probably had little to do with differences in fire severity among patch types. By contrast, alteration of characteristics such as fuel distribution, biomass, and structure of the fuel bed had a large effect on fire characteristics.

Van Wilgen and Richardson (1985) used runs of Rothermel's (1972) fire spread simulation model to examine the effect of altered fuel characteristics on fire spread rate and flame length (intensity) in invaded versus uninvaded fynbos shrublands in southern Africa. Their invaded sites were structurally similar to uninvaded sites in that all were shrub dominated. The main differ-

ence between the "native" and "exotic" fuels was a higher density and biomass of fine fuels per unit area of ground surface in invaded sites. For *Hakea*-invaded shrubland, the increased biomass of fine fuels and decreased fuel moisture did not lead to the expected increase in fire severity because they were counteracted by a densely packed fuel bed that presumably reduced oxygen to the fire. The increased fuel biomass of shrublands invaded by *Acacia* species also did not lead to increases in fire severity because of high fuel moisture in live tissue of the invader. Van Wilgen and van Hensbergen (1992) thus predict that the altered fuel bed characteristics will result in less-frequent fires because it will take more extreme weather conditions for fires to spread, but that fire severity will increase because of the altered fuel loads and extreme conditions under which they will burn. Fire intensity in woody vegetation is known to influence native species survival and regeneration (e.g., Moreno and Oechel 1994). Thus changes in fire severity can have important impacts, even when fire frequency is not changed.

Lippincott (in press) empirically examined alterations in fire intensity in Florida pine sandhills invaded by the Asian grass *Imperata cylindrica*, in contrast to pine sandhills patches containing only native grass fuels. She found that the exotic grass fuels were more continuously distributed and resulted in a more continuous fire. In addition, the *Imperata* fuels were more dense vertically, which resulted in higher fire intensity at 0.5 to 0.99 meters above the ground surface. This increased intensity resulted in greater mortality among saplings of the dominant native pine species.

In contrast to the studies described above, investigators examining the spread of fire in ecosystems where the invaders are structurally very different from native species have shown strong effects of changing fuel characteristics on fire frequency or spread rates. Using fuel and microclimate parameters estimated from field sampling, Freifelder et al. (1998) found that the most significant parameter affecting fire spread rates through seasonally dry grass-invaded sites in Hawaii was wind speed. This was much greater over a smooth grass canopy than over the native woodland canopy, and when these differences were entered into Rothermel's (1972) fire spread model, they resulted in enormous differences in fire spread rates. By contrast, variation among fuel types in moisture content or density did not have a large effect on fire characteristics. Thus it is the structural change from a heterogeneous to a smooth canopy that had the most profound effect on fire regime. The smooth grass canopy (see Figure 4.1) was the result of two sequential exotic-grass-fueled fires that eliminated the dominant trees and shrubs of the native woodland (see Hughes et al. 1991) and had a strong effect on plant species richness (D'Antonio and Dudley 1995).

Whisenant (1990a) empirically examined the horizontal frequency of fine

## Conclusions

Chapin et al. (1996) suggest that species with ecosystem impacts, including altering the disturbance regime of a site, are those that are qualitatively different from the rest of the species in a community. Mack and D'Antonio (1998) define "qualitatively different" invaders as species with no functional analogues in the invaded system. Functional analogy is further defined as sharing a suite of traits that influence a particular ecosystem function such as disturbance regime. The scant literature on fuel characteristics of native versus non-native species suggests that where invaders are similar in overall life-form to natives (see van Wilgen and Richardson 1985; Bilbao 1995; Lippincott, in press), they tend to alter primarily fuel biomass per unit area of ground. This in turn has the potential to influence fire intensity. By contrast, where invaders have no functional analogues in terms of fuel characteristics in the invaded system, such as in the case of annual or perennial grasses invading desert shrublands (see Whisenant 1990a; Burquez and Quintana 1994; Brooks 1998), they have the potential to alter fire frequency and indeed introduce fire to ecosystems where it had no evolutionary role. In other words, if an invader is simply more of the same (e.g., van Wilgen and Richardson 1985; Bilbao 1995; Lippincott, in press), it may alter fire intensity or slightly modify an existing fire regime. However, if an invader is something very new ("qualitatively different"), then it has the potential to introduce a novel type of disturbance to the ecosystem. But do the former invaders have less severe impacts than the latter? Both are impacts on fire regime, but the latter is a complete alteration rather than a modification. In terms of impacts on native species, invasive alien shrubs in South African fynbos clearly have a devastating effect on native species, although this effect is not solely through fire. However, the potential for restoration of these ecosystems may be higher (see Holmes and Cowling 1997) than in desert shrubland (see Whisenant 1990a), Hawaiian woodlands (see Hughes et al. 1991), or other sites where fire is a novel disturbance and the invaders have set in motion a fire cycle where none previously existed.

In spite of the large number of cases found where invaders promote fire, it is not appropriate to assume that the majority of invaders have the potential to do so. Many people have suggested that less than 20 percent of all invaders have important ecological impacts, and I suspect that less than 5 percent alter fire regime. These invaders should be easy to identify beforehand since many are grasses and/or woody species that come from fire-prone ecosystems, and we are already amassing a large database on them. What is difficult to predict is how fast they will move across the landscape and how abundant they must become before their impacts are felt. These issues are particularly important in light of the numerous ongoing global changes that are discussed in the following section.

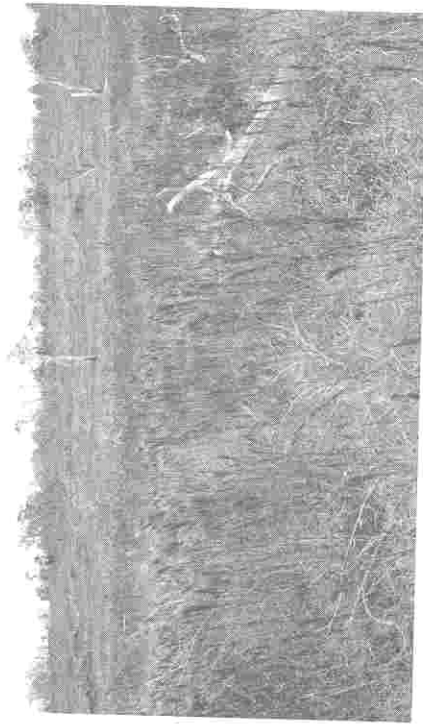


Figure 4.1. The introduced  $C_4$  grasses *Schizachyrium condensatum* (beardgrass) and *Melinis minutiflora* (molasses grass) form a relatively smooth canopy in a site that used to be dominated by native woody species, including several shrub species and the native tree *Metrosideros polymorpha* (ohia). These introduced grasses invade the understory of the woodlands and fuel large and intense fires. Fires in turn alter the system from a diverse native woodland with a heterogeneous canopy to a simple low-diversity system dominated by grasses. Photo taken by author at 850-meter elevation in Hawaii Volcanoes National Park.

fuels in grass-invaded and burned Great Basin desert in western North America where, historically, fires were rare but are now common occurrences. He found that the horizontal frequency of fine fuels increased with grass invasion of sagebrush steppe by *Bromus tectorum* (cheatgrass) and that this relationship between fine-fuel frequency and grass species abundance does not exist for native grasses in this system. Biomass of *B. tectorum* fuels was not as important as frequency since it reached an asymptote as cheatgrass cover increased. He and others (Beatley 1966; Billings 1990) have surmised that the increase in fire frequency in the Great Basin ecosystems is the result of an increase in the horizontal continuity of fine fuels that persist during the summer lightning season compared to uninvaded vegetation. Beatley (1966) described characteristics of invaded desert shrublands in Nevada and found that the exotic grass *Bromus rubens* (red brome), unlike native annuals, can germinate with spring rains and then stalks persist throughout the summer drought when lightning strikes are common. Thus it appears to be a combination of phenology and horizontal distribution of fuels that promotes fire in these ecosystems. Fire in these habitats has severe effects on native species richness (Whisenant 1990a; Billings 1990).

## Interaction of Fire and Biological Invasions with Other Aspects of Global Change

### Land-Use/Land-Cover Change

Land-use/land-cover change is without a doubt the most profound impact that humans have had on the biosphere. In arid and semiarid ecosystems, livestock production has resulted in a reduction in native woody species and the introduction of grazing-tolerant grasses. Parsons (1972) documented the flow of grazing-tolerant, African pasture grasses to the New World. Their further spread there is the result of both land-use change (beef production) and natural spread. The impacts of this flow on the desire to preserve native ecosystems is now being manifested. For example, *Hyparrhenia rufa* (jaragua grass) was introduced to Costa Rica for livestock production and is now widespread throughout the Guanacaste province. In this same region, it is considered the largest single impediment to reforestation of tropical dry forest (Janzen 1988) because of its propensity to fuel large, intense fires. Likewise, in the state of Sonora, Mexico, the African grass *Pennisetum ciliare* has been planted widely for beef production at the expense of native lowland desert and thornscrub vegetation. It is spreading rapidly throughout the region, fueling repeated fires and leading to massive decline in native species over a very large area (Alberto Búrquez, personal communication, and see Figure 4.2). Clearly, the conversion of land for livestock production, combined with the introduction of fire-promoting grasses, will continue to cause spread of the grass-fire cycle in many regions of the world.

Forest fragmentation after logging or type conversion for livestock grazing is impacting enormous areas of tropical forest each year. In Australia, livestock grazing and fire in dry-open tropical forests has promoted invasion of wet-forest fragments that abut more open vegetation types by unwanted exotic woody species such as *Lantana camara* (Gentle and Duggin 1997; Duggin and Gentle 1998). While *Lantana* itself does not promote further fire, it does interfere with native species recruitment. Thus, the process of forest fragmentation in a fire-prone ecosystem with fire-responsive exotics will lead to the degradation of forest fragments.

Changes in land cover in many regions of the world have resulted directly from the construction of dams and the impoundment of rivers. In the western United States, the large-scale control of the Colorado River by successive impoundment has led to invasion of thousands of hectares of floodplain forest by the Eurasian salcedar, *Tamarix ramosissima*. Fire, once a rare phenomenon in riparian areas in this region, is now quite common (Busch 1995). Busch believes this is the result of the buildup of woody fuels throughout these forests due to physiological stress caused by altered water table conditions for riparian trees. *Tamarix* itself does not promote the spread of fire



Figure 4.2. *Top:* Buffel grass (*Cenchrus ciliaris*), introduced to Mexico from Africa, has been widely planted for use as cattle forage. Today thousands of hectares of diverse Sonora plains and thornscrub vegetation have been replaced by this African grass. This photo shows a site purposefully converted to buffel pasture at 300-meter elevation in Sonora, Mexico. *Bottom:* Buffel grass invades away from planted areas into native vegetation. Here it can be seen growing in a desert riparian woodland near Hermosillo, Sonora, Mexico. Eventually, it carries fire into these unique and diverse sites that historically have not experienced fire. Photographs by author.



since its litter is largely nonflammable, but it responds positively to fire (Busch 1995). In turn, it can reduce water availability to native species, adding to the physiological stress they are already experiencing from human land-use activities (see Zavaleta, this volume).

Land-use change frequently brings with it the construction of roads that can serve as conduits for the spread of unwanted exotic organisms. Lonsdale and Lane (1994) found that tourist vehicles were vectors of weed seeds in a remote Australian national park. Others (e.g., Forcella and Harvey 1983; Milberg and Lamont 1995; D'Antonio et al. 1999) have demonstrated that roadsides are replete with nonnative species that then invade away from these corridors into adjacent native vegetation. Because fires also frequently begin along roadsides, fire-promoted exotics should be expected to spread from roadsides into adjacent habitat, and road construction should accelerate this phenomenon.

### Other Global Changes

The impact of climate change on fire frequency will depend both on its impact on possible ignition sources as well as on the likelihood that an ignition will result in a fire. Very few investigators have attempted to evaluate how the anticipated global climate change over the next 1 to 200 years will affect possible ignitions and the actual frequency of fire. Fosberg et al. (1993) review some of the difficulties with making these sorts of predictions. Nonetheless, palynological evidence clearly shows that fire frequencies are higher under warmer, drier conditions (e.g., Clark 1988, 1990; Johnson and Larson 1991). Recently, there have been several attempts to evaluate how a doubled- $\text{CO}_2$  climate might affect fire spread rates, assuming that ignition has already occurred. For example, Torn and Fried (1992) found increases in area burned and frequency of escaped fires using four different versions of available general circulation models (GCMs) when comparing current to projected climate for northern California. They found that the magnitude of the increase in fire spread was dependent on the choice of GCM and fuel type. Further, they found that projected changes in wind speed were much more important than changes in temperature in driving fire spread. Changes in wind speed can occur both by external climate forcing and by changes in the vegetation canopy within a site. The latter may be a direct result of biological invasion.

The spread of introduced, fire-promoting exotic species such as grasses in North American deserts or tropical woodlands, regardless of changes in ignition frequency, should increase the ratio of possible ignitions to actual fires because of changes in fuel and canopy characteristics. Climate change alone or in combination with elevated atmospheric  $\text{CO}_2$  may change the competitive relationship between native and exotic plant species in a way that favors

exotics. Alternatively, severe droughts associated with climate change may increase the fuel potential of vegetation by reducing fuel moisture or decomposition time, by promoting pathogen outbreaks that kill woody vegetation (e.g., Riggan et al. 1994) or increasing the amount of xerophytic vegetation surrounding wetlands (Hogenbirk and Wein 1991). The latter authors experimentally simulated drought and fire in a seasonally flooded wetland ecosystem in Alberta, Canada, and found that both drought and fire enhanced invasion by Eurasian forbs (mainly thistles) in this system. On this basis, they predict that climate change will shift these systems from ones in which flooding controls species dynamics to ones in which drought and fire are important controlling forces. Thus even if climate change does not alter possible ignition frequencies within a region, it might alter real fire frequency solely by favoring growth of fire-promoting exotics or by causing fuel accumulation. Indeed, the frequency of drought is expected to increase, as is interannual variability in precipitation over North America under projected climate change (Rind et al. 1989, 1990). This should lead to an increase in conditions that favor fire.

Will an increase in the frequency of exotic-species-fueled fires contribute to increased trace gases in the atmosphere? Current knowledge suggests that this will not be the case. D'Antonio and Vitousek (1992) estimated that exotic-grass-fueled fires were responsible for less than 1.5 percent of the total increase in stable gases released from biomass burning on a global scale (see Crutzen and Andreae 1990). Even if exotic-grass-fueled fires double in occurrence, we do not anticipate their contribution to atmospheric trace gases to be large.

Several authors have shown that addition of nitrogen to ecosystems can result in the promotion of exotic species at the expense of natives (e.g., Huenneke et al. 1990; Maron and Connors 1996). Recently, Brooks (1998) and Brooks and Allen (personal communication) have suggested that atmospheric nitrogen deposition in parts of semiarid and arid southern California is responsible for a large increase in the abundance of introduced annual grasses. These grasses, in turn, have carried fire into shrubland sites in Riverside County, California, where it occurred at a much lower frequency, or into the Mojave Desert where fire was previously largely absent. The experimental evidence of Brooks (1998) and others (e.g., Hobbs et al. 1988; Huenneke et al. 1990) that added nitrogen can greatly increase the abundance of exotic grasses is largely on infertile soils. Thus, we can expect that atmospheric nitrogen deposition will strongly interact with the spread of fire-promoting exotic species in these sorts of situations and that low-fertility ecosystems are significantly at risk. Hobbs and Atkims (1988) showed that nutrient addition increased the abundance of exotic species, particularly an exotic annual grass, when combined with soil disturbance in a woodland in



the atmosphere. Biomass burning does contribute significantly to the global rise in greenhouse gases, but exotic-grass-fueled fires are only a tiny fraction of this increase.

Atmospheric nitrogen deposition is expected to contribute to the spread of fast-growing exotic grasses that may introduce fire into areas where it was previously absent or increase the intensity of fire in places where it already existed. More data is needed to elucidate this potentially important interaction.

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Australia. The interaction of nitrogen deposition with land-use disturbance as it relates to subsequent invasion and the potential for fire should be further explored.

### Conclusions

Most studies show that fire increases invasion by introduced species. Even in several studies where fire was specifically used to control an invasive exotic species, other nontarget exotics increased after fire or exotics were not effectively reduced by fire. Thus fire should be used with great caution as a management tool, and almost all fires should be viewed as creating a window of opportunity for exotics to invade an ecosystem.

Naturally fire-prone ecosystems, such as the fynbos of South Africa or coastal chaparral in California, can be heavily invaded by exotic species. Thus the occurrence of a "natural fire regime" will not guard against invasion if fire-responsive exotic propagules are available or if that natural fire regime is severely altered.

Examples are now extremely common of where invaders create conditions that favor the spread of fire. This occurs when invaders are different in their life-form or phenology from natives and thus increase both the continuity and biomass of fine fuels in a community where fire is a relatively novel event. The most common such invaders are grasses invading desert shrubland or dry forest ecosystems. These are formidable invaders that are difficult to control and are spreading rapidly throughout the world.

In ecosystems where fire has been a common part of the historic disturbance regime, invaders often change fuel biomass or vertical distribution, and by so doing tend to increase fire intensity. In these cases, invaders have the potential to have a negative impact on native species but do not convert the community entirely to exotics. Their impacts via changes in fire regime at this point are not as severe as those cases where invaders introduce fire into systems where it was previously uncommon.

The effect of climate change on the invader-fire interaction will depend on how climate affects the frequency of weather conditions that will either ignite vegetation or favor the spread of fire from an ignition source. Currently, there has been very little research on how climate change will affect fire frequency, and this will depend on the particular geographic region in question and the pool of potential invaders. From a modeling perspective, the particular GCM used will also affect the projected impact on fire independent of fuel type or species responses. Because of the enormous impact that grass-fueled fires can have on native biological diversity and ecosystem function, more research is needed into how fire regimes might change with climate change.

Exotic-grass-fueled fires will likely not affect the changing composition of

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