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# Fire Management Impacts on Invasive Plants in the Western United States

JON E. KEELEY

U.S. Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon National Parks, Three Rivers, CA 93271-9651, U.S.A., email jon\_keeley@usgs.gov; and Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, U.S.A.

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**Abstract:** *Fire management practices affect alien plant invasions in diverse ways. I considered the impact of six fire management practices on alien invasions: fire suppression, forest fuel reduction, prescription burning in crown-fire ecosystems, fuel breaks, targeting of noxious aliens, and postfire rehabilitation. Most western United States forests have had fire successfully excluded for unnaturally long periods of time, and this appears to have favored the exclusion of alien plant species. Forest fuel reduction programs have the potential for greatly enhancing forest vulnerability to alien invasions. In part this is due to the focus on reestablishing pre-Euro-American fire regimes on a landscape that differs from pre-Euro-American landscapes in the abundance of aggressive non-native species. We may be forced to choose between restoring "natural" fire regimes or altering fire regimes to favor communities of native species. Intensive grazing in many western forests may exacerbate the alien problem after fire and temporally decoupling grazing and fire management may reduce the alien threat. Many shrubland ecosystems such as the Intermountain West sagebrush steppe or California chaparral have a natural, high-intensity crown fire regime that is less amenable to forest restoration tactics. Historical use of prescribed fire for type conversion of shrublands to more useful grazing lands has played some role in the massive annual grass invasion that threatens these shrublands. Fuel breaks pose a special invasive plant risk because they promote alien invasion along corridors into wildland areas. Use of prescription burning to eliminate noxious aliens has had questionable success, particularly when applied to disturbance-dependent annuals, and success is most likely when coupled with ecosystem restoration that alters the competitive balance between aliens and natives. Artificial seeding of alien species as a form of postfire stabilization appears to cause more problems than it solves and may even enhance alien invasion.*

**Key Words:** exotic plants, fire suppression, fuel breaks, fuel reduction, non-native plants, postfire rehabilitation, prescription burning

Impactos de la Gestión de Fuego sobre Plantas Invasoras en el Oeste de Estados Unidos

**Resumen:** *Las prácticas de gestión de fuego afectan de diversas maneras a las invasiones de plantas. Consideré el impacto de seis prácticas de manejo de fuego sobre las invasiones: supresión de fuego, reducción de combustible forestal, quema prescrita en ecosistemas con fuego de dosel, guardarrayas, eliminación de invasoras dañinas y rehabilitación post fuego. En la mayoría de los bosques del oeste de Estados Unidos el fuego ha sido excluido exitosamente por largos períodos de tiempo no naturales y esto parece haber favorecido la exclusión de especies de plantas exóticas. Los programas de reducción de combustible forestal tienen el potencial para incrementar la vulnerabilidad de bosques a las invasiones de plantas exóticas. En parte, esto se debe al enfoque en el reestablecimiento de regímenes de fuego pre-Euroamericanos en un paisaje que difiere de paisajes pre-Euroamericanos en la abundancia de especies no nativas agresivas. Podremos ser forzados a elegir entre la restauración de regímenes de fuego "naturales" o la alteración de regímenes de fuego para favorecer a comunidades de especies nativas. El pastoreo intensivo en muchos bosques occidentales puede exacerbar el problema de invasoras después del fuego y la reducción temporal de pastoreo y gestión de incendios puede reducir la amenaza de las invasoras. Muchos ecosistemas con matorrales como la estepa de artemisa*

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*West Intermountain o el chaparral California tienen un régimen natural de fuego de alta intensidad que es menos dócil a las tácticas de restauración de bosques. El uso histórico de quemas prescritas para la conversión de terrenos con matorrales a tierras de pastoreo más útiles ha jugado un papel en la invasión masiva anual de pastos que amenaza a estos terrenos con matorrales. Las guardarrayas constituyen un riesgo especial porque promueven la invasión de áreas silvestres a lo largo de corredores. El éxito del uso de quemas prescritas para eliminar invasoras dañinas es cuestionable, particularmente cuando se aplica a anuales dependientes de perturbación, y el éxito es más probable cuando se combinan con restauración de ecosistemas que altera el balance competitivo entre invasoras y nativas. La diseminación artificial de semillas de especies invasoras como una forma de estabilización posterior al fuego parece causar más problemas que los que resuelve e incluso puede favorecer la invasión de exóticas.*

**Palabras Clave:** guardarrayas, plantas exóticas, plantas no nativas, quema prescrita reducción de combustible, rehabilitación post fuego, supresión de fuego

## Introduction

U.S. federal policies incorporate alien plant concerns into management of public lands. For example, the U.S. National Park Service policy (U.S. Department of Interior 2001) mandates that “exotic species will not be allowed to displace native species if displacement can be prevented.” The chief of the U.S. Department of Agriculture Forest Service (USFS) has identified invasive species as one of the four significant threats to U.S. forest and rangeland ecosystems (U.S. Department of Agriculture Forest Service 2004), and the USFS manual states that “determining the risk of noxious weed introduction or spread as part of the NEPA process for proposed actions, especially for ground-disturbing and canopy-altering activities” is the explicit responsibility of managers (U.S. Department of Agriculture Forest Service 1995). Here I explore how these policies may be complicated, and sometimes compromised, by fire management practices. I examined impacts from six fire management practices: (1) fire suppression, (2) fuel reduction in forests, (3) prescription burning in shrublands, (4) fuel breaks, (5) prescription burning to target noxious aliens, and (6) postfire rehabilitation.

## Fire Suppression

Fire suppression policy over the past century has worked toward excluding fires from forests. For some forest types, such as Southwest ponderosa pine (*Pinus ponderosa* Laws.), the natural fire regime of frequent, low-intensity surface fires has been particularly amenable to fire suppression tactics. Consequently fires have been excluded over a significant portion of the landscape for much of the twentieth century (Allen et al. 2002). There is little debate about the critical nature of the fire hazard due to unnatural accumulation of understory fuels in these and many other western U.S. forest types. These fuels increase the probability of large, high-intensity wildfires and pose a

threat to the long-term sustainability of these ecosystems (Graham et al. 2004).

Under this management policy of fire suppression, however, forests appear to have fared well in terms of minimal alien plant invasion (Pierson & Mack 1990a, 1990b; Weaver et al. 2001; Keeley et al. 2003). One of the major reasons for the resilience to invasion of undisturbed forests is that the closed forest canopy is highly inhibitory to aliens, most of which require high light levels (Rejmanek 1989; Pierson et al. 1990; Charbonneau & Fahrig 2004). Other factors that potentially play a role are the accumulation of surface litter, which diminishes sites for alien establishment, and reduced propagule sources (dense, closed canopy forests have little herbaceous growth to attract livestock).

## Fuel Reduction in Forests

The National Fire Plan (U.S. Department of Agriculture Forest Service 2001) addresses the threat of catastrophic fires by reducing fuels with prescription burning or mechanical thinning. The Healthy Forests Restoration Act of 2003 (House Resolution 1904) increases the ability of resource managers to perform necessary fuel reduction projects and is called forest restoration because one of its goals is to return forests to their prefire-suppression-era structure and function. Fire lines and firefighting equipment associated with prescription burning directly favor alien species by creating soil disturbances and introducing alien propagules (Harrod & Reichard 2001; Backer et al. 2004), but the impact is potentially much broader. There is growing evidence that these fuel reduction projects alter ecosystem structure in ways that promote alien plant invasion.

Ponderosa pine forests in the Cedar Grove section of Kings Canyon National Park in the southern Sierra Nevada of California have been managed with prescription burning for more than two decades. The primary goal is to return a quasi-natural fire cycle for the resource benefit of

these forests. In 1998, however, fire management voluntarily halted this program because of the recognition that associated with prescription burning was an explosion of cheatgrass (*Bromus tectorum* L.) in the burned forests (Caprio et al. 1999). Results of experiments on the interaction between cheatgrass and fire show that burning stimulates cheatgrass populations, regardless of whether it is late spring or early fall (T. McGinnis & J.E.K., unpublished data). Based on these studies, the only parameter with potential for inhibiting cheatgrass is accumulation of pine-needle litter, which suggests that lengthening the fire-return interval to significantly exceed the natural cycle may be one of the few options for controlling this alien invader.

Restoration includes restoring not only natural processes such as fire but also natural structure through mechanical thinning of forests, and these practices also may enhance alien invasion. Extensive forest restoration is currently under way in many western U.S. ponderosa pine forests. These treatments alone or in combination with burning of slash increase both the diversity and abundance of alien plant species (Griffis et al. 2001; Dodson 2004; Wienk et al. 2004). Longer-term studies are needed, however, to determine whether this is a short-lived invasion or whether such practices provide an opportunity for invasives to gain a foothold that will allow long-term persistence in these forests.

These examples suggest a potential conundrum. Forest restoration often has as one of its goals returning the system to historical fire regimes of high fire frequency (Covington & Moore 1994). These historical fires, however, occurred on a landscape that lacked a background of diverse alien species poised to take advantage of such disturbance regimes. This situation may force a choice between restoring "natural" fire regimes or altering those fire regimes to favor communities of native species. In reality, though, the question is not that simple because reducing the incidence of fire in these ecosystems has long-term impacts on forest structure, with potential cascading effects on alien species.

Many western U.S. forests have historically had rather complex fire regimes that included a mixture of surface fires and localized crown fires (Odion et al. 2004b). Low-intensity surface fires removed dead wood and thinned the sapling population, and localized patches of crown fire created gaps that were essential for reproduction (Keeley & Stephenson 2000). A century of fire suppression, coupled with other management activities such as grazing and logging, has added greatly to the amount and continuity of understory fuels such that now these perturbed forests face the reality that gaps created by high-intensity crown fire will be potentially orders of magnitude larger (Fig. 1). These canopy gaps are sinks for alien invasion (Keeley et al. 2003). Crawford et al. (2001) reported more than a dozen alien species in gaps produced by high-severity wildfires in northern Arizona ponderosa

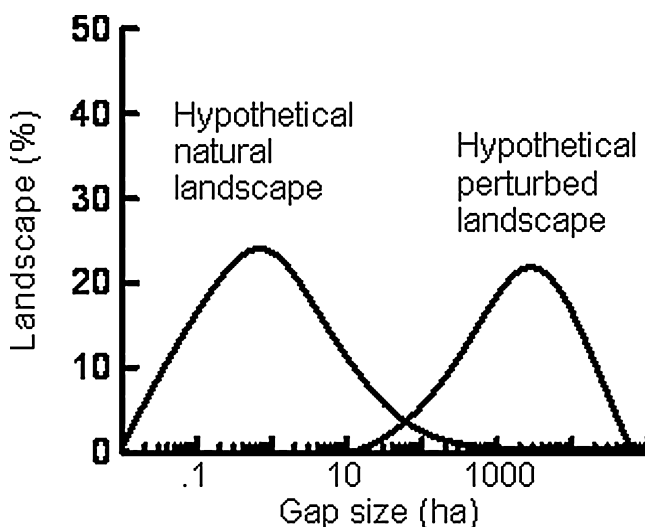


Figure 1. Hypothetical distribution of fire-generated gaps expected for natural fire regimes and future fire regimes in Sierra Nevada mixed conifer forests perturbed by a century of fire exclusion (from Keeley & Stephenson 2000).

forests, and these aliens constituted more than a quarter of the understory cover. These invasive species change the fuel structure of forests (Brooks et al. 2004) and are capable of setting back both natural and artificial regeneration of the dominant forest trees.

There are perhaps ways to minimize effects of alien species in fuel reduction projects. For example, many of the aliens Crawford et al. (2001) recorded in their burned sites were weeds that are often transported by cattle (Arnold 1950; Wuerthner & Matteson 2002); thus, prescription burning or logging, when coupled with grazing, may be a dangerous combination, exacerbating the alien invasion problem. This is supported by the report that wildfires in ungrazed ponderosa forests of northern Arizona have relatively few alien species (Laughlin et al. 2004). If there is a connection, then it could be rather large because 70% of the western United States is grazed, including wilderness areas, national forests, and some national parks (Fleischner 1994). I suggest that rotating grazing areas so that livestock are removed for an extended period of time before prescription burning might be one means of reducing alien species' response to necessary fuel reduction treatments.

Manipulating fire severity during prescription burning can also affect the alien response because high-severity gaps are more vulnerable to invasion than low-severity gaps (Keeley et al. 2003). This, however, is complicated by the requirement of many dominant trees in high-severity gaps for successful seedling recruitment (Keeley & Stephenson 2000).

Manipulating treatment patch size may be another way of altering the invasive threat. For example, the size of

burned patches affects postfire colonization by opportunistic species (Turner et al. 1997). Small patches have a greater perimeter-to-area ratio, making the burned area more vulnerable to invasion, whereas large burn patches have a smaller ratio, making the bulk of the burned area less susceptible to colonization from outside alien invaders. The landscape pattern of alien distribution, however, complicates drawing conclusions about community vulnerability to invasion. For example, forest patches adjacent to open habitat are much more susceptible to invasion than forests surrounded by more closed canopy forest (Charbonneau & Fahrig 2004). If aliens are sparsely distributed across the landscape, then small burn patches, despite their high perimeter-to-area ratio, are less likely to encounter alien populations, whereas large patches, with a greater absolute perimeter size, would have a higher probability of encountering alien populations.

In short, grazing history, alien distribution patterns, treatment size, and fire severity are all factors that might be manipulated to reduce the alien threat linked to necessary fuel-reduction projects. Roads and recreational use are other parameters that interact with fire and invasives (e.g., Gelbard & Belnap 2003) and could be manipulated in conjunction with fuel treatments to reduce alien invasion.

### Prescription Burning in Shrublands

Many shrubland ecosystems such as the Intermountain West sagebrush steppe or California chaparral have a natural fire regime of high-intensity crown fires. These ecosystems provide fewer options for fuel reduction because mechanical treatments are both expensive and unlikely to provide commercial profit. Prescription burning is one of the more economically feasible treatments but there are increasing constraints on its widespread use in shrubland ecosystems because of the hazards of high-intensity fires on populated landscapes. One of the realities of doing prescription burning in crown-fire ecosystems is the difficulty of defining controllable prescriptions (Keeley 2002a). This is particularly problematic for burns in the normal late summer through autumn fire season. One approach is to conduct burns outside the normal fire season, but such manipulations have the potential for extreme resource damage, as illustrated by the poor recovery of the native community and massive alien invasion following a winter burn in one California park (Fig. 2).

For shrublands as well as forests, prescription burning is justified if it provides either resource benefits to the ecosystem or reduces fire hazard for people. In California chaparral, prescription burning is primarily justified on the basis of fire-hazard reduction, whereas in the Intermountain West sagebrush, the primary justification is benefit to ecosystem resources. The most commonly cited resource benefits are improved rangeland



*Figure 2. Alien-grass-dominated scar in chaparral shrublands 10 years after an out-of-season winter burn in chaparral at Pinnacles National Monument (central coastal California) (photograph by J. Keeley). A similar effect was also reported for another cool-season chaparral prescription burn in northern California (Parker 1987).*

for wildlife (Beardall & Sylvester 1976; Holechek 1981) or livestock (Pechanec 1944; Sapsis & Kaufmann 1991). Other justifications include returning these ecosystems to their historical structure, which is considered by some to have been a landscape of more open sagebrush steppe vegetation. Indeed, rangeland literature commonly refers to the unnaturally dense stands of sagebrush in need of prescription burning (Blaisdell et al. 1982; Miller et al. 1994). In light of the massive cheatgrass invasion across much of this landscape (Mack 1981), coupled with the potential for burning to favor cheatgrass expansion (Harnis & Murray 1973; Knapp 1997; Young & Allen 1997), there is need for a closer examination of prescription burning in these Intermountain West ecosystems.

Prescription burning in sagebrush ecosystems is a highly effective method of improving rangelands for livestock grazing. The dominant shrub, *Artemisia tridentata* Nutt., is immediately replaced by more palatable herbaceous plants and recovers slowly over a period of decades (Stewart & Young 1939; Pechanec 1944; Ralphs & Busby 1979). On the other hand, prescription burning for enhancement of wildlife habitat appears to be justifiable in very few cases, and generally the loss of sagebrush following burning represents important habitat loss (Miller & Eddleman 2001; Welch & Criddle 2003). Restoring historical fire regimes is perhaps the weakest justification for prescription burning because many lines of evidence suggest fire-rotation intervals are currently at the low end of the historical range of variability (Menakis et al. 2003). The natural fire regime in sagebrush ecosystems appears to have been one of infrequent fires at 60- to 110-year intervals (Whisenant 1990; Welch & Criddle 2003; W. Baker, personal communication), although at the mesic end of

the gradient it may have been shorter (Winward 1984). Thus, except on rangelands where livestock production is the only goal, prescription burning may not be a desirable fire-management treatment because of the potential threat of exacerbating the cheatgrass invasion.

In California chaparral and sage scrub shrublands, a similar annual grass invasion has also occurred, although fire-management practices for rangeland improvement appear to have played a much bigger role. This began with burning by the Native Americans, largely to favor herbaceous vegetation over shrublands, which set much of the landscape in a quasi-disequilibrium vulnerable to rapid annual plant invasion upon the arrival of Europeans (Keeley 2002b). By the late nineteenth century rangelands were in short supply, widespread burning expanded the grazing lands, and the coastal analogues of cheatgrass, specifically *Bromus madritensis* L., *B. bordeaceus* L., and *B. diandrus* Roth., and forbs such as *Erodium cicutarium* (L.) L'Her., rapidly expanded to fill the void created by removing natural shrub dominants (Keeley 1990, 2001, 2004b). Initially these burning practices were unregulated, but in the mid-twentieth century organized efforts at rangeland expansion into shrublands was a state-sanctioned practice that resulted in substantial conversion to alien grasslands (Keeley & Fotheringham 2003).

Typically a repeat fire within the first postfire decade is sufficient to provide an initial foothold for aliens (Fig. 3). With the first entry of alien annuals into these shrubland ecosystems, there is a potential shift from a crown-fire regime to a mixture of surface and crown fires, where highly combustible grass fuels carry fire between shrub patches that have not yet attained a closed canopy capable of carrying crown fire under most weather conditions. As fire frequency increases there is a threshold beyond which the native shrub cover cannot recover (Zedler et al. 1983; Haidinger & Keeley 1993; Jacobson et al. 2004). Not only do alien grasses increase the probability of burning,

but also the shift from crown fires to a mixture of surface and crown fires increases the probability of alien seed-bank survivorship (Keeley et al. 2005) because grass fuels generate lower temperatures (Zschaechner 1985). In these shrublands and in other ecosystems, alien grasses alter fire regimes in ways that enhance their own success, in what has been described as a “grass/fire cycle” (D’Antonio & Vitousek 1992), “niche construction” (Keeley 2001), or “invasive engineering” (Cuddington & Hastings 2004).

In recent years ineffective fire prevention has allowed an unnaturally high number of wildfires on chaparral landscapes, which has resulted in conversion to alien-dominated grasslands (Fig. 4). Such type conversions not only affect biodiversity, but replacing slopes dominated by natural shrublands with grasslands also makes these landscapes highly vulnerable to major changes in hydrological processes. For example, experimental type conversions performed for fire hazard reduction have resulted in soil slips and other major geomorphological changes (Keeley 2002a).

On shrubland landscapes where the excessive load of anthropogenic fires has stressed natural ecosystems to the point of collapse, fire managers need to be prudent about adding further fire in the form of prescription burning. Currently this applies to much of the Great Basin and all of the lower-elevation foothills in southern California, where type conversion to alien grasslands is happening at an alarming rate (J.K., personal observations). To be avoided are prescription burning at fire-return intervals of 5 years in southern California chaparral (Loomis et al. 2003; Gonzalez-Caban et al. 2006), which are likely to lead to type conversion to alien grassland and even exacerbate

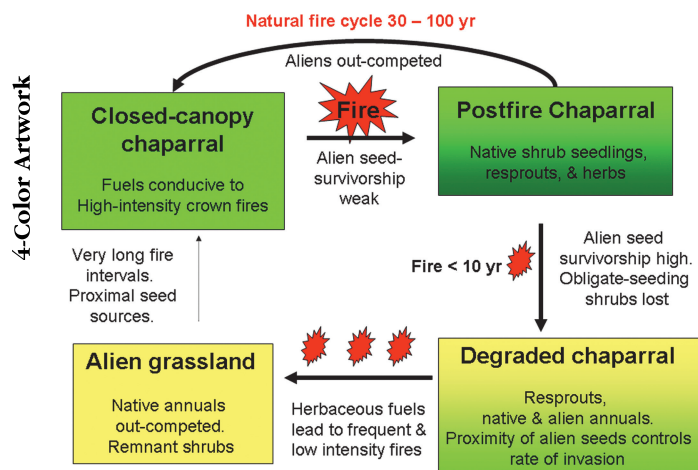


Figure 3. Model of fire and alien species interactions in California chaparral.

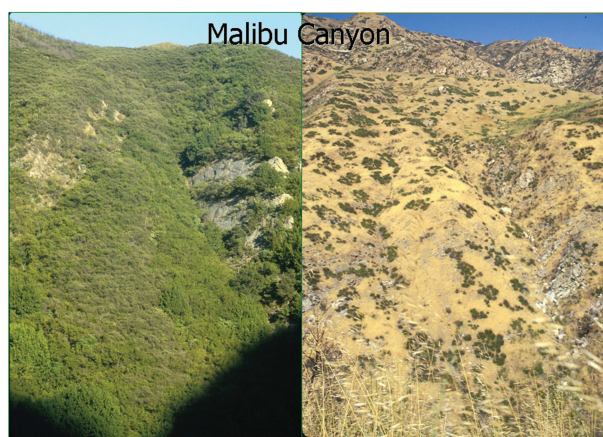


Photo by Anna Jacobsen, Pepperdine University

Figure 4. Type conversion recorded for Malibu Canyon, Santa Monica Mountains, California: left, natural chaparral landscape representative of chaparral in Malibu Canyon; right, landscape dominated by alien annual grass after three fires in 12 years (based on Jacobson et al. 2004; photograph by Steve Davis).

4-Color Artwork

the sedimentation problems they are supposed to reduce (Keeley et al. 2004).

## Fuel Breaks

Forests and shrublands, particularly in California, have had a long history of experimentation with different types of fuel breaks. They are constructed to create barriers to fire spread and to provide access and defensible space for fire-suppression crews during wildfires. These activities have the potential for creating suitable sites for alien plant invasion, and invasion is closely tied to the loss in over-story cover. In a recent study of 24 fuel breaks distributed throughout California, alien plants constituted as much as 70% of the plant cover and the proportion of aliens varied significantly with distance to roads, fuel break age, construction method, and maintenance frequency (J. K. Merriam and J. L. Beyers, unpublished data). The association of alien species with fuel breaks raises two critical concerns. One is that the linear connectedness of these disturbance zones acts as corridors for alien invasion into wildland areas. Another is that these zones of reduced fuels produce lower temperatures and thus safe sites for alien propagules during wildfires, ensuring survivorship of seed banks (Keeley 2001, 2004b). Consequently, following fires these fuel breaks represent a major source area capable of providing a seed bank for alien invasion of adjacent wildlands (Fig. 5).

## Prescription Burning to Target Noxious Aliens

Fire has diverse effects on alien species, and except for a small handful of cases, it generally promotes persistence of aliens (e.g., Grace et al. 2001; Harrod & Reichard

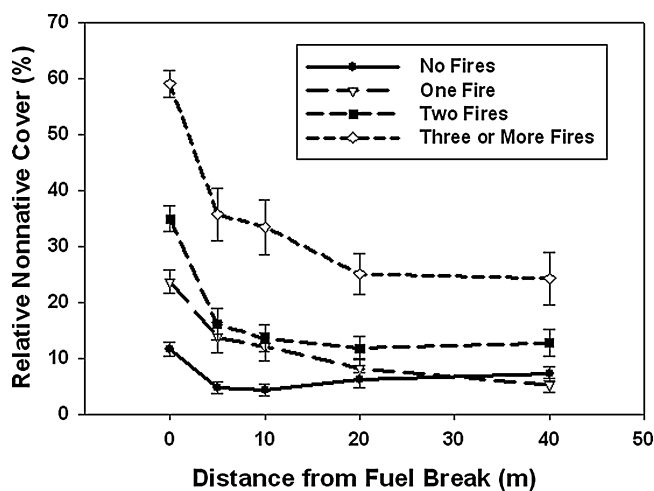


Figure 5. Interaction between number of fires and distance from the fuel break. Error bars represent  $\pm 1$  SE (from J. K. Merriam, and J. L. Beyers, unpublished data).

2001; Brooks et al. 2004). Invasive species in the western United States that seem to be controlled by fire include Mediterranean Basin macchi shrubs known collectively as "brooms." Some of these are vigorous resprouters after fire and thus are not readily controlled by burning. Others (e.g., Scot's broom, *Cytisus scoparius* [L.] Link) are weak resprouters, and burning shows promise of control. All have dormant, fire-stimulated seed banks; thus several repeat fires appear to be required to extirpate brooms from a site (Tveten & Fonda 1999; Alexander & D'Antonio 2003; Odion & Haubensak 2004), not unlike what happens to native shrublands in the face of repeat fires (Figs. 3 & 4). Burning, however, typically replaces these noxious woody aliens with herbaceous alien species (Keeley 2001).

Several lines of evidence point to precisely timed prescription burning as an effective treatment for eliminating certain noxious alien annuals with transient seed banks that are vulnerable to fire during spring seed dispersal. One example widely cited in recent alien plant review articles as a demonstration of such success is the application of spring burning in the control of yellow starthistle (*Centaurea solstitialis* L.). This European pest is distributed from Idaho to California and has been targeted as a particularly noxious alien because it alters range conditions and severely reduces soil water resources (Gerlach 2004). Confidence in prescribed burning treatment as a control for this species is based on the results of annual burning for 3 consecutive years in very dense stands that demonstrated 90–100% reduction in starthistle (DiTomaso et al. 1999; Odion et al. 2004a). Burn plans written by agencies undertaking prescribed burns in annual grasslands often use this as one of their primary goals (e.g., East Bay Regional Parks, <http://www.ebparks.org/fire/rxfire>). This species, however, like many aliens, has a relatively long-lived seed bank (Callihan et al. 1993), and longer-term study shows that this thistle rapidly reestablishes once burning is halted (Fig. 6). Clearly, prescribed burning provides only temporary reduction, does not effect sustainable control of this alien, and may exacerbate the alien situation.

Most alien herbs are opportunistic species that capitalize on disturbance. I offer the hypothesis that when it comes to eliminating such noxious aliens, control is most likely under conditions that limit the use of further disturbances such as fire (or grazing, mowing, or herbicides). In some cases prescribed fire may be appropriate if applied in a manner that affects the noxious target species more than potential native competitors and if coupled with active ecosystem restoration that alters the competitive balance between aliens and natives. Sustainable control of these aggressive weeds is most likely going to occur only when natural, intact ecosystems are restored. In the case of yellow starthistle, it invades annual grasslands that owe their origin to disturbance, either displacement of native perennial grassland or type conversion of shrublands



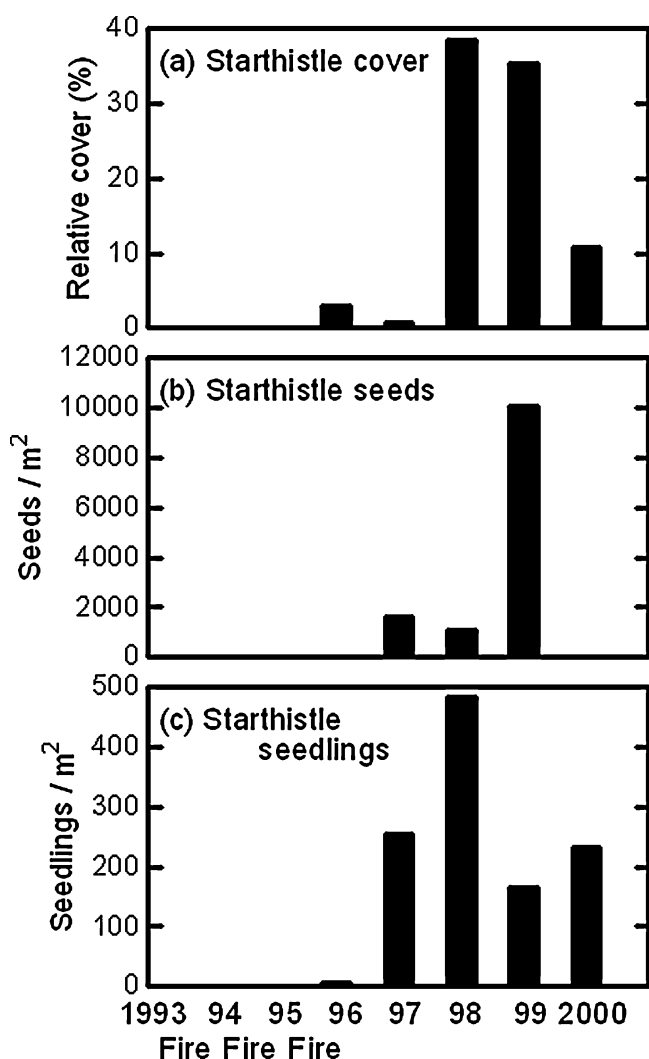


Figure 6. Yellow starthistle (a) cover, (b) seed, and (c) seedling production following three consecutive annual burns applied to extremely dense populations of this noxious alien weed. Immediate postfire results were promising (DiTomaso et al. 1999), but follow-up studies indicate that burning destabilized these grasslands and allowed subsequent reinvasion once burning was stopped (Kyser & DiTomaso 2002).

and woodlands (Huenneke 1989; Keeley 1990; Hamilton 1997). In the absence of community restoration, prescription burning is likely to provide only temporary control of this, and other, noxious annual weeds, and not be cost-effective.

### Postfire Rehabilitation

Propagule source is often the limiting step in the invasion process (D'Antonio et al. 2001) and thus postfire management practices such as site stabilization by seeding of non-natives must be considered a potential influence on

alien plant invasion. These postfire rehabilitation projects illustrate well the Severide Principle, after the newscaster Eric Severide, who is quoted as saying, "Most problems begin as solutions."

Early efforts at such revegetation projects may have played a role in the spread of some noxious weeds. For example, postfire seeding in southern California chaparral in the 1940s aerially seeded black mustard (*Brassica nigra* [L.] Koch and possibly related taxa) on steep southern California watersheds (Gleason 1948). These aggressive weeds soon found their way into citrus orchards and other agricultural fields and were eventually abandoned by fire managers as a suitable slope stabilizer. These species, however, produce polymorphic seed banks with dormant fire-stimulated germination (Went et al. 1952), and decades later on many of the previously seeded slopes in the Los Angeles Basin this species still figures prominently in the postfire flora as a ghost of seedings past (Keeley et al. 2005). Eventually postfire seeding projects replaced mustard with various grass species (e.g., ryegrass, *Lolium multiflorum* Lam., zorro fescue *Vulpia myuros* [L.] C. Gmelin, crested wheatgrass *Agropyron cristatum* [L.] Gaertn.) that appear to lack persistent seed banks. Although these grasses are not persistent on chaparral or forested slopes (Barclay et al. 2004; Beyers 2004), they are capable of invading adjacent grassland and savanna communities.

Because they lack an ability to invade communities, "sterile" or "nonpersistent" cereal grains have been considered a more desirable species for reseeding (Beyers 2004). Although seeding of these species may have achieved some of the intended goals of slowing soil erosion, they have introduced other problems. In one study in the Sierra Nevada the success of wheat seeding was so extraordinary (Fig. 7) that it resulted in the loss of substantial native plant diversity and pine reproduction (Keeley



Figure 7. Postfire ponderosa pine forest reseeded with a nonpersistent variety of wheat after fire in the Giant Sequoia National Monument, Fresno County, California (photograph by J. Keeley).

2004a), a pattern common in many seeding projects (Beyers 2004). Seeding nonpersistent species also carries with it the problem that a marked loss of plant cover in the second postfire year will create an ecological vacuum, and aggressive alien invaders are well suited to exploit this situation.

Increasingly it is apparent that mechanical rehabilitation treatments, including straw mulch and hay bales, are more predictable means of reducing soil erosion and other postfire hydrological problems (Robichaud et al. 2000). Mulching treatments, however, are particularly hazardous in terms of introducing and promoting alien establishment (Kruse et al. 2004). In fact, accidental introduction of alien propagules is possible with any "burned area emergency rehabilitation" project. For example, following the 2000 Cerro Grande Fire it is estimated that contamination of aerial seeding sources was responsible for inadvertently broadcasting more than 1 billion cheatgrass seeds on recently burned sites (C. Allen, personal communication).

## Conclusions

Fire management practices could have widespread effects on invasions of alien species. This linkage is best understood when these problems are placed in a context of community ecology theory. Fire suppression and prefire fuel manipulations have ecological equivalents in that the former attempts to maintain ecosystem equilibrium by preventing disturbance and the latter introduces disequilibrium.

In western U.S. forests, a century of successful fire suppression policy has shifted the competitive balance in favor of long-lived trees that create ecosystem conditions unfavorable to alien invasion. Although greater ecosystem equilibrium appears to exclude alien plants, fire exclusion has set these forests on a trajectory of undesirable conditions for both forest sustainability and human fire hazard. Thus, forest thinning, fuel breaks, and prescribed burning are necessary and inevitable. But accompanying these management activities is a shift in ecosystem properties that favor early successional species, and when done in the context of a landscape with alien species it is likely to alter the balance of native and non-native species. The impact of these management practices may be altered by considering management practices that decouple grazing and burning practices and manipulate burning patterns in light of prefire alien presence.

In many western U.S. shrubland ecosystems, fire suppression policy—despite valiant efforts—has not kept up with an ever-increasing frequency of fires. These communities exhibit weak resilience to major deviations from the natural crown-fire regime and the dominant life forms have been lost, creating an ecological vacuum that has

been rapidly filled by alien weeds. In both the Intermountain West sagebrush and California chaparral (including sage scrub) this alien invasion has historically been exacerbated by fire management practices that included prescription burning for range improvement. Current infestations of annual grasses in both regions require enhanced efforts at fire prevention, fire suppression, and avoidance of prescribed burning under most situations.

## Acknowledgments

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## Literature Cited

- Alexander, J. M., and C. M. D'Antonio. 2003. Seed bank dynamics of French broom in coastal California grasslands: effects of stand age and prescribed burning on control and restoration. *Conservation Biology* 11:185–197.
- Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12:1418–1433.
- Arnold, J. F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *Journal of Forestry* 48:118–126.
- Backer, D. M., S. E. Jensen, and G. R. McPherson. 2004. Impacts of fire-suppression activities on natural communities. *Conservation Biology* 18:937–946.
- Barclay, A. D., J. L. Betancourt, and C. D. Allen. 2004. Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest. *International Journal of Wildland Fire* 13:183–194.
- Beardall, L. E., and V. E. Sylvester. 1976. Spring burning for removal of sagebrush competition in Nevada. *Tall Timbers Fire Ecology Conference Proceedings* 14:539–547.
- Beyers, J. L. 2004. Postfire seeding for erosion control: effectiveness and impacts on native plant communities. *Conservation Biology* 18:947–956.
- Blaisdell, J. P., R. B. Murray, and E. D. McArthur. 1982. Managing Intermountain rangelands—sagebrush-grass ranges. U.S. Department of Agriculture Forest Service, Intermountain Forest and Range Experiment Station, Provo, Utah.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. M. DiTomaso, J. B. Grace, R. J. Hobbs, J. E. Keeley, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677–688.
- Callihan, R. H., T. S. Prather, and F. E. Northam. 1993. Longevity of yellow starthistle (*Centaurea solstitialis*) achenes in soil. *Weed Technology* 7:33–35.
- Caprio, A., S. Haultain, M. B. Keifer, and J. Manley. 1999. Problem evaluation and recommendations: invasive cheatgrass (*Bromus tectorum*) in Cedar Grove, Kings Canyon National Park. Pages 88–107 in 1999 annual fire report on research, monitoring, and inventory. U.S. National Park Service, Sequoia National Park, Three Rivers, California.
- Charbonneau, N. C., and L. Fahrig. 2004. Influence of canopy cover and amount of open habitat in the surrounding landscape on proportion of alien plant species in forest sites. *Ecoscience* 11:278–281.



- Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure. Changes since Euro-American settlement. *Journal of Forestry* 92:39–47.
- Crawford, J. A., C.-H. A. Wahren, S. Kyle, and W. H. Moir. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12:261–268.
- Cuddington, K., and A. Hastings. 2004. Invasive engineers. *Ecological Modeling* 178:335–347.
- D'Antonio, C., J. Levine, and M. Thomsen. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *Journal of Mediterranean Ecology* 2:233–245.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. *Weed Science* 47:233–242.
- Dodson, E. K. 2004. Monitoring change in exotic plant abundance after fuel reduction/restoration treatments in ponderosa pine forests of western Montana. M.S. thesis. Department of Forestry, University of Montana, Missoula.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629–644.
- Gelbard, J., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17:420–432.
- Gerlach, J. D., Jr. 2004. The impacts of serial land-use changes and biological invasions on soil water resources in California, USA. *Journal of Arid Environments* 57:365–379.
- Gleason, C. H. 1948. How to sow mustard in burned watersheds of southern California. California Forest and Range Experiment Station, Berkeley.
- Gonzalez-Caban, A., P. Wohlgemuth, J. B. Loomis, and D. R. Weise. 2006. Costs and benefits of reducing sediment production from wildfires through prescribed burning: the Kinneloa fire case study. In press in general technical report PSW-GTR-xxx. U.S. Department of Agriculture Forest Service Pacific Southwest Experiment Station, Albany, California.
- 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, editors. *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species*. Miscellaneous publication 11. Tall Timbers Research Station, Tallahassee, Florida.
- Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. General technical report RMRS-GTR-120, U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Missoula, Montana.
- Griffis, K. L., J. A. Crawford, M. R. Wagner, and W. H. Moir. 2001. Understorey response of management treatments in northern Arizona ponderosa pine forests. *Forest Ecology and Management* 146:239–245.
- Haidinger, T. L., and J. E. Keeley. 1993. Role of high fire frequency in destruction of mixed chaparral. *Madroño* 40:141–147.
- Hamilton, J. G. 1997. Changing perceptions of pre-European grasslands in California. *Madroño* 44:311–333.
- Harnis, R. O., and R. B. Murray. 1973. 30 years of vegetal change following burning of sagebrush-grass range. *Journal of Range Management* 26:322–325.
- Harrod, R. J., and S. Reichard. 2001. Fire and invasive species within the temperate and boreal coniferous forests of western North America. Pages 95–101 in K. E. M. Galley and T. P. Wilson, editors. *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species*. Miscellaneous publication 11. Tall Timbers Research Station, Tallahassee, Florida.
- Holechek, J. L. 1981. Brush control impacts on rangeland wildlife. *Journal of Soil & Water Conservation* 36:265–269.
- Huenneke, L. F. 1989. Distribution and regional patterns of Californian grasslands. Pages 1–12 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function*. California annual grasslands. Kluwer Academic, Dordrecht, Netherlands.
- Jacobson, A. L., S. D. Davis, and S. L. Babritius. 2004. Fire frequency impacts non-sprouting chaparral shrubs in the Santa Monica Mountains of southern California. In M. Arianoutsou and V. P. Panastasis, editors. *Ecology, conservation and management of mediterranean climate ecosystems*. Millpress, Rotterdam, Netherlands.
- Keeley, J. E. 1990. The California valley grassland. Pages 2–23 in A. A. Schoenherr, editor. *Endangered plant communities of southern California*. Southern California Botanists, Fullerton.
- Keeley, J. E. 2001. Fire and invasive species in mediterranean-climate ecosystems of California. Pages 81–94 in K. E. M. Galley and T. P. Wilson, editors. *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species*. Miscellaneous publication 11. Tall Timbers Research Station, Tallahassee, FL.
- Keeley, J. E. 2002a. Fire management of California shrubland landscapes. *Environmental Management* 29:395–408.
- Keeley, J. E. 2002b. Native American impacts on fire regimes in California coastal ranges. *Journal of Biogeography* 29:303–320.
- Keeley, J. E. 2004a. Ecological impacts of wheat seeding after a Sierra Nevada wildfire. *International Journal of Wildland Fire* 13:73–78.
- Keeley, J. E. 2004b. Invasive plants and fire management in California mediterranean-climate ecosystems. In M. Arianoutsou, editor. *10th MEDECOS—international conference on ecology, conservation and management*. Rhodes, Greece.
- Keeley, J. E., and C. J. Fotheringham. 2003. Impact of past, present, and future fire regimes on North American mediterranean shrublands. Pages 218–262 in T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. *Fire and climatic change in temperate ecosystems of the western Americas*. Springer-Verlag, New York.
- Keeley, J. E., and N. L. Stephenson. 2000. Restoring natural fire regimes in the Sierra Nevada in an era of global change. Pages 255–265 in D. N. Cole, S. F. McCool, and J. O'Loughlin, editors. *Wilderness science in a time of change conference*. RMRS-P-15, Vol. 5. U. S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Missoula, Montana.
- Keeley, J. E., C. J. Fotheringham, and M. A. Moritz. 2004. Lessons from the October 2003 wildfires in southern California. *Journal of Forestry* 102(7):26–31.
- Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien plant dynamics following fire in mediterranean-climate California shrublands of California. *Ecological Applications* 15:2109–2125.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13:1355–1374.
- Knapp, P. A. 1997. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. *Global Environmental Change* 6:37–52.
- Kruse, R., E. Bend, and P. Bierzychudek. 2004. Native plant regeneration and introduction of non-natives following post-fire rehabilitation with straw mulch and barley seeding. *Forest Ecology and Management* 196:299–310.
- Kyser, G. B., and J. M. DiTomaso. 2002. Instability in a grassland community after the control of yellow starthistle (*Centaurea solstitialis*) with prescribed burning. *Weed Science* 50:648–657.
- Laughlin, D. C., J. D. Bakker, M. T. Stoddard, M. L. Daniels, J. D. Springer, C. N. Gilar, A. M. Green, and W. W. Covington. 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management* 199:137–152.
- Loomis, J., P. Wohlgemuth, A. Gonzalez-Caban, and D. English. 2003. Economic benefits of reducing fire-related sediment in southwestern fire-prone ecosystems. *Water Resources Research* 39:1–8.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145–165.

- Menakis, J. P., D. Osborne, and M. Miller. 2003. Mapping the cheatgrass-caused departure from historical natural fire regimes in the Great Basin, USA. Pages 281–287 in *Proceedings RMRS-P-29*. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Missoula, Montana.
- Miller, R. E., and L. L. Eddleman. 2001. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Technical bulletin 151. Agricultural Experiment Station, Oregon State University, Corvallis.
- Miller, R. E., T. J. Svejcar, and N. E. West. 1994. Implications of livestock grazing in the intermountain sagebrush region: plant composition. Pages 101–146 in M. Vavra, W. A. Laycock, and R. D. Pieper, editors. *Ecological implications of livestock herbivory in the West*. Society for Range Management, Denver, Colorado.
- Odion, D. C., and K. A. Haubensak. 2004. Response of French broom to fire. Pages 296–307 in N. G. Sugihara, M. E. Morales, and T. J. Morales, editors. *Proceedings of the symposium: fire in California ecosystems: integrating ecology, prevention and management*. Miscellaneous publication 2. Association for Fire Ecology, Berkeley, California.
- Odion, D. C., J. Alexander, and M. Swezy. 2004. Use of short rotation burning to combat non-natives and their seed banks in California North Coastal Prairie. Pages 46–57 in N. G. Sugihara, M. E. Morales, and T. J. Morales, editors. *Proceedings of the symposium: fire management: emerging policies and new paradigms*. Miscellaneous publication 2. Association for Fire Ecology, Berkeley, California.
- Odion, D. C., E. J. Frost, J. R. Stritholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. *Conservation Biology* 18:927–936.
- Parker, V. T. 1987. Effects of wet-season management burns on chaparral vegetation: implications for rare species. Pages 233–237 in T. S. Elias, editor. *Conservation and management of rare and endangered plants*. California Native Plant Society, Sacramento.
- Pechanec, J. F. 1944. Sagebrush burning—good and bad. *Farmers' Bulletin* No. 1948. U.S. Department of Agriculture, Washington, D.C.
- Pierson, E. A., and R. N. Mack. 1990a. The population biology of *Bromus tectorum* in forests: distinguishing the opportunity for dispersal from environmental restriction. *Oecologia* 84:519–525.
- Pierson, E. A., and R. N. Mack. 1990b. The population biology of *Bromus tectorum* in forests: effect of disturbance, grazing, and litter on seedling establishment and reproduction. *Oecologia* 84:526–533.
- Pierson, E. A., R. N. Mack, and R. A. Black. 1990. The effect of shading on photosynthesis, growth, and regrowth following defoliation for *Bromus tectorum*. *Oecologia* 84:534–543.
- Ralphs, M. H., and F. E. Busby. 1979. Prescribed burning: vegetative change, forage production, cost, and returns on six demonstration burns in Utah. *Journal of Range Management* 32:267–270.
- Rejmanek, M. 1989. Invasibility of plant communities. Pages 369–388 in J. A. Drake, H. A. Mooney, F. diCasti, R. H. Groves, F. J. Kruger, and M. Rejmanek, editors. *Biological invasions: a global perspective*. John Wiley & Sons, New York.
- Robichaud, P. R., J. L. Beyers, and D. G. Neary. 2000. Evaluating the effectiveness of postfire rehabilitation treatments. General technical report RMRS-GTR-63. U.S. Department of Agriculture, Rocky Mountain Research Station, Fort Collins, Colorado.
- Sapsis, D. B., and J. B. Kauffman. 1991. Fuel consumption and fire behavior associated with prescribed fires in sagebrush ecosystems. *Northwest Science* 65:173–179.
- Stewart, G., and A. E. Young. 1939. The hazard of basing permanent grazing capacity on *Bromus tectorum*. *Journal of the American Society of Agronomy* 31:1002–1015.
- Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67:411–433.
- Tveten, R. K., and R. W. Fonda. 1999. Fire effects on prairies and oak woodlands on Fort Lewis, Washington. *Northwest Science* 73:145–158.
- U.S. Department of Agriculture Forest Service (USFS). 1995. *U.S. Forest Service manual*. USFS, Washington, D.C.
- U.S. Department of Agriculture Forest Service (USFS). 2001. *National fire plan*. USFS, Washington, D.C.
- U.S. Department of Agriculture Forest Service (USFS). 2004. *National strategy and implementation plan for invasive species management*. USFS, Washington, D.C.
- U.S. Department of the Interior (USDI). 2001. *National Park Service policy*. USDI, National Park Service, Washington, D.C.
- Weaver, T., D. Gustafson, and J. Lichthardt. 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky Mountain environments (HTs). *Western North American Naturalist* 61:417–427.
- Welch, B. L., and C. Criddle. 2003. Countering misinformation concerning big sagebrush. Research paper RMRS-RP-40. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.
- Went, F. W., G. Juhren, and M. C. Juhren. 1952. Fire and biotic factors affecting germination. *Ecology* 33:351–364.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. Pages 4–10 in D. D. McArthur, E. M. Romney, S. O. Smith, and P. T. Tueller, editors. *Proceedings, symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management*. General technical report INT-276. U.S. Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah.
- Wienk, C. L., C. H. Sieg, and G. R. McPherson. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. *Forest Ecology and Management* 192:375–393.
- Winward, A. H. 1984. Fire in the sagebrush-grass ecosystem—the ecological setting. Pages 2–6 in K. Sanders and J. Durban, editors. *Rangeland fire effects, a symposium*. U.S. Department of Interior, Bureau of Land Management, Boise, Idaho.
- Wuerthner, G., and M. Matteson. 2002. *Welfare ranching. The subsidized destruction of the American West*. Island Press, Covelo, California.
- Young, J. A. and F. L. Allen. 1997. Cheatgrass and range science: 1930–1950. *Journal of Range Management* 50:530–535.
- Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809–818.
- Zschiehner, G. A. 1985. Studying rangeland fire effects: a case study in Nevada. Pages 66–84 in K. Sanders and J. Durham, editors. *Rangeland fire effects, a symposium*. U.S. Department of Interior, Bureau of Land Management, Boise, Idaho.