

# **The Role of Wildfire in the Establishment and Range Expansion of Nonnative Plant Species into Natural Areas**

*A review of current literature*

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## FOREWORD

Discussions of nonnative plant species and wildfire present excellent opportunities to integrate knowledge from different disciplines, but they also present significant challenges. As both wildfire and nonnative plant species elicit emotionally charged reactions, researchers are challenged to provide quantitative information to replace current opinions and dogma based on emotion and conjecture. The conventional wisdom is that many notorious nonnative plant species will dramatically increase and change future fire frequency following wildfire. A surprising number of papers draw conclusions about nonnative plant species and wildfire using this conventional wisdom as the null hypothesis, rather than using the more traditional and testable null hypothesis that the abundance of nonnative plants is not altered by wildfire.

We set out to review the scientific literature on the response of nonnative plant species to wildfire. We were focused on an objective assessment of responses based on quantitative data. That is, we did not accept conclusions not well supported by data and statistical analysis. We intentionally did not use information from the grey literature; in fact, we used information only from quantitative studies published in journals, proceedings, books, and websites. We held the null hypothesis that there would be no response by nonnative species following wildfire, and looked for evidence that would allow one to reject this null hypothesis. Thus, we may have erred on the side of conservatism with regard to integrating nondata-based knowledge that often finds its way into conclusions. However, one can be certain that our assessment was as objective as possible. We hope this review will provide context for researchers to determine which issues need to be studied and how best to conduct those studies to further contribute to this important issue.

—Mara Johnson, Lisa Rew, Bruce Maxwell, and Steve Sutherland

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# INTRODUCTION

Nonnative invasive plants are one of the greatest threats to natural ecosystems worldwide (Vitousek et al. 1996). In fact, their spread has been described as “a raging biological wildfire” (Dewey et al. 1995). Disturbances tend to create conditions that are favorable for germination and establishment of plant species. Nonnative plant species are often characterized as weeds, exotics, and invasives that can exploit such conditions (Rejmánek 1996) and many of them possess traits such as rapid germination, high fecundity, and effective means of seed dispersal (Stohlgren et al. 1998).

Natural resource managers responding to a 1995–6 survey of 21 national forests in the Northern Rocky Mountains estimated that 2 million out of approximately 46 million acres of those forests had been invaded by nonnative plant species (Markin 2004). Respondents of a survey of all U.S. Fish and Wildlife Service Wilderness Areas identified invasive plants as a major problem in 12 out of the 68 responding areas (Tempel et al. 2004). In the western United States, numerous anthropogenic disturbances such as grazing, vehicle use, logging, and development have been linked to nonnative plant species introductions and population expansion, especially since Euro-American settlement (Kemp and Brooks 1998; Young et al. 1972). Wildfire, a natural disturbance in many areas of the western United States, has recently received considerable attention for its purportedly significant role in nonnative plant species introductions and subsequent invasions (Asher and Spurrer 1998; Asher et al. 2001; Mason 2002; Ririe 2001).

Wildfire is a natural process in many ecosystems of the western United States. Many native plants are adapted to fire; that is, they have characteristics that allow them to persist with repeated burning (Agee 1993; Wright and Bailey 1982). However, the impact, frequency, and scale of wildfires has changed in some ecosystems as a result of anthropogenic pres-

ence, manipulation, and management. Prior to Euro-American settlement, Native Americans used fire to alter vegetation in many areas of the West (Barrett and Arno 1982; Humphrey 1958; Samuels and Betancourt 1982). Euro-American settlement intensified disturbances through land management activities (e.g., logging and grazing) and fire suppression. Because of this, fuels have accumulated for the past century and have resulted in unusually large and severe wildland fires in certain ecosystems in recent years (USDA 2000). In 1999 wildfires burned 1.6 times the 10-year average of acres burned; in 2000 wildfires burned 2.3 times the 10-year average; in 2001 wildfires burned the 10-year average; and in 2002 wildfires burned two times the 10-year average (NIFC 2004). The Federal Wildland Fire Management Policy recognizes that fire is a critical natural process in many ecosystems and further contends that it should be reintroduced where it has been suppressed (Glickman and Babbitt 1995).

More recently, maintaining natural processes has been considered a critical part of preserving natural areas. Natural areas as defined for this review are those areas that are composed of predominantly native vegetation and have not been impacted or have been minimally impacted by anthropogenic disturbances, particularly post-European settlement disturbances. Wildfire is considered a natural process necessary for maintaining many natural ecosystems in the western United States. Maintaining native vegetation and the natural process of wildfire in these systems is complicated by the potential for nonnative plant species invasions following wildfire. In addition, suppressing wildfires in natural areas also represents a possible avenue for dispersion of nonnative plant species into natural areas (Ririe 2001).

A clearer understanding of the relationship between wildfire and responses of nonnative plant species in natural areas will assist land

managers in allocating limited resources to control or monitor for specific plant species following wildfires. In addition, clarifying the scope and gaps of research on responses of nonnative plant species to wildfire will help direct future research. In this document, we collate and synthesize the literature of nonnative plant species' responses to wildfire in the intermountain West. Additional information resulting from a web-based survey sent to land managers concerning wildfire and nonnative species management can be found at <http://landresources.montana.edu/rew/index.html> (Rew 2005).

### Previous Literature Reviews

Although there have been many case studies on the impact of fire on nonnative plant species, there have been few attempts at synthesizing these studies and examining the results to determine general patterns of fire effects on the establishment and expansion of nonnative plant species. These reviews have not typically separated effects of wildfire from prescribed fire and have not distinguished between natural areas and degraded areas. Galley and Wilson (2001) reviewed the relationship between fire (prescribed and wildfire) and the control and spread of invasive plant species throughout the United States by broad eco-regions. The Fire Effects Information System (FEIS) at the USDA Forest Service's Fire Sciences Laboratory in Missoula, Montana, is an online database that provides reviews of fire effects on 100 animal and 900 plant species – including 60 nonnative species (USDA 2003). Although these reviews provide species-specific responses to fire (prescribed and natural/wild), there has been no attempt at synthesizing these fire effects in a wider ecological framework. The

USDA Forest Service published a synthesis of fire effects on flora (Brown and Smith 2000) that describes fire regimes throughout the United States pre- and post- Euro-American settlement and fire autecology, but it focuses on native plant responses. The document includes limited information on nonnative plant species, primarily a section on *Bromus tectorum* L. (downy brome/cheatgrass)-dominated grasslands in the West.

There is considerable information on nonnative plant species' responses to fire, but many of these studies are on prescribed-fire effects. Although information from prescribed-fire studies is useful for understanding potential responses to wildfire, it must be used with caution if applied to wildfire situations because the two types of fire have generally different characteristics and potential effects on vegetation (Wright 1974). Wildfire is more likely to occur in very dry years when drought stress will compound the effects, and prescribed fires tend to be conducted in wet years (Wright 1974) and at a different time/season than wildfire. In addition, prescribed fires are conducted under certain weather and with particular fuel conditions and are typically smaller than wildfires (Wright and Bailey 1982). Information on wildfire and nonnative plant species is also available for areas that have a history of anthropogenic disturbances and an abundance of nonnative plant species (Young and Evans 1974, 1978; Young et al. 1976). However, nonnative plant species' responses in these areas may be very different from responses in natural areas (West and Hassan 1985).



# APPROACH AND METHODS

Every relevant experiment provides a piece of the puzzle to understanding the role of wildfire in the introduction and establishment of non-native plant species. The goal of this project was to try to put together that puzzle by synthesizing the current research and identifying key pieces that were missing. Following are the methods we used to find, evaluate, and integrate the research studies.

## Literature Search

In March 2001, the initial literature search was conducted in the U.S. Forest Service's Rocky Mountain Research Station using AGRICOLA, TreeCD, and EcoDisc databases to identify literature on fire and weeds published since 1990. Various combinations of the keywords "burn," "fire," "weed," "noxious," "invasive," "exotic," "alien," and the names of the 50 states were used, which resulted in 179 citations. In 2003 a search of the FEIS database was conducted regarding wildfire and nonnative plant species for each of the 60 nonnative plant species in that database, which includes articles from journals, books, conference proceedings, websites, and reports, as well as personal communications. In addition, online databases accessed through the Montana State University library (Biological Abstracts, Web of Science, AGRICOLA, and JSTOR) were searched using keywords "fire," "wildfire," "nonnative," "exotic," and "weed," as well as combinations and variations of these words. These databases covered publications from the 1970s and 1980s to present. Finally, we searched the bibliographies and cited literature in our selected publications to identify additional publications, typically older publications unavailable through the online databases.

## Literature Selection

Literature was included in this synthesis based on the following criteria:

1. Only responses to wildfires were used; responses to intentionally conducted prescribed fires were not included unless they were paired with wildfire responses in the same study. The prescribed fires we did not include were those that were intentionally lit under carefully prescribed conditions with certain management objectives. We did not find any "prescribed natural fires" in the relevant literature. When articles about prescribed fires are used, we clearly state this in the text.
2. Only "natural areas" were selected. These were defined as areas containing predominantly native vegetation and negligible anthropogenic disturbances. Preferably, information on the pre-fire plant species composition and documentation of anthropogenic disturbances were used to determine this; sometimes the author's qualitative assessment of the site was used. When nonnative species comprised the dominant vegetation (typically measured as percent cover) of a life form (forb, grass, shrub, and tree), it was not considered a natural area.
3. Nonnative plant species were defined as those not occurring before Euro-American settlement in each area. A species encroaching on areas where it did not occur in recent history, such as juniper growing in adjacent grasslands, was not defined as a nonnative plant species.
4. Only studies containing primary evidence or quantitative measures of plant responses to wildfire were included. These types of publications were primarily located in peer-reviewed documents. However, proceedings and conference papers were used if they presented research that contained quantitative measures. Opinion papers and other such publications were not used to synthesize plant species' responses although they were used in some of the introductory statements and were qualified as such.
5. Although there are many critical issues related to nonnative plant species' responses to wildfire, information on the key questions was specifically extracted and synthesized.

## Key Questions

1. Which nonnative plant species are most invasive (i.e., increasing in abundance and/or area) after wildfire in natural areas?
2. In areas of predominantly native vegetation, do existing nonnative plant populations increase or decrease after wildfire? Which existing nonnative plant populations increase or decrease after wildfire?
3. What plant characteristics are associated with the introduction or expansion of nonnative plants after wildfire?
4. Which wildfire characteristics – such as severity, size, and pattern – are associated with the establishment or expansion of nonnative plant species?
5. Which environmental characteristics – such as slope, aspect, and topographical position – are associated with the introduction or expansion of nonnative plant species after wildfire?
6. Which climatic variables – such as pre- and post-fire precipitation – contribute to the introduction or expansion of nonnative plant species after wildfire?
7. Do nonnative plant species that are introduced after wildfire persist and under which conditions?
8. Do wildfires contribute to the dominance of nonnative plant species in natural areas?
9. Which fire management activities, such as fire suppression and rehabilitation, contribute to the introduction, expansion, or decrease of nonnative plant species after wildfire?
10. Which factors are related to nonnative plant species' invasion and at what scales?

## Synthesis of Relevant Literature

D'Antonio (2000) attributed the difficulty in making generalizations about fire and nonnative plant relationships to the diversity of ecosystems subject to invasions and the variable role of natural fire in these systems as well as its variation in frequency. To better generalize the results of relevant studies, the information is separated into sections according to vegetation types based on the Forest and Range Environmental Studies. A brief introduction of the vegetation type, its general anthropogenic disturbance history, and pre- and post-European settlement fire regimes is provided. Subsequently, the research studies are synthesized in subsections that address the key questions.

Scientific names of nonnative plant species are used throughout, with the common name in parentheses at the first mention. The scientific names provided in the text are those used in the original manuscripts. Where the scientific names differ from the current nomenclature as provided by the USDA NRCS Plants Database (<http://plants.usda.gov>), the current nomenclature is also provided in parentheses. A table of all the nonnative plant species, with both scientific and common names, used in this review is provided in Appendix 1. Conversely, common names are used for native species with the scientific name provided at the first mention.

# RESULTS

## Southwestern Shrubsteppe (Desert Grasslands)

Southwestern shrubsteppe, also called desert grasslands, occurs in southeastern Arizona, south-central and southwestern New Mexico, southwestern Texas, and into Mexico. Precipitation ranges from 12 to 18 inches in the west to 20 to 30 inches in the east and occurs mainly during two separate periods, the summer and winter (Humphrey 1974; Paysen et al. 2000). The most common grass genera are *Bouteloua*, *Hilaria*, and *Aristida* (Humphrey 1974). Although dominated by grasses, these areas also contain numerous woody species including yucca (*Yucca* spp.), mesquite (*Prosopis juliflora*), and creosotebush (*Larrea tridentata*) (Humphrey 1974; Paysen et al. 2000).

Historical records are the only source of information on the pre-European fire regime since evidence of fires in the form of fire scars does not persist in grasslands as it does in forests (Humphrey 1974). Various estimates of the pre-European-settlement fire frequency, or mean fire interval (MFI), have been given for these grasslands. Wright (1980) estimated 10 years for southeastern Arizona desert grasslands, although he questioned that estimate in the same publication. Humphrey (1974) reviewed several historical records documenting fires in these desert grasslands and concluded that fires were merely “frequent” prior to European settlement, whereas around the time of his publication in 1974, fires were only “occasional.” Paysen et al. (2000) suggested that fire could occur “in any given year” in grasslands if fuels were dry enough.

Euro-American settlement saw the commencement of active fire suppression in these grasslands (Paysen et al. 2000). There is general agreement that shrubs have increased in density and invaded new areas in desert grasslands over the last century (Bahre and Shelton 1993; Hastings and Turner 1965; Humphrey 1974; Wright and Bailey 1982). However, the factors

enhancing shrub encroachment are not agreed upon (see Bahre and Shelton 1993). Some authors (Bahre and Shelton 1993; Humphrey 1974; Wright 1980) concluded that frequent fires occurred in the desert grasslands prior to livestock grazing. They further theorized that overstocking of the rangelands, which occurred mainly in the late 1800s, resulted in the reduction of area and intensity of grassland fires, thus resulting in the encroachment of shrubs into these grasslands. Harris (1966) attributed shrub encroachment to grazing and fire suppression, which was accentuated by climatic fluctuations. Bahre and Shelton (1993) concluded that there was no clear relationship between mesquite increases and precipitation variations, and suggested that the probable cause of encroachment was livestock grazing and/or fire suppression. Wright (1980) concluded that vegetation changes from predominantly grass to shrub since the beginning of the 20th century were caused by several factors related to increased livestock grazing. However, Hastings and Turner (1965) rejected the theory that wildfires historically occurred over large areas of desert grassland and that fire suppression was correlated with shrub encroachment. They argued that changes in climatic factors were responsible for the changes in shrub vegetation.

## Disturbance History

Livestock grazing in the southwestern states dates back to the 1500s (Humphrey 1958). Seeding of *Eragrostis* spp. (*Eragrostis lehmanniana* and *Eragrostis curvula* var. *conferta*) (Bock and Bock 1992) occurred extensively in the Southwest semi-desert during the mid-20th century (Cable 1973). Thus, it is not surprising that natural grassland sites that have recorded nonnative plant species' responses to wildfire have adjacent areas of seeded *Eragrostis* spp. as well as a history of grazing (Bock and Bock 1992; Cable 1965). Cable's (1965) study of native black grama (*Bouteloua eriopoda*)

plots and adjacent *Eragrostis* spp. vegetation was within a fenced enclosure that had not been grazed by cattle for “many years.” Bock and Bock (1992) studied vegetation responses to wildfire in two types of sites designated “exotic grassland” and “native grassland.” The exotic grassland sites had previously been seeded with *Eragrostis* spp. for erosion control and forage production though the area of the study had been ungrazed for nearly two decades prior to the wildfire.

### **Time Since Fire**

Only short-term first year (Cable 1965) and four-year post-fire (Bock and Bock 1992) responses to wildfire have been studied in native desert grasslands. Bock and Bock (1992) found that after four years, most of the species had reached their pre-burn abundances.

### **Response of Nonnative Plant Species**

Very few studies have documented the response of nonnative plant species to wildfire in natural areas of the desert grasslands, perhaps because there has been more interest in the use of fire to decrease shrubs and improve range forage (Cable 1967; Humphrey and Everson 1951; White 1969). As a result of such human manipulation in the late 19th and early 20th centuries, nonnative plant species have invaded desert grasslands either unintentionally or through planned introductions, in particular the seeding of *Eragrostis* spp. Anable et al. (1992) documented the spread of *Eragrostis* spp. for 35 years (1954 to 1989) at the Santa Rita Experimental Range. By the end of the study, *Eragrostis* spp. occurred on >85% of unseeded sampled plots; disturbance was not necessary for its increase. Cattle graze selectively on native grasses which may further favor the invasion of *Eragrostis* spp. (Cox et al. 1990). Managers regard this nonnative grass positively or negatively depending on management goals; it stabilizes soils in disturbed areas but it is not palatable to cattle and is a threat to native grasslands (Ruyle et al. 1988).

In a review of studies conducted throughout the Americas on nonnative grasses introduced from Africa, Williams and Baruch (2000) con-

cluded that these grasses are generally stimulated by and promote fire and in many cases respond more positively (e.g., have greater regrowth) than native species. Cox and Ruyle (1986) state that *Eragrostis* spp. is adapted to fire and has invaded more than 200,000 hectares of southeastern Arizona grasslands. In the quantitative studies found in this review, the response of nonnative plant species to wildfire in native grasslands was far from conclusive because of a lack of studies. The most observed nonnative species, *Eragrostis* spp., showed an initial increase in both native and nonnative dominated stands (Cable 1965), as well as an initial decrease followed by a slight increase then slight decline through four years of post-fire observation in stands dominated by native grass (Bock and Bock 1992).

Bock and Bock (1992) studied 25 native and 25 nonnative grassland plots in Santa Cruz County, Arizona, for two years (1984 and 1985) before a wildfire burned nearly half of the plots in each group in 1987. The native grassland plots were composed of grasses, shrubs, and scattered mesquite trees. Nearby nonnative grass plots were predominantly composed of *Eragrostis* spp. (*E. lehmanniana* and *E. curvula* var. *conferta*) that had been seeded 40 years previously. The authors continued to sample the plots for four years following the July 1987 wildfire. Fire severity was not measured but the authors stated that almost all aboveground vegetation was consumed by the fire. Four years after the fire, nearly all the vegetation had returned to pre-fire abundances (% cover). They compared measurements from burned and unburned plots with repeated measures analysis of variance after first subtracting the pre-burn values from each post-fire year. Very few nonnative grasses were in the native grass plots prior to the wildfire, but those that were “showed little response to burning.” *E. curvula* var. *conferta*, which was the most common nonnative grass on the study sites, declined initially after the fire then slightly increased from 1988 to 1989 but decreased somewhat in 1990. However, because it was nearly absent on the unburned plots the authors stated that it prevented statistical comparisons (Table 1).

Year	Burned	Unburned
1984 (pre-fire)	0.91 (1.70)	0
1987	0.18 (0.60)	0
1988	1.36 (3.04)	0
1989	3.73 (9.28)	0.21 (0.80)
1990	2.73 (6.13)	0

**Table 1.** Mean percent canopy of *Eragrostis curvula* var. *conferta* (standard deviation in parentheses) in unburned and burned plots pre-fire and four years following a 1987 fire. Results are from repeated measures analysis of variance, from Bock and Bock (1992).

Two nonnative forbs were also recorded on the native grassland sites – *Sida procumbens* (now called *Sida abutilifolia* [spreading fanpetals]) and *Ipomoea coccinioides*. (*I. coccinodes* was cited in the text, but as this species does not exist it is presumed to be *I. coccinea* [redstar]). The authors described these as species that “readily invade” disturbed areas. However, the effect of wildfire was not significant, although year was, for both species. The interaction between year and burn was significant for both species in native grasslands ( $P < 0.01$ ). The authors concluded that prescribed fire would not be a useful tool for controlling these nonnative grasses, although wildfire would not likely result in the displacement of native species (Bock and Bock 1992).

Cable (1965) observed the response of *Eragrostis* spp., the native grass black grama, and mesquite to an “accidental fire” on June 28, 1963, that killed most of the top growth of all of the grasses at the Santa Rita Experimental Range 40 miles south of Tucson, Arizona. Four plots were located immediately after the fire in each of two sites, one area dominated by *Eragrostis* spp. and the other dominated by a mix of native grasses including black grama. The pre-fire density of *Eragrostis* spp. for the *Eragrostis* spp. plots was 2.67 plants/ft<sup>2</sup> and the pre-fire density of black grama in the black grama plots was 3.59 plants/ft<sup>2</sup>. At the end of the first season post-fire, less than 2% of *Eragrostis* spp. resprouted compared with 10% of the black grama. However, no new seedlings of black grama were observed on any plots, whereas *Eragrostis* spp. seedlings were found

on all plots. New *Eragrostis* spp. plant density was 13.23 plants/ft<sup>2</sup> in the *Eragrostis* spp. plots and 17.04 plants/ft<sup>2</sup> in the black grama plots. Statistical analysis of these data was not performed.

### Conclusions

- Very little information is available on the response of nonnative plant species to wildfire in the natural areas of desert grasslands of the southwestern United States.
- *Eragrostis* spp. (lovegrasses) have received most of the attention in studies on nonnative plant species in desert grasslands. These species were intentionally seeded for erosion control and forage production in many areas during the 20th century.
- Short-term responses of nonnative grasses to wildfire in desert grasslands has shown both initial increases and decreases in the metric used, and one study showed a slight increase after four years post-wildfire.

### Chaparral-Mountain Shrub

Chaparral is the general term used to describe the sclerophyllous shrublands predominantly found in California, but also in Arizona and parts of the Rocky Mountains. Chaparral types are generally referred to as “evergreen chaparral” in California, “coastal sage scrub” on the West/Pacific coast, “petran chaparral” in the Rocky Mountains, and “interior chaparral” of Arizona and northern Mexico (Keeley and Keeley 1988). Few plant species are common to both the California chaparral and the petran chaparral (Hanes 1971).

California chaparral has received the most attention in discussions of chaparral types (Biswell 1974; Keeley and Keeley 1988; Sweeney 1956). Several different shrub species occur in the California chaparral shrublands depending on the biophysical condition and fire history of the site (Biswell 1974; Keeley and Keeley 1988). Chaparral occurs as the dominant vegetation type in many areas, but it is also found intermixed with adjacent forests, grasslands, and oak woodlands (Hanes 1971). Information on specific species and distributions can be found in Keeley and Keeley (1988). In California, evergreen chaparral



occurs in an area characterized by a Mediterranean climate of wet winters and hot, dry summers (Biswell 1974; Keeley and Keeley 1988), and the most common chaparral species is chamise (*Adenostoma fasciculatum*). This species and the other shrubs typically form dense, contiguous stands with little understory vegetation in mature stands (Hanes 1971; Keeley and Keeley 1988). Further north in California, chaparral is less dense and becomes more restricted to drier sites (Keeley and Keeley 1988).

The extensive Native American populations in California likely utilized wildfire to convert shrublands to grasslands prior to Euro-American settlement and this practice had been continued by Euro-American settlers (Keeley 2002). The distribution and composition of California chaparral has been affected by mining, logging, grazing, farming, and Euro-American settlement (Hanes 1971; Keeley and Fotheringham 2001). For example, the native vegetation of the East Bay Hills in the San Francisco Bay Area changed into nonnative tree and shrub species over a period of 50 years starting in the 1880s (Rowntree 1994).

### **Fire Regime**

Chaparral shrublands are characterized by frequent stand-replacing fires and are considered to be a fire-adapted system (Biswell 1974; Hanes 1971). Following wildfire, herbaceous species dominate an area, peaking in abundance one to five years after the fire, until the shrubs regrow and the canopy closes. Chaparral shrublands consist of species that revegetate from seed and resprout from belowground material. Some species will resprout from charred stumps and others have seeds that have long-term viability and resistance to fire (Biswell 1974; Hanes 1971; Keeley and Keeley 1988). Extensive information on the effects of fire on chaparral can be found in Biswell (1974).

Fires probably have occurred in California shrublands for at least 100,000 years (Jepson 1925, as cited in Biswell 1974). The exact MFI for chaparral shrublands is unknown, but the range of fire-free periods has been estimated at

less than five to more than 100 years. Biswell (1974) suggested that wildfires typically occurred in chaparral shrublands approximately every 15 years. Sweeney (1956) estimated that fires typically recurred every 20 to 25 years. Wright and Bailey (1982) estimated that large fires (5,000 acres or greater) occurred every 20 to 40 years in California.

Fires in these shrublands have been extensively suppressed during the mid-20th century (Biswell 1974; Hanes 1971). However, increased fire ignitions have occurred as a result of the expanding human population within the chaparral range (Keeley and Keeley 1988). It has been suggested that suppression activities may have balanced out the increased occurrence of human ignitions resulting in little change in the fire regime of chaparral (Keeley and Fotheringham 2001; Paysen et al. 2000). More regional studies have highlighted subtle differences in fire frequencies. A study of the regional fire regimes of San Diego County, California, concluded that the rate of burning in chaparral vegetation had remained stable in the 20th century but had increased in the lower-elevation coastal sage scrub stands (Wells et al. 2004). However, Minnich (1983) and Minnich and Hong Chou (1997) concluded that fire suppression had resulted in fewer and larger fires in San Diego County, which departed from the natural fire regime of frequent, small fires.

The response of native and nonnative plant species to wildfire in chaparral has been the subject of research since the mid-20th century (Sampson 1944; Sweeney 1956) and was recently reviewed by Keeley (2001). Nearly 25% of the flora in California is nonnative (Hickman 1993). Nonnative species are more dominant in terms of number of species and percent cover in lower elevations of California (Keeley 2001). Many of the native plants are dependent upon disturbance such as wildfire for regeneration. However, disturbance of these closed-canopy shrublands also results in invasion by Mediterranean annuals, which also respond favorably to disturbance (Keeley 2001). In many cases a nonnative seed source

is in close proximity to chaparral areas. Many areas of burned chaparral are often reseeded with grasses, commonly *Lolium multiflorum* (annual ryegrass), to prevent erosion or improve livestock grazing (Biswell 1974), further increasing the occurrence and density of non-native plant species.

### **Fire Frequency and Disturbance History**

It was difficult to determine how “natural” many of the chaparral areas were before burning because of a lack of information about anthropogenic disturbances and pre-fire vegetation in a region that has been extensively utilized by humans and invaded by nonnative plant species.

Keeley (2001) concluded that frequency of disturbance may determine which species benefit from or are harmed by the disturbance. He stated that high fire frequency has contributed to the conversion of the native shrublands and woodlands of California to annual grasslands dominated by nonnative grasses and forbs. Studies have shown that although native chaparral species benefit from frequent fire, nonnative annuals have the potential to dominate sites with higher fire frequencies (Haidinger and Keeley 1993; Zedler et al. 1983). However, the role played by adjacent degraded areas and anthropogenic disturbances – such as post-wildfire seeding (Zedler et al. 1983) – in the conversion of native to predominantly nonnative vegetation is unclear.

Haidinger and Keeley (1993) studied the effects of multiple fires on chaparral sites in the Verdugo Mountains of southern California. No information was available on the disturbance history of the sites other than fire history and fire severity. Relative species composition (%) and density of individual species were used to evaluate plant responses to wildfire. The authors concluded that generally the percentage of nonnative species increased in the sites with more frequent fires. They also observed that both the percentage of annuals and nonnative species increased with increasing fire frequency. *Brassica nigra* (black mustard) was significantly more dense (number/ha at  $P < 0.05$ ,  $n = 10$ )

on the sites burned in years 1, 4, and 6 than on any of the other sites. *Bromus* spp. were significantly denser on the sites burned in years 1, 4, and 6 than on the sites burned in years 1 and 6 or 4 and 6, but their density was not significantly different on these sites than on the site burned in year 6 only. In contrast, *Schismus barbatus* (common Mediterranean grass) was not densest on the more frequently burned sites; it was significantly denser on the site burned in years 1 and 6 than on any of the other sites. The authors concluded that this study supports the theory that high fire frequency could alter the dominant vegetation in these California systems from shrubs to herbs.

Zedler et al. (1983) studied the response of California chaparral and coastal scrub to multiple fires on an area that burned once in 1979 and an adjacent site that burned in 1979 and again in 1980 in San Diego County in southern California. Anthropogenic disturbances played a key role in this study as the 1979 wildfire was started by an arsonist. The site was then seeded with a nonnative grass, *L. multiflorum*, to control erosion. Part of the site burned again in 1980. Information on pre-fire occurrence of native and nonnative plant species was not available. Density and frequency of shrubs and shrub seedlings were recorded in 1981 at both sites and the data quantitatively analyzed. Frequency of native shrub species did not significantly change following the first fire, but substantial declines were noted in many shrub species after the second fire in 1980. In terms of nonnative species, the site that burned only in the 1979 fire had high abundance of *Bromus rubens* (red brome), *Avena* spp., and *Erodium cicutarium* (redstem stork's bill) compared to the part of the site that reburned in 1980. No quantitative information was provided for these species. The authors concluded that increased fire frequency and the introduction of nonnative annual grasses contributed to an abrupt change in vegetation composition.

### **Fire Severity**

The effects of fire severity and intensity have both been discussed in relation to nonnative plant responses to chaparral wildfire. How-

ever, the definition used for these terms is not consistent and the effects of these parameters are not conclusive (Christensen and Muller 1975; Safford and Harrison 2004; Tyler 1995). Tyler (1995) studied a burned and adjacent unburned ridge of chaparral in the Santa Ynez Mountains northwest of Santa Barbara, California. Areas that had been cleared of shrubs prior to the wildfire were considered to be low-intensity sites and those sites that contained mature shrubs prior to the fire were defined as high-intensity sites. The responses of subgroups of vegetation, shrubs, subshrubs, perennial herbs, and annual herbs were recorded although species-specific responses were not. Only three out of 17 annual herbs were nonnative species – *Bromus mollis* (*Bromus hordeaceus* ssp. *hordeaceus* [soft brome]), *Sonchus* spp. (sowthistle), and *Silene gallica* (common catchfly). The author observed that fire intensity was significantly related to many of the subgroups, although never to perennial herbs, in the year following the fire.

Safford and Harrison (2004) studied the effects of an arson-caused wildfire in 1999 for three subsequent years in serpentine and sandstone chaparral near the junction of Napa, Lake, and Yolo counties in California. Fire severity was assessed by measuring the stem diameter of four randomly chosen stems of the dominant shrub species, as well as by estimating shrub mortality. The results showed that mean and maximum fire severity was greater in sandstone than in serpentine soils. However, heterogeneity in mean fire severity was higher in serpentine soils. Nonnative species richness was significantly higher on burned than on unburned sites the year following wildfire ( $P < 0.0001$ ). It was also higher on sandstone soils ( $P < 0.05$ ).

### **Response of Nonnative Plant Species**

Responses of nonnative plant species to wildfire may vary by biophysical variables such as aspect (Guo 2001), soil type and the productivity of the area (Safford and Harrison 2004), and precipitation patterns (Keeley et al. 1981). In addition, the time since fire will affect the abundance and density of nonnative

plant species. Generally nonnative species were rare the first year following fire (Haidinger and Keeley 1993; Horton and Kraebel 1955; Keeley and Keeley 1981; Sweeney 1956; Tyler 1995), but peaked within the first four years following fire (Horton and Kraebel 1955; Safford and Harrison 2004; Sweeney 1956), after which nonnative species declined (Horton and Kraebel 1955; Sweeney 1956).

Plant responses to seven wildfires that occurred over a period of 17 years were collected on chaparral sites in the San Bernardino and San Gabriel Mountains of southern California between 1927 and 1952 (Horton and Kraebel 1955). Permanent plots were nonrandomly placed in the areas burned by wildfire and sampled annually for the first several years after burning and then at 2- to 5-year intervals. At first, total crown density was recorded; later, density by species was also recorded. Occurrence (average number of seedlings per milacre [1/1000th of an acre]) of herbaceous species was recorded for 1, 2, 3, 4, 5, 7, 10, 15, 20, and 25 years after burning. Four nonnative species were recorded over the course of the study, all of them annual herbs and grasses: *B. nigra*, *B. rubens*, *B. tectorum*, and *Festuca megalura* (*Vulpia myuros* [rat-tail fescue]). *B. rubens*, *B. tectorum*, and *F. megalura* were present along trails, firebreaks, and openings in the area before the fires. These species reached peak abundance 3 to 5 years following the fire and then decreased as the shrub cover closed the canopy. *B. nigra* was seeded at two of the sites for erosion control but only established on one site where it peaked in the second year and was absent by the fifth. No nonnative species occurred on the 20-year post-burn site and only one *B. nigra* seedling occurred on the 25-year post-burn site. *B. rubens* had the highest density of any nonnative species at any point in time after wildfire, but only on one site, where it peaked at 423.5 seedlings/milacre four years after burning, decreased to 30.5 seedlings/milacre seven years post-burn, and was absent by 20 years post-burn. Also, on one site *B. tectorum* peaked the fourth year following fire with 202.0 seedlings/milacre, but was absent by the 15th year. The nonnative perennial or biennial



*Brassica incana* (*Hirschfeldia incana* [short-pod mustard]), although not listed in the occurrence table, was stated to have appeared after a 1942 burn at one of the sites, after which it became common along trails, firebreaks, and other open areas.

Sweeney (1956) studied herbaceous plant succession on 10 sites following wildfire in Lake County north of San Francisco, California. All sites were on lower slopes in mixed chaparral, had comparable habitat conditions and similar aspects, but were on six different soil series. Sweeney observed the following patterns in relation to the abundance of nonnative species post-fire: *B. tectorum* was rare one year post-burn, *B. mollis* ranged from rare to common one year post-burn, and *B. rubens* and *Bromus rigidus* (ripgut brome) were common one year post-burn. In subsequent years, *B. mollis* and *B. rubens* increased in abundance 2, 3, and 4 years after burns. *B. tectorum* became common locally 2 to 6 years after burns, although it was found the least often of the *Bromus* spp. (on only three sites). Only *B. rigidus* decreased after the first year. All *Bromus* spp. were common to abundant on adjacent roads and areas near the burn sites. Other nonnative species included *Aira caryophyllea* (silver hairgrass) and *Avena fatua* (wild oats), which were rare one year after burns but became more common through year four after fire. *A. caryophyllea* and *Draba verna* (spring draba) were common on open sites adjacent to the burns, whereas *Sisymbrium altissimum* (tumble mustard) was common on open grassy and disturbed sites adjacent to the burns. *D. verna* was also present but rare one year post-burn. *Sanguisorba officinalis* (official burnet) was found on only one burn site and was rare at that location. *Filago gallica* (narrowleaf cottonrose) was common, *E. cicutarium* and *Centaurea melitensis* (Maltese starthistle) were rare to common, and *Anagallis arvensis* (scarlet pimpernel) was rare one year post-burn, but all became abundant over time. *F. gallica*, *E. cicutarium*, *C. melitensis*, and *A. arvensis* species were abundant on open and disturbed sites adjacent to the burns. *Anthemis cotula* (stinking chamomile) was rare to frequent one year post-burn and common

on older burns. It was also common on open sites adjacent to the burns.

Christensen and Muller (1975) studied the effects of wildfire in chaparral in the Santa Ynez Mountains near Santa Barbara, California, for 18 months. They located adjacent plots of similar slope and aspect in burned and unburned sites. The focus of the research was to assess the effects of several factors including soil moisture, texture, chemistry, light, bacteria, and fungi on the dominant shrub chamise (*Adenostoma fasciculatum*) after wildfire, but some information on nonnative plant species was also presented. The sites were predominantly covered with chamise prior to the wildfire and had not burned in the preceding 40 years. However, the area was subject to several anthropogenic disturbances and nonnative plant species were most common in heavily disturbed areas such as alongside roads that ran through the burn area. There were also nonnative plant species in the adjacent grasslands and on associated roadsides. Species were listed by their occurrence under shrub cover or in artificial clearings created in the unburned sites for the first and second year following fire. The following annual nonnative species appeared in both the first and second years following fire: *B. mollis*, *B. rubens*, *C. melitensis*, *E. cicutarium*, and *L. multiflorum*. *A. fatua* and *A. arvensis* occurred only in the second year following fire. *Lactuca serriola* (prickly lettuce) and *Senecio vulgaris* (old-man-in-the-Spring) occurred both years following fire as well as in artificial clearings. Some nonnative species such as *S. vulgaris*, *C. melitensis*, and *L. serriola* were described as abundant in nearby roadsides and grasslands. However, these species did not occur under the unburned canopy of the chaparral and some of them appeared to be negatively affected by an allelopathic mechanism of the shrubs.

Keeley et al. (1981) studied four years of herbaceous plant succession in southern California chaparral following a wildfire in San Diego County. The responses of four herbaceous groups were studied post-wildfire: "generalized herbaceous perennials" that

were present before and after fire, “generalized annuals” that occurred in the openings before fire and peaked in population size a few years after the fire, “fire annuals” that mainly occurred one year after fire, and “fire perennials” that were rare before fire, established the first year following fire, and peaked three or four years later. Two types of studies were conducted – one with short-term intensive information on post-fire responses and the other on a broader range of areas and time since wildfire. All sites were near or adjacent to roads. Intensive study sites (ISS) were located on the four cardinal aspects at three different elevations (500 m, 1000 m, and 1670 m) after the 1970 burn. All of the ISS had been seeded with nonnative grass, *L. multiflorum*, post-fire to prevent erosion which was reported to have a negative effect on native plant cover, especially fire annuals. However, *L. multiflorum* decreased by 75% in relative dominance in the second year and by the fourth year following fire was absent from the two lowest-elevation sites. Changes in herbaceous cover in the ISS may have been related to different precipitation patterns at the different sites. Nonnative species such as *Bromus* spp. and *E. cicutarium* were usually present only the first year following fire in the ISS.

The following nonnative plant species occurred on at least one site post-wildfire: *Avena barbata* (slender oat), *B. mollis*, *B. rubens*, *B. tectorum*, *Centaurea cyanus* (garden cornflower), *C. melitensis*, *Ehrharta erecta* (panic veldtgrass), *E. cicutarium*, *Hypochaeris glabra* (smooth catsear), *L. multiflorum*, and *Trifolium repens* (white clover). Only a few species that were not seeded had greater than 0.1% ground surface cover, but only on Site 1 for the first year after wildfire (*B. rubens* and *C. cyanus*) or second year after wildfire (*B. mollis*). The percent cover of native species by site and years since wildfire are given in Table 2; nonnatives make up the difference.

<b>Site and Years Since Fire</b>	<b>% Native Species</b>	<b>% Native Cover</b>
<b>Alpine Site (500 m):</b>		
Year 1	92	32
Year 2	80	87
Year 3	91	66
Year 4	100	100
<b>Boulder Creek Site (1000 m):</b>		
Year 1	96	67
Year 2	71	82
Year 3	89	81
Year 4	91	97
<b>Kitchen Creek Site (1670m):</b>		
Year 1	92	92
Year 2	84	92
Year 3	85	76
Year 4	85	81

**Table 2.** Percent (%) of native species and native species cover at three sites of different elevations for 1 to 4 years following wildfire, from Keeley et al. (1981)

To assess the effects of wildfire over a greater period of time and across a broader area, a number of sites were selected within 1 to 16 years post-fire (Keeley and Keeley 1981). These were termed the extensive study sites (ESS). On these study sites, shrub cover was near pre-fire levels by the fifth year post-fire. The 9-year post-fire ESS had been heavily grazed and had a higher herbaceous cover than other older sites; the herbaceous cover included *B. rubens* and *E. cicutarium* as well as native grasses.

Tyler (1995) studied a burned and adjacent unburned ridge of chaparral in the Santa Ynez Mountains northwest of Santa Barbara, California. The ridges were similar in pre-fire vegetation, topography, soil type, and fire history. Previous to the 1990 fire that burned one ridge, both sites had last burned in 1964. The study focused on the response of four plant subgroups (shrubs, subshrubs, perennial herbs, and annual herbs) to fire intensity and herbivory. Areas that had been cleared of shrubs prior to the wildfire were considered to be low-intensity sites while those sites that contained mature shrubs prior to the

fire were defined as high-intensity sites. Sites were caged to create controls for responses to herbivory. The results were presented only for the subgroups and indicated that perennial herbs were not significantly affected by fire intensity but that the emergence of subshrubs and herbs was higher in burned areas but lower in the highest-intensity areas. The density (maximum number observed per 0.25 m<sup>2</sup>) was listed for all species. Only three of the 17 annual herbs listed by species were nonnative species and all had relatively low densities on all sites. The nonnative species listed were: *B. mollis* at five plants/0.25 m<sup>2</sup> on the burned site and absent on the unburned site; *S. gallica* at three plants/0.25 m<sup>2</sup> on the burned site and one plant/0.25 m<sup>2</sup> on the unburned site; and *Sonchus* spp. at 1 plant/0.25 m<sup>2</sup> on both the burned site and unburned site.

Guo (2001) observed the temporal variations in species richness, cover, and biomass for four years following a fire on the Stunt Ranch on the Santa Monica Mountains Reserve in southern California. The pre-fire vegetation was described as nearly 100% cover of evergreen chaparral species, which varied in composition by aspect. Permanent plots were sampled within the burn area for four seasons following the wildfire, two on south-facing slopes and one on a north-facing slope. After the wildfire, all of the nonnative species recorded were annuals. Nine species of nonnative annuals were found on the north-facing slope and six on the south-facing slopes over the course of the study. *Bromus diandrus* (*ripgut brome*) and *Vulpia myuros* (rat-tail fescue) were found on both aspects and were the most common nonnatives. *A. barbata*, *B. nigra*, and *Galium aparine* (stickywilly) occurred only on the north-facing slope. *L. serriola* and *Melilotus indica* (sour clover) occurred only on the south-facing slopes. The number of nonnative plant species on the north-facing slope peaked at approximately 10 the second year following fire and then declined to <5 by the fourth year. Guo (2001) suggested that the decline in nonnative plant species was the result of a large increase in native species biomass in the third year that suppressed nonnative plant growth.

The number of nonnative plant species on south-facing slopes rose from <5 the first year to 5 to 10 species the second year post-fire and remained at that level through the fourth year of the study. The author concluded that the effects of the nonnative plant species on the community were not yet apparent.

Safford and Harrison's (2004) study on the effects of an arson-caused wildfire in 1999 found that chaparral vegetation was more productive on the sandstone than on serpentine soils. Forty pairs of burned and unburned plots were studied. The results indicated that diversity of both native and nonnative plant species increased more on sandstone than serpentine chaparral by plot and across the entire study. In the mature stands on both soils there were few nonnative plant species. Nonnative species richness was significantly higher on the burned than on unburned sites the first year following wildfire ( $P < 0.0001$ ); it was also higher on sandstone soils ( $P < 0.05$ ). The first year following fire a total of 33 nonnative plant species were found on both sandstone and serpentine chaparral. The total number of nonnative plant species significantly increased after fire from seven in the unburned to 22 on burned sites in the serpentine chaparral and from 9 to 30, respectively, in the sandstone chaparral. The number of species on the two burned sites was also significantly different between the serpentine and sandstone sites ( $P < 0.05$ ). Post-fire recovery in serpentine chaparral was slower than in sandstone chaparral.

### **Fire Management Activities**

Keeley's (2001) review concluded that several aspects of fire management have contributed to the invasion of nonnative plant species, including the inability to suppress fires ignited by the increasing human population, pre-fire fuel manipulations, fuel breaks, and the use of nonnative species for seeding in fire rehabilitation programs in Mediterranean California vegetation. Studies of vegetation responses to wildfire include areas that have been seeded after wildfire for erosion control (Horton and Kraebel 1955; Keeley et al. 1981; Zedler et al. 1983), although some studies avoided selecting

such areas for study plots (Christensen and Muller 1975). Seeding after chaparral fires is a common practice to prevent erosion, but it is difficult to determine whether study areas have or have not been seeded unless this information is specifically stated in the experimental design (Safford and Harrison 2004). In addition, the type of wildfire varies – several studies were conducted after wildfires that were initiated by humans as opposed to “natural” ignitions of lightning strikes (Safford and Harrison 2004; Zedler et al. 1983). Other disturbances studied included pre-fire fuel treatments (Tyler 1995), native herbivory (Tyler, 1995 #201), or livestock grazing (Keeley and Keeley 1981). Keeley et al. (1981) noted that one of their sites had been heavily grazed by cattle and the vegetation response to wildfire was markedly different from other sites that had not been grazed by cattle.

Possibly because the chaparral shrublands have been heavily utilized by humans for hundreds of years and are often adjacent to disturbed lands, numerous study sites may be affected by their proximity to disturbed areas. Horton and Kraebel (1955) observed that the nonnative perennial or biennial *B. incana* appeared after a 1942 burn on one of their sites and became common along trails, firebreaks, and other open areas in the chaparral after that. In addition, *B. rubens*, *B. tectorum*, and *F. megalura* were present in the area before the fires along trails, firebreaks, and openings. Sweeney (1956) observed that most of the nonnative plant species present at some point following a wildfire in chaparral were also common to abundant on open and disturbed sites adjacent to the burns. Christensen and Muller (1975) stated that nonnative plant species were most common in heavily disturbed areas, such as alongside roads that ran through their burned sites and in adjacent grasslands. Thus, in many of the studies the interaction or additional affect of different disturbances, plus the proximity to nonnative species propagules makes determining the effect of wildfire on the vegetation composition difficult to quantify and predict with confidence.

### Conclusions

- A frequent fire return interval is necessary for native chaparral species to survive and reproduce, but too frequent fires may favor nonnative annuals. However, the effect of fire return interval is difficult to isolate from other site variables and disturbances.
- Nonnative and native plant species appear to respond differently to fire on more productive sandstone chaparral sites than on serpentine chaparral sites.
- Numerous biophysical variables such as precipitation, aspect, and soil potentially affect the response of nonnative plant species to wildfire in chaparral.
- Numerous fire management activities may directly or indirectly introduce nonnative plant species into chaparral.
- Nonnative plant species may potentially decline following wildfire as the shrub canopy closes.
- It is difficult to determine whether research on responses of nonnative plant species to wildfire has been conducted in natural areas unless the authors specifically state such. Many chaparral sites are adjacent to anthropogenic disturbances, which are often impacted by nonnative plant species, thus providing a seed source.
- Much of the research on responses of nonnative plant species to wildfire has been conducted in southern California chamise chaparral. More data are required on the responses of nonnatives post-wildfire over the entire range of chaparral vegetation in New Mexico, Arizona, and the Rocky Mountains.

### Desert Shrublands

Desert shrublands occur in the four major deserts of the western United States: the Great Basin or Sagebrush Desert, the Mojave Desert, the Sonoran Desert, and the Chihuahuan Desert. Although the deserts are considered floristically distinct, they are all arid and have low-growing woody plants. Similar species are found in the latter three deserts (Humphrey 1974).

Although different vegetation types within the desert shrublands do not have distinct boundaries, Paysen (2000) divides the desert shrublands according to the Forest and Range Environmental Studies (FRES) ecosystems



(Paysen et al. 2000). These groups are Great Basin sagebrush, blackbrush, saltbush-grease-wood, creosote bush, Joshua tree, creosote-bursage, paloverde-cactus shrub, southwestern shrubsteppe (also called desert grasslands), and chaparral-mountain shrub. For descriptions of these types and details on their pre- and post-Euro-American settlement fire regimes, refer to Paysen (2000).

Most of the information about responses of nonnative plant species to wildfire in desert shrubland types comes from studies on sagebrush vegetation types, including higher elevation sites (Cook et al. 1994; Hosten and West 1994; Humphrey 1984; Ratzlaff and Anderson 1995; West and Hassan 1985; West and Yorks 2002; Whisenant 1990). Other studies on desert shrubland types are predominantly on blackbrush vegetation of the transition zone between the Great Basin and Mojave Deserts (Beatley 1966; Brooks and Matchett 2003; Callison et al. 1985) and creosote bush vegetation types in the Mojave and Sonoran Deserts (Brown and Minnich 1986; Cave and Patten 1984; O'Leary and Minnich 1981; Rogers and Steele 1980). Because of the abundance of information on sagebrush and its broad environmental range, sagebrush desert shrublands will be discussed, then other desert shrubland types in the Mojave, Sonoran, and Chihuahuan Deserts will be reviewed in the section *Other Desert Shrublands*.

### **Sagebrush Desert Shrublands**

The Great Basin Desert includes Nevada, southern Oregon, southern Idaho, southwestern Wyoming, western and southeastern Utah, and parts of northern Arizona. The dominant overstory species are big sagebrush (*Artemisia tridentata*) and/or shadscale (*Atriplex confertifolia*) (Humphrey 1974; MacMahon 1988). It is considered a "cold desert," one in which the majority of precipitation comes in the form of snow (MacMahon 1988).

Sagebrush rangelands cover approximately 247 million acres in the western United States (Blaisdell et al. 1982). They occur mainly between 610 and 2135 m elevation between

the Sierra Nevada and Rocky Mountain ranges (Wright 1985). Several species of sagebrush (*Artemisia* spp.) dominate throughout the range. The major sagebrush species, big sagebrush (*A. tridentata*), has four subspecies that occur on different sites. These subspecies are Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*), basin big sagebrush (*A. tridentata* ssp. *tridentata*), mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) (Bunting et al. 1987; West 1988), and "species X" (*A. tridentata* ssp. *vaseyana* form *xericensis*) (Bunting et al. 1987). Associated species vary depending on climatic factors but typically include more perennial grasses in the northern portion of the range (West 1988). Information on sagebrush species and the environmental conditions where they are located can be found in West (1988). Sagebrush species are susceptible to fire and easily killed. They reproduce by seed following fire (West 1988).

The sagebrush type and other adjacent shrublands have received a considerable amount of attention because of the rapid degradation of these systems since Euro-American settlement (Roberts 1996; Vail 1994). Threats to sagebrush shrublands include grazing, changes in fire regimes, juniper invasion, noxious weed invasion, conversion to agriculture, and recreation (Roberts 1996; Sparks et al. 1990; Vail 1994). Nonnative plant species now dominate many plant communities in this type (Klemmedson and Smith 1964; Sparks et al. 1990; Vail 1994). The most common nonnative plant species in these shrublands is *B. tectorum*, which has become dominant in many areas of sagebrush shrublands in the last century due to grazing and agriculture (Peters and Bunting 1994; Pickford 1932; Piemeisel 1951; Vail 1994). *Taeniatherum caput-medusae* (medusahead), another nonnative annual grass, may become an even worse problem than *B. tectorum* (Vail 1994; West and Hassan 1985). Other nonnative plant species invading these sites include *Euphorbia esula* (leafy spurge), *Chondrilla juncea* (rush skeletonweed/hogbite), *Centaurea* spp. (knapweeds including yellow starthistle) (Sparks et al. 1990), *Aegilops cylindrica* (goat grass), *Salvia aethiopis* (Mediterranean sage), and *Chenopodium album* (weed).

anean sage), and *Isatis tinctoria* (dyer's woad) (West and Hassan 1985). Young et al. (1972) suggested that none of the native annual grasses were competitive equivalents to *B. tectorum* in sagebrush shrublands. They suggested this lack of competition with *B. tectorum* may explain why it has invaded sagebrush communities so successfully. Mack (1981) described three possible native colonizing grasses (*Festuca octoflora*, *Festuca microstachys*, and *Bromus carinatus*) that may have been displaced by *B. tectorum* in some areas. Suggested solutions to nonnative plant problems in sagebrush shrublands include improved rangeland management, aggressive fire suppression, and new fire rehabilitation programs (Vail 1994).

Nonnative plant species invasion has been more intense in some areas of the sagebrush shrubland range. Bunting et al. (1987) reported that *B. tectorum* was more likely to invade big sagebrush communities in Great Basin and Wyoming big sagebrush vegetation types than in mountain big sagebrush vegetation types. Peters and Bunting (1994) observed that lower-elevation sagebrush shrublands in the Snake River Plain of Idaho have been most affected by the invasion of nonnative plant species.

Before European settlement, the frequency of stand-replacing wildfires in sagebrush steppe and Great Basin sagebrush has been reported as between 20 and 70 years (Paysen et al. 2000). However, the exact nature of pre-European settlement fire regimes is not well understood. Most information on historic fire regimes comes from historic accounts because methods used for fire history studies in forested landscapes cannot be used in sagebrush shrublands (Peters and Bunting 1994). However, the information obtained from these accounts is questionable (Paysen et al. 2000). Other methods for determining changes in sagebrush and historic fire regimes consist of dating fire scars on adjacent forests (Houston 1973) and comparing current to historic photographs (Arno and Gruell 1983).

Anecdotal accounts suggest that fires were uncommon in the Lower Snake River Plain of Idaho, probably because of the lack of fine

fuels to carry a fire (Peters and Bunting 1994). In contrast, the Upper Snake River Plain and the Camas Prairie north of the Snake River Plain historically had more fine grasses and wildfires were more common. These areas are higher in elevation and have higher mean precipitation than the Lower Snake River Plain (Peters and Bunting 1994). Houston (1973) determined that the pre-European settlement MFI for the Douglas fir/sagebrush ecotone in Yellowstone National Park, Wyoming, was 32 to 70 years by studying fire scars in Douglas fir trees. Houston (1973) also observed that reduced fire frequency contributed to an increase in sagebrush into the steppe vegetation. Photo comparisons in southwestern Montana between the late 1800s, early 1900s, and 1970s showed an increase in sagebrush cover, which was attributed to fire suppression (Arno and Gruell 1983). The pre-European settlement MFI at that forest/sagebrush ecotone was estimated to be 35 to 40 years and shorter in the adjacent grassland.

### **Disturbance History**

Very little information is available on responses of nonnative plant species to wildfire in sagebrush rangelands that have predominantly native vegetation and a history of little anthropogenic disturbance. Most studies describe a considerable amount of *B. tectorum* (West and Hassan 1985) or other nonnatives (Ratzlaff and Anderson 1995) interspersed with native vegetation or a history of some grazing, although such sites are not necessarily considered degraded (Cook et al. 1994). Few of the studies that were conducted in "natural areas" had pre-fire vegetation data that would allow researchers to confirm whether nonnative plant species found post-wildfire were introduced before or after the fire (Ratzlaff and Anderson 1995).

### **Time Since Fire**

Although relatively few studies have been conducted on responses of nonnative plant species to wildfire in natural sagebrush shrublands, one site was studied for more than 20 years following wildfire (Houston and West 1994; West

and Hassan 1985; West and Yorks 2002). To collect information over an ecologically longer time frame but a shorter study period, many researchers perform a chronosequence study by examining a series of areas/stands that burned at different times. For example, a chronosequence study would consist of selecting sites that burned 1, 5, 10, 15, 20, 50, and 100 years previously and recording the vegetation at each during one season to represent trends over time. Humphrey (1984) performed a chronosequence by selecting sites that had experienced wildfire 2 to 36 years previously to observe long-term successional trends. Whisenant (1990) selected sites that had burned 1 to 6 and 100+ years previously to study the relationship between fire frequency and *B. tectorum*. Two other studies (Cook et al. 1994; Ratzlaff and Anderson 1995) evaluated short-term responses 1 to 3 years following wildfire.

### **Response of Nonnative Plant Species**

Research on the responses of nonnative plant species to wildfire in sagebrush natural areas have predominantly focused on *B. tectorum* dynamics (Cook et al. 1994; Hosten and West 1994; Humphrey 1984; Ratzlaff and Anderson 1995; Sparks et al. 1990; West and Hassan 1985; West and Yorks 2002; Whisenant 1990). Some studies documented no significant short-term changes in *B. tectorum* (Ratzlaff and Anderson 1995) or in grass production (Cook et al. 1994). At a site in Utah authors observed short-term increases in *B. tectorum* in both burned and unburned sites coinciding with above-average precipitation (West and Hassan 1985), a decline to a trace after 11 years coinciding with drought (Hosten and West 1994), an increase during a wetter period over the following seven years, and then a decrease in the final year of the study (West and Yorks 2002). In a chronosequence study, negligible amounts of *B. tectorum* were recorded in 2-, 22-, and 36-year-old post-burn sites, but 6% cover was recorded on 18- and 32-year-old post-burn sites (Humphrey 1984). Among other nonnative plant species that were observed following wildfire, *Salsola kali* (Russian thistle) cover was negligible until year 10, but increased in year

11 with high site variability (Hosten and West 1994). *Poa pratensis* (Kentucky bluegrass) was recorded as 6% cover on 2- to 18-year-old post-burn sites, but was negligible on older sites (Humphrey 1984).

Ratzlaff and Anderson (1995) measured mean cover of *B. tectorum* for the first and second year post-fire in seeded and unseeded sites in southeastern Idaho. An emergency management plan written for the site recommended seeding to minimize *B. tectorum* invasion with an objective of a maximum of “10% composition” within three years of wildfire. In 1988, the first year after fire, mean cover of *B. tectorum* was 0.3% and 0.1% in seeded and unseeded sites, respectively. In 1989, mean cover of *B. tectorum* was 1.6% and 1.2% in seeded and unseeded sites, respectively. No significant difference was found between treatments in either year (1988  $P < 0.316$ ; 1989  $P < 0.381$ ). Another nonnative annual grass, *P. bulbosa*, was reported to have high densities in both treatments and was relatively more abundant (6.9% cover) in unseeded areas, but this was not considered a problem because *P. bulbosa* was “naturalized” in the area.

West and Hassan (1985) recorded vegetation recovery following a 1981 wildfire on a site in central Utah that was considered in “good condition” with a significant component of perennial grasses. Mean percent cover of *B. tectorum* was recorded as 0% in 1981, 35.7% in 1982, and 50% in 1983 on burned sites. On the unburned control plots, *B. tectorum* cover was 6.8% in 1981, 11% in 1982, and 24% in 1983. Hosten and West (1994) continued to study these sites and reported changes for 11 years following the 1981 wildfire. In 1982, the second year post-wildfire, grazing was introduced as a treatment to provide burned and grazed, unburned and grazed, and burned and ungrazed treatment sites. Cover values for both burned treatments were similar and much larger than the unburned and grazed treatment. Exact cover values were not reported in the publication, although bar graphs and a narrative presented the results. All treatments showed sharp increases in *B. tectorum* cover

following wildfire and cattle grazing, peaking two years following the 1981 wildfire. *B. tectorum* cover then declined sharply on all treatments and was found only as a trace in years 10 and 11 post-fire. The sharp decline in *B. tectorum* cover coincided with the worst drought during the study. *S. kali* was also found on the sites and percentage cover was negligible until 10 years after wildfire (1990) when it increased to a mean cover of approximately 8% on burned and grazed sites and approximately 5% on burned and ungrazed sites. However, the data showed high site variation.

From observing more than 20 years of change on the same central Utah site, West and Yorks (2002) noted that *B. tectorum* increased during a wetter period from 1993 to 2000 in all treatments. However, in 2000 cover of *B. tectorum* decreased in all treatments, coinciding with a drop in precipitation to levels below the long-term average. Thus, ultimately *B. tectorum* did not remain dominant after an initial exponential increase, especially in ungrazed plots.

Cook et al. (1994) studied the effects of wildfire on wildlife forage for three years in high-elevation and high-precipitation sagebrush sites in Wyoming. Their study showed no significant differences in annual grass production between burned and unburned sites, except during the second year on burned sites with a southwest aspect. These sites had significantly higher *B. tectorum* production (25 to 30 g/m<sup>2</sup>) than the unburned sites (10 g/m<sup>2</sup>), but by the third season there was no significant difference in grass production (approximately 7 g/m<sup>2</sup>) on burned and unburned southwest-aspect sites. The southwest-aspect sites were the only sites listed as having *B. tectorum* in the pre-burn vegetation. The other two sites, with east-southeast and east-northeast aspects, had less than 3.0 g/m<sup>2</sup> *B. tectorum* for all three years.

Humphrey (1974) studied eight environmentally similar sites that had burned between 2 and 36 years previously in southeastern Idaho to document successional trends following wildfire. Relative cover of *B. tectorum* ranged from negligible on two-year post-burn sites, approximately 6% on 18-year post-burn sites,

negligible on 22-year post-burn sites, approximately 6% on 32-year post-burn sites, and negligible on 36-year post-burn sites. *P. pratensis* was found at approximately 6% relative cover on the 2- to 18-year post-burn sites but had negligible cover on the rest of the sites in the chronosequence.

Whisenant (1990) compared fire frequency with fine fuel frequency and quantity on 12 sites that had burned between 1 and 6, 55, and >100 years previously in the Snake River Plains of Idaho. The sites that had burned one to six years previously either had *B. tectorum* as the dominant species or, in two cases, as one of but not the most dominant species. The site that had burned 55 years previously and two sites that had burned more than 100 years ago did not list *B. tectorum* as a dominant species. The sites had different potential vegetation types and there were no sites at comparable successional stages. Regardless, it is interesting that the older sites had no *B. tectorum*, but they were also equal to or higher in elevation than other sites in the study.

Interestingly, *B. tectorum* was located in all sites in a southeastern Oregon area not subjected to human use and surrounded by rugged lava flows, and thus considered “pristine” (Kindschy 1994). These sites were sampled irregularly over 14 years. From 1980 to 1991, *B. tectorum* increased from 0 to 10% abundance. The authors suggested the increase in *B. tectorum* was due to heavy spring precipitation during the study period. However, using statistical analyses (ordination, regression, and analysis of variance) to assess data, West and Yorks (2002) found no stabilization of a sagebrush plant community that had burned 20 years previously and was in “good condition.” The results indicated that *B. tectorum* came to dominate in the first few years. The perennial grasses recovered and began to dominate, especially in ungrazed areas. They speculated that *B. tectorum* will be transitory only on sites similar to those in their study area with “low stores of and capacities to fix nitrogen and other critical elements to plant growth.” In contrast, Young and Evans (1978) concluded that *B. tectorum*



became dominant in their degraded sites post-wildfire and within four years had reached a new dynamic equilibrium.

### **Native Plants**

West and Yorks (2002) found a significant inverse relationship between perennial grass cover and *B. tectorum* cover. Many native perennial grasses associated with sagebrush shrublands are damaged by fire only during certain times of the year. Wright and Klemmedson (1965) tested effects of the season of burn for several native bunchgrasses from sagebrush-grass regions of southern Idaho. They concluded that squirreltail (*Sitanion hystrix*) was damaged only by July burning when tested in June, July, and August. Sandberg bluegrass (*Poa secunda*) was not affected by burning. Needle and thread (*Stipa comata*) was damaged in June and July, but was relatively resistant to fire in August. Thurber's needlegrass (*Stipa thurberiana*) followed the same pattern as needle and thread but with less damage.

### **Fire Severity**

Very little information is available on the effect of fire severity on the responses of nonnative plant species to wildfire in sagebrush shrublands. None of the papers reviewed defined fire severity classes for their sites or measured its relationship to nonnative plant species invasion. Humphrey (1984) reported that no fire intensity data were available for his study sites that had burned 2 to 36 years previously in a southeastern Idaho study. He did state that charred sagebrush stumps were visible on the sites indicating that the fire had been severe enough to kill all aboveground vegetation. Ratzlaff and Anderson (1995) studied paired seeded and unseeded plots that had both been burned by wildfire. The authors stated that burn intensities were similar for unseeded and seeded plots, though they did not state what that intensity was. However, native perennial grasses resprouted rapidly indicating that the wildfire had not been severe enough to kill the vegetative bases. The fire severity in a central Utah study (West and Hassan 1985) was not measured, but it was described as killing most aboveground vegetation.

### **Livestock Grazing**

The interactive effect of livestock grazing and wildfire on nonnative plant species is not clearly understood. Sparks et al. (1990) used the same methods and descriptions of vegetation and land use as the General Land Office surveyors at the time of Euro-American settlement; they then compared their 1988 data with the older data for two counties in Utah. They determined that *B. tectorum* had attained the greatest dominance in mid-elevation, shadscale (*Atriplex confertifolia*)/sagebrush shrublands exposed to high fire and livestock grazing, whereas high-elevation, "rugged" sites that had experienced wildfire but little human use, such as livestock grazing, had experienced little *B. tectorum* invasion. Hosten and West (1994) did not observe a definite impact to vegetation dominance when wildfire was followed by grazing. However, they did observe that areas that did not have grazing after wildfire had higher cover of native perennial grasses.

### **Rehabilitation and Seeding**

It has been recommended that when *B. tectorum* is present in sagebrush shrublands, the shrublands should be seeded after wildfire to prevent *B. tectorum* invasion (Young et al. 1976) and/or to prevent erosion (Ratzlaff and Anderson 1995). However, a potential problem is that many of the perennial grasses used in seed mixtures are also nonnative species (Wright and Bailey 1982). To determine whether seeding was necessary following an August wildfire in southeastern Idaho, Ratzlaff and Anderson (1995) recorded plant recovery on seeded and unseeded areas for two consecutive years. The results indicated that seeding had no effect on the mean cover of *B. tectorum*. The authors used a two-way analysis of variance to analyze mean cover of *B. tectorum* by treatment (seeded or unseeded), site (upper, middle, and lower plots), and site by treatment. The results of the analysis for *B. tectorum* by treatment in 1988 and 1989 were insignificant ( $P < 0.316$  and  $P < 0.381$ , respectively). Interestingly, the results for mean cover of *B. tectorum* by site were significant in 1988 ( $P < 0.006$ ) but not in 1989 ( $P < 0.056$ ).

The authors concluded that results of treatment were insignificant because the establishment of the seeded plants was poor, possibly because of drought conditions in 1987 and 1988, and that many perennials resprouted from vegetative bases that did not burn in the fire. The authors also concluded that drill-seeding caused additional disturbance that was unnecessary and may have been detrimental. Although *B. tectorum* was the focus of the study, authors noted that the nonnative grass *P. bulbosa* occurred in both treatments but was relatively more abundant in unseeded areas.

### Conclusions

- Very little information is available on the responses of nonnative plant species to wildfire in natural sagebrush desert shrublands.
- Most study sites have either a history of livestock grazing, or *B. tectorum* and other nonnative plant species already exist in substantial amounts on the sites.
- The little long-term information found on *B. tectorum* responses to wildfire have shown large variation over time, but no studies have shown that *B. tectorum* eventually dominates these sites.
- Several environmental and disturbance factors such as post-wildfire precipitation, aspect, and grazing appear to affect the response of nonnative plant species to wildfire.
- Seeding after wildfire to reduce *B. tectorum* invasion may be no more successful than not seeding.
- *B. tectorum* has been the most commonly studied nonnative plant species in post-wildfire studies of sagebrush desert shrublands. However, several other nonnative plant species have been recorded in sagebrush desert shrublands after wildfire and warrant research.
- A “new equilibrium” consisting of *B. tectorum* dominance which prevents native vegetation from regrowing was not observed at sites considered to be in good condition and having a high density of perennial grasses pre-fire in one long-term (20-year) study.

### Other Desert Shrublands

MacMahon (1988) calls the Mojave, Sonoran, and Chihuahuan deserts the “warm deserts” because the majority of the precipitation occurs as rain. The Mojave Desert spans southern Nevada, southeastern California, and the edge of northwestern Arizona. It is bordered by the Great Basin Desert to the north and the Sonoran Desert to the south. Creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) are the dominant shrub species over much of this desert. Other general vegetation types include shadscale (*A. confertifolia*), saltbush (*Atriplex* spp.), blackbrush (*Coleogyne ramosissima*), and Joshua tree (*Yucca brevifolia*), which is unique to the Mojave Desert (Humphrey 1974; MacMahon 1988).

The Sonoran Desert covers the southwestern third of Arizona, the southeastern corner of California, and most of the Baja California/Mexico peninsula, and extends into Sonora, Mexico. The vegetation in the Sonoran Desert is highly variable because of the desert’s expanse and consequent variety of environmental conditions, but is generally characterized by a large variety of woody species and an abundance of cacti. Many areas are dominated by creosote bush and white bursage, but there are also expanses of sand dunes, perennial grasslands, wash vegetation, brittlebrush (*Encelia farinosa*), saguaro (*Carnegiea gigantea*), and several other shrub species (Humphrey 1974; MacMahon 1988).

The Chihuahuan Desert occurs in southcentral New Mexico and southwestern Texas but is located mainly in Mexico. Its vegetation consists of medium-size shrubs, few cacti, and some perennial grasses at higher elevations (Humphrey 1974; MacMahon 1988).

Approximately 25 nonnative plant species are widespread in the natural areas of the Mojave and Sonoran Deserts in southeastern California. Most are annuals of Eurasian origin from the Poaceae, Chenopodiaceae, and Brassicaceae families. Most of these nonnative plant species were introduced to the deserts in the mid and late 19th century but did not become common and abundant until after the 1930s.

Several factors are suggested as related to the establishment and spread of nonnative plant species in the desert including human-induced atmospheric changes and competitive ability of the species (Kemp and Brooks 1998). Other anthropogenic disturbances that have led to the degradation of these deserts include agriculture, urbanization, transportation and utility corridors, and military training activities (Lovich and Bainbridge 1999).

Nonnative plant species provide fuel for wildfires in areas where fuels were historically discontinuous and sparse; therefore, wildfires have become more frequent and intense (Brooks and Pyke 2001; Kemp and Brooks 1998). Using data collected from 34 sites in central, southern, and western Mojave Desert in 1995, Brooks (1999) observed that the nonnative annual grasses *Bromus* spp. and *Schismus* spp. were the only annual species that were abundant and that they created continuous fine fuels that persisted into the summer fire season. He concluded that these nonnatives were necessary for fire to spread in the Mojave Desert. It is not clear what role wildfire plays in the response of nonnative plant species in areas that do not have a predominant element of nonnative grasses in the understory before the fire.

### **Fire Regime**

There is no agreement on the MFI of desert shrublands prior to European settlement (Payson et al. 2000). Humphrey (1974) suggested that deserts have fewer and less severe fires than other ecosystems because of lack of fuel. For the Mojave Desert, there is very little fire history information although Humphrey (1974) suggested fires were rare. Humphrey (1974) concluded that fires in the Sonoran Desert also were rare despite greater opportunities of ignition by lightning because fuels are sparse. When wildfires did occur, they were ignited by Native Americans or lightning prior to Euro-American settlement (Humphrey 1974).

Fires most often occur in the ecotone between the desert and desert grasslands and in above-average precipitation years that result in dense annual plant growth (Humphrey 1974).

McLaughlin and Bowers (1982) observed that above-average precipitation resulted in a high production of winter annuals and that several fires occurred the following spring and summer in the deserts of Arizona. Rogers and Vint (1987) analyzed the difference between areas burned by wildfire after one or two wet winters and concluded that many more hectares burned after consecutive wet winters on the deserts in the Tonto National Forest. They stated that this supported McLaughlin and Bowers' (1982) conclusions. Schmid and Rogers (1988) reviewed Forest Service records of fires between 1955 and 1983 in the Arizona Upland Subdivision of the Sonoran Desert. They concluded that fire occurrence increased over this period of time and suggested that the increase may have been due to winters with above-average precipitation, increased fuel from nonnative plant species, improved fire detection and reporting, and increased human-caused ignitions. Brooks (1999) stated that urban areas and transportation corridors, as well as wilderness areas of the Mojave Desert, that have increased in fire frequency between the 1970s and 1990s are dominated by nonnative grasses.

### **Disturbance History**

It has been observed that many natural areas in these deserts contain nonnative plant species (Kemp 1998; Brooks 2002). Numerous anthropogenic disturbances have been recorded in these areas (Lovich and Bainbridge 1999). Brooks (1999) found that nonnative annuals were more frequent than native annuals on randomly selected sites in the Mojave Desert. He randomly selected 34 sites in the public lands of the central, western, and southern Mojave Desert that were 50 m from dirt roads and 2 km from paved roads for a study of nonnative plant species. Averaged over the 34 sites, the absolute frequency of the nonnative annuals *Bromus* and *Schismus* spp. was significantly higher ( $P < 0.05$ ) than that of other annual plants.

It appeared that most of the study sites had a significant amount of nonnative vegetation in the control sites as well as the burned sites and may not have clearly met the criteria for "natural areas" (Beatley 1966; Brooks and Matchett 2003;

Brown and Minnich 1986; Callison et al. 1985; O'Leary and Minnich 1981). However, the information on prefire nonnative vegetation and anthropogenic disturbances was not explicit so the following studies were included and any indication of the nature of prefire sites was described as well as possible. Brown and Minnich (1986) did not explicitly describe nonwildfire disturbances in their study, but the site map shows that the four sites were located adjacent to or within 2 km from the nearest highway and near Palm Springs, California. In the same study, more than half of the herbaceous cover at unburned sites (used to represent the pre-burn vegetation) was composed of nonnatives (26% of the total 42% cover), suggesting that these may not have been sites that would be considered "natural." O'Leary and Minnich (1981) observed that there was little difference in the "ephemeral" vegetation between unburned and burned plots; nonnatives occurred in nearly the same percentage in each, but did not dominate the annual vegetation. Although information on disturbances in the area was not specifically stated, the sites were located within 500 m of the Snow Creek Road and near a collection of buildings. Beatley (1966) noted that *B. rubens* and *B. tectorum* were common throughout her study area, which had been partially or entirely denuded in many places from military testing activities. Several sites in the study by Callison et al. (1985) had been seeded with nonnative grasses. In that study nonnative annual grasses, nonnative annual forbs, and the seeded perennial grasses dominated the understory at all sites including the unburned site. Brooks and Matchett (2003) stated that their Beaver Dam site had a history of grazing and was currently being grazed by cattle at moderate levels, which may have allowed nonnative plant species to establish and reach higher levels of richness and cover in the unburned sites. The other two sites in their study had not been grazed by livestock for several decades and had "much lower" levels of nonnative plant species richness and cover. The authors concluded that the effects of fire on previously disturbed blackbrush sites might not affect the dominance of nonnative plant species if those species were abundant prior to the disturbance.

### **Time Since Fire**

Some authors commented that their studies were limited by being conducted for only one or a few years (Brooks and Matchett 2003; Brown and Minnich 1986). However, this was the case with all of the studies. The same site was sampled consecutively after a wildfire three times at most (Beatley 1966). However, the wildfires had occurred at different times at each site in that study so time since fire was 4 to 6 years at one site, 5 to 7 years at the second site, and approximately 13, 14, and 15 years at the third site (although the exact date of that fire was unknown). Another study sampled the same sites for two consecutive years (Cave and Patten 1984). Rogers and Steele (1980) sampled two sites the first year following fire, and then resurveyed one site three years later and the other four years later. Brown and Minnich (1986) sampled two sites one season, then resurveyed one site three years and the other five years after wildfire. They commented that a limitation of their study was that it examined only a limited period in the post-fire succession and that the future succession could not be determined from the study. O'Leary and Minnich (1981) sampled sites once five years following fire. Callison et al. (1985) sampled several sites in one year as a fire chronology. Wildfires had occurred at 1, 2, 6, 12, 17, 19.5, and 37 years previously on the different sites. Brooks and Matchett (2003) sampled two sites in one year where wildfire had occurred 6 and 14 years previously, respectively. They, too, commented that their study was conducted at only one point in time and that their limited results should be interpreted with that in mind.

### **Fire Severity**

Fire severity was described in some studies by its effect on the overstory shrubs (Beatley 1966; Brown and Minnich 1986; O'Leary and Minnich 1981). Brown and Minnich (1986) recorded fire damage on their burned sites by qualitatively ranking plants as burned, scorched, or green. O'Leary and Minnich (1981) described the wildfires that burned their sites as severe enough to consume all the leaves of the creosote bushes at the site,



although most of them resprouted. Beatley (1966) described the fire severity at her blackbrush-shrub-association sites as totally destroying the plant cover.

### **Response of Nonnative Plant Species**

*Bromus* spp. (Beatley 1966; Brooks and Matchett 2003; Brown and Minnich 1986; Callison et al. 1985; Cave and Patten 1984; O'Leary and Minnich 1981; Rogers and Steele 1980), *Schismus* spp. (Brooks and Matchett 2003; Brown and Minnich 1986; Cave and Patten 1984; O'Leary and Minnich 1981), and *E. cicutarium* (Brooks and Matchett 2003; Brown and Minnich 1986; Callison et al. 1985; Cave and Patten 1984; O'Leary and Minnich 1981; Rogers and Steele 1980) were the most commonly observed nonnative plant species in desert shrubland post-fire communities of the Mojave and Sonoran deserts.

Inconsistent responses of nonnative annuals were reported when authors compared burned to adjacent unburned sites at various times following wildfire in desert shrublands. In one study (Brown and Minnich 1986), nonnative plant species cover increased after wildfire, but the data were not statistically analyzed. In another study little difference was found between nonnative plant species on burned and unburned sites (O'Leary and Minnich 1981). Cave and Patten (1984) recorded for *Schismus* spp., a decrease for *Bromus* spp., and no significant difference for *E. cicutarium*. Rogers and Steele (1980) described the annual post-fire communities at two different sites as dominated by nonnatives, especially *E. cicutarium* at one site and *B. rubens* at the other. Beatley (1966) recorded that density and cover of *B. rubens* were greater on two out of three of the burned sites than on unburned sites for three years, but trends (increases and decreases) on each site varied. Callison et al. (1985) observed that nonnative annual grasses, nonnative annual forbs, and seeded perennial grasses dominated the understory at all burned and unburned sites in their study. Brooks and Matchett (2003) recorded significantly higher percent cover of *E. cicutarium* on one burn site and *E. cicutarium*, *B. rubens*, and *B. tectorum*

on a second burn site compared to unburned sites. Relevant details of each study are provided in the following paragraphs.

Brown and Minnich (1986) studied sites in paired burned and unburned plots on the border of the Mojave and Sonoran Deserts in creosote bush scrub. They stated that the wildfires had been preceded by heavy precipitation from 1976 to 1983, which resulted in abundant growth of native and nonnative annuals. The authors speculated that the wildfires reported in their study may have been fueled by the abundant and persistent nonnative grasses, especially *B. tectorum*, *B. rubens*, and *S. barbatus*, resulting from prior wet years. In the previous decade almost no fires had occurred in the area. Sites were sampled once in 1983 when "desert annuals were decreasing," which was three growing seasons post-fire at three sites and five growing seasons post-fire at another site; data were merged. The unburned vegetation included the nonnative grasses *B. rubens* and *S. barbatus*, which were described as being "nearly everywhere." The percent cover of the three nonnative plant species in unburned and burned sites was approximately 17% in unburned sites and 21% in burned sites for *B. rubens*, 7% and 16%, for *S. barbatus*, and 2% and 6%, respectively, for *E. cicutarium*. Statistical differences were not determined between these treatments, but total herbaceous cover was higher overall on burn sites (65% on burn sites and 42% on unburned sites). Shrub reproduction was dominated by goldenhills (*Encelia farinosa*), a native shrub, on burned sites.

O'Leary and Minnich (1981) studied the post-fire recovery of several desert shrubs on creosote bush scrub sites in the Western Colorado Desert (Sonoran Desert) in southern California. The fire occurred in early July 1973 and spread into the desert scrub through an "unusually dense herb layer" resulting from the previous winter's rains. The authors compared unburned stands to adjacent burned stands in post-fire succession, primarily of shrubs, by sampling in 1978 (five years after the fire). The authors observed little difference in the

“ephemeral” vegetation between unburned and burned plots. The species with the highest cover (30% on both unburned and burned sites) was whitemargin sandmat (*Euphorbia albomarginata*), a native plant. The other primary ephemeral species on unburned and burned areas included the nonnative plant species *E. cicutarium*, which had 6% and 10% cover, *S. barbatus* with 6% and 5% cover, followed by another native, sand pygmyweed (*Crassula erecta* [*Crassula connata* var. *connata*]) with 3% cover on each area, and the nonnative *B. rubens* with 2% and 1% cover, respectively. Although the authors did not draw conclusions about the nonnative vegetation responses to wildfire in particular, it appears that the wildfire had not substantially changed the composition of the nonnatives in the community at the sampling time.

Cave and Patten (1984) studied short-term vegetation responses to a 1981 controlled burn and a 1980 wildfire in the Tonto National Forest in the Upper Sonoran Desert near Phoenix, Arizona. The authors indicated that pre-fire herbaceous vegetation had been unusually lush because of above-normal precipitation. Palo Verde cactus (mostly *Opuntia* spp. and *Carnegiea gigantea*) and shrub (mostly *Ambrosia deltoidea* [triangle burr ragweed]) association characterized their sites. Changes in plant density and biomass in two different microhabitats

(open/shrub and shaded sites), as well as the density and survival/recovery of trees, shrubs, and cacti were recorded for two years following fire. Sites were in an area burned by a May 1980 wildfire and in two adjacent unburned sites – one used for a prescribed fire and the other as the unburned control. (Only results for the wildfire and unburned control sites are reviewed here.) The results indicated that only *B. rubens* and *Schismus* spp. grasses had significant, although opposite, responses to the wildfire out of the nine most abundant annual plants. *B. rubens* density was significantly lower both years following wildfire in both the shade and open/shrub sites on the burned sites compared to the unburned sites (Table 3). However, *Schismus arabicus* (Arabian schismus) density was significantly higher on the burned compared to the unburned sites both years following fire, except in 1981 in the open/shrub sites (Table 3). The other nonnative annual, *E. cicutarium*, showed no significant response to burning (Table 3). The authors suggested that *B. rubens* would recover its pre-fire density in a few more years.

Following human-caused wildfires in 1974, Rogers and Steele (1980) set up permanent plots at two sites about 45 km north and east of Phoenix, Arizona, in the Sonoran Desert. Paired plots in the unburned and burned vegetation were sampled twice. However, the

<b>Species Microhabitat</b>	<b>Variable</b>	<b>Unburned 1981</b>	<b>Burned 1981</b>	<b>Unburned 1982</b>	<b>Burned 1982</b>
<i>Bromus rubens</i> (red brome) <b>Open/Shrub</b>	Density	396a	20b	120x	20y
	Biomass	12.4a	3.8b	5.6x	2.5y
<i>Bromus rubens</i> (red brome) <b>Shade</b>	Density	824a	11b	258x	105xy
	Biomass	26.3a	1.2b	29.0x	34.7xy
<i>Schismus arabicus</i> (Arabian schismus) <b>Open/Shrub</b>	Density	27a	66a	26x	186y
	Biomass	0.3a	13.8b	0.4x	32.8y
<i>Schismus arabicus</i> (Arabian schismus) <b>Shade</b>	Density	20a	98b	48x	284y
	Biomass	0.7a	11.1b	1.9x	63.2y
<i>Erodium cicutarium</i> (redstem stork's bill) <b>Open/Shrub</b>	Density	29a	10a	49x	26x
	Biomass	0.6a	4.1a	3.9x	1.8x
<i>Erodium cicutarium</i> (redstem stork's bill) <b>Shade</b>	Density	7a	10a	61x	18x
	Biomass	0.3a	1.2a	4.7x	8.8x

**Table 3.** Mean annual plant density (number/m<sup>2</sup>) and biomass (g/m<sup>2</sup>) followed by the same letter (a or b for 1981 and x or y for 1982) are not significantly different ( $P < 0.05$ ), from Cave (1984).

study focused on the effects to perennials so data on annuals was not presented although descriptions were given. The post-fire annual community was dominated by nonnatives, especially *E. cicutarium* at one site and *B. rubens* at the other.

Beatley (1966) studied three paired plots of unburned and burned blackbrush-shrub-association vegetation in Nye County, Nevada. Dominant shrubs on the sites were creosote bush, blackbrush, natal bottlebrush (*Grayia* spp.), sagebrush, saltbrush, and desert thorn (*Lycium* spp.), as well as a few other desert shrubs. The author stated that the blackbrush shrub associations with *B. rubens* were the most susceptible to fire because of the community structure and flammability of both species. The sites had burned at three different times – prior to 1950, and in 1958 and 1959. Density, frequency, cover, and average height of *B. rubens* were recorded for all sites in 1963, 1964, and 1965. Paired plots were within approximately 100 feet of each other. The density and cover of *B. rubens* were greater on the burned than the unburned sites and decreased each year on each of the sites, except sites 41 and 42 in years 1964 and 1965 (Table 4). The results indicated that *B. rubens* cover was usually much higher on disturbed sites, but that local environmental conditions during different seasons also affected the results (Table 4). These results were not statistically analyzed and only trends could be discussed.

Callison et al. (1985) presented information on eight sites that had been burned 1 to 37 years previously in a blackbrush community in southwestern Utah. It was not clear whether prescribed fire or wildfire had burned the sites. The focus of the study was not to determine the response of nonnative plant species to fire. Paired plots were located in burned and adjacent unburned sites and absolute cover values at each site were compared. Three of the sites (those 2, 6, and 12 years since burning) had been seeded with perennial grasses. Cryptogammic soil crusts and blackbrush were reported to be severely damaged by the fires and did not show signs of recovery after

approximately 20 and 37 years. Other native shrubs did return to dominance on the sites. Four nonnative plant species that were not seeded were identified to species: *Melilotus officinalis* (yellow sweet-clover), *B. rubens*, *B. tectorum*, and *E. cicutarium* (Table 5). Nonnative plant species dominated the annual understory in both unburned and burned sites. Statistical analyses of the differences between sites were not performed.

Brooks and Matchett (2003) studied the plant community patterns in blackbrush shrublands of the Mojave Desert at three sites located in southwestern Utah, southern Nevada, and southern California. The authors selected paired sites in mature blackbrush and adjacent burned sites on similar soils and topography. Wildfires in 1987 and 1995 were responsible for the southwestern Utah and southern Nevada burns, but a prescribed fire created the southern California site and will not be reviewed. The southwestern Utah site was sampled once 6 years post-fire and the southern Nevada site was sampled once 14 years post-fire. Species richness, cover, and frequency were recorded at four pairs of 4-ha plots at each site.

Species richness was measured at four spatial scales at each site. The results of nonnative plant species richness at the Utah site were not significant at any spatial scale. However, at the Nevada site burn effects were positively related to nonnative plant species richness at  $P \leq 0.001$  at the 1-m<sup>2</sup>, 10-m<sup>2</sup>, and 100-m<sup>2</sup> scales, and positively related at  $P \leq 0.01$  at the 1000-m<sup>2</sup> scale. When all sites (including the prescribed-burn site) were summed, nonnative species richness increased and native richness decreased after fire ( $P=0.0031$ ) compared to the unburned plots (Brooks and Matchett 2003). Nonnative species frequency increased significantly with burning ( $P < 0.0012$ ) at the Nevada site but changed only from 96% to 98% ( $P=0.6704$ ) at the Utah site (Brooks and Matchett 2003).

The Utah burned site was dominated in order of abundance by the nonnative forb *E. cicutarium*, three native species, and *Bromus*

*madritensis* spp. *rubens* (compact brome). The Nevada burned site was dominated by a native species, *E. cicutarium*, four other native species, and then *B. madritensis* spp. *rubens* (Brooks and Matchett 2003). *E. cicutarium* was the only nonnative significantly ( $P \leq 0.01$ ) positively related to fire at the Utah site. At the Nevada site, all categories of nonnatives were significantly ( $P \leq 0.01$ ) positively related to fire (Brooks and Matchett 2003). The authors speculated that the previous years of below-average precipitation may have negatively affected the annual grass cover, especially the *Bromus* spp. (Brooks and Matchett 2003).

**Conclusions**

- Limited studies on the responses of nonnative plant species to wildfire in natural areas of desert shrublands have been conducted throughout the Mojave and Sonoran deserts.
- Many areas where the responses of nonnative plant species to wildfire have been studied are of questionable “natural” composition. Nonnative plant species were documented in all unburned vegetation, sometimes as the dominant component in the annual vegetation, even when overstory species were native.

- Many sites were located near transportation corridors and developed areas.
- In several studies, wildfire had occurred following higher-than-average periods of precipitation.
- Fire severity was measured as it affected the overstory shrub species.
- Very few studies were conducted for consecutive years and most were conducted at one point in time. Time since fire ranged from the first year post-fire to 37 years post-fire and varied greatly between studies.
- The annual plants *Bromus* spp., *Schismus* spp., and *E. cicutarium* were the most common nonnatives found in the studies.
- No consistent responses of nonnative plant species were documented among all of the studies. Some nonnative plant species increased and some decreased after wildfire. In some studies, differences in nonnative plant species on burned and unburned sites were not noticeable, while in one study nonnative species were greater in unburned than in burned sites.

Plot # and site	Shrub association for the site pairs	1963			1964			1965		
		#/5 m <sup>2</sup>	% freq	% cov	#/5 m <sup>2</sup>	% freq	% cov	#/5 m <sup>2</sup>	% freq	% cov
18 U	Blackbrush	494	94	2.6	292	78	2.5	68	38	1.5
19	Fire in 1958	3394	100	26.2	2301	100	16.4	2117	100	10.6
39 U	Blackbrush–natal bottlebrush	5	8	0.2	32	18	0.4	48	28	1.0
40	Fire prior to 1950	393	82	3.6	141	70	2.0	121	68	1.7
41 U	Blackbrush	376	94	3.6	995	100	8.8	615	100	7.3
42	Fire in 1959	429	92	4.0	451	94	2.9	1626	98	13.6

**Table 4.** Number of plants, frequency, and percent cover of *Bromus rubens* in 50 0.1-m<sup>2</sup> samples on three pairs of burned and unburned (U) sites, from Beatley (1966).

Year	Unburned		1		2		6		12		17		19.5		37	
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
<i>Melilotus officinalis</i>	0.0	0.0	0.0	0.0	1.3	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bromus rubens</i>	3.4	3.1	3.9	2.4	2.4	3.9	10.7	8.2	0.4	0.4	6.9	2.2	1.5	0.6	1.4	0.9
<i>Bromus tectorum</i>	2.8	2.7	2.5	2.7	6.6	8.7	33.5	12.2	11.3	5.3	20.6	4.9	0.0	0.0	4.3	3.3
<i>Erodium cicutarium</i>	0.2	0.7	11.1	4.5	7.1	11.5	1.7	3.1	0.0	0.0	2.5	1.6	0.0	0.0	0.2	0.4

**Table 5.** Mean (M) and standard deviation (SD) of absolute percent cover values for *Melilotus officinalis*, *Bromus rubens*, *Bromus tectorum*, and *Erodium cicutarium* in unburned (U) and adjacent sites that had burned 1, 2, 6, 12, 17, 19.5, and 37 years previously, from Callison et al. (1985).



## Pinyon-Juniper

Pinyon-juniper woodlands refer to areas composed of a combination of pinyon pines (*Pinus monophylla*, *Pinus edulis*) and junipers (*Juniperus* spp.) in the overstory, except in the northwestern Great Basin and Columbia Basin where western juniper (*Juniperus occidentalis*) occurs without a pinyon pine component. Approximately 17 million ha in the semi-arid western United States from eastern Oregon to New Mexico support pinyon-juniper assemblages (Wright and Bailey 1982). These woodlands occur elevationally above semi-desert shrublands and grasslands, mainly in foothills, low mountains, mesas, and plateaus (West 1988). They grow in a wide range of environmental conditions and with a diverse assemblage of tree, shrub, and understory herbaceous species in varied densities and cover (Evans 1988; West 1988). In general, typical pinyon-juniper assemblages occur with understory perennial grasses in Arizona and New Mexico (Dwyer and Pieper 1967), Great Basin sage-scrub and some grasses throughout the Great Basin and the Colorado Plateau (Erdman 1970; Koniak 1985), and Great Basin sage-scrub and chaparral in California (Wangler and Minnich 1996).

Although people occupied and used pinyon-juniper woodlands before Euro-American settlement (Samuels and Betancourt 1982), intensive use of these woodlands began with Spanish colonization of the Southwest in the 1600s (Evans 1988) and continued with European settlement in the 1800s in the intermountain region (Evans 1988; Miller and Wigand 1994). This intensive use consisted mainly of livestock grazing and fuelwood gathering (Evans 1988). Some areas of pinyon-juniper were cleared for use in mining. This was especially true in the intermountain west, particularly in Nevada in the late 1800s (Evans 1988; Young and Budy 1987).

The current utilization of pinyon-juniper woodlands varies by region. However, livestock grazing is a major use throughout the range. According to Evans (1988), about 80% of the total pinyon-juniper area is grazed, much of which is heavily grazed.

## Fire Regime

In *The Effects of Fire on Flora* (Paysen et al. 2000), pinyon-juniper woodlands are categorized as having a mixed fire regime. However, little is known about pre-European settlement fire history in pinyon-juniper woodlands (Bunting 1994; Floyd et al. 2000). Fire histories are difficult to determine with pinyon pine and juniper because they do not consistently form fire scars (but see Baker and Shinneman 2004; Floyd et al. 2000). However, fire histories have been estimated using fire scars (Gruell 1999; Young and Evans 1981) as well as other methods such as stand age structure (Floyd et al. 2000) and collecting supporting evidence of fire histories in adjacent stands of ponderosa and Jeffrey pine (Gruell 1999).

Estimates of MFIs for pinyon-juniper woodlands vary across its range and by aspect, topography, understory vegetation, and ignition source (Gruell 1999). Burkhardt and Tisdale (1976) concluded that the MFI for pinyon-juniper woodlands in southwestern Idaho was 25 to 30 years between 1650 and 1900. Young and Evans (1981) determined that the MFI was approximately 50 years with up to 90 years between fires during the same period at a northern California pinyon-juniper site. However, the researchers commented that technologies for reconstructing fire histories were “woefully inadequate” for that environment. Gruell (1999) reported that in Great Basin National Park more frequent fires, with MFIs of 15 to 20 years, occurred on north-facing slopes and other areas that had fine fuels. Native Americans ignited some of the fires that resulted in shorter return intervals. On rocky slopes without fine fuels, wildfires occurred infrequently with MFIs of up to 100 years (Gruell 1999). Baker and Shinneman (2004) concluded through a systematic review of the evidence on fire history studies in pinyon-juniper woodlands that there are no reliable estimates of low-severity surface fires in these systems because of methodological problems. Furthermore, they deemed that only two studies had adequate information to assess changes in fire frequency since Euro-American settlement.

Fires that occurred before European settlement were believed to be of mixed severity with lethal surface fires in dense stands and periodic light surface fires (Paysen et al. 2000). However, considerable debate on the exact nature of pinyon-juniper fire regimes exists. Bunting (1994) suggested that nested fire cycles consisting of frequent low- to moderate-intensity fires and infrequent, large, high-severity fires occurred in pinyon-juniper woodlands. Romme et al. (2003) hypothesized that historic pinyon-juniper fire regimes could be subdivided into three classes. They suggested that the first class – termed piñon-juniper grass savannas and found in New Mexico, Arizona, and northern Mexico – had frequent, low-severity surface fires carried by grasses. The second class – termed pinyon-juniper shrub woodlands and were found in the Great Basin of the Colorado Plateau – had moderately frequent, high-severity crown fires. The third class – categorized as pinyon-juniper forest and occurring in small stands throughout the Colorado Plateau, Great Basin, Central Oregon, southern Rocky Mountains, and southern California mountains – experienced very frequent, very high-severity crown fires.

Since Euro-American settlement, many changes have occurred in pinyon-juniper woodlands. Pinyon-juniper woodlands have increased in density and expanded into adjacent areas including the southwestern desert grasslands, the sagebrush-grass vegetation of the Great Basin, and aspen groves and riparian communities (Barney and Frischknecht 1974; Burkhardt and Tisdale 1976; Miller and Wigand 1994). These changes have been attributed to alterations in fire frequency, grazing, and climatic conditions (Burkhardt and Tisdale 1976; Miller and Wigand 1994). However, Baker and Shinneman (2004) concluded that evidence to support change in fire frequency is lacking. Fire may scar large juniper trees but it does not typically kill them (Burkhardt and Tisdale 1976; Wink and Wright 1973). However, younger trees are easily killed by fire (Burkhardt and Tisdale 1976). Therefore, it has been suggested that livestock grazing (which reduced fine fuels) and fire

suppression resulted in the expansion of this fire-sensitive tree (Barney and Frischknecht 1974; Burkhardt and Tisdale 1976; Miller and Wigand 1994).

On the Owyhee Plateau of southern Idaho, Burkhardt and Tisdale (1976) reported a decrease in fire occurrence since 1910. They attributed the change to fire suppression, the construction of roads and other artificial fire breaks, heavy grazing, and a climate shift to drier and warmer conditions. The historic fire regime was characterized by frequent fires. With the decrease in fire frequency, juniper has invaded sagebrush steppe vegetation.

Gruell (1999) studied fire histories for three diverse areas in the Great Basin. The results suggested that fire frequency varied with fine fuels and site production characteristics. For example, in Great Basin National Park, the MFI ranged from as low as eight years in an area of abundant perennial grasses to as high as 50 to 100 years on dry slopes. He also observed that the frequency and severity of fires has increased due to livestock grazing and fire suppression, which have resulted in more woody fuels and nonnative grasses.

A fire history study in Mesa Verde National Park, Colorado, indicated that there had been no change to the pinyon-juniper woodlands fire regime in that area (Floyd et al. 2000). The authors concluded that Mesa Verde National Park had a history of infrequent, large, stand-replacing fires occurring about every 400 years with a few nonlethal surface fires between times. The authors reasoned that this fire regime had not been significantly affected by recent events such as fire suppression or other management activities.

### **Disturbance History**

Pre-fire vegetation data can assist researchers in determining actual invasion or introduction of nonnative plant species related to wildfire. As previously stated, most sites in pinyon-juniper studies have experienced intensive post-European settlement disturbance, especially from livestock grazing. Many of the studies reviewed here had histories of livestock grazing and

also contained nonnative plant species, even in unburned areas (Barney and Frischknecht 1974; Koniak 1985; Ott et al. 2001). Other sites were seeded with native and nonnative plant species post-wildfire (Erdman 1970; Koniak 1985).

Ott et al. (2001) recorded *B. tectorum* at approximately 20% cover on all of their 16 unburned sites. These authors also noted that their study area had been previously disturbed by livestock grazing. *B. tectorum* occurred on 49% of the late-successional stands sampled by Koniak (1985) that were used as controls to compare to recent burns. On 7% of the sampled successional stands, *B. tectorum* had  $\geq 5\%$  cover. On 4% of the same successional stands, *S. altissimum* was present but at  $< 5\%$  cover. Eight of the burned sites had also been seeded with nonnative perennial grasses, but the author did not list these species or provide details on the livestock grazing history of any of the sites. Barney and Frischknecht (1974) did not have quantitative data on the grazing history of their sites, but stated that, in general, Utah rangelands were heavily grazed from the late 1800s to early 1900s. *B. tectorum* was found on all of the sites they used for their chronosequence study. They also mentioned that some of the sites had been aerially seeded with perennial nonnatives post-wildfire.

Seeding of perennial native and nonnative plant species often occurs after wildfires in semiarid areas to discourage *B. tectorum* invasion (Evans 1988; MacDonald 1999). Erdman (1970) studied three sites that had been burned in 1959, 1934, and 1873 in Mesa Verde National Park, Colorado. He recorded that directly after the 1959 burn, nonnative perennial grasses were aerially seeded and 30 lbs. of pinyon seeds were also planted on a one-acre plot. The 1934 fire was planted with 42,000 trees in 1942 and then 200,000 seedlings a few years later. In general, the author described the pinyon-juniper forests of Mesa Verde National Park as having “widespread” *B. tectorum*. No further evaluation of these added disturbances was provided. In the study by Koniak (1985), eight of the 21 sites were

seeded with nonnative grasses post-wildfire. *B. tectorum* had significantly lower occurrence on seeded sites than on nonseeded sites. The annual forbs *E. cicutarium* and *S. altissimum* also were significantly higher on the nonseeded sites. However, seeding was also significantly detrimental to several native species and growth forms including shrubs, grasses, and forbs. Ott et al. (2001) also observed that, in a west-central Utah study, the cover of *B. tectorum* was lowest in the site that had been seeded with perennial grasses and forbs post-wildfire.

### **Topographical and Environmental Variables**

The occurrence and population growth rate of species are likely to respond differently to topographical and environmental variables. Quantifying and evaluating such responses will improve our understanding of the response of nonnative and native plant species to wildfire. Koniak (1985) studied variation in species composition by aspect, which proved to be important for *B. tectorum*. *B. tectorum* occurred significantly more often on west-facing aspects than north-, east-, or south-facing slopes, while nonnative forbs occurred more often on south- and west-facing slopes. Ott et al. (2001) attributed the large increase in *B. tectorum* after wildfire, in part, to above-average precipitation.

### **Time Since Fire**

Two basic types of studies contained information on the responses of nonnative plant species to wildfire in pinyon-juniper woodlands. The first was chronosequence studies conducted to define long-term successional patterns in pinyon-juniper woodlands (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985). The second dealt with short-term (1- to 5-year) plant responses on individual sites (Floyd-Hannah et al. 1997; Floyd-Hannah et al. 1998; Koniak 1985; Ott et al. 2001).

### Pre-Fire Vegetation

None of the wildfire studies reviewed here recorded pre-fire vegetation (Barney and Frischknecht 1974; Erdman 1970; Floyd-Hannah et al. 1997, 1998; Koniak 1985; Ott et al. 2001), which is common in research on unplanned disturbances. However, some authors concluded that post-fire responses in pinyon-juniper would be based in part on pre-fire vegetation (Barney and Frischknecht 1974; Koniak 1985). Several authors (Dwyer and Pieper 1967; Koniak 1985; Ott et al. 2001) compared recently burned sites to adjacent unburned stands.

### Response of Nonnative Plant Species

As most of the studies found in the literature did not target nonnative plant species, it was often difficult to determine exactly how nonnative species changed over time. Results from long-term chronosequence studies (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985) suggested that nonnative plant species are present in earlier successional stages but will eventually decline to a trace or less in late successional stages approximately 60 to 100 years following wildfire. *B. tectorum* was the most commonly recorded nonnative (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985; Ott et al. 2001). However, a study after a southwestern wildfire did not note any *B. tectorum* or other nonnative plant species (Dwyer and Pieper 1967). Nonnative annual forbs commonly increased soon after wildfire (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985; Ott et al. 2001). Annual forbs and grasses varied greatly between sites and between years (Koniak 1985). Svejcar (1999) suggested that research needs to focus on several nonnative plant species (such as *Centaurea* spp.) to better understand their responses to wildfire.

Only two nonnative plant species had more than a trace of cover on three Mesa Verde National Park sites studied by Erdman (1970). On a site burned four years previously, he recorded that *S. kali* and *B. tectorum* were present (Table 6), although each had less than a mean of 4% cover. Based on 50 subplots

per site, percent frequency of *S. kali* was 46% and *B. tectorum* 42%. This site also had several nonnative grasses that had been seeded but had less than 4% mean cover. In the 29-year post-burn site, *B. tectorum* was present as a trace in 22% of the subplots. In the 90-year post-burn site, *B. tectorum* was also only a trace in 22% of subplots; however, the authors remarked that *B. tectorum* was “widespread.”

Barney and Frischknecht (1974) noted that *B. tectorum* was the only annual grass found in their chronosequence study (Table 6). *B. tectorum* cover was 12.6% in the three years following fire and declined over the three subsequent sampling periods (6, 11, and 22 years). For the remaining sampling times (36, 46, 71, 86, and 100+ years), *B. tectorum* remained sparse, measuring approximately 0.9% cover in the oldest stands. The most abundant nonnative annual forbs were *Alyssum alyssoides* (pale madwort), *Descurainia sophia* (herb Sophia/flixweed tansy-mustard), and *Salsola pestifer* (*Salsola tragus* [prickly Russian lettuce]). In general, annual forbs were most abundant three and four years following fire, after which they declined. *A. alyssoides* and *D. sophia* were present at all successional stages but were most abundant in recently burned sites.

Koniak (1985) observed that *B. tectorum* exhibited broad ecological amplitude by occurring over many successional stages and locations. It was the most frequently encountered nonnative species, found on 95% of the burned sites in Nevada and California. Koniak (1985) selected 21 post-fire sites for a chronosequence study and grouped them as early (1 year post-wildfire), early-mid (4 to 8 years post-wildfire), mid (15 to 17 years post-wildfire), and late-mid (22 to 60 years post-wildfire) successional stages. Replicates for the successional stages were as follows: early (3); early-mid (7); mid (5); and late-mid (5). She observed that *B. tectorum* cover peaked in mid-successional stages, unlike Barney and Frischknecht's (1974) and Erdman's (1970) studies where it peaked in early successional stages. Koniak also observed that *B. tectorum* had lower percent cover at late successional



stages, as did Barney and Frischknecht (1974) and Erdman (1970). She reported cover only for understory species that occurred on  $\geq 5\%$  of the actual sites. On average, *B. tectorum* cover occupied 13% in early; 76% in early-mid, 71% in mid, 48% in late-mid, and 7% in the mature forest or late successional stages. The percentage cover of *B. tectorum* in early and late successional stages did not differ significantly, but both were significantly different from cover at mid-successional stages. *B. tectorum* occurred significantly ( $P < 0.05$ ) more frequently on west-facing slopes than on north-, south-, and east-facing slopes.

Several nonnative annual forbs were also found in this study (Koniak 1985) (Table 6). In general, annual forb cover in different successional stages varied more than the other growth forms (trees, shrubs, grasses, and perennial forbs). *E. cicutarium* had only 3% cover in the early-mid, but on late-mid successional sites its cover was 60%. *L. serriola* occurred in only trace amounts at all stages. *S. altissimum* achieved an average of 30% cover in early-mid and declined to 21% cover in mid-successional stages. These three forbs occurred more often on south- and west-facing slopes.

In a three-year study following a wildfire in west central Utah, *B. tectorum* had an “explosive” early response to wildfire (Ott et

al. 2001). However, the high occurrence of *B. tectorum* coincided with above-average precipitation. In 1997, one year after fire, *B. tectorum* cover was 28.6%, 69.8% in 1998, and 54.7% in 1999. These percentages were significantly different from those in unburned plots in the second and third year when values were paired by year. *B. tectorum* density increased in all three years following wildfire from 55 stems/m<sup>2</sup> to 157 stems/m<sup>2</sup> in the second year and reaching 345 stems/m<sup>2</sup> in the third year (1999). Density of *B. tectorum* on unburned plots remained relatively stable in all three years – 84.1, 76.3, and 89.2 stems/m<sup>2</sup>, respectively. The second year following wildfire *B. tectorum* increased in the interspaces of pinyon-juniper stumps. In the third year following wildfire, *B. tectorum* increased in average percent cover in sub-canopy areas. Another nonnative grass, *Bromus japonicus* (Japanese brome), showed a decreasing trend over the same period. In the same study, some nonnative forbs increased while others showed a decreasing trend: *Camelina microcarpa* (false flax), *S. altissimum*, and *L. serriola* tended to increase while others – *Ranunculus testiculatus* (syn. *Ceratocephala testiculata* [curvedseed butterwort]), *A. alyssoides*, and *Malcolmia africana* (African mustard) – showed decreasing trends. Nonnative forb cover was not significantly different between years or between treatments

<b>Nonnative Plant Species</b>	<b>Study</b>
<i>Bromus tectorum</i> (downy brome/cheatgrass)	Erdman (1970), Barney and Frischknecht (1974), Koniak (1985), Ott et al. (2001)
<i>Salsola kali</i> (Russian thistle)	Erdman (1970)
<i>Salsola pestifer</i> - as stated in text (Russian thistle)	Barney and Frischknecht (1974), Ott et al. (2001)
<i>Alyssum alyssoides</i> (pale madwort)	Barney and Frischknecht (1974), Ott et al. (2001)
<i>Descuriana sophia</i> (herb Sophia)	Barney and Frischknecht (1974)
<i>Sisymbrium altissimum</i> (tumble mustard)	Koniak (1985), Ott et al. (2001)
<i>Erodium cicutarium</i> (redstem stork's bill)	Koniak (1985)
<i>Lactuca serriola</i> (prickly lettuce)	Koniak (1985), Ott et al. (2001)
<i>Camelina microcarpa</i> (false flax)	Ott et al. (2001)
<i>Bromus japonicus</i> (Japanese brome)	Ott et al. (2001)
<i>Ranunculus testiculatus</i> (pale butterwort)	Ott et al. (2001)
<i>Malcolmia africana</i> (African mustard)	Ott et al. (2001)
Miscellaneous nonnative grasses and forbs with trace amounts	Ott et al. (2001)

**Table 6.** Nonnative plant species documented in pinyon-juniper vegetation types following wildfire.

although percent cover was greater on burned sites. The authors concluded that not all nonnative plant species were aggressive invaders post-wildfire. They also suggested that adverse effects of nonnative plant species on native species varied (Ott et al. 2001).

A summary of the nonnative plant species reported after fire appears in Table 6. *B. tectorum* was the most commonly documented nonnative in the pinyon-juniper studies.

### Fire Severity

There is a noticeable lack of information on the relationship between wildfire severity and nonnative plant species in pinyon-juniper woodlands. Relevant literature alluded to severity, sometimes using “intensity” for fire severity, but did not quantify or stratify by severity. Erdman (1970) alluded to fire severity by describing the fire effects as “vegetation was leveled by fire” for recently burned sites, but gave no fire severity measurement. Floyd-Hannah et al. (1993), in a brief article on a wildfire, reported that researchers found an increase in nonnative plant species in “areas subjected to hot fires” in pinyon-juniper sites in Mesa Verde National Park, but did not elaborate on the definition of “hot.” Koniak (1985) recommended that effects of severity on nonnative plant species be a key component of future research.

### Conclusions

- Vegetation responses to wildfire are generally site-specific in pinyon-juniper woodlands as a result of variable pre-fire assemblages and post-fire climate, aspect, seed reserves, anthropogenic disturbances (including grazing), and other biophysical variables.
- Nonnative plant species found in pinyon-juniper woodlands were primarily annual grasses and forbs. *B. tectorum* was one of the most common nonnative grass species in this vegetation type. *S. altissimum* and *S. kali* were the most commonly documented nonnative annual forbs.
- Nonnative annual grasses and forbs may or may not dominate a site soon after wildfire.
- Nonnative annual grasses and forbs, if they

occur post-wildfire, are generally found in early and mid-successional stages. The studies suggest that they will likely decline in late successional stages. However, studies reaching this conclusion are based on chronosequence data that may not have revealed assumptions, used adequate successional stage replicates, or satisfactorily addressed site similarity issues.

- In one study, aspect was significantly related to responses of nonnative plant species; another study observed *B. tectorum* at significantly higher occurrences on west-facing aspects. In another study *B. tectorum* rapidly increased post-wildfire with above-average precipitation. The effect of environmental variables such as elevation, aspect, soil type, and post-wildfire climate on nonnative plant species establishment and reproduction needs to be addressed more directly in future studies.
- The relationship between wildfire variables – such as severity, timing, size, spatial pattern – and responses of nonnative plant species also needs further study.
- Pinyon-juniper woodlands are heavily utilized vegetation types. Co-occurring disturbances and variable disturbance histories need to be considered in evaluating the effects of wildfire on the responses of nonnative plant species in these vegetation types.

### Ponderosa Pine

Ponderosa pine (*Pinus ponderosa*) forests are traditionally considered one of the most common, nonlethal, understory-fire-regime forest types in the western United States. Ponderosa pine occurs as early seral and climax dominant species in forests from southern British Columbia to northern Mexico (Little 1971). Over the past century, ponderosa pine forests have declined in distribution throughout their range (Covington and Moore 1994a) and now occur primarily in dense stands with smaller trees (Cooper 1960; Covington and Moore 1994b). The National Biological Service (Noss et al. 1995) categorized old-growth ponderosa pine forests as endangered ecosystems in the northern Rocky Mountains, intermountain West, and eastside Cascade Mountains. This decline has been attributed to timber harvest, fire suppression, and succession to other tree species.

Increasing tree densities in ponderosa pine forests increase their susceptibility to destructive crown fires due to ladder fuels and dense conditions. Changes to late successional species, such as those in mixed-conifer forests, make such forests more susceptible to insect and disease outbreaks due to the higher susceptibility of late seral species to insects and diseases. Some researchers believe the window of opportunity for changing these conditions through ecological restoration is fairly small, perhaps 15 to 30 years (Covington et al. 1994). The intent to act on this problem was underscored in 2000 when the U.S. Forest Service published a cohesive strategy for addressing concerns about wildfire that focused on restoring ecosystems such as ponderosa pine forests (USDA 2000) that evolved with a frequent, low-intensity fire regime.

The pre-European natural fire regime in ponderosa pine forests was characterized by frequent, nonlethal, understory wildfires (Arno 1980; Cooper 1960). The actual MFI varied across ponderosa pine's range but was typically less than 30 years (Arno 1988; Gruell et al. 1982; Steele et al. 1986; Veblen et al. 2000). In western Montana, one study determined that understory fires occurred, on average, every seven years between the 1600s and the 1900s (Gruell et al. 1982). Ponderosa pine and ponderosa pine-larch stands in the northern Rocky Mountains were subjected to frequent low-intensity surface fires every 5 to 30 years (Arno 1988). A fire history study in central Idaho's ponderosa pine/Douglas-fir forest determined that MFIs were 10 to 22 years pre-1895 (Steele et al. 1986). In southwestern ponderosa pine forests, frequent surface fires probably occurred every 2 to 12 years (Cooper 1960; Weaver 1951). Researchers in the Colorado Front Range determined that, like other western ponderosa pine forests, lower-elevation ponderosa pine forests had frequent surface fires, but that higher-elevation ponderosa pine/Douglas-fir/lodgepole pine forests had much lower fire frequencies and were characterized by a mixed fire regime that included stand-replacing and surface fires (Veblen et al. 2000).

Restoration of a natural fire regime in ponderosa pine forests creates the potential for the introduction of nonnative plant species (Keeley 2004). However, the potential for stand-replacing wildfires that may occur without natural fire regime restoration may pose an even greater risk of introducing nonnative plant species, as high-severity fire severely damages the native vegetation that is adapted to an understory fire regime and not stand-replacing wildfire.

### ***Disturbance History***

Understanding wildfire and nonnative plant species' relationships is complicated by variable disturbance histories pre- and post-fire. Differences can occur at a fine scale between local stands, affecting post-fire recovery and interpretation of the effect of wildfire on nonnative plant species. Many ponderosa pine forests have a history of livestock grazing, which may confound the results of studies. Griffis et al. (2001) noted that the stands in their study had varying disturbance histories and different seed sources, which may have affected the results. In a study on the effects of a May wildfire in northern Arizona, wildfire resulted in increased forage production and temporarily increased forage quality for wildlife and livestock grazers (Pearson et al. 1972). Merrill et al. (1980) suggested that the deteriorated condition of their central Idaho study area was caused by a history of intensive wildlife and livestock grazing.

Obviously, seeding of nonnatives will have a direct impact on the post-fire nonnative vegetative component. Following a northern Arizona wildfire, the highest production increases occurred in grass and grass-like plants where nonnative grasses had been seeded (Pearson et al. 1972).

### ***Spatial Variables***

The spatial scale at which data are sampled may affect the results, yet this topic is not often addressed. However, Acton (2003) observed that across multiple scales the only consistent results were the relationship between low-severity fire and low nonnative plant species richness.

Keeley et al. (2003) observed that all of the nonnative plant species in their study colonized from adjacent source populations. They suggested that the pattern of burns may have an important effect on nonnative plant species invasion by increasing the proximity of peripheral seed sources to open sites that are often created by high-severity fires. However, the researchers caution that these open sites are also important for native flora.

### **Time Since Fire**

Without long-term research, it is difficult to determine whether the nonnative plant species establishing immediately post-fire ultimately will become invasive. Many of the nonnative plant species and wildfire studies reviewed here were conducted at one point in time and often within a few years of the wildfire (Cooper and Jean 2001; Crawford et al. 2001; Griffis et al. 2001). Crawford et al. (2001) hypothesized that the nonnative plant species identified in their study may be dominant for only a few years, and ultimately may only be a minor component of the forest. It also can be difficult to distinguish yearly variation from overall change when long-term sampling is not conducted. The cover and frequency of some nonnative plant species varied by year in a four-year study in central Idaho (Merrill et al. 1980).

Keeley et al. (2003) sampled stands that were categorized as either first-year post-fire (though some second-year burns were included) or third-year post-fire (though some four- and five-year-old burns were included). Both nonnative species richness and cover were significantly related to time since fire (Table 7). The authors concluded that persistence of nonnatives that colonize burned sites would depend on the rate and extent of canopy closure.

Griffis et al. (2001) pointed out that a shortcoming of their study was that it did not account for temporal changes, underscoring the importance of this issue. Fornwalt et al. (2003) studied nonnative plant invasions in ponderosa pine and Douglas-fir forests in Colorado and concluded that year of last fire and year of last

stand-replacing fire were not significant variables in predicting nonnative species richness or cover. They suggested this may indicate that fire effects on nonnative plant species may be short-term and not long-term.

### **Pre-Fire Vegetation**

Pre-fire vegetation data are useful for determining the role of wildfire, but are usually impossible to obtain with such unplanned disturbances. Several studies used nearby unburned sites to compare to burned sites (Cooper and Jean 2001; Crawford et al. 2001; Griffis et al. 2001; Merrill et al. 1980). However, the pre-fire vegetation composition in burned sites may have been different from the composition controls for many reasons. For example, Griffis et al. (2001) suggested that their paired control and test plot sites might have had different disturbance histories and potential seed sources. Most of the studies attempted to use unburned controls in the same general area as the burned sites to minimize variability (Crawford et al. 2001; Griffis et al. 2001; Merrill et al. 1980). Some studies selected sites with similar biophysical variables such as slope and aspect (Merrill et al. 1980).

### **Fire Severity**

Various definitions of severity and methods to determine severity were used in the relevant literature. Griffis et al. (2001) used prescribed fires, thinning treatments, and a stand-replacing wildfire to represent a range of treatment intensities from unmanaged to high-severity in a northern Arizona ponderosa pine community. They analyzed their data using ranked species abundance and richness values. The study indicated that five years post-wildfire and several years after thinning and prescribed fire, nonnative forbs increased significantly in ranked species richness and abundance with intensity of treatment. However, ranked species richness and abundance of nonnative graminoids did not significantly change with treatment intensity.

Another study in northern Arizona also noted increases in nonnative plant species richness and abundance related to increased burn sever-



ity (Crawford et al. 2001). The bulk of the increases were observed in annual forbs. Two years post-wildfire, vegetative recovery was measured once in three levels of burn severity: unburned, moderate severity, and high severity in ponderosa pine-dominated forests. “High severity” was defined as all or most trees killed. “Moderate severity” was defined as most trees having lower canopy crown scorch, but few killed. The results for each class were significantly different. Total mean cover of nonnative plant species, forbs, and graminoids was <1% in unburned stands, 59% in mixed-severity fire stands, and 116% in high-severity fire stands. Nonnative species diversity increased with fire severity; however, native species diversity did not. The authors noted that the occurrence of nonnative plant species was related to little litter and bare soil, while native plant recovery was related to moderate litter and bare soil.

Keeley et al. (2003) studied fire impacts on plant diversity and nonnative plant invasions in coniferous forests in the southern Sierra Nevada. Results for all coniferous forests were presented together though they consisted of ponderosa pine forests, generally at lower elevations, as well as mixed coniferous forests composed of white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), sugar pine (*Pinus lambertiana*), ponderosa pine, and giant sequoia (*Sequoiadendron giganteum*) – the latter at higher elevations. Burned sites experienced either wildfire or prescribed fire, but this information was not differentiated in the results. The burns occurred between 1994 and 1998, and sampling occurred in the first or third year post-fire. High-severity fires were defined as those with “heavy tree mortality,” low-severity sites were selected from adjacent sites with “little canopy tree mortality,” and control sites were adjacent to the other two treatments on slopes and aspects similar to the burned sites. There was a significant inverse relationship between the cover of all annual species and tree canopy ( $P \leq 0.001$  and  $r^2=0.30$ ). All of the annual species were not listed, but the authors stated that *B. tectorum* was a dominant component of the nonnative plants on three out of five sites. Fire

severity was significantly related to nonnative plant species richness but not cover (Table 7).

Source	SS	df	F	P
<b>Nonnative plant species richness</b>				
Severity	7.220	2	31.419	0.000
Time	7.113	1	61.905	0.000
Severity x time	1.438	1	12.506	0.000
<b>Nonnative plant cover (% understory cover)</b>				
Severity	274.675	1	1.222	0.290
Time	8827.222	2	18.023	0.000
Severity x time	920.720	1	3.780	0.050

**Table 7.** Nonnative plant species richness and cover in ponderosa pine forest from a two-way analysis of variance ( $n=2060$ ;  $1 \text{ m}^2$  subplots), from Keeley et al. (2003). SS represents sums of squares values, df the degrees of freedom, F represents the F-value, and P the probability value as given in Keeley et al. (2003).

Acton (2003) also noted that increased fire severities were related to increased nonnative plant species richness in ponderosa pine-dominated forests in west-central Idaho five years post-fire. However, this author also documented that at multiple scales the only consistent result was that low nonnative species richness was related to low-severity fires.

A study of wildfire succession in ponderosa pine and Rocky Mountain juniper communities in central Montana noted that higher severity fires resulted in increased *B. japonicus* and other nonnative species sampled four years post-fire (Cooper and Jean 2001). Three fire intensities were defined: low, medium, and high. Direct information on fire severity was not obtained, so the authors used “post-fire undergrowth survival, recovery, and differential response as an index of severity.” Areas that burned with low severity had negligible increases in nonnative plant species. High-severity fires resulted in a distinct increase in *B. japonicus* and less dramatic responses for several nonnative forbs. *Cirsium arvense* (Canada thistle) accounted for up to 15% of the canopy cover after “hot” fires. However, the authors noted that there was high variability among responses of the herbaceous component of severely burned stands. The authors did not publish their data

in the paper cited; rather, they only stated their narrative conclusions as described above.

**Response of Nonnative Plant Species**

It is difficult to determine which nonnative plant species are the most invasive after wildfire since not all studies report responses by nonnative plant species. Some used broad categories such as nonnative forbs or graminoids. The same species are not all present at each study site. Among the research reviewed, a few studies noted greater increases in nonnative forbs than nonnative graminoids as a short-term response to wildfire (Crawford et al. 2001; Griffis et al. 2001). The most common nonnative graminoids found post-wildfire were the annual bromes *B. tectorum* and *B. japonicus* (Cooper and Jean 2001; Crawford et al. 2001; Merrill et al. 1980).

Griffis et al. (2001) found that the ranked species richness of nonnatives forbs increased with treatment intensity, and nonnative forb ranked abundance was significantly different between all treatments and wildfires (Table 8). Nonnative graminoid responses were not significantly different among treatments when the sites were sampled in the summer of 1999, but time since treatment varied. (Unmanaged stands had not had density treatments for 30 years, thinned and prescribed burns had occurred 3 to 4 years previously, thinned stands had been treated between 6 and 12 years previously, and other stands had experienced stand-replacing wildfires within the previous five years).

Crawford et al. (2001) determined that annual forbs accounted for the overall increase in nonnatives two years after wildfire (Table 9). The most common nonnative species included *B. tectorum*, *Chenopodium album* (lambsquarters), *Conyza*

<b>Nonnative plant group</b>	<b>Unmanaged</b>	<b>Thinned</b>	<b>Thinned and prescribed burn</b>	<b>Wildfire</b>
Nonnative forbs – ranked abundance	<5a	<5a	~5a	~50b
Nonnative forbs – ranked sp. richness	<2a	<2a	~4b	~7c
Nonnative graminoids	No significant response			

**Table 8.** Nonnative plant group responses to unmanaged, thinned, thinned and prescribed burn, and wildfire, from Griffis et al. (2001). Different letters after value indicate rank numbers were significantly different.

<b>Nonnative Plant Species</b>	<b>Plant group</b>	<b>Unburned (%)</b>	<b>Mixed severity (%)</b>	<b>High severity (%)</b>
<i>Bromus tectorum</i> (cheatgrass)	Annual grass	<0.5	3	19
<i>Bromus inermis</i> (smooth brome)	Perennial grass	<0.5	2	<0.5
<i>Chenopodium album</i> (lambsquarters)	Annual forb	<0.5	11	39
<i>Conyza canadensis</i> (Canadian horseweed) *	Annual forb	-	27	18
<i>Dactylis glomerata</i> (orchard grass)	Perennial grass	-	<0.5	1
<i>Lactuca serriola</i> (prickly lettuce)	Annual forb	-	1	2
<i>Lappula occidentalis</i> (flatspine stickseed) *	Annual forb	-	<0.5	4
<i>Melilotus officinalis</i> (yellow sweet clover)	Annual forb	<0.5	<0.5	1
<i>Poa pratensis</i> (Kentucky bluegrass)	Perennial grass	-	1	2
<i>Salsola kali</i> (Russian thistle)	Annual forb	-	<0.5	24
<i>Taraxacum officinale</i> (dandelion)	Perennial forb	<0.5	11	1
<i>Teloxys graveolens</i> (fetid goosefoot) *	Annual forb	<0.5	1	<0.5
<i>Verbascum thapsus</i> (common mullein)	Annual forb	<0.5	1	5

**Table 9.** Nonnative plant species with at least 0.5% mean cover in unburned, mixed-, and high-severity fire ponderosa pine sites, from Crawford et al. (2001). Values equal mean percentage cover of nonnative species.

\*Species considered as native by the USDA/NRCS PLANTS Database for the state in which the study took place.

*canadensis* (Canadian horseweed), and *S. kali* (Table 9). In mixed-severity fires, annual forbs had 42% canopy cover and perennial forbs had 11% canopy cover. In high-severity fires, annual forbs had 93% canopy cover and perennial forbs had 1% canopy cover. In contrast, in mixed-severity fires, annual (primarily *B. tectorum*) and perennial grasses had 3% cover each. In high severity stands, annual grasses had 19% canopy cover and perennial grasses had 3% cover.

In a study of first- and third-year post-fire responses to wildfire in the southern Sierra Nevadas (Keeley et al. 2003), *B. tectorum* was determined to be the dominant nonnative plant species in coniferous forests at lower elevations. All nonnative plant species in this study represented only 0.3% of understory plants in unburned and 3.4% in burned coniferous forests. Thus the authors concluded that, at the time of the study, nonnative plant increases were not a major problem after wildfire on forest sites.

In a ponderosa pine-Rocky Mountain juniper plant association in Montana, Cooper and Jean (2001) found a marked increase in *B. japonicus* with increased fire intensity and lesser increases in nonnative forbs four years after a wildfire burned the area (Table 10). The most significant forb to increase was *C. arvense*.

All of the studies cited above were conducted at one point in time post-fire. The response of annual versus perennial plants may vary over time following wildfire. Thus, it must be remembered that the results of the studies may be relevant only to the point in time in which they were conducted.

In a study with more than one year of sampling following fire (two years for cover and four years for production), Merrill et al. (1980) recorded significant differences in yield (g/m<sup>2</sup>) for annual grasses (primarily *B. tectorum*) between unburned and burned sites the first season following fire. The second year there was no difference in annual grass production between burned and unburned sites, but in the third and fourth years, annual grass production was significantly higher on the burned sites, although the yields for these two years were significantly less than the first year (Table 11). The authors remarked that canopy cover of *B. tectorum* was almost twice as great on burned than on unburned sites in 1974 and 1976. However, it appears from their data that there was a great deal of variability among the seven sites and no conclusive difference between *B. tectorum* on burned and unburned sites in the 1976 results (Table 11).

<b>Nonnative Plant Species</b>	<b>High severity wildfire response</b>
<i>Bromus japonicus</i> (Japanese brome)	Dramatic increases
<i>Cirsium arvense</i> (Canada thistle)	As much as 15% canopy cover
<i>Cirsium vulgare</i> (bull thistle)	The remaining species are in approximate order of decreasing importance.
<i>Lactuca serriola</i> (prickly lettuce)	
<i>Melilotus officinalis</i> (yellow sweet clover)	
<i>Lepidium</i> spp. (pepperweeds)	
<i>Collomia linearis</i> (tiny trumpet)	
<i>Sisymbrium altissimum</i> (tumble mustard)	
<i>Filago arvensis</i> (field cottonrose)	
<i>Descurainia pinnata</i> (western tansy mustard)	
<i>Descurainia sophia</i> (herb Sophia)	
<i>Tragopogon dubius</i> (yellow salsify)	
<i>Euphorbia serpyllifolia</i> ( <i>Chamaesyce serpyllifolia</i> ssp. <i>hirtella</i> ) (thyme-leaf sandmat)	
<i>Conyza canadensis</i> (Canadian horseweed)	

**Table 10.** Responses of nonnative plant species to high severity fires, from Cooper and Jean (2001).

Nonnative Plant species	Plant group	1974	1974	1976	1976
		% cover $\pm$ SD Burned	% cover $\pm$ SD Unburned	% cover $\pm$ SD Burned	% cover $\pm$ SD Unburned
<i>B. tectorum</i> (cheatgrass)	Annual grass	24 $\pm$ 12	9 $\pm$ 12	10 $\pm$ 6	6 $\pm$ 9
<i>Rumex acetosella</i> (common sheep sorrel)	Perennial forb	Trace $\pm$ 1	Trace	2 $\pm$ 3	1 $\pm$ 2
<i>Tragapogon</i> spp. (salsify)	Perennial forb	2 $\pm$ 2	1 $\pm$ 1	1 $\pm$ 1	2 $\pm$ 1

**Table 11.** Mean percent canopy coverage of the three most frequently encountered nonnative plant species on seven paired plots in the Selway-Bitterroot Wilderness, Idaho, from Merrill et al. (1980). SD = standard deviation.

### Environmental Variables

Post-wildfire environmental conditions may be an important factor in determining responses of nonnative plant species. After a fall wildfire in central Idaho, annual forb production increased dramatically the first year post-fire and then appeared to vary with environmental conditions (Merrill et al. 1980). Cooper and Jean (2001) described *B. japonicus* as having a dramatic increase after wildfire when conditions had been “relatively dry.” They noted that this contrasted with the results from Whisenant and Uresk (1990) who studied *B. japonicus* responses to prescribed fire in Badlands National Park in South Dakota. Whisenant and Uresk (1990) concluded that April burns had the greatest negative effect on *B. japonicus* abundance after below-average precipitation.

Keeley et al. (2003) analyzed the relationship between elevation and the richness and cover of nonnative plant species. Generally, there were more nonnative plant species and greater cover of those species in the lower-elevation sites (Table 12). However, the coefficient of determination ( $r^2$ ) or amount of variation in richness and cover that could be accounted for by changes in elevation was low, indicating that elevation contributed only a small amount to the variation in richness and cover between

sites. The dominant nonnative plant in the Cedar Grove, Lewis Creek, and Mineral King sites was *B. tectorum* (Table 12). *B. tectorum* was not common at the two highest-elevation sites.

### Conclusions

- Higher-severity burns were related to increases in nonnative plant species. In all the studies, increases of nonnative species occurred within five years of wildfire and so were representative of only short-term responses. However, no studies were conducted for more than five years.
- Several studies showed greater increases in nonnative forbs than nonnative graminoids in the short term after wildfire.
- Many of the study sites had a history of livestock grazing, but the frequency, intensity, or variability by site of grazing was not documented.
- Most of the studies used adjacent unburned sites as controls to compare to burned sites. Among the studies, little detailed information existed on conditions of plots pre-fire, such as vegetation composition and disturbance (e.g., grazing histories).
- Most of the sites that experienced wildfire had moderate- and high-severity fires, which are not typically considered the natural fire regime for ponderosa pine forests. Some studies used prescribed fire and thinning treatments to create burns of varying severities. It may

Parameter	Cedar Grove	Lewis Creek	Mineral King	Giant Forest	Sugarloaf	P
Mean elevation (m)	1480	1884	1975	2050	2170	<0.001
# sites	38	16	13	18	18	
<i>Nonnative plant species richness (#/1000 m<sup>2</sup>)</i>						
	1.6	0.7	1.2	2.2	0.3	<0.001
<i>Nonnative plant species cover (% of understory cover)</i>						
	10	0.1	0.0		0.6	<0.001

**Table 12.** Comparisons of nonnative plant species richness and cover averaged across burned and unburned plots at five different sites. P values from one-way analysis of variance. From Keeley et al. (2003).

be appropriate to study the effects of wildfires occurring outside the natural range of severity considering that ponderosa pine forests' fire regimes have changed from lower predominantly severity before European settlement to high-severity fires after European settlement. Such higher-severity fires are likely to continue without considerable intervention. However, responses of nonnative plant species to naturally occurring low-severity wildfires should also be studied to understand how a natural fire regime in ponderosa pine will affect nonnative plant species.

- Most of the studies reviewed were conducted in Arizona. Considering the broad range of ponderosa pine forests, more studies are needed in other areas such as the northern Rocky Mountain region and under diverse environmental conditions and wildfire characteristics.
- Long-term studies that consider the landscape/environmental variation would help to determine which areas are invaded by nonnative plant species and where these species become invasive. These data would help managers prioritize eradication or management of nonnative plant species after fire.
- More information is needed on the effects on nonnative plant species of restoring fire regimes to help guide the reintroduction of a natural fire regime to ponderosa pine forests.

### **Lodgepole Pine and Spruce/ Sub-alpine Fir**

Several coniferous forest types in the western United States have historically experienced periodic stand-replacing wildfires. In *The Effects of Fire on Flora*, Arno (2000) associated seven forest types with stand-replacing fire regimes in this region. These types are coastal Douglas fir, coastal true fir/mountain hemlock, interior true fir/Douglas-fir/western larch, Rocky Mountain lodgepole pine, western white pine/cedar/hemlock, spruce/sub-alpine fir/white-bark pine, and aspen. Most of the information available on the responses of nonnative plant species to stand-replacing wildfires in western forests is from studies on lodgepole pine and spruce/sub-alpine fir forests.

Several of the studies reviewed here included fire effects on nonnative plant species in both lodgepole pine and spruce/sub-alpine fir forests

in the same study so they will be addressed concurrently in this section. Lodgepole pine occurs in the middle- to high-elevation zones of the inland West from the Yukon Territory to southern Colorado. In the inland West from central British Columbia to New Mexico, spruce/sub-alpine fir forests occur in high-elevation zones. Lodgepole pine occurs on the broad plateaus while sub-alpine fir and spruce forests occur in the more mesic areas such as ravines in the greater Yellowstone area (Romme and Knight 1981). The forest types or habitat types reviewed in this section varied somewhat depending on the study, though several are based in the greater Yellowstone area (Anderson and Romme 1991; Doyle et al. 1998; Romme et al. 1995; Turner et al. 1997). All contained either spruce/sub-alpine fir or lodgepole pine or both. Some of the sites contained western larch and Douglas-fir cover pre-fire, but were considered sub-alpine fir habitat types. All of the sites appeared to have a history of infrequent stand-replacing fires.

Various MFIs have been reported for lodgepole pine and spruce/sub-alpine fir forests throughout their range. Romme (1982) concluded that stand-replacing fires occurred on average every 300 to 400 years in Yellowstone National Park. In other parts of the northern Rocky Mountains, fire return intervals for sub-alpine stands have been reported as much lower – from 22 to 153 years (Arno 1980). Within sub-alpine forests, lodgepole pine stands tend to burn more frequently than the adjacent spruce/sub-alpine fir stands. Romme and Knight (1981) determined that the MFI for spruce/sub-alpine fir drainage bottoms was longer than the 300 years in the adjacent lodgepole pine forests. Lodgepole pine forests may also experience mixed-severity fires but those sites were not addressed. Barrett (2000) identified several stands of lodgepole pine in the montane and lower sub-alpine zones of central Idaho that had burned in a mixed-severity fire regime.

Brown et al. (1994) found several variations of fire regimes and MFIs while conducting fire histories in central Idaho (Table 13). The authors also compared the area of pre-European



Forest Type	Pre-European Settlement MFI	Fire Regime
Lodgepole pine/sub-alpine fir	112	Stand-replacing fires
Lodgepole pine/sub-alpine fir	47	Understory and mixed
Whitebark pine/sub-alpine fir forests	180	Stand-replacing
Whitebark pine/sub-alpine fir forests	56	Understory and mixed
Alpine larch-englemann spruce/sub-alpine fir	166	Stand-replacing
Engleman spruce/Douglas-fir/lodgepole pine/sub-alpine fir	166	Stand-replacing

**Table 13.** Pre-European settlement mean fire return interval (MFI) and fire regime type, from Brown et al. (1994).

settlement and recent burns and concluded that the area that had experienced pre-European settlement stand-replacing fires was 1.7 times greater than the area that had experienced recent wildfires for the upper-elevation fire regime types.

Fire suppression appears to have affected those forests that had historically shorter MFIs, typically shorter than the period over which fire suppression has been conducted. Barrett et al. (1991) concluded that fire suppression had altered fire regimes in the drier areas of western larch-lodgepole pine forests that had historic MFIs of 25 to 75 years versus the moister forests of the same type with longer MFIs of 140 to 340 years. In contrast, fire suppression activities appeared not to have affected sub-alpine fir forest fire regimes because of the difference between the relatively short period of active fire suppression and the much longer interval between fires in Yellowstone National Park (Romme 1982).

Fire behavior varies within the same forest type due to topography and environmental conditions (Arno 1980). Barrett et al. (1991) determined that fire regimes for western larch-lodgepole pine forests in Glacier National Park consisted of 25- to 75-year MFIs and mixed-severity fires in the drier, gentler topographical areas while the wetter and more rugged areas of the park saw infrequent, stand-replacing fires with MFIs of 140 to 340 years.

### **Time Since Fire**

Long-term studies are especially useful for observing changes in understory vegetation (Stickney 1980) and provide an indication of the persistence of nonnative species after wildfire. Several of the studies reviewed here

focused on early successional changes post-wildfire (Benson and Kurth 1995; Romme et al. 1995; Turner et al. 1997) (Table 14). Turner et al. (1997) commented that although sites that experienced crown fire had provided the greatest opportunity for opportunistic species (those not present in pre-fire vegetation) to invade soon after the wildfire, the three-year study did not show whether or not they would persist.

A few studies observed changes for a longer time period, between 9 and 17 years post-wildfire (Doyle et al. 1998; Lyon and Stickney 1976; Stickney 1980). Stickney (1980) found only 1% cover of *Cirsium vulgare* (bull thistle) in years seven and eight of a nine-year study, declining to insignificant cover by the final year of the study. Doyle et al. (1998) observed that although *C. arvense* increased to approximately 5% cover nine years into the study, it ultimately decreased to 1% by 17 years following wildfire. *Taraxacum* spp. steadily increased in severely burned areas to 10% cover in the seventeenth, and final, year of the study, but showed only a slight increase in moderately burned areas in Grand Teton National Park.

### **Fire Severity**

Vegetation recovery following wildfire depends upon the interaction between fire severity and plant regeneration strategies (Miller 2000). Native species in Rocky Mountain lodgepole pine and spruce/sub-alpine fir forest types have evolved with stand-replacing fires and have various strategies for reproduction post-wildfire. However, high-severity fires may reduce pre-fire vegetation and provide opportunities for different species to enter the community (Turner et al. 1997).

Although stand-replacing fires characterize these forest types, a mosaic of fire severities – including unburned areas, severe surface burns, and severe canopy burns – still occurs within any fire (Turner et al. 1997). The lack of uniform fire severity definitions among studies makes it difficult to compare and summarize fire severity effects. Doyle et al. (1998) used three categories for fire severity: unburned, moderate, and severe. They defined “moderate severity” areas to be those with greater than 40% canopy of trees alive one year post-fire, and defined “severe” areas as those where all trees were killed and aboveground understory species consumed. Turner et al. (1997) divided severe burns into severe surface burns and crown fire. “Severe surface burns” were defined as areas where the canopy needles were not consumed in the wildfire, leaving a layer of litter post-fire. “Crown fires” were defined as areas where the canopy needles were consumed in the wildfire. They also defined “light surface burn areas” where the stems were scorched, though the canopy survived and the soil organic layer was not consumed. Unfortunately, some studies did not indicate burn severity at all so data from different fire severity areas are presumably combined (Benson and Kurth 1995; Lyon and Stickney 1976; Stickney 1980).

### **Pre-Fire Vegetation**

Adjacent unburned sites were often used as reference sites to indicate which plants would have been present in the pre-fire vegetation (Benson and Kurth 1995; Doyle et al. 1998; Turner et al. 1997). In general, pre-fire vegetation may be the most important indicator of post-fire vegetation (Doyle et al. 1998). Most of the plant species found on a site previous to wildfire will reestablish soon after wildfire (Anderson and Romme 1991; Doyle et al. 1998; Lyon and Stickney 1976; Turner et al. 1997). Lyon and Stickney (1976) concluded that initial vegetation following wildfires in the northern Rocky Mountains was dominated by species that were present pre-fire. Anderson and Romme (1991) came to similar conclusions in a study in Yellowstone National Park. At all their sites one year post-fire, the vegetation was largely the same as pre-fire vegetative composition.

Turner et al. (1997) acknowledged that there are problems with using reference sites as controls in wildfire studies since they are defined after the event. Instead of using before-and-after data, the authors compared the initial effects of the wildfire and subsequent recovery of vegetation. This approach was recommended as possibly more useful by Wiens and Parker (1995) than the before-and-after studies.

Turner et al. (1997) concluded that this was a valid approach for answering their questions regarding the effects of disturbance size and pattern in early vegetation succession post-fire. They studied two nonnative plant species, *C. arvensis* and *L. serriola*. *C. arvensis* was common along trails and roads in Yellowstone National Park; however, they stated that it was not in most of the burnt areas before the wildfire. *L. serriola* was not noticeable in the adjacent unburned sites. Therefore, the authors hypothesized that these species and other opportunistic species would invade the open sites created by the wildfire.

### **Response of Nonnative Plant Species**

Only one study clearly indicated that one of the primary objectives of the research was to document the responses of nonnative plant species to wildfire (Benson and Kurth 1995). The other studies were primarily focused on general early vegetative responses to wildfire and patterns of succession (Anderson and Romme 1991; Doyle et al. 1998; Lyon and Stickney 1976; Romme et al. 1995; Stickney 1980; Stickney 1990). Turner et al. (1997) focused on relating spatial characteristics of fire to early vegetation succession. In that study, responses of only two nonnative species, *C. arvensis* and *L. serriola*, were recorded and no information was provided on other nonnative species, if there were any.

*C. arvensis* was the most commonly observed or studied post-fire nonnative species in the relevant studies (Benson and Kurth 1995; Doyle et al. 1998; Romme et al. 1995; Turner et al. 1997). It was defined mainly as an opportunistic or transient species that was not present or was scarce in the mature forest or in unburned sites (Doyle et al. 1998; Turner et al.

1997). This does not necessarily indicate that it is the most abundant or invasive species after wildfire, but that the most information exists on its response to wildfire in these forests.

The study that reported the highest number of nonnative plant species post-fire (Benson and Kurth 1995) was conducted in old-growth Douglas-fir, dog-hair lodgepole pine, and Englemann spruce sites in the North Fork Valley of the Flathead National Forest in Montana. The researchers presented the total number of species for all forest types in the study by bulldozer lines, burned areas, and adjacent unburned sites. Twenty-three nonnative plant species were observed in the bulldozed plots, five in the burned plots, and three in the undisturbed areas.

No consistent pattern of responses of nonnative plant species to wildfire in natural areas was discernable from the few studies that have been conducted. Studies showed negligible amounts of *C. vulgare* (Anderson and Romme 1991) and *Phleum pratense* (timothy) (Stickney 1980) soon after wildfire. Short-term increases of *C. arvensis* were observed (Doyle et al. 1998; Turner et al. 1997), followed by an eventual long-term decrease after 17 years (Doyle et al. 1998). *Taraxacum officinale* (dandelion) showed a long-term increase (Doyle et al. 1998). *L. serriola* initially increased then decreased within three years of wildfire (Turner et al. 1997).

Doyle et al. (1998) concluded that moderate-severity burns had higher percentage cover of sprouting forbs and shrubs (which they termed "persistent" in this study) than did high-severity burns, whereas species establishing from seed, termed "transient," were more abundant in high-severity stands. The two nonnative species in this study were *C. arvensis* and *Taraxacum* spp., both transient species, which the authors believed were introduced from off-site seed sources since the species were absent in the adjacent mature forest. Although *C. arvensis* established two to three years post-fire, it increased to 5% on both severe and moderately burned sites, then declined to 1% cover on severely burned sites, and to only a trace

in moderately burned sites by the seventeenth year after fire. In the moderately burned sites, *Taraxacum* spp. were recorded as a trace the first year following fire and were not recorded again until the eighth year when they provided a 1% cover, which was the same for the final (seventeenth) year of sampling. In the severely burned sites, *Taraxacum* spp. were recorded in trace amounts in the second and third year and then increased to 7% by the eighth year and 10% in the final year of the study.

To analyze vegetation responses to wildfire, Turner et al. (1997) used a repeated measures analysis of variance (ANOVA). This method was used to minimize errors due to pseudoreplication resulting from the inability to replicate the wildfire. They statistically analyzed density of *C. arvensis* and *L. serriola*, and trends in between-subject effects of their Yellowstone National Park data from 1990 to 1993 in areas that had been burned in the 1988 fires. (The between-subject effects included year, location, patch, burn severity, slope, distance to light surface burn, distance to severe surface burn, aspect, location x patch, location x burn, patch x burn, and location x patch x burn). Site locations included Cougar Creek, Fern Cascades, and Yellowstone Lake. Patch sizes were described as large, moderate, and small. The burn severity categories were light surface burn, severe surface burn, and crown fire. *C. arvensis* and *L. serriola* were selected to represent opportunistic species; i.e., species relatively absent in the pre-fire vegetation. The amount of variation in density of *C. arvensis* accounted for by all of the predictor variables was an  $r^2$  of 0.30, indicating that only about a third of the variation in density of this species could be accounted for by changes in the predictor variables. The analysis indicated that *C. arvensis* densities were increasing by year. *C. arvensis* was denser in crown-fire sites than severe surface burn sites, which in turn had denser *C. arvensis* than light-surface-burn sites. This species had highest densities at the Yellowstone Lake site. The other variables were not significant. *C. arvensis* continued to increase over the four years of the study (1990 to 1993) in all burn severities. The fourth year of the study, *C.*

*arvensis* had an average of approximately 800 stems/ha in the crown-fire areas. The amount of variation in density of *L. serriola* explained by the predictor variables was less than that explained for *C. arvensis* ( $r^2 = 0.19$ ), with only two significant variables: density of *L. serriola* increased with burn severity but was also positively related to distance to severe-surface burns. Density of *L. serriola* remained low in the light-surface burns throughout the period of the study. However, *L. serriola* reached around 100 stems/ha in the severe-surface burns and crown-fire stands in 1991 and then decreased to less than 50 stems/ha by the end of the study in 1993.

Anderson and Romme (1991) also studied the effects of wildfire on vegetation in Yellowstone National Park following the 1988 wildfires. They selected paired plots in severe and moderate-severity burns and measured density of vascular plants one year following the fire. *P. pratense* was the only nonnative species identified in the publication. Out of seven paired sites, it was only found on one moderate-severity site at an average density of 0.02 individuals/m<sup>2</sup>.

After a stand-replacing wildfire in sub-alpine fir habitat type in Montana, only one of three sites had any nonnative plant species throughout the nine years of surveys (Stickney 1980). At this site, *C. vulgare* was recorded at 1% cover in years 7 and 8, but was not present in years 1 through 6, nor in the ninth year after fire. The exact definition of burn severity was not given for the sites except that the wildfire was stand-replacing with no surviving trees or stump cover.

### **Post-Fire Regeneration Strategy**

Post-fire vegetation regenerates or germinates from on-site propagules as well as off-site propagule sources. It is important to identify the source of nonnative plant species propagules post-fire in order to understand their ability to persist or invade and establish after fire. Different regeneration strategies may require different management actions. Authors use various terms to describe regeneration from

on-site and off-site sources (Doyle et al. 1998; Stickney 1990; Turner et al. 1997). Stickney (1990) defined three groups: survivor, a plant that regrows from vegetative parts that did not die in the fire; residual colonizer, which grows either from cones in the crowns of on-site trees or seeds surviving in the soil; and off-site colonizer, which establishes from seeds dispersed from surrounding unburned sites. Doyle et al. (1998) grouped plant species as “persistent” or “transient.” Persistent species are those found in the first year post-fire and in the mature forest. Transient species are those that are short-lived in burned areas and absent in the mature forest. Turner et al. (1997) categorized the plants in their study as “forest species” if they grew from vegetative parts or from seeds that were present before the fire and “opportunistic species” if the plants were absent or incidental before the fire.

Stickney (1990) suggested that, in general, more severe fires will result in less on-site regeneration from resprouting or surviving seeds because of the damage to these sources by wildfire. He suggested that the ability of off-site sources to colonize burned sites is related to several circumstances coinciding: a seed crop, a dispersal event, and a burn site. Stickney (1986; 1990) also concluded that off-site sources will establish post-fire but will have little effect on succession of the initial post-fire community. In a discussion on general post-wildfire vegetation, Lyon and Stickney (1976) concluded that the survival of on-site seeds was part chance and that off-site seed introduction was unpredictable. They observed that few species introduced from off-site sources could dominate the site except trees and species that could regenerate from both root-crown regrowth and off-site seeds.

The most commonly observed or studied post-fire nonnative plant species among these studies was *C. arvensis* (Benson and Kurth 1995; Doyle et al. 1998; Romme et al. 1995; Turner et al. 1997). Although *C. arvensis* was introduced from off-site seed sources in these studies, it is capable of resprouting from crowns post-wildfire (Romme et al. 1995).

In their study of post-fire regeneration in Grand Teton National Park, Doyle et al. (1998) noted that none of the species arriving after the first year had greater than 5% cover in the moderate burn over the course of the 17-year study. The authors suggested that both the *C. arvense* and the *Taraxacum* species' seeds had been dispersed long distances to the burn since they were absent or scarce in adjacent, unburned areas and have light, wind-dispersed seeds. In contrast, Bakker (1960) as cited by Wilson (1979) observed that *C. arvense* wind dispersal is not highly efficient because the pappus breaks off easily. However, he noted that its seed might remain viable in the soil for 20 years or longer.

Turner et al. (1997) determined that most post-fire plant species cover was from on-site resprouting. They studied *C. arvense* and *L. serriola*, which were transient, absent, or scarce in the pre-burn community and thus were thought to establish from off-site seed sources.

Anderson and Romme (1991) studied six paired moderately and severely burned sites for the first year following wildfire in Yellowstone National Park. The following proportion of individual vascular plants by sources of reestablishment or introductions was recorded: 67% were considered to be from vegetative regrowth, 29% from seed stored in the canopy (lodgepole pine), 1.7% from an unknown source, 1.5% from seed stored in soil, and 0.8% from seed dispersed from an off-site source. *P. pratense*, the one nonnative species identified to species in this study, reestablished on only one out of the seven sites. It established through vegetative regrowth.

### **Spatial Variables**

Turner et al. (1997) included several spatial variables related to fire size and pattern, as explained above. From among these variables, they found that location was a significant factor in predicting the density of *C. arvense*; density of *C. arvense* was greater at Yellowstone Lake (approximately 1100 stems/ha) than at the other two sites. Location was not significant in predicting *L. serriola* density.

### **Fire Management Activities**

Fire suppression and rehabilitation activities to reduce the risk and impact of wildfire may inadvertently introduce nonnative plant species and therefore warrant further investigation. Although not clearly described, post-fire vegetation recovery was "compromised" in several study plots by rehabilitation management activities in the Bitterroot National Forest (Lyon and Stickney 1976). Benson and Kurth (1995) observed vegetation recovery on rehabilitated bulldozer lines after a wildfire in Glacier National Park. The results indicated that nonnative plant species were more abundant on bulldozer lines than in adjacent burned and undisturbed forests. Unfortunately, the sites were not clearly paired based on key environmental characteristics such as slope, aspect, and vegetation similarities so it would be difficult to attribute the differences to the treatments alone.

### **Conclusions**

- Most stand-replacing fires and studies of nonnative plant species in natural areas have occurred in Rocky Mountain lodgepole pine and sub-alpine fir and spruce habitats.
- Most of the studies were not focused specifically on the responses of nonnative plant species to wildfire.
- Most of the studies used adjacent unburned stands as controls. Little pre-fire vegetation information existed for any of the study areas.
- Higher severity fires were related to greater increases in nonnative plant species in the short-term.
- The most commonly observed/studied nonnative plant species were *C. arvense* or other thistle species.
- Most of the nonnative plant species observed following wildfire established from off-site seed sources, if the studies indicated the seed source. However, most of the overall vegetation post-fire came from regeneration of on-site vegetation.
- Several studies observed short-term, early-successional changes post-fire and therefore could not confirm the persistence of the nonnative plant species observed.
- The few long-term studies show both eventual decline of *Cirsium* spp. and an increase in cover of *Taraxacum* spp.



- One study evaluated the effect of spatial variables on nonnative species following wildfire and found that location was a significant predictor of *C. arvensis* density. Future research should incorporate spatial variables in studies and analyses.
- One study concluded that bulldozing for fire suppression was significantly related to nonnative plant species abundance. More research is needed on the effect of fire suppression and rehabilitation on nonnative plant species in lodgepole pine/sub-alpine fir and spruce habitats.



# CONCLUSION

In synthesizing the peer-reviewed literature on the response of nonnative plant species to wildfire in predominantly natural areas, we have identified a developing body of information with little consistency in the findings. Identification of key variables and methods for researching the responses of nonnative plant species to wildfire are still evolving. Much of the scientific information available concerning nonnative plant species and wildfire is observational and/or descriptive, which makes it challenging to interpret exactly how the many different processes and variables affect nonnative plant occurrence and invasion.

Overlapping issues emerged from our review which inhibit one from drawing conclusions or generalizations about wildfire and nonnative plant species invasions. D'Antonio (2000) made a similar statement and listed the following issues: Wildfire characteristics and vegetation responses are extremely variable within any one fire, and fire intensity and severity are rarely quantified or lack consistent criteria in their estimation. Pre-fire conditions are often not known or reported in many of the descriptive studies. There is no consensus on the definition of "invasion" (D'Antonio 2000). In addition, wildfires are often accompanied by anthropogenic disturbances resulting from fire suppression activities, which may increase the amount of suitable habitats for invasion of ruderal nonnative species.

Wildfire should not be considered independently as a disturbance influencing nonnative plant species invasion. In many of the relevant studies, wildfire disturbance was not separated from other forms of disturbance and the intentional introduction of plant species that often follow wildfire. The effect of each different type of disturbance as well as their cumulative effects must be evaluated if we are to accurately predict the responses of nonnative plant species to different combinations of disturbance. All of these issues contribute to the confusion about factors that drive nonnative plant species invasion.

To address these issues, we extracted information from each study on wildfire characteristics and the measurements or definitions used, especially for fire severity. We also extracted information on issues that we considered relevant to determining invasion of nonnative plant species such as the persistence of nonnative plant species that were introduced following wildfire and the dominance of these plants in the composition of the native vegetation.

A general difficulty with synthesizing information on the responses of nonnative plant species to wildfire is that many studies are not focused specifically on nonnative plant species. Thus it was not always apparent whether all nonnative plant species at a site were recorded. As a result, processes or activities that could be driving nonnative species dispersal, establishment, and survival were not necessarily addressed. For example, most stand-replacing fires and nonnative plant species studies in natural areas have occurred in Rocky Mountain lodgepole pine, sub-alpine fir, and spruce habitats. Only one study reviewed for stand-replacing fire regimes in forests clearly indicated that one of the primary objectives of the research was to document responses of nonnative plant species to wildfire (Benson and Kurth 1995). The other studies primarily focused on general early vegetative responses to wildfire and patterns of succession (Anderson and Romme 1991; Doyle et al. 1998; Lyon and Stickney 1976; Romme et al. 1995; Stickney 1980; Stickney 1990).

We also were cautious about determining whether a site was "natural." We defined natural as being composed of predominantly native vegetation with little or no anthropogenic disturbances. Since many authors were not necessarily researching the response of nonnative plant species to wildfire, the condition of the pre-fire site was not always clearly stated. Thus, we were as selective of studies that used natural sites as the information reported allowed.

In the following paragraphs we have synthesized the information from all of the sections in the review as they relate to the key questions described in the Approach and Methods section. Some of the key questions were combined because the answers were interrelated.

**Which nonnative plant species are most invasive after wildfire in natural areas? In natural areas with predominantly native vegetation, do existing nonnative plant populations increase or decrease after wildfire? Which existing nonnative plant populations increase or decrease after wildfire? Do wildfires contribute to the dominance of nonnative plant species in natural areas?**

The overall goal of this review was to synthesize information on the role of wildfire in the introduction or expansion of nonnative plant species in natural areas. “Natural areas” were defined as sites with predominantly native vegetation and little or no anthropogenic impact. Nonnative plant species populations were generally only a minor component of the plant community. To determine whether a species was introduced, it was necessary to know whether it existed on-site prior to the wildfire. If it did, it was important to have some measure of the populations of the nonnative plant species before the fire to determine the extent of expansion. Although this scenario would be optimal, such data were rarely available because wildfires are unplanned events. As a consequence, adjacent unburned sites were frequently used as reference sites to indicate which species were present in the pre-fire vegetation (Beatley 1966; Benson and Kurth 1995; Brooks and Matchett 2003; Brown and Minnich 1986; Callison et al. 1985; Cave and Patten 1984; Christensen and Muller 1975; Cook et al. 1994; Cooper and Jean 2001; Crawford et al. 2001; Doyle et al. 1998; Dwyer and Pieper 1967; Griffis et al. 2001; Koniak 1985; Merrill et al. 1980; O’Leary and Minnich 1981; Ott et al. 2001; Rogers and Steele 1980; Safford and Harrison 2004; Turner et al. 1997; Tyler 1995). Using adjacent reference sites was practical and probably representative of pre-fire vegetation, especially when numerous edaphic site variables were matched between unburned

and burned sites. However, when a nonnative plant species was found in the burned area and not in the unburned site, it was not irrefutable proof that a new introduction had occurred.

Another goal of this review was to identify which nonnative species were most invasive. This is a difficult generalization to make for several reasons. Not all studies report species-specific responses, but instead use broad categories such as nonnative forbs, graminoids, etc., and obviously the same species are not present at each study site. This is true even among studies in the same forest, shrubland, or grassland type. Particular species (e.g., *B. tectorum*, *C. arvensis*) have been extensively studied, or at least defined to the species level in many of the studies so we have a better understanding of how they respond to fire and other variables. Other species may respond equally or more or less to wildfire but if they are not defined to the species level nor present at the site we cannot draw any conclusions. Following are summaries – organized by vegetation type – on the introduction and expansion of nonnative plant species following wildfire and information on which species have been studied.

Few studies have been conducted on responses of nonnative plant species to wildfire in natural **desert grasslands**. The most commonly documented nonnative species, *Eragrostis* spp., showed an initial increase in both native- and nonnative-dominated stands (Cable 1965), as well as an initial decrease followed by a slight increase through four years of post-fire observation in native-grass-dominated stands (Bock and Bock 1992).

Inconsistent responses of nonnative plant species were reported when authors compared burned to unburned adjacent sites at various times following wildfire in **desert shrublands**. Negligible differences were found between nonnative plant species on burned and unburned sites in a study in the Western Colorado Desert (O’Leary and Minnich 1981). Mixed results were recorded in most studies with responses varying by species, site, and year. No difference for *E. cicutarium* and

a short-term significant density increase for *Schismus* spp. and decrease for *Bromus* spp. were all observed in the same study (Cave and Patten 1984). Density and cover of *B. rubens* was greater on two out of the three burned sites than on the unburned sites studied for three years, but trends (increases and decreases) on each site varied (Beatley 1966). Brooks and Matchett (2003) recorded significantly higher percent cover of *E. cicutarium* on one site and *E. cicutarium*, *B. rubens*, and *B. tectorum* on a second site on burned plots compared to unburned plots. Callison et al. (1985) recorded variations in nonnative species cover depending on time since burning, site differences, and site treatments and there was no clear trend for the nonnative species. The post-fire annual community was described as dominated by nonnatives in one Sonoran Desert study (Rogers and Steele 1980), but according to the authors the dominant species at each site varied although they did not provide numbers. In another study, nonnative plant species were reported to increase in cover after wildfire, but there was no significance testing (Brown and Minnich 1986). *Bromus* spp. (Beatley 1966; Brooks and Matchett 2003; Brown and Minnich 1986; Callison et al. 1985; Cave and Patten 1984; O'Leary and Minnich 1981; Rogers and Steele 1980), *Schismus* spp. (Brooks and Matchett 2003; Brown and Minnich 1986; Cave and Patten 1984; O'Leary and Minnich 1981), and *E. cicutarium* (Brooks and Matchett 2003; Brown and Minnich 1986; Callison et al. 1985; Cave and Patten 1984; O'Leary and Minnich 1981; Rogers and Steele 1980) were the most commonly documented nonnative species in post-fire desert shrubland communities of the Mojave and Sonoran Deserts.

Research on the responses of nonnative plant species to wildfire in **sagebrush** natural areas have predominantly focused on *B. tectorum* dynamics (Cook et al. 1994; Hosten and West 1994; Humphrey 1974; Ratzlaff and Anderson 1995; Sparks et al. 1990; West and Hassan 1985; West and Yorks 2002; Whisenant and Uresk 1990). Some studies documented no significant short-term changes in *B. tectorum* (Ratzlaff and Anderson 1995) or in grass

production (Cook et al. 1994). At a long-term study site in Utah, authors observed short-term increases in *B. tectorum* in both burned and unburned sites (West and Hassan 1985) coinciding with above-average precipitation, a decline to a trace after 11 years coinciding with drought (Hosten and West 1994), and an increase during a wetter period over the following 7 years, followed by a decrease in the final year of the study (West and Yorks 2002). West and Yorks (2002) found a significant inverse relationship between perennial grass cover and *B. tectorum* cover. In a chronosequence study (Humphrey 1984), negligible amounts of *B. tectorum* were recorded on two sites 22 and 36 years after fire, but 6% cover was recorded 18 and 32 years following fire. Among other nonnative species that were observed following wildfire, *S. kali* percent cover was negligible until year 10, then increased in year 11 following wildfire but with high variability in percent cover between sites (Hosten and West 1994). *P. pratensis* was recorded as 6% 2 through 18 years after fire, but was negligible on older sites (Humphrey 1984).

General information on other nonnative plant species' responses to wildfire in sagebrush included data on *T. caput-medusae* (Blank et al. 1992), *S. kali* (Hosten and West 1994; West and Yorks 2002), nonnative bunch grasses (Sparks et al. 1990), *Descurainia pinnata* (western tansy mustard) (West and Yorks 2002), general nonnative annual forbs (West and Hassan 1985), *P. bulbosa* (Ratzlaff and Anderson 1995), and *L. serriola* (Ratzlaff and Anderson 1995; West and Yorks 2002), but no general patterns were observed. Vail (1994) stated that other nonnative plant species of concern in sagebrush areas are *Halogeton glomeratus* (halogeton/saltlover), *S. kali*, *E. esula*, *Centaurea* spp. (including yellow starthistle), and *T. caput-medusae*. However, research on the relationship between these plant species and wildfire is largely lacking.

Generally, nonnative plant species were rare the first year following fire in **chaparral shrublands** (Haidinger and Keeley 1993; Horton and Kraebel 1955; Keeley et al. 1981; Sweeney 1956; Tyler



1995), but typically peaked within the first four years following fire (Horton and Kraebel 1955; Safford and Harrison 2004; Sweeney 1956), after which nonnative species declined (Horton and Kraebel 1955; Sweeney 1956).

In **pinyon-juniper woodlands**, short-term increases (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985; Ott et al. 2001) and decreases (Ott et al. 2001) and long-term decreases (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985) of nonnative plant species were observed. Nonnative annual forbs commonly increased soon after wildfire (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985; Ott et al. 2001). However, at least in one study, annual forbs and grasses had high variability between sites and between years making it difficult to determine trends (Koniak 1985). In a three-year study following a wildfire in west-central Utah, *B. tectorum* had an “explosive” early response to wildfire and then continued to increase in density the next two years (Ott et al. 2001). However, the high occurrence of *B. tectorum* coincided with above-average precipitation. Another nonnative grass, *B. japonicus*, showed a decreasing trend over the same period (Ott et al. 2001). In the same study, some nonnative forbs increased while others showed a decreasing trend. In late successional stages, *B. tectorum* had lower percent cover in several studies than in earlier successional stages (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985). *B. tectorum* was the most commonly recorded nonnative after wildfire (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985; Ott et al. 2001). However, a study after a southwestern pinyon-juniper wildfire did not record any *B. tectorum* or other nonnative species (Dwyer and Pieper 1967). Other nonnative species recorded in more than one study included the annual species *L. serriola* (Koniak 1985; Ott et al. 2001), *S. altissimum* (Koniak 1985; Ott et al. 2001), *A. alyssoides* (Barney and Frischknecht 1974; Ott et al. 2001), and *S. kali* (Barney and Frischknecht 1974; Erdman 1970; Ott et al. 2001), but again responses were inconsistent.

In **ponderosa pine forests**, areas experiencing high-severity fire were related to short-term increases in nonnative forb species richness and abundance but not nonnative graminoids species richness and abundance (Griffis et al. 2001), increases in nonnative plant species richness and abundance (Crawford et al. 2001), nonnative plant species richness but not cover (Keeley et al. 2003), increases in nonnative plant species richness but not at all scales (Acton 2003), and increases in *B. japonicus* and other nonnative plant species (Cooper and Jean 2001). The most common nonnative graminoids found post-wildfire in ponderosa pine forests were the annual bromes *B. tectorum* and *B. japonicus* (Cooper and Jean 2001; Crawford et al. 2001; Merrill et al. 1980).

No consistent pattern in responses of nonnative plant species to wildfire in **lodgepole pine, spruce and sub-alpine fir forests** were discernable from the studies that were reviewed. Two studies showed negligible amounts of *C. vulgare* and *P. pratense* following wildfire (Anderson and Romme 1991; Stickney 1980). Short-term increases of *C. arvensis* were observed (Doyle et al. 1998; Turner et al. 1997), and its eventual long-term decrease was also observed in a study that followed 17 years of post-fire succession (Doyle et al. 1998). *T. officinale* showed a long-term increase (Doyle et al. 1998). *L. serriola* initially increased then decreased in a three-year period following wildfire (Turner et al. 1997). *C. arvensis* was the most commonly observed or studied nonnative plant species after stand-replacing fires in lodgepole pine and spruce/sub-alpine fir forests (Benson and Kurth 1995; Doyle et al. 1998; Romme et al. 1995; Turner et al. 1997). It was defined mainly as an opportunistic or transient species that was not present or was scarce in the mature forest or in unburned sites (Doyle et al. 1998; Turner et al. 1997). This does not necessarily indicate that it is the most abundant or invasive species after wildfire, but that the most information exists on its response to wildfire in these forests. The study that reported the highest number of nonnative plant species post-fire (Benson and Kurth 1995) was conducted in old-growth Douglas-

fir, dog-hair lodgepole pine, and Englemann spruce sites in the Flathead National Forest in Montana. The researchers presented the total number of species for all forest types in the study by bulldozer lines, burned areas, and adjacent unburned sites. Twenty-three nonnative plant species were observed in the bulldozed plots, five in the burned plots, and three in the undisturbed areas.

One may generalize from the literature reviewed that annual species, particularly grasses (e.g., *B. tectorum* and *B. japonicus*) and long-distance-dispersing forbs (e.g., *L. serriola*), are most likely to invade, although the exact species vary with vegetation type. In addition, chronosequence and repeated observation studies indicate that these annual species decline as native perennial species reoccupy sites in the years following fire. The perennial nonnatives *C. arvensis* and *T. officinale* may be notable exceptions to this generalization.

#### **What plant characteristics are associated with the introduction or expansion of nonnative plants after wildfire?**

It is not clear which plant characteristics are related to the increase or expansion of nonnative plants after wildfire, but some information has been gathered and a few generalizations suggested. The most commonly studied plant characteristic was regeneration strategy, i.e., whether plants regenerated vegetatively following fire or established from existing seed banks or off-site seed sources.

Post-fire vegetation regenerates or germinates from on-site propagules as well as off-site propagule sources. Stickney (1990) suggested that more severe fires will result in less on-site regeneration from resprouting or surviving seeds because of the damage to these sources by wildfire. He proposed that the ability of off-site sources to produce propagules to colonize burned sites is related to several coinciding circumstances – a seed crop, a dispersal event, and a burn site. Stickney (1986; 1990) concluded that seed from off-site seed sources will establish post-fire but will have little effect on succession of the initial post-fire community. In a discussion on general post-

wildfire vegetation, Lyon and Stickney (1976) concluded that the survival of on-site seeds was part chance and that off-site seed introduction was unpredictable. They observed that few species introduced from off-site sources could dominate the site, except trees and species that could regenerate from both the root crown and off-site seeds. Unfortunately, this research was not designed to address the dynamics of nonnative plant species following fire.

On-site regeneration versus off-site seed introduction was most commonly studied in lodgepole pine, spruce, and sub-alpine fir forests that experienced stand-replacing forest fires. In these studies, authors used various terms to describe regeneration from on-site and off-site sources (Doyle et al. 1998; Stickney 1990; Turner et al. 1997). Stickney (1990) defined three groups: survivor, a plant that regrows from vegetative parts that did not die in the fire; residual colonizer, which grows either from cones in the crowns of on-site trees or seeds surviving in the soil; and off-site colonizer, which establishes from seeds dispersed from surrounding unburned sites. Doyle et al. (1998) grouped plant species as “persistent” or “transient.” Persistent species are those found in the first year post-fire and in the mature forest. Transient species are those that are short-lived in burned areas and absent in the mature forest. Turner et al. (1997) categorized the plants in their study as “forest species” if they grew from vegetative parts or from seeds that were present before the fire and “opportunistic species” if they were absent or incidental before the fire.

The most commonly observed or studied nonnative plant species among burned lodgepole pine and spruce/sub-alpine fir forest studies was *C. arvensis* (Benson and Kurth 1995; Doyle et al. 1998; Romme et al. 1995; Turner et al. 1997). In all of these studies, *C. arvensis* was introduced from off-site seed sources. However, it is capable of resprouting from root crowns and rhizomes after wildfire (Romme et al. 1995). In their study of post-fire regeneration in Grand Teton National Park, Doyle et al. (1998) noted that none of the species arriving after the first year had greater than 5%

cover in the moderate burn over the course of the 17-year study. The authors suggested that both the *C. arvense* and the *Taraxacum* species' seeds had been dispersed long distances to the burn since they were absent or scarce in adjacent unburned areas and they have light seeds that are dispersed by wind. In contrast, Bakker (1960) as cited by Wilson (1979) observed that *C. arvense* wind dispersal is not highly efficient because the pappus breaks off easily from the seed. However, he noted that the seed might remain viable in the soil for 20 years or longer. Thus, seed longevity coupled with long-distance dispersal could build seed banks in the years between fires, and these are traits that could be associated with successful post-fire invasion. However, it must be remembered that the aboveground appearance of a species after wildfire and its absence in adjacent unburned areas does not necessarily mean the species arrived directly after fire. It may have arrived at an earlier time by some other means such as wind, animals, gravel, etc., but germinated only after wildfire created the opportunity for its establishment and survival by creating bare ground and increasing availability of limited resources such as light.

Turner et al. (1997) determined that most post-fire plant species cover originated from resprouting. Anderson and Romme (Anderson and Romme 1991) studied vascular plants on six paired moderate and severely burned sites for the first year following wildfire in Yellowstone National Park: 67% were considered to be from vegetative regrowth; 29% from seed originating in the canopy (*P. contorta*); 1.7% from an unknown source; 1.5% from seed stored in soil; and 0.8% from seed dispersed from an off-site source. *P. pratense*, the one nonnative identified to species in this study, reestablished from vegetative regrowth on only one out of the seven sites. The best predictor of success of post-fire native or nonnative species may be their capacity for vegetative regrowth from structures not destroyed by the fire. Thus, fire severity or degree to which fire destroys regeneration potential from existing species will define the plant community composition immediately following fire.

**Which wildfire characteristics (e.g., severity, size, and pattern) are associated with the establishment or expansion of nonnative plant species?**

Disturbances such as wildfire are commonly characterized by their areal extent, magnitude (intensity and severity), frequency, predictability, and turnover rate or rotation period (Sousa 1984). Fire regimes in particular are typically described by extent, season, frequency, intensity, and severity (Wright and Bailey 1982). In describing wildfire effects on vegetation, researchers often focus on fire severity because it has the greatest importance to the survival and recovery of vegetation (Neary et al. 1999; Ryan and Noste 1985). Of the various wildfire characteristics, fire severity was most often studied in the literature of this review. However, a few scientists also examined effects of wildfire frequency and pattern on nonnative plant species.

Brown (2000) defined fire severity as: "A qualitative measure of the immediate effects of fire on ecosystems. It relates to the extent of mortality and survival of plant and animal life both aboveground and belowground and the loss of organic matter. It is determined by heat released aboveground and belowground." Vegetation recovery following wildfire results from the interaction between fire severity and plant regeneration strategies (Brown 2000). Different vegetation communities are adapted to different historic fire regimes and exhibit various adaptations to persist with burning (Agee 1993). However, even in communities adapted to high-severity fires, these types of fires may provide opportunities for species not present prior to the fire to enter the community by reducing the survival of pre-fire vegetation (Turner et al. 1997). Several publications have extensive descriptions of the general effects of fire severity on plants without specific attention to nonnative species (Agee 1993; Brown and Smith 2000; Wright and Bailey 1982).

Numerous methods exist to measure fire severity (Goodwin et al. 2002; Ryan and Noste 1985). Researchers need to use more consistent measures of wildfire characteristics that may affect nonnative plant species invasion, such as

fire severity. The lack of uniform fire severity definitions between studies makes it difficult to compare and summarize fire severity effects (Christensen and Muller 1975; Cooper and Jean 2001; Crawford et al. 2001; Doyle et al. 1998; Griffis et al. 2001; Keeley et al. 2003; Safford and Harrison 2004; Turner et al. 1997; Tyler 1995). Some studies did not categorize fire severity at all (Benson and Kurth 1995; Lyon and Stickney 1976; Stickney 1980). However, some authors used clear definitions of fire severity and discussed the ecological significance of the fire severity definitions they used (Turner et al. 1997). Studies in forested landscapes tended to measure the responses of nonnative plant species to wildfire severity more than studies in shrublands or grasslands.

Little information was available on the response of nonnative plant species to fire severity in the shrublands and grasslands of the western United States. The effects of fire severity and intensity were both discussed in relation to the responses of nonnative plant species to chaparral wildfire. However, the definition used for these terms was not consistent and the effects of these parameters were not conclusive (Christensen and Muller 1975; Safford and Harrison 2004; Tyler 1995). In desert shrublands, fire severity was described in some studies only by its effect on the overstory shrubs (Beatley 1966; Brown and Minnich 1986; O'Leary and Minnich 1981). There was a noticeable lack of information on the relationship between wildfire severity and nonnative plant species in pinyon-juniper woodlands and sagebrush shrublands.

The effects of fire frequency on nonnative plant species were studied on chaparral sites and sagebrush sites. Haidinger and Keeley (1993) studied the effects of multiple fires on chaparral sites in the Verdugo Mountains of southern California. The authors concluded that, generally, the percentage of nonnative plant species increased in the sites with more frequent fires. They also observed that both the percentage of annuals and nonnative plant species increased with increasing fire frequency. Whisenant (1990) studied 12 sagebrush shrub-

land sites that had burned from 1 to 6 and more than 100 years previously in the Snake River plains of Idaho in order to compare fire frequency with fine fuel frequency and quantity. The sites that had burned 1 to 6 years previously, and more frequently, either had *B. tectorum* as the dominant species or, in two cases, as one of but not the most dominant species. The site that had burned 55 years previously and two sites that had burned more than 100 years ago did not have *B. tectorum* listed as one of the dominant species. The author concluded that higher fire frequencies were related to *B. tectorum* in sagebrush. However, the author also stated that the sites had variable potential vegetation and also had variable site characteristics, such as elevation differences. The sites with *B. tectorum* had also burned more recently so the persistence of *B. tectorum* was not known.

In ponderosa pine forests, higher fire severity was related to increases in annual forbs (Crawford et al. 2001; Griffis et al. 2001) and *B. japonicus*, plus a few nonnative forbs (Cooper 1998), as well as nonnative plant species richness (Acton 2003; Keeley 2004). In a study that used prescribed fire, thinning, and wildfire to represent treatment intensities, nonnative forbs but not graminoids increased with intensity of treatment (Griffis et al. 2001). Another study in northern Arizona also observed increases in nonnative plant species, especially annual forbs, related to increased burn severity (Crawford et al. 2001). In ponderosa pine and pinyon-juniper sites, increases in nonnative plant species were observed with more severe fires but not low-severity fires (Cooper 1998). However, the authors noted that there was high variability among responses of the herbaceous component of severely burned stands (Cooper 1998). Fire severity was significantly related to nonnative plant species richness but not cover in coniferous forests, including ponderosa pines, of the Sierra Nevadas (Keeley et al. 2003). Acton (2003) also noted that increased fire severities were related to increased nonnative plant species richness in ponderosa pine-dominated forests in west-central Idaho five years post-fire. This author



also documented that at multiple scales the only consistent result was that low nonnative species richness was related to low-severity fires but the conflicting results were not reconciled. However, in general, annual species occurrence/richness increased with fire severity in ponderosa pine forests.

In lodgepole pine and spruce/sub-alpine fir forests, severe fires (Doyle et al. 1998; Turner et al. 1997) and moderate fires (Doyle et al. 1998) were related to short-term increases and the long-term decline of *C. arvensis* (Doyle et al. 1998). High fire severities were related to the eventual increase of *Taraxacum* spp. (Doyle et al. 1998). Density of *L. serriola* showed short-term increases with increased burn severity (Turner et al. 1997). Anderson and Romme (1991) recorded negligible amounts of nonnative plant species with no difference between moderate and severe fires.

Turner et al. (1997) included several spatial variables related to fire size and pattern, in addition to commonly observed variables such as fire severity, in their analysis of post-wildfire vegetation responses in lodgepole pine forests. These variables included location (Yellowstone Lake, Cougar Creek, or Fern Cascades), patch size (small, moderate, and large), distance to light-surface and severe-surface burns, plus interactive effects among the variables. They found that location was a significant factor in predicting the density of *C. arvensis*. Location was not significant in predicting *L. serriola* density. Keeley (2003) suggested that the pattern of burn may also be related to nonnative plant species invasion following wildfire in ponderosa pine forests, but burn pattern was not included as an independent variable in the study.

**Which environmental characteristics (e.g., slope, aspect, topographical position) are associated with the introduction or expansion of nonnative plant species after wildfire?**

The relationship between site characteristics and the responses of nonnative plant species after wildfire was emphasized in most of the relevant studies. In most of the paired unburned and burned site research designs several site

factors – such as aspect, elevation, etc., in all vegetation types – were considered in selecting paired sites. Site characteristics may affect the responses of plant species, so future research should investigate the relationship between site variables and nonnative plant species' responses to wildfire. Site characteristics and the responses of nonnative plant species to wildfire were not a significant part of studies in desert grasslands, desert shrublands, or ponderosa pine forests.

Cook et al. (1994) observed no significant differences in annual grass production in burned and unburned sagebrush sites except during the second year on burned sites with southwest aspects. These sites had significantly higher *B. tectorum* production ( $\text{g}/\text{m}^2$ ) than the unburned sites, but by the third season following fire there was no significant difference in grass production on burned and unburned southwest aspects.

Responses of nonnative plant species to wildfire in chamise chaparral vegetation types may vary by biophysical variables such as aspect (Guo 2001), soil type, and the productivity of the area (Safford and Harrison 2004). In a study of wildfire effects on chaparral in serpentine versus sandstone soils, nonnative plant species richness was significantly higher on burned than on unburned sites and it was also higher on sandstone soils. The results also demonstrated that diversity of both native and nonnative species increased more in sandstone than in serpentine chaparral by plot and across the entire study (Safford and Harrison 2004).

Vegetation responses to wildfire were generally site-specific in pinyon-juniper woodlands as a result of variable pre-fire vegetation assemblages and post-fire climate, aspect, seed reserves, anthropogenic disturbances including grazing, and other biophysical variables. Koniak (1985) observed that *B. tectorum* occurred significantly more frequently after fires on west-facing slopes than on north-, south-, and east-facing slopes in pinyon-juniper woodland sites.

In the lodgepole pine forests of Yellowstone National Park, one study indicated that site location was one of the significant variables related to *C. arvensis* densities following wildfire



(Turner et al. 1997).

Environmental characteristics clearly can influence the distribution of vegetation and thus should influence the response of nonnative plant species to fire. However, based on this literature review there has been incomplete study of this question and thus no generalizations can be made.

***Which climatic conditions (e.g., pre- and post-fire precipitation) contribute to the introduction or expansion of nonnative plant species after wildfire?***

The occurrence and population growth rate of species is likely to vary in response to different climatic conditions. Understanding such responses in more detail will provide a better interpretation of the responses of both nonnative and native species to wildfire. For example, some studies (Hosten and West 1994; Ott et al. 2001; West and Yorks 2002) suggested that increases in *B. tectorum* were related to increased precipitation. Without information on precipitation, it may have been concluded that the increases were related to wildfire alone. Many studies lacked statistical information on relationships between climatic conditions and post-wildfire nonnative plant species.

Historically, desert shrubland wildfires typically occurred in above-average precipitation years that resulted in dense annual plant growth (Humphrey 1974). Pre-fire precipitation patterns were considered important to the occurrence of wildfire in several recent desert shrubland studies (Cave and Patten 1984; McLaughlin and Bowers 1982; Rogers and Vint 1987; Schmid and Rogers 1988). However, it was inconclusive whether increases in annual nonnative plant species resulted in different wildfire patterns than would be observed with only native plants.

Precipitation patterns were also linked to *B. tectorum* dynamics at a sagebrush site in Utah that was studied for several years by different researchers and at a pinyon-juniper site. Authors observed short-term increases in *B. tectorum* in both burned and unburned sites (West and Hassan 1985) coinciding with

above-average precipitation, a decline to a trace after 11 years coinciding with drought (Hosten and West 1994), an increase during a wetter period over the following seven years, then a decrease in the final year of the study corresponding with below-average precipitation (West and Yorks 2002). At pinyon-juniper sites, Ott et al. (2001) attributed the large increase in *B. tectorum* after wildfire, in part, to above-average precipitation.

It was suggested that responses of nonnative plant species to wildfire in chaparral shrublands may be related to precipitation patterns among other variables, but no data were provided (Keeley et al. 1981).

In ponderosa pine forests, both above-average precipitation (Oswald and Covington 1984) and relatively dry conditions (Cooper and Jean 2001) were related to increases in nonnative plant species following wildfire. After a fall wildfire in central Idaho, annual forb production varied with “environmental conditions” (Merrill et al. 1980). Keeley et al. (2003) observed that there were generally more nonnative plant species and greater cover at lower elevations in their study in the Sierra Nevadas.

A broad-scale assessment of potential nonnative plant species invasion in the lodgepole pine, sub-alpine fir, and spruce forests of Yellowstone National Park concluded that global climate change may increase the fire frequency, which in turn may create more opportunities for nonnative species invasion and establishment within the Greater Yellowstone ecosystem (Whitlock and Millspaugh 2001).

Post-fire precipitation may be a good predictor of the success of nonnative plant species following wildfire because water is a dominant limiting factor to plant growth through most of the intermountain West. Pre-fire precipitation in more arid areas may also increase fuels for wildfires. When precipitation occurs at the the appropriate plant phenological stage, nonnative plant species (e.g., *B. tectorum*) may increase seed production and subsequent seed banks, which may contribute to future post-fire populations. These are logical generalizations that can be drawn from the

studies outlined above, but they are speculative hypotheses that have largely gone untested.

***Do nonnative plant species that are introduced after wildfire persist and under which conditions?***

Although “explosive” increases in nonnative plant species immediately following wildfire generally invoke panic, they do not necessarily result in long-term persistence of such species. The initial response of nonnative plant species to wildfire may be transitory. It is difficult to determine whether nonnative plant species are invasive after wildfire (i.e., increase in density and/or spatial extent) without long-term research. Long-term studies provide an indication of the persistence of nonnative plant species after wildfire. Such studies are especially useful for observing changes in understory vegetation (Stickney 1980), but must be conducted for sufficient lengths of time so that responses to the treatment – in this case wildfire – can be detected (Korb et al. 2003). Without studying an area for a sufficient length of time, changes can be masked by yearly climatic variation (Korb et al. 2003). In the few long-term studies that were conducted, most nonnative plant species declined in later successional stages (Barney and Frischknecht 1974; Doyle et al. 1998; Erdman 1970; Horton and Kraebel 1955; Humphrey 1984; Koniak 1985; Stickney 1980; Sweeney 1956) and fire effects on nonnative plant species were mainly short-term (Fornwalt et al. 2003). However, some studies showed increases or significant relationships to fire in later successional stages (Brooks and Matchett 2003; Doyle et al. 1998).

One method for determining long-term successional changes in vegetation is to use chronosequence studies. In this context, chronosequence refers to the use of vegetation succession stages post-fire to examine a series of similar stands that burned at different times. For example, a chronosequence study would consist of selecting sites that burned 1, 5, 10, 15, 20, 50, and 100 years previously and recording the vegetation at each site during one season to represent trends over time. To maximize the validity of chro-

nosequence studies, West and van Pelt (1987) recommended that assumptions of the study be stated, similarity of the sites described, and that studies contain replicates in each successional stage. The documentation of these study attributes was not included for most of the studies in this review that used this method. In the future, researchers using chronosequence studies should consider these factors when conducting their research.

Only short-term, first-year (Cable 1965), and four-year post-fire (Bock and Bock 1992) responses to wildfire have been studied in native desert grasslands. The most observed nonnative species, *Eragrostis* spp., showed an initial increase in both native- and nonnative-dominated stands (Cable 1965), as well as an initial decrease followed by a slight increase then a slight decline through four years of post-fire observations in native grass-dominated stands (Bock and Bock 1992). Bock and Bock (1992) observed that after four years, most of the species at their research site had returned to their pre-burn abundances, suggesting that this period of time was sufficient to observe recovery following fire in this vegetation type.

The length of time over which studies were conducted following wildfire varied for desert shrublands. A couple of authors commented that their studies were limited by being conducted for only one or a few years (Brooks and Matchett 2003; Brown and Minnich 1986), though this was a common limitation of many studies. For example, a desert shrubland site was sampled consecutively after a wildfire no more than three times (Beatley 1966). Another study (Cave and Patten 1984) sampled sites for two consecutive years. Rogers (1980) sampled the same two sites at two different times. Brown (1986) sampled two different sites one season, one site three years after wildfire, and the other five years after wildfire. O’Leary and Minnich (1981) sampled sites once five years following fire. Callison et al. (1985) sampled several sites in one year; wildfires had occurred at 1, 2, 6, 12, 17, 19.5, and 37 years previously on the different sites. Nonnative plant species dominated both post-fire and unburned

communities (Callison et al. 1985). There appeared to be negligible differences in the mean cover of nonnative plants between burned and unburned sites; however, differences were not statistically analyzed. Brooks and Matchett (2003) sampled two sites in one year; wildfire had occurred 6 and 14 years previously on the respective sites. Inconsistent responses of nonnative plant species included anecdotal observations of increases in cover of nonnatives (Brown and Minnich 1986); little difference between burned and unburned conditions (O'Leary and Minnich 1981); simultaneous short-term increase, decrease, and no change in three different nonnative species (Cave and Patten 1984); and nonnative species' domination in both post-fire and unburned communities with apparent negligible differences in the mean cover of nonnative plants between burned and unburned sites (Cave and Patten 1984). At a site burned 14 years previously, all categories of nonnative plant species were significantly positively related to fire compared to unburned adjacent sites (Brooks and Matchett 2003).

In sagebrush shrublands, it has been suggested that wildfire followed by *B. tectorum* dominance can create a "new equilibrium" in which *B. tectorum* dominance prevents native vegetation from regrowing (Young et al. 1972). This hypothesis was statistically tested in one 20-year study and results indicated that it did not occur at sites considered to be in good condition and having a high density of perennial grasses pre-fire (West and Yorks 2002). In a chronosequence study of several sagebrush shrubland sites, relative cover of *B. tectorum* ranged from negligible on sites 2 years after wildfire, approximately 6% on sites 18 years after wildfire, negligible on sites 22 years after fire, approximately 6% on sites 32 years after fire, and negligible 36 years after fire (Humphrey 1984).

In the relevant chaparral studies, nonnative plant species generally were rare the first year following fire (Haidinger and Keeley 1993; Horton and Kraebel 1955; Keeley and Keeley 1981; Sweeney 1956; Tyler 1995), then typically peaked within the first four years after fire (Horton and Kraebel 1955; Safford and Har-

ison 2004; Sweeney 1956), after which nonnative species declined (Horton and Kraebel 1955; Sweeney 1956).

In pinyon-juniper woodlands chronosequence studies were conducted to define long-term successional patterns (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985). Collecting information on the responses of nonnative plant species to wildfire was secondary to documenting the changes in overall plant assemblage in this research (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985). Results from these studies (Barney and Frischknecht 1974; Erdman 1970; Koniak 1985) suggested that nonnative plant species are present in earlier successional stages, but will eventually decline to a trace or less in late-successional stages approximately 60 to 100 years following wildfire.

In ponderosa pine forests, several studies were conducted within five years following wildfire (Cooper and Jean 2001; Crawford et al. 2001; Griffis et al. 2001; Keeley et al. 2003). Crawford et al. (2001) suggested that the nonnative plant species observed in their study in ponderosa pine forests may be dominant for a few years, but may ultimately become a minor component of the forest. Fornwalt et al. (2003) suggested that fire effects on nonnative plant species may be short-term and not long-term in the ponderosa pine and Douglas-fir area they studied in Colorado. Fornwalt et al. (2003) examined the relationships between nonnative plant species and numerous biophysical and management variables (including year of last fire and last stand-replacing fire) in ponderosa pine and Douglas-fir forests of Colorado. The lack of a relationship between nonnative species and either of their fire variables suggested that fire effects on nonnative plant species may be short-term and that other variables were far more important to long-term dynamics of nonnative species.

Several of the studies reviewed in lodgepole pine and sub-alpine fir forests focused on early successional changes after wildfire (Benson and Kurth 1995; Romme et al. 1995; Turner et al. 1997). Two studies observed changes for

a longer time period (between 9 and 17 years) after wildfire (Doyle et al. 1998; Stickney 1980). Negligible amounts of *C. vulgare* were observed 9 years following wildfire in one study (Stickney 1980). *C. arvense* eventually decreased after an initial increase in a 17-year study in Grand Teton National Park (Doyle et al. 1998). In the same study *T. officinale* showed a long-term increase (Doyle et al. 1998).

The conclusion to be drawn from the available data is that nonnative plant species do not typically persist at high levels or dominate in predominantly natural areas in any of the reviewed systems after wildfire. None of the authors studied whether or not the nonnative plants changed ecosystem processes following the fire events. *Both of these findings are contrary to current dogma, and additional studies are required to evaluate the persistence and impact of nonnative plant species after wildfire.*

**Which fire management activities (e.g., fire suppression and rehabilitation) contribute to the introduction or expansion of nonnative plant species after wildfire?**

Fire suppression and rehabilitation activities to reduce the risk and impact of wildfire may be related to the introduction or population expansion of some nonnative plant species. In a review of nonnative plant species and wildfire in Mediterranean vegetation, Keeley (2001) suggested that several aspects of fire management have contributed to the invasion of nonnative species in chaparral. These aspects included the inability to suppress fires ignited by the increasing human population, pre-fire fuel manipulations (such as thinning under- and over-story vegetation), fuel breaks, and the use of nonnative plant species in seeding for post-fire rehabilitation of Mediterranean California vegetation. These aspects may be relevant to all of the vegetation types of the western United States. Considering the lack of research on this topic and the extent of these activities, further research is required.

Only one relevant study (Benson and Kurth 1995) was focused on the effects of fire

suppression and rehabilitation activities on nonnative plant species. Benson and Kurth (1995) observed vegetation recovery on rehabilitated bulldozer lines after a wildfire in old-growth Douglas-fir, dog-hair lodgepole pine, and Englemann spruce sites in the North Fork Valley of the Flathead National Forest in Montana. The results indicated that nonnative plant species were more abundant on bulldozer lines than in adjacent burned and undisturbed forests. Unfortunately, the sites were not clearly paired based on key environmental characteristics such as slope, aspect, and vegetation similarities so it would be difficult to attribute the differences in species composition to the treatments alone.

In general, specific nonnative plant species are often seeded to stabilize the soil, reduce erosion and inhibit the invasion of undesirable nonnative plant species as part of a wildfire rehabilitation program. In semiarid areas, perennial native and nonnative plant species are often seeded post-wildfire to discourage *B. tectorum* invasion (MacDonald 1999; Young and Evans 1978). In pinyon-juniper sites, post-wildfire seeding of nonnative grasses has been conducted in several areas (Erdman 1970; Koniak 1985; Ott et al. 2001) including Mesa Verde National Park (Erdman 1970). In the study by Koniak (1985), eight of the 21 sites were seeded with nonnative grasses after wildfire. In this study, *B. tectorum* had significantly lower occurrence on seeded sites than on nonseeded sites. The nonnative annual forbs *E. cicutarium* and *S. altissimum* also occurred less frequently on the seeded sites. Ott et al. (2001) also observed in their west-central Utah study that the cover of *B. tectorum* was lowest on the site that had been seeded with perennial grasses and forbs after wildfire. In contrast, in sagebrush shrublands of southeastern Idaho, Ratzlaff and Anderson (1995) measured mean cover of *B. tectorum* for the first and second year post-fire in seeded and unseeded sites. No significant difference was found between treatments in either year (1988  $P < 0.316$ ; 1989  $P < 0.381$ ). Although seeding of nonnative plant species may inhibit targeted nonnative plant growth, seeding can also be significantly detri-



mental to several native species including trees, shrubs, grasses, and forbs (Koniak 1985). This effect needs to be considered when deciding to seed nonnative species after wildfire, and more studies need to be conducted to determine the long-term tradeoffs of these practices.

Seeding of nonnative plant species may have a direct impact on the desired post-fire vegetation. Following a northern Arizona wildfire in ponderosa pine forests where nonnative grasses had been seeded, the highest biomass production increases occurred in grass and grass-like plants (Pearson et al. 1972). Several desert shrubland sites in the study by Callison et al. (1985) had been seeded with nonnative grasses. In that study, nonnative annual grasses, nonnative annual forbs, and the seeded perennial grasses dominated the understory at all sites including the unburned site. Many areas of burned chaparral are often reseeded with grasses, commonly annual ryegrass (*L. multiflorum*) to prevent erosion or improve livestock grazing (Biswell 1974). The role that anthropogenic disturbances, such as seeding which often occurs post-wildfire in chaparral shrublands (Zedler et al. 1983) and other vegetation types, play in the conversion of native to predominantly nonnative vegetation is unclear.

The disturbances caused by vegetation removal and soil movement associated with fire suppression activities are extreme in terms of area and extent of soil disturbance, and thus create safe sites for germination, establishment, and survival of short-lived ruderal species. In addition, seeding of nonnative species to aid soil stabilization directly introduces species that could become invasive. Accidental introduction of nonnative species as contaminants in seed mixes is also a potential point of introduction and was listed as an issue in a survey of wildfire and nonnative plant species management (Rew 2005). Very little research is published on these potentially important avenues of nonnative plant species introduction.

### **How do site disturbance histories affect the results of studies on nonnative plant species and wildfire?**

Since Euro-American settlement in the western United States, anthropogenic disturbances have sharply increased. These disturbances are numerous and include urban and rural housing development, transportation corridor construction, livestock grazing, recreation, wildfire suppression, and agriculture. Many of these disturbances provide opportunities for nonnative plant species introductions or expansions. It is difficult to isolate the effects of wildfire on nonnative plant species without acknowledging the history of anthropogenic disturbances on each site considered. This was not always explicitly stated in the studies in this review, but is recommended for future research.

Very few studies have documented the response of nonnative plant species to wildfire in natural areas of the desert grasslands, perhaps because there has been more interest in the use of fire to decrease shrubs and improve range forage (Cable 1967; Humphrey and Everson 1951; White 1969). As a result of such human manipulation in the late 19th and early 20th centuries, nonnative plant species have invaded desert grasslands either unintentionally or through planned introductions. The seeding of *Eragrostis* spp. (*E. lehmanniana* and *E. curvula* var. *conferta*) and their subsequent invasion illustrates the point (Bock and Bock 1992). Livestock grazing in the southwestern states dates back to the 1500s (Humphrey 1958) and seeding of *Eragrostis* spp. for forage occurred extensively in the semi-desert Southwest during the mid-20th century (Cable 1973). Thus, it is not surprising that natural grassland sites that have recorded the responses of nonnative plant species to wildfire have adjacent areas of seeded *Eragrostis* spp. as well as a history of grazing (Bock and Bock 1992; Cable 1965). Cable (1965) studied native black grama plots and adjacent *Eragrostis* spp. vegetation within a fenced enclosure that had not been grazed by cattle for “many years.” Bock and Bock (1992) studied sites after wildfire that had been previously seeded with *Eragrostis* spp. for erosion control and forage production, and



adjacent sites of native grasslands that were not seeded on a sanctuary owned by the National Audubon Society in Arizona. The area of study had been ungrazed for nearly two decades prior to the wildfire. They observed initial increases of nonnative plant species in both native- and nonnative-dominated stands (Cable 1965). *Eragrostis curvula* percent cover initially decreased, then slightly increased for two years, then declined the last year of observation in native grass-dominated stands through four years of post-fire observation (Bock and Bock 1992).

Many natural areas contain nonnative plant species in the Mojave and Sonoran Desert shrublands (Brooks and Esque 2002; Kemp and Brooks 1998) where numerous anthropogenic disturbances have been recorded (Lovich and Bainbridge 1999). It was difficult to determine whether desert shrubland studies were conducted in areas of predominantly native vegetation with minimal anthropogenic disturbances because detailed information was not provided on pre-fire vegetation or current or past disturbances, such as proximity to roads and buildings (Brown and Minnich 1986; O'Leary and Minnich 1981), military testing activities (Beatley 1966), seeding with nonnatives (Callison et al. 1985), and livestock grazing (Brooks and Matchett 2003).

Very little information is available on the responses of nonnative plant species to wildfire in areas that have predominantly native vegetation and a history of little anthropogenic disturbance in sagebrush rangelands. Most studies in these areas have observed a considerable amount of *B. tectorum* (West and Hassan 1985) or other nonnatives (Ratzlaff and Anderson 1995) interspersed with native vegetation, or a history of some grazing even if the sites are not considered degraded (Cook et al. 1994).

The distribution and composition of Californian chaparral has been affected by Native American burning (Keeley 2002), mining, logging, grazing, farming, and Euro-American settlement (Hanes 1971; Keeley 2001, 2002), making determinations of a "natural" pre-fire condition difficult. Studies of the responses of

nonnative plant species to wildfire in chaparral included areas that had been seeded after wildfire for erosion control (Horton and Kraebel 1955; Keeley et al. 1981; Zedler et al. 1983), although some studies avoided selecting such areas for study plots (Christensen and Muller 1975). Other disturbances studied included pre-fire fuel treatments (Tyler 1995), native herbivory (Tyler 1995), or livestock grazing (Keeley et al. 1981). Keeley et al. (1981) noted that one of their sites had been heavily grazed by cattle and the vegetation response to wildfire was markedly different from other sites that had not been grazed by cattle.

Most sites in pinyon-juniper studies have experienced intensive disturbance since European settlement, especially from livestock grazing. Many of the studies reviewed had histories of livestock grazing and contained nonnative plant species even in unburned areas (Barney and Frischknecht 1974; Koniak 1985; Ott et al. 2001), while others were seeded with native and nonnative plant species after wildfire (Erdman 1970; Koniak 1985).

Variable disturbance histories of sites may make it difficult to interpret the effects of wildfire on nonnative plant species in ponderosa pine forests (Griffis et al. 2001). In ponderosa pine forests, wildfire may result in increased forage production that could attract wildlife and livestock to burned sites (Pearson et al. 1972). Histories of livestock grazing and intensive wildlife use can affect the condition of sites (Merrill et al. 1980).

Site disturbance histories may be a very important aspect of predicting the response of nonnative plant species to wildfire. This review indicated that there is anecdotal evidence but few quantitative studies that allow solid conclusions.

# FINAL REMARKS

Wildfire is a natural process in many ecosystems in the western United States. In the last century, numerous anthropogenic disturbances have altered how this natural process operates in the forests, shrublands, and grasslands of the West. The intentional and/or unintentional introduction of nonnative plant species and the ongoing invasion of these species into natural areas is one of the anthropogenic disturbances that causes grave concern. In particular, the potential response of nonnative plant species to wildfire has alarmed resource managers in the West. Unfortunately, the overall conclusion of this review is that little specific information is available on the response of nonnative plant species to wildfire in natural areas. The majority of research has occurred in semiarid vegetation of the West, though much of this research has been conducted in areas impacted by other anthropogenic disturbances. Less information is available on the responses of nonnative plant species to wildfire for forested landscapes of the West. Fortunately, as of 2005, several studies are being conducted throughout the West on this topic and should be available in the near future.

However, some generalizations are possible. Most nonnative plant species tend to be associated with the more severely burned areas. In these areas relatively short-lived (often annual or biennial) species are the first colonizers, whereas in less severely burned areas, existing perennial understory native species often respond first. Most of the nonnatives are short-lived ruderal species that are not likely to maintain aboveground populations following tree or shrub canopy closure under typical successional pathways. The idea that nonnative species like *B. tectorum* can change successional pathways by increasing fire frequency and thus selecting against regeneration of native perennial species seems logical, but there is little quantitative scientific evidence to indicate that this phenomenon is the rule rather than the exception.

As previously stated, each study provides a piece of the puzzle in understanding the relationship of nonnative plant species and wildfire. This review has identified numerous missing pieces and several important issues that warrant future research. Future research should focus on more completely integrating aspects of invasion biology and fire ecology in formulating hypotheses and in study designs. Specifically, research should address not only introductions of nonnative plant species and short-term responses, but issues of persistence and dominance of these species and their impacts on native species following wildfire. Borrowing from fire ecology, researchers should address not only the effects of fire severity, but also the effect of wildfire frequency and the aerial extent and spatial pattern on nonnative plant species' responses. Standard measures of these characteristics also need to be used to determine patterns of response among studies. In addition, because the western United States has experienced numerous anthropogenic disturbances that affect the invasion of nonnative plant species, site disturbance histories need to be explicitly documented in studies of wildfire and nonnative plant species. Where possible, these disturbance effects should be integrated into the study design along with the effect of wildfire. Finally, the relationship between fire management activities such as fire suppression and rehabilitation requires far more research, although some resource managers have data on these issues (Rew 2005). Quantitative research on this topic was notably under-represented in the literature located for this review. Considering the extent of ongoing fire management activities and the intuitively great potential for them to affect nonnative plant species invasion through introduction of propagules and creation of suitable sites, immediate attention is required.



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# APPENDIX 1:

## Scientific and common names of nonnative plant species in this review

Scientific name as given in the relevant citation, with authority and common names from USDA/NRCS Plants Database (<http://plants.usda.gov/>). Where the current nomenclature differs from that provided in the citation, the new name is given in the third column. \* signifies species that the author listed as “exotic” but USDA/NRCS PLANTS Database lists as native for the state in which the study took place.

Scientific name (as given in citation) and authority	Common names	Current nomenclature if different from cited
<i>Aegilops cylindrica</i> Host	goat grass	
<i>Aira caryophylla</i> L.	silver hairgrass	
<i>Anagallis arvensis</i> L.	scarlet pimpernel	
<i>Anthemis cotula</i> L.	stinking chamomile	
<i>Avena barbata</i> Pott ex Link	slender oat	
<i>Avena fatua</i> L.	wild oats	
<i>Brassica incana</i> Tenore	short-pod mustard	<i>Hirschfeldia incana</i> (L.) Lagrèze-Fossat
<i>Brassica nigra</i> (L.) W.D.J. Koch	black mustard	
<i>Bromus diandrus</i> Roth	ripgut brome	
<i>Bromus japonicus</i> Thunb. ex Murr.	Japanese brome	
<i>Bromus mollis</i> auct. non L.	soft brome	<i>Bromus hordeaceus</i> L. ssp. <i>Hordeaceus</i>
<i>Bromus rigidus</i> Roth	ripgut brome	
<i>Bromus rubens</i> L.	compact brome	
<i>Centaurea cyanus</i> L.	garden cornflower	
<i>Centaurea melitensis</i> L.	Maltese starthistle	
<i>Centaurea</i> spp.	knapweeds	
<i>Chenopodium album</i> L.	lambsquarter	
<i>Chondrilla juncea</i> L.	rush skeletonweed/hogbite	
<i>Cirsium arvense</i> (L.) Scop.	Canada thistle	
<i>Cirsium vulgare</i> (Savi) Ten.	bull thistle	
<i>Collomia linearis</i> Nutt.	tiny trumpet	
<i>Conyza canadensis</i> (L.) Cronq.	Canadian horseweed	
<i>Dactylis glomerata</i> L.	orchard grass	
<i>Descurainia pinnata</i> (Walt.) Britt.	western tansymustard	
<i>Descurainia sophia</i> (L.) Webb ex Prantl	herb Sophia	
<i>Draba verna</i> L.	spring draba	
<i>Ehrharta erecta</i> Lam.	panic veldtgrass	
<i>Eragrostis curvula</i> var. <i>conferta</i> (Schrad.) Nees	weeping lovegrass	
<i>Eragrostis lehmanniana</i> Nees	Lehmann lovegrass	
<i>Euphorbia esula</i> L.	leafy spurge	

<i>Euphorbia serpyllifolia</i> Pers. ssp. <i>hirtella</i> (Engelm. ex S. Wats.) Oudejans	thyme-leaf sandmat	<i>Chamaesyce serpyllifolia</i> (Pers.) Small ssp. <i>hirtella</i> (Engelm. ex S. Wats.) Koutnik
<i>Festuca megalura</i> Nutt.	rat-tail fescue	<i>Vulpia myuros</i> (L.) K.C. Gmel.
<i>Filago arvensis</i> (L.) Holup	field cottonrose	
<i>Filago gallica</i> (L.) Coss. & Germ.	narrowleaf cottonrose	<i>Logfia gallica</i> (L.) Coss. & Germ.
<i>Galium aparine</i> L.	stickywilly	
<i>Halogeton glomeratus</i> (Bieb.) C.A. Mey.	saltlover/halogeton	
<i>Hypochaeris glabra</i> L.	smooth catsear	
<i>Ipomoea coccinioides</i> (no species with this name - assumed to be <i>I. coccinea</i> )	redstar	<i>Ipomoea coccinea</i> L.
<i>Isatis tinctoria</i> L.	dyer's woad	
<i>Lactuca serriola</i> L.	prickly lettuce	
<i>Lappula occidentalis</i> (S. Wats.) Greene	flatspine stickseed *	
<i>Lepidium</i> spp.	pepperweeds	
<i>Lolium multiflorum</i> Lam.	annual ryegrass	
<i>Melilotus indica</i> (L.) All.	sour clover	
<i>Melilotus officinalis</i> (L.) Lam.	yellow sweet clover	
<i>Poa bulbosa</i> L.	bulbous bluegrass	
<i>Poa pratensis</i> L.	Kentucky bluegrass	
<i>Salsola kali</i> L.	Russian thistle	
<i>Salvia aethiopsis</i> L.	Mediterranean sage	
<i>Sanguisorba officinalis</i> L.	official burnet	
<i>Schismus barbatus</i> (Loefl. ex L.) Thellung	common Mediterranean grass	
<i>Senecio vulgaris</i> L.	old-man-in-the-Spring	
<i>Sida abutilifolia</i> P. Mill	spreading fanpetals	
<i>Silene gallica</i> L.	common catchfly	
<i>Sisymbrium altissimum</i> L.	tumble mustard	
<i>Taeniatherum caput-medusae</i> (L.) Nevski	medusahead	
<i>Taraxacum officinale</i> G.H. Weber ex Wiggers	dandelion	
<i>Teloxys graveolens</i> Willd.	fetid goosefoot *	
<i>Tragopogon dubius</i> Scop.	yellow salsify	
<i>Trifolium repens</i> L.	white clover	
<i>Verbascum thapsus</i> L.	common mullein	



