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Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems

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Abstract Fire regimes influence and are influenced by the structure and composition of plant communities. This complex reciprocal relationship has implications for the success of plant invasions and the subsequent impact of invasive species on native biota. Although much attention has been given to the role of invasive grasses in transforming fire regimes and native plant communities, little is known about the relationship between woody invasive species and fire regime. Despite this, prescribed burning is frequently used for managing invasive woody species. In this study we review relationships between woody exotic plant invasions and fire in invaded ecosystems worldwide. Woody invaders may increase or decrease aspects of the fire regime, including fire frequency, intensity and extent. This is in contrast to grass invaders which almost uniformly increase fire frequency. Woody plant invasion can lead to escape from a grass-fire cycle, but the resulting reduction in fire frequency can sometimes lead to a cycle of rare but more intense fires. Prescribed fires may be a useful management tool for controlling woody exotic invaders in some systems, but they are rarely sufficient to eliminate an invasive species, and a dearth of controlled experiments hampers evaluation of their benefits. Nevertheless, because some woody invaders have fuel properties that differ substantially from native species, understanding and managing the impacts of woody invaders on fire regimes and on prescribed burns should become an important component of resource and biodiversity management.

Keywords Management · Community ecology · Fire regime · Invasive species · Prescribed burning · Woody invasions

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Introduction

Fire is a common disturbance in many temperate and tropical ecosystems around the world (Bond and Keeley 2005). Fire both influences and is influenced by plant community composition and structure, resulting in a complex relationship between fire and exotic plant invasion. Because of the potential for elucidating ecological principles underlying invasion, as well as improving management of invasive species and conservation of ecosystems threatened by invasion, understanding the relationships between fire, plant invasion and plant communities is of great interest to both scientists and managers (e.g. Brooks et al. 2004; Fisher et al. 2009; Rahlao et al. 2009).

Fire regime describes the average fire characteristics and patterns for a given site during a particular time period, including fire intensity (the amount of heat released when plant material is burned), frequency, seasonality, and extent or patchiness, all of which influence vegetation structure and have the potential to influence plant invasion (Brooks et al. 2004; Moritz et al. 2005; Whelan 1995). Each fire event has unique characteristics and consequences for individual organisms and populations including biomass loss and death of plants, plant parts, and propagules due to high temperatures. The effects of fire continue into subsequent years: post-fire conditions include higher solar radiation and wind levels, higher water loss, and more extreme temperature oscillations. Fire can also affect the edaphic environment, increasing erosion and changing soil properties, including water holding capacity and short-term soil nutrient availability (Certini 2005; Whelan 1995). All these factors may alter the success of invasive and native plant species within a community.

Reciprocally, the intrinsic fuel properties of plants within a community—a result of the ecology and physiology of the plant species—affect fire frequency, seasonality and intensity. Intrinsic fuel properties include the amount of moisture present in plant tissues, ignitability, and the heat released during combustion. Traits which increase fire frequency and/or intensity may be adaptive when fire gives flammable plants a competitive advantage (Brooks et al. 2004; Schwilk and Ackerly 2001).

The effects of grass invasion and subsequent increases in fire frequency have been studied extensively (Brooks et al. 2004 and references therein; D'Antonio and Vitousek 1992). However, the effects of woody plant invasion on fire regimes remain poorly understood. Here, we examine the effects of woody exotic plant species on fire regimes and associated plant communities worldwide and compare our findings in the literature to the well-documented grass-fire cycle (D'Antonio and Vitousek 1992). We then examine the use of prescribed fire to manage woody invasions and discuss the conditions under which prescribed fires can effectively control them.

Methods

Literature search

To locate studies on the relationship between woody exotic plant invasions and fire, we searched the online database Web of Science for sources that included the following key words: ("tree" or "shrub" or "vine" or "wood*") and 'fire' and "invas*" and ("exotic" or "alien" or "non-native" or "introduced") and "plant." We also included references cited within sources obtained from the Web of Science search. We did not attempt to systematically search gray literature. We restricted our search to species found outside their native range, excluding studies on woody encroachment by native species.

Results and discussion

Fire regimes and woody invasions

In total we located studies involving 16 woody invaders that clearly altered fire regimes in at least one invaded ecosystem (Table 1). Among these 16 woody invasive species, eight increased fire frequency or intensity, five decreased aspects of the fire regime and three had mixed effects. The high number of species that increase aspects of the fire regime may reflect a bias in study species, as plants that increase fire, especially grasses, tend to receive the most attention (Brooks et al. 2004). The interaction between invasions and fire in the South African fynbos has been extensively studied and six of the 16 species identified are invasive in the fynbos. Species that increase aspects of the fire regime belong primarily to the families Fabaceae *senso lato* and Pinaceae. The five species found to decrease fire frequency or intensity come from four different families and are invasive in a diversity of ecosystems, including temperate and tropical regions (Table 1).

Woody plants can increase aspects of the fire regime such as fire intensity, frequency or extent through traits associated with high flammability. Biomass accumulation through high production and shedding of leaves and branches increases fuel load, the amount of fuel per area (Brooks et al. 2004). Eurasian saltcedar (*Tamarix* spp.), invasive in the southwest United States and Mexico, sheds dead

Table 1 Woody exotic plant invaders documented to alter fire regimes

Invasive species	Family	Region of origin	Region invaded	Growth form	Community invaded	Interaction with plant community	Changes in fire regime				Selected references
							Overall	Fuel	Fire intensity, frequency	Fire spread, type	
Acacia saligna	Fabaceae	Australia	South Africa	Shrub	Fynbos	Forms dense stands, reduces understory	+/−	Increases fuel load	Increases intensity, decreases frequency	Decreases spread, promotes crown fires	Van Wilgen and Richardson (1985)
Cryptostegia grandiflora	Asclepiadaceae	Madagascar	Australia	Vine, shrub	Woodlands, riparian forest	Reduces grass, smothers trees	−−			Promotes shift from grass to crown fires	Grice (1997)
Cytisus scoparius	Fabaceae	Europe	United States, Canada	Shrub	Grasslands, woodland gaps	Forms dense stands	++	Increases flammability	Increases intensity	Promotes crown fires in dry seasons	Tveten and Fonda (1999), Richburg et al. (2000), Richburg et al. (2004)
Eucalyptus spp.	Myrtaceae	Australia	Mediterranean ecosystems	Tree	Shrubland, woodland		+/−	Extremely flammable leaves		Decreases spread and flame length	Dimitrakopoulos and Papaioannou (2001), Dicus and Anderson (2004)
Genista monspessulana	Fabaceae	Mediterranean	Chile	Shrub	Forest	Forms dense stands	++	Increases fuel load, highly flammable	Increases intensity, frequency	Promotes crown fires	Pauchard et al. (2008)
Hakea gibbosa	Proteaceae	Australia	South Africa	Tree	Fynbos		++	Increases fuel load	Increases intensity		Van Wilgen et al. (2007)
Hakea sericea	Proteaceae	Australia	South Africa	Shrub	Fynbos	Forms dense stands, reduces understory	+/−	Increases fuel load and packing ratio	Increases intensity, decreases frequency	Decreases spread, promotes crown fires	Van Wilgen and Richardson (1985), Holmes et al. (2000), Van Wilgen et al. (2007)
Melaleuca quinquenervia	Myrtaceae	Australia	Florida	Tree	Wetlands, wet prairies	Decreases diversity, changes structure	++	Highly flammable leaves, bark	Increases intensity, frequency	Increases spread, promotes crown fires	Gordon (1998), Serbesoff-King (2003), Silvers et al. (2007)
Mimosa pigra	Fabaceae	Tropical America	Australia	Shrub, tree	Wetlands, riparian forest	Reduces herbaceous species richness and native tree regeneration	−−			Decreases spread of understory-fueled fires	Braithwaite et al. (1989), Lonsdale and Miller (1993)
Pinus spp. (including *patula*, *pinaster* and *radiata*)	Pinaceae	Northern hemisphere	Argentina, South Africa, New Caledonia	Tree	Grasslands, fynbos, open woodlands	Forms dense stands	++	Increases fuel load	Increases intensity, frequency	Increases fire extent, promotes crown fires	Holmes et al. (2000), Richardson and Brown (1986), Simberloff et al. (2010), Van Wilgen et al. (2007)

Table 1 continued

Invasive species	Family	Region of origin	Region invaded	Growth form	Community invaded	Interaction with plant community	Changes in fire regime				Selected references
							Overall	Fuel	Fire intensity, frequency	Fire spread, type	
Robinia pseudoacacia	Fabaceae	Southeast US	Northeast United States	Tree	Pine barrens		−−	Less flammable			Richburg et al. (2004)
Schinus terebinthifolius	Anacardiaceae	South America	Florida	Shrub, small tree	Pine savanna		−−		Decreases intensity, frequency		Stevens and Beckage (2009), Stevens and Beckage (2010)
Tamarix spp.	Tamaricaceae	Eurasia	Southwest United States, Mexico	Shrub, small tree	Arid and semi-arid riparian zones	Outcompetes natives by resprouting	++	Increases fuel load	Increases intensity, frequency		Busch and Smith (1993), Ellis et al. (1998), Nagler et al. (2005)
Triadica sebifera	Euphorbiaceae	Asia	Southern United States	Tree	Coastal prairie	Excludes fuel species	−−	Poorly flammable, low ignition			Grace (1998)

Species are classified by their overall effect on fire regime, where species that increase all studied aspects of the fire regime (fuel, fire intensity, frequency and/or spread) are rated ++, species that decrease all studied aspects of the fire regime are rated −− and species with mixed effects, i.e., increase some aspect(s) of the fire regime but decrease other(s), are rated ±. The impact of these changes on the native community is highly context-dependent

branches which increase fire frequency and intensity in invaded areas (Busch 1995; Ellis et al. 1998). Some plants have flammable oils (e.g. many eucalypts) which facilitate ignition of plant materials and thus increase the frequency of fire (Allen 2008). Red river gum (*Eucalyptus camaldulensis*), a native of Australia and invasive in Mediterranean regions, including in California, has highly flammable volatile oils (Dimitrakopoulos and Papaioannou 2001). *Genista monspessulana*, a widely invasive European shrub (Alexander and D'Antonio 2003a; Bossard 2000; Holmes et al. 1987; Pauchard et al. 2008), enhances fire frequency and intensity by significantly increasing fuel load and flammability. In south-central Chile's Mediterranean ecosystem, *G. monspessulana* also changes fire behavior, promoting crown fires through vertical accumulation of fine fuel (Pauchard et al. 2008).

In some systems, however, woody species decrease fuel load and fire frequency. Fire suppression can result when woody plant tissues have a low surface area-to-volume ratio and retain moisture (Grace 1998). By retaining such tissues, either during the growing season or year-round, woody plants may shorten the length of the fire season. *Hakea sericea*, introduced to South Africa from Australia, produces high fuel loads with a high packing ratio, which generally leads to reduced fire intensity and spread (van Wilgen and Richardson 1985), since highly packed fuels stifle fire by excluding oxygen. Woody species can also out-compete grasses and forbs by blocking sunlight, leading to decreased surface plant cover, reduced ground fuel loads and continuity, and decreased fire frequency and extent (Brooks et al. 2004; Grace 1998; Peterson and Reich 2007). Chinese tallow (*Triadica sebifera*) shades out the native fuel-producing coastal prairie species in the southern United States, thus reducing fire frequency and extent (Grace 1998). Black locust, *Robinia pseudoacacia*, a North American species, is invasive in parts of the United States and Canada and is less flammable than many native species (Richburg et al. 2004 and references therein). An increased prevalence of tall woody species and decreased abundance of surface fuels can also result in a fire-type shift from frequent surface fires to less frequent but more intense crown fires, which move along tree tops and can kill large trees (Brooks et al. 2004; van Wilgen and Richardson 1985). Rubber vine (*Cryptostegia *grandiflora*), a woody vine from Madagascar that is invasive in Australia, promotes crown fires by functioning as a ladder fuel (Grice et al. 2008) while reducing the frequency of low-intensity ground fires by suppressing grasses (Grice 1997).

Complex interactions between fuel characteristics and environmental conditions can mediate the impact of woody invaders on fire regime. In South Africa, simulations suggest that two prominent woody invaders of the fire-prone fynbos, *Hakea sericea* and *Acacia saligna*, suppress fire under most, but not all, conditions (van Wilgen and Richardson 1985). *Acacia saligna*, introduced from Australia, may reduce fire spread and intensity because it retains moisture well, resulting in poor ignition. Furthermore, both *Acacia saligna* and *Hakea sericea* dramatically reduce the density of native understory species, further suppressing fire. Van Wilgen and Richardson (1985) note, however, that extreme weather events such as prolonged drought can increase the flammability of *A. saligna*, increasing the frequency of high-intensity fires, which are rare under normal conditions. Thus the effect of woody invasions may depend not only on species characteristics, but also on weather and stochastic environmental events.

Fire, invasion and the plant community: contrasts between grasses and woody invaders

How plant populations and communities respond to each fire event depends on the previous fire regime and the functional traits of the species present (Allen 2008). In fire-prone communities dominated by woody species, invasive species that resprout from roots or rapidly recruit from seeds following fire may out-compete natives and form dense stands, further exacerbating their effect on the local fire regime. By contrast, species with high moisture content or which exclude understory species by shading can reduce community flammability and fuel continuity, thus reducing the frequency of fire (Brooks et al. 2004).

A high relative abundance of grasses in the community (e.g. in savannas) can drive a fire regime characterized by high-frequency surface fires with relatively low intensity and broad extent (Brooks et al. 2004). Many grasses readily resprout after fire from surface-level or below-ground buds, promoting continued dominance of the grasses (Brooks et al. 2004). Though these fires have little effect on mature woody plants, which have thick bark and can resprout (Grace 1998; Stevens and Beckage 2009), seedlings are often vulnerable to fire and many woody species, including invaders, can only recruit during fire-free periods (e.g. invasive Chinese tallow, *Triadica sebifera*, Grace 1998; invasive Brazilian pepper, *Schinus terebenthifolius*, Stevens and Beckage 2009). Thus the presence of frequent, grass-fueled fires can limit or prevent the establishment of woody species and facilitate the continued existence of a grass-dominated community (Peterson and Reich 2007). This is known as the grass-fire cycle (Fig. 1), and it has received much attention because it is a common mechanism by which introduced grasses transform and dominate native ecosystems (D'Antonio and Vitousek 1992).

Anthropogenic disturbances like land-use change or changes in fire regime can allow exotic grasses to establish and initiate grass-fire cycles (D'Antonio and Vitousek (1992). In contrast, disturbances such as fire may promote woody plant invaders that either promote or tend to inhibit fires (Table 1). As with invasive grasses, invasive woody species can alter fire regimes through a positive feedback that creates an alternate invaded community (Fig. 1). Woody species that invade native or non-native grass-dominated ecosystems can disrupt the grass-fire cycle, suppressing fire and leading to positive feedbacks that promote woody invasion—an "escape" from the grass-fire cycle (Brooks et al. 2004; Grace 1998). In our review of the literature, we found two species of woody invaders documented to disrupt grass-fire cycles: *Cryptostegia grandiflora* (Grice 1997) and *Triadica sebifera* (Grace 1998). *Mimosa pigra* may also suppress fire where it invades sedgelands and reduces understory cover, though many invaded areas are floodplains that may not usually carry ground fires prior to invasion (Braithwaite et al. 1989; Lonsdale and Miller 1993 and references therein). The impact of *M. pigra* invasion on the fire regime of paperbark and monsoon forests is not documented.

Examples of non-native woody species inhibiting grass-fire cycles in non-native grasslands are primarily anecdotal and have not been well-documented. D'Antonio (2000) suggests that the low flammability and low litter production of firetree (*Morella faya*, Myricaceae) may reduce the spread of understory fires in Hawaiian woodlands, disrupting a recent grass-fire cycle associated with exotic grass invasion. Introduced *Leucaena leucocephala* and *Prosopis juliflora* (both Fabacaeae) also form dense stands in exotic grass communities in Hawai'i that reduce understory grass densities (C. C. Daehler, personal observation), though their effect on the grass-fire cycle has not been studied. *Cytisus scoparius* and *Genista monspessulana* invade areas dominated by exotic grasses in California, but this appears to be in response to, rather than the cause of, reductions in fire frequency (Keeley 2001). Nevertheless, shading by aggressively invading woody plants can reduce grass biomass and increase surface humidity, reducing fire risks and promoting escape from the classic grass-fire cycle. Many woody legumes are capable of resprouting after fire and have propagules that persist through fire or use fire as a germination cue (Bond and Keeley 2005; Pausas et al. 2006), These traits may make legumes particularly capable of establishing and increasing in abundance following fire, potentially disrupting understory grass-fire cycles.

Alternately, invasive woody species can promote fire or increase aspects of a pre-existing fire regime. Woody plant species that have been documented to increase fire frequency or intensity in the invaded range come from a variety of habitats and families (Table 1), but most are relatively fast-growing species well adapted to fire or disturbance. These species are likely to benefit from fire by surviving fire (e.g. *Melaleuca quinquenervia,* Gordon 1998) or establishing quickly after fire either through resprouting or a robust seed bank (e.g. *Pinus* spp, Schwilk and Ackerly 2001). For example, in Chile, the invasive European shrub *Genista monspessulana* is killed by fire but germinates readily from seeds, quickly forming dense monocultures (Pauchard et al. 2008). Flammable tissues and dense stands can promote the ignition and spread of fire, further exacerbating the invasion in a potentially self-promoting manner (Brooks et al. 2004; Schwilk and Ackerly 2001). In the southern United States, Eurasian saltcedar (*Tamarix* spp.) resprouts rapidly post-fire, out-competing natives and creating dense stands that carry fire well, creating a positive feedback cycle (Busch and Smith 1993; Ellis et al. 1998). Some pines, which often promote fire in the invaded range, have serotinous seeds and depend on fire for successful recruitment. Schwilk and Ackerly (2001) found evidence for a suite of traits which promote fire in serotinous pine species, thus promoting their own regeneration.

The impacts of woody invaders can be substantial in ecosystems where fire is a common natural disturbance. The well-studied invaders of the South African fynbos, which is adapted to frequent, low-intensity

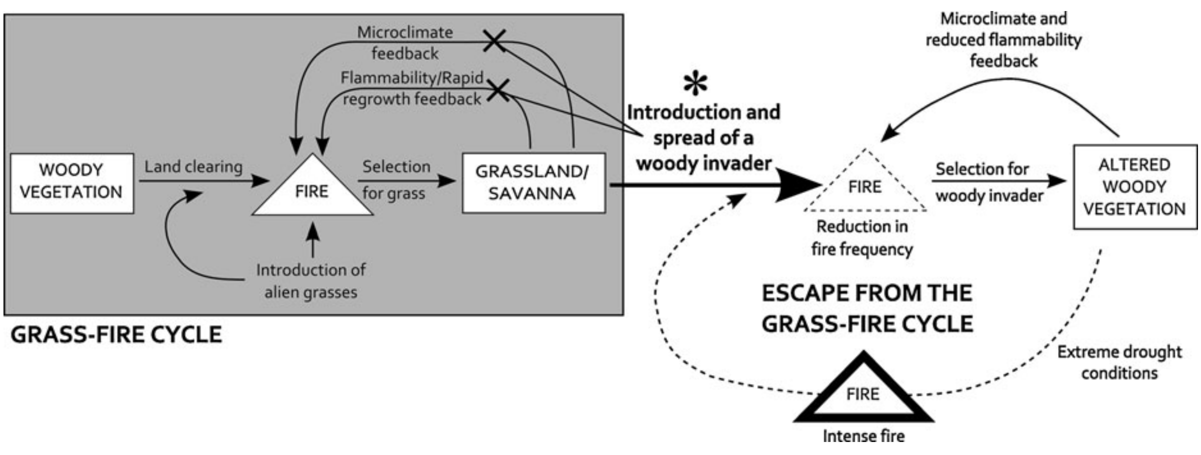

Fig. 1 Escape from the grass-fire cycle (*) can be triggered by the arrival and spread of an introduced woody invader. Shading and vertical biomass alter the surface microclimate, reducing biomass of highly flammable, sun-loving grasses, and increasing humidity. Fires then become less frequent; however, an intense fire may be carried by this system under particular circumstances, such as during unusual drought conditions. The grass-fire cycle (*gray box*) is redrawn from D'Antonio and Vitousek (1992). *Triangles* represent fire regimes with a bold triangle indicating an increase in one or more aspects of the fire regime (e.g. frequency, intensity or extent), and a *dashed triangle* indicating a reduction. *Boxes* represent plant communities. The grass-fire cycle is reprinted with permission, from the *Annual Review of Ecology and Systematics,* Volume 23, © 1992 by Annual Reviews www.annualreviews.org

fires, generally decrease overall fire frequency but increase the occurrence of rare, high-intensity fires with severe consequences for native fynbos vegetation (Holmes et al. 1987; van Wilgen and Richardson 1985). Pines (*Pinus* spp.) are adapted to frequent fires and invasive pines may increase the frequency, intensity and extent of fires in the invaded region, including invasions of fynbos (van Wilgen and Richardson 1985) and the pampas grasslands of Argentina (Simberloff et al. 2010). In contrast, woody invaders of pine barren ecosystems (*Schinus terebinthifolius* and *Robinia pseudoacacia*) reduce fire frequency or intensity (Richburg et al. 2004; Stevens and Beckage 2009). Eucalyptus leaves are extremely flammable (Dimitrakopoulos and Papaioannou 2001), but models of fire behavior in fire-adapted California chaparral predict reduced flame length and fire spread in areas invaded by eucalyptus compared to the native vegetation (Dicus and Anderson 2004). While eucalyptus has been implicated in disastrous, high intensity fires in urban areas of California (e.g. Boyd 1997), it is not clear whether eucalyptus invasion has caused a change in fire regime or how the native vegetation in the area would have responded under similar conditions.

Fire and management of woody invasive species

Reestablishing pre-invasion fire regimes is one proposed technique for controlling or eradicating invasive plant species that alter fire regimes (Brooks et al. 2004). In instances where an invasive plant increases fire frequency or intensity, reduction of fuel loads and ignition sources and active fire suppression could break the cycle. Where an invasive plant suppresses aspects of the fire regime, prescribed fires in conjunction with altering fuel beds (e.g. adding dry biomass) to increase flammability might facilitate control and eradication.

Most examples of invasive species control through fire regime management involve grasses. The role of prescribed fire frequency and intensity in controlling woody invasives has rarely been tested (but see Radford et al. 2008). Nevertheless, we identified 46 studies examining how fire regime may be used to hinder or control exotic woody plant invasions (Table 2). From these studies, it is clear that the risks and benefits of prescribed fire are highly location specific, making it difficult to draw general conclusions. Furthermore, these studies are limited in scope: most come from temperate ecosystems, especially within North America and South Africa.

Fire applied during the growing season is often most effective at controlling woody invasive plants (Grace 1998; Richburg et al. 2004; Schierenbeck 2004), but this may not coincide with the season when prescribed fires are easiest to administer or safest to control (Rice 2004) and may also differ from the timing of most natural pre-invasion fires. Manipulation of fire regime alone is seldom enough to fully eradicate woody invasive species (Table 2). For example, Dooley (2003) found that prescribed fire was successful at preventing invasion of pine barren ecosystems by several invasive woody species in the eastern United States, but did not eradicate established invaders. Fire may be effective at reducing or eliminating seed banks, especially for woody invasive legumes (e.g. Holmes et al. 1987; Pieterse and Boucher 1997; Pieterse and Cairns 1988). However, repeated fires or herbicide applications are necessary to kill newly germinated seedlings before they mature and seed banks are re-established. Fire often only impacts juveniles or small individuals of woody species. DiTomaso et al. (2006) reviewed the use of prescribed fire for controlling weeds (both native and exotic) in the United States and concluded that fire is an effective management only for a few woody species, and is best integrated with other management techniques such as mechanical removal or herbicide application. Even when fire is not a successful stand-alone technique, it can reduce costs and limit the amount of time devoted to more labor-intensive control methods such as hand removal (Bossard 2000).

For any invasive plant, it is theoretically possible to implement a fire regime in which that species could not persist. However, the fire regimes necessary to manage woody invasive plants may not be feasible to implement across the spatial scale necessary for control or eradication of the invasive species. For example, annual prescribed fires on an abandoned farmland site in the Florida Everglades suppressed individuals of Brazilian pepper (*Schinus terebinthifolius*) in small size classes (Doren and Whiteaker 1990). However, the patchiness of fuel production precludes the possibility of large annual fires and therefore prescribed fire is not a good management tool at the landscape-level scale of invasion. Similarly, old fields invaded by Chinese tallow (*Triadica sebifera*) in the coastal prairie of Texas had low fuel loads that could not support fires of adequate intensity to kill small Chinese tallow individuals (Grace 1998). The high number of repeated annual burns needed to eradicate Japanese honeysuckle (*Lonicera japonica*) makes prescribed fire a potential tool for control, but not for eradication of this species (Schierenbeck 2004). A study comparing treatments for controlling *Hakea sericea* and *Pinus radiata* found that burning after felling and removing trees was optimal (Holmes et al. 1987). However, inaccessible terrain in many areas would make it impossible to remove trees. Alternate control treatments, including burning trees while standing or burning after felling without clearing, either promote invasive species or produce high-intensity fires that are difficult to control. While the combination of felling and fire implemented in the 1970s is likely predominately responsible for the reduction in *H. sericea* across South Africa from 1979 to 2001, prescribed fire faltered as a management technique in the 1980s due to increased regulation and lack of funding (Esler et al. 2010). More recent success at halting the spread of *H. sericea* is attributed to the introduction of biological control agents (Esler et al. 2010).

The role of invasive species as drivers of community change or passengers of ecosystem degradation is an ongoing debate in invasion ecology (Didham et al. 2005; MacDougall and Turkington 2005). Changes in fire regime may facilitate initial establishment of invasive species, with an invasive plant–fire cycle further promoting dominance and spread. Reduced fire frequency has been implicated in facilitating the invasion of *Cryptostegia grandiflora* in riparian habitats in northern Australia (Grice 1997) and Chinese tallow (*Triadica sebifera*) in the United States (Grace 1998). Understanding the complex relationship between woody exotic plant invasions and disturbance is crucial to the implementation of appropriate prescribed fire regimes. Rather than re-establishing pre-invasion fire regime, control may require identifying and establishing the fire regime that existed before the disturbance or degradation that facilitated the initial invasion.

Manipulation of fire regimes to control invasive woody species must consider plant communities beyond the targeted species, especially negative effects on native species (Radford et al. 2008; Tveten and Fonda 1999). Furthermore, the optimal prescribed fire regime for one invader might have no effect on or even promote other invasive species, limiting the success of management (Murphy and Lusk 1961). Even within natural ecosystems, different species have different optimal fire regimes (Keith et al. 2002). Thus, a patchwork mosaic of fire is often thought to increase diversity by creating patches which are beneficial to fire-sensitive and fire-tolerant species (Allen 2008). This variation in fire regimes may be important to maintaining a diverse native community, but is difficult to incorporate into a prescribed fire regime for invasive species control.

The prevalence of anecdotal information and lack of accessible supporting data is a major limitation to demonstrating which woody exotic species have impacted fire regimes and which invaded ecosystems might successfully be managed with prescribed fires. Hiremath and Sundaram (2005) acknowledge that they must rely primarily on anecdotal and descriptive information in proposing a *Lantana*-fire cycle in Indian forests, but anecdotal information for many species is propagated without being evaluated. Gray literature contains valuable information about the management of invasive woody species, but most of it remains inaccessible or difficult to locate.

Conclusions

Changes to fire regime following woody invasion are often undocumented and the true cause of alterations in fire regime can be difficult to determine. This is confounded by the opportunistic nature of invasions, where woody species may take advantage of, rather than cause, changes in fire regime. Management intuitively seeks to reverse the effects of invaders on fire regimes, but a lack of well-documented studies on pre-invasion fire regimes makes fire management largely guesswork. Changes in fire regime as a result of management can actually promote the invasion of woody species, making prescribed fire a very sensitive and context-specific control method.

Woody invasive species could be expected to generally inhibit fire in an alternative pathway to the grass-fire cycle (Fig. 1). Current research based predominately in South Africa, Australia and the United States, however, has focused on woody invasive species that increase fire frequency or intensity. More research is needed to determine whether this is representative of woody invasive

Table 2 Studies reporting the effectiveness of prescribed burns for controlling woody plant invasions

Invasive species	Family	Region of origin	Region invaded	Life form	Reduces seed bank	Kills adults	Cut before fire	Requires follow-up	Return interval	Fire recommended for control?	Selected references
Acacia cyclops	Fabaceae	Australia	South Africa	Shrub	x		x	x		In fynbos, but not in fire-sensitive coastal zones	Holmes et al. (1987)
Acacia longifolia	Fabaceae	Australia	South Africa	Shrub	x	x		x		Can control seed bank	Pieterse and Cairns (1988)
Acacia mearnsii	Fabaceae	Australia	South Africa	Tree	x		x	x		Standing plants resprout, only recommended if fell first	Pieterse and Boucher (1997)
Acacia nilotica	Fabaceae	Africa, India	Australia	Tree	x		x	x		Causes seed and seedling mortality	Radford et al. (2001)
Acacia saligna	Fabaceae	Australia	South Africa	Shrub	x		x	x		Felling followed by fire is most effective	Van Wilgen and Richardson (1985), Holmes et al. (1987)
Berberis thunbergii	Berberidaceae	Asia	Northeast US	Shrub				x		Successful when used with herbicide	Richburg et al. (2000), Ward et al. (2009)
Cryptostegia grandiflora	Asclepiadaceae	Madagascar	Australia	Vine, shrub		x				Low-intensity fires killed invasive with minimal impact on natives; grass required to carry fire	Grice (1997), Bebawi and Campbell (2002), Grice et al. (2008), Radford et al. (2008)
Cytisus scoparius	Fabaceae	Europe	Australia, US	Shrub	x		x	x	1–3 years	Often negatively impacts native species	Downey and Smith (2000), Alexander and D'Antonio (2003a , b), Richburg et al. (2004)
Elaeagnus umbellata	Elaeagnaceae	Asia	Northeast US	Shrub						No	Richburg et al. (2000)
Frangula alnus	Rhamnaceae	Eurasia	Northeast US	Shrub, small tree				x	1–2 years	Fire controls seedlings, only controls mature plants with herbicide	Richburg et al. (2000)
Genista monspessulana	Fabaceae	Mediterranean	California	Shrub	x		x	x	1–3 years	Often negatively impacts natives; other methods needed to kill adults	Boyd and Rafael (1995), Swezy and Odion (1997), Alexander and D'Antonio (2003a), 6), Boyd and Rafael (1995)
Hakea sericea	Proteaceae	Australia	South Africa	Shrub	x	x	x		12 years	Yes	Van Wilgen and Richardson (1985), Holmes et al. (2000), Esler et al. (2010)
Lantana camara	Verbenaceae	Tropical America	Global	Shrub			x	x		Only with other methods	Sharma et al. (2005)
Ligustrum vulgare and L. sinense	Oleaceae	Europe, North Africa, Asia	Southeast US	Shrub					1 year	Successful in some areas, but not in others	Batcher (2000)
Lonicera japonica	Caprifoliaceae	Japan, Korea, Eastern China	Global	Vine				x		No, but may be used as a pretreatment to herbicide application	Richburg et al. (2000), Rice (2004), Schierenbeck 2004
Melaleuca quinquenervia	Myrtaceae	Australia	Florida	Tree	x		x	x		Repeated fires destroy seed bank, felling and herbicide needed to control adults	Turner et al. 1997; Myers et al. (2000), Serbesoff-King (2003), Silvers et al. (2007)

Table 2 continued

Invasive species	Family	Region of origin	Region invaded	Life form	Reduces seed bank	Kills adults	Cut before fire	Requires follow-up	Return interval	Fire recommended for control?	Selected references
Mimosa pigra	Fabaceae	Tropical America	Australia	Shrub, tree	x			x		Fires just before the wet season effective if seedlings and resprouts are flooded post-fire	Lonsdale and Miller (1993), Paynter and Flanagan (2004)
Pinus halepensis	Pinaceae	Mediterranean	South Africa	Tree	x					Frequent fires kill seedlings	Richardson (1988), Zalba and Villamil (2002)
Pinus radiata	Pinaceae	California	South Africa	Woody	x		x	x		Felling followed by fire is most effective, but difficult in many areas	Holmes et al. (2000), Zalba and Villamil (2002), Williams and Wardle (2005)
Pittosporum undulatum	Pittosporaceae	Australia	Australia	Tree	x	x				Yes, controls seeds in canopy seed bank, seedlings and adults	Gleadow and Narayan (2007)
Prosopis pallida	Fabaceae	South America	Australia	Tree	x	x		x		Fire with follow-up treatments can be effective	Campbell and Setter (2002)
Rhamnus cathartica	Rhamnaceae	Europe, Asia, North Africa	Northeast US	Tree			x			Repeated fires necessary to control resprouting	Rice (2004), Richburg et al. (2004)
Robinia pseudoacacia	Fabaceae	Southeast US	Northeast US	Tree			x			Repeated fires necessary to control resprouting	Richburg et al. (2004)
Rosa multiflora	Rosaceae	Asia	US	Shrub						Frequent fires may be effective in some areas, but not recommended in others	Richburg et al. (2004), Glasgow and Matlack (2007)
Schinus terebinthifolius	Anacardiaceae	South America	Florida	Shrub, small tree			x		3–7 years	Repeated fire maintains low densities in pine forests, but is not effective on abandoned fields or at high densities	Doren and Whiteaker (1990), Doren et al. (1991), Stevens and Beckage (2009), Stevens and Beckage (2010)
Tamarix spp.	Tamaricaceae	Eurasia	Southwest US, Mexico	Tree, shrub			x	x		Fire suppression and pulse flooding promote natives, fire removes biomass after felling and before herbicide	Brock (1994), Ellis et al. (1998), Nagler et al. (2005), Shafroth et al. (2005)
Triadica sebifera	Euphorbiaceae	Asia	Southern US	Tree				x		Fire may be effective in prairies (but not abandoned fields) if used with other control methods	Grace (1998)
Ziziphus mauritiana	Rhamnaceae	Southeast Asia	Australia	Shrub						No, plants resprout readily	Grice (1997)

species globally. The reciprocal impacts of fire and woody invasions are not clearly understood and are likely species and community specific. However, understanding the interaction between woody invaders and fire regime and the impact on plant community dynamics is important for the control of invasive species and native community management, especially where the fire regime is being manipulated for management purposes. An international database of information from managers and scientists could help expedite the synthesis of existing knowledge on the relationship between invasion and fire and improve the success of management with prescribed fires.

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