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Chapter 2:

Effects of Fire on Nonnative Invasive Plants and Invasibility of Wildland Ecosystems

Considerable experimental and theoretical work has been done on general concepts regarding nonnative species and disturbance, but experimental research on the effects of fire on nonnative invasive species is sparse. We begin this chapter by connecting fundamental concepts from the literature of invasion ecology to fire. Then we examine fire behavior characteristics, immediate fire effects, and fire regime attributes in relation to invasion potential. These concepts form the basis for examining the literature that supports or refutes several common generalizations regarding fire effects on nonnative invasives. We conclude with a summary of management implications regarding fire effects on nonnative invasive plants.

Invasion Ecology

Invasion ecology is influenced by interactions of ecosystem properties, properties of native and nonnative plant species, and nonnative propagule pressure (Lonsdale 1999) (fig. 2-1). Ecosystem properties include disturbance regimes and fluctuations in

resource availability. In the context of invasion, this is the availability of resources needed by a nonnative species to establish, persist, and spread. Morphological properties, phenological properties, and competitive ability of native species influence resistance to invasion, while the same properties of nonnative species influence potential to invade. Native and nonnative plant responses to fire, such as damage or stimulation from heat and increases or decreases in postfire years, are particularly important for our discussion. Propagule pressure is the availability, abundance, and mobility of propagules in and around a plant community.

In this chapter, we examine several generalizations that have been suggested about wildland invasion by nonnative species after fire. We treat these generalizations as questions that can be examined in light of current research.

- Question 1. Does fire generally favor nonnative over native species?
- Question 2. Do invasions increase with increasing fire severity?

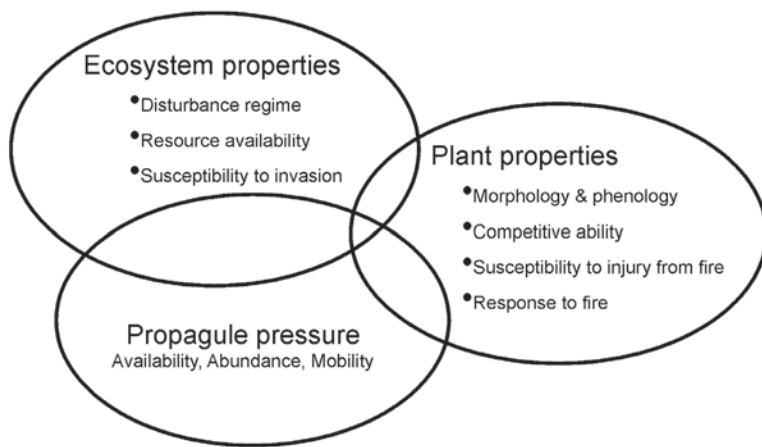


Figure 2-1—Susceptibility of a plant community to invasion by nonnative species after fire depends on properties of the ecosystem itself, properties of plant populations (both native and nonnative) and availability of nonnative plant propagules (following Lonsdale 1999).

- Question 3. Does additional disturbance (before, during, or after fire) favor invasions?
- Question 4. Do invasions become less severe with increasing time after fire?
- Question 5. Do invasions increase with disruption of the presettlement fire regime?
- Question 6. Are postfire invasions less common in high elevation ecosystems?

We will return to these questions after reviewing the connections between invasion concepts and fire.

Ecosystem Properties and Resource Availability

Invading species must have access to resources, including light, nutrients, and water, so community susceptibility to invasion can be explained to some extent by changes in resource availability. A species will “enjoy greater success in invading a community if it does not encounter intense competition for these resources from resident species” (Davis and others 2000). Therefore, a plant community becomes more susceptible to invasion when the amount of unused resources increases. Fire can increase resource availability by reducing resource use by resident vegetation (through mortality or injury) or by altering the form and availability of nutrients. Reports of postfire increases in nonnative species, often attributed to increased light or other resources, are available in the literature (for example, D’Antonio 2000, review; Hunter and others 2006; Keeley and others 2003).

Disturbed areas are often considered vulnerable to invasion (Sakai and others 2001), and burned areas are no exception. However, some plant communities that have evolved with recurring fire, such as California chaparral, are not considered highly invasible under

their historic fire regime (Keeley 2001; Keeley and others 2003). Furthermore, divergence from the historic fire regime in the “opposite” direction—with reduced fire frequency or severity—may also increase invasibility. For invasion to actually occur, community susceptibility and resources adequate for the spread of nonnative species must coincide with availability of propagules of nonnative species that can successfully compete with native vegetation for those resources (Davis and others 2000).

Properties of Native and Nonnative Plants

Several plant characteristics influence their susceptibility to fire injury, ability to recover and compete for resources following fire, and changes in cover and dominance over time after fire. Fire has less potential to kill individuals and impact populations if the species’ meristem tissues, buds, and seeds are protected from heat-caused damage. Avoidance of heat damage can be based on structural features, location of meristematic tissues, or phenology (see “Influence of Fire Season and Plant Phenology on Postfire Invasions” page 18). Elevated buds, thick bark, and underground vegetative structures can provide protection.

Fire survivors and species that form persistent seed banks, native or nonnative, have early access to resources on a burned site (see “Influence of Fire on Resource Availability and Interactions Between Plant Species” page 10). They can spread by regenerating from surviving structures or establishing from the seed bank, then producing abundant seeds that establish on the exposed mineral soil seedbed (see “Downward heat pulse effects on plant survival” page 14). Many nonnative invasives are annuals or biennials with short generations, ability to self pollinate, and low shade tolerance (Sutherland 2004). A review by

Barrett (2000) highlights the relationship between disturbance and opportunistic or invasive species with short life cycles, well-developed dispersal powers, and high reproductive output. These typically ephemeral species can establish on burned sites only if abundant propagules are available from the soil bank or nearby unburned areas. Unless they alter ecosystem processes to perpetuate early-seral conditions, ephemerals are often replaced by perennials within a few years after fire (see “Question 4” page 25).

Nonnative Propagule Pressure

The spatial distribution of nonnative source populations and their mode of propagule dispersal influence their establishment and spread in new areas (Amor and Stevens 1975; Giessow and Zedler 1996; Wisser and others 1998), including burns (Keeley and others 2003). Some seeds are heat tolerant and therefore may survive a fire onsite (Volland and Dell 1981). Postfire establishment and spread of nonnative species depends, in part, on propagule pressure (*sensu* Colautti and others 2006; Drake and Lodge 2006; Lockwood and others 2005)—the abundance of nonnative propagules occurring onsite and within dispersal distance of the burned area. D’Antonio and others (2001b) contend that variation in propagule supply interacts with the “ecological resistance” of an ecosystem (*sensu* Elton 1958) such that when resistance is low, few propagules are needed for successful invasion, and as resistance increases it takes proportionately more propagules for invaders to establish. In a meta-analysis designed to examine characteristics of invasiveness and invasibility, Colautti and others (2006) found that while propagule pressure was rarely considered in studies of biological invasions, it was a significant predictor of invasibility. More disturbance and higher resource availability are also significant predictors of invasibility (Colautti and others 2006), though field studies rarely isolate these factors and measure their influence quantitatively.

The scientific literature provides numerous examples of a positive relationship between anthropogenic disturbance and nonnative invasive species richness

and abundance. Where burns are associated with anthropogenic disturbance, they are likely to be subject to greater propagule pressure and may therefore be more susceptible to postfire invasion than burns in less disturbed areas (see “Question 3” page 22). The generally positive relationship between nonnative invasive species and anthropogenic disturbance (for example, Dark 2004; Johnson and others 2006; McKinney 2002; Moffat and others 2004) may have implications for plant communities and bioregions that currently show relatively little effect of fire on nonnative plant invasions. Fire appears only weakly related to spread of nonnative species in the Northeastern bioregion (chapter 5), but the plethora of nonnative invasive species present in this region (Mehrhoff and others 2003) and the prevalence of anthropogenic disturbance suggest that, if burning increases, impacts from nonnative species may increase as well. Similarly, while fire-caused increases in nonnative invaders are currently uncommon in Alaska (chapter 10), expanding human influences on wildlands coupled with climate change may increase problems with nonnative plants in that state. Similar concerns have been voiced regarding invasive species in Colorado shortgrass steppe (Kotanen and others 1998) and may apply in many areas of the United States.

Influence of Fire on Invasions

The responses of plants to fire depend on both fire attributes and plant attributes relating to survival and establishment (Pyke and others, in review). Nonnative plants that survive on site, establish from the seed bank, or disperse seed into burns soon after fire have early access to resources that are more plentiful or more available after fire. Fire behavior characteristics, immediate fire effects, and fire regime attributes (table 2-1) influence persistence of on-site populations and postfire establishment from on- and off-site sources. While fire behavior characteristics are often measured and recorded on wildfires, they are not as clearly related to invasiveness and invasibility

Table 2-1—Fire attributes that can influence invasion by nonnative plant species. Concepts listed here are defined in greater detail in chapter 1 and the glossary.

Fire behavior attributes	Immediate fire effects	Fire regime attributes
Fire type (ground, surface, and/or crown fire)	Fuel consumption Soil heating pattern	Fire type (ground, surface, and/or crown fire)
Fireline intensity	Total heat release	Intensity
Rate of spread	Burn pattern	Frequency
Residence time	Crown scorch	Severity
Flame length	Crown	Size
Flame depth	Consumption	Spatial complexity
Reaction intensity	Smoke production	Seasonality

as immediate fire effects (most of which relate to fire severity) and fire regime attributes. Fire type, severity, and frequency affect the persistence of invasive populations and their potential for spread within burned areas. Spatial characteristics (fire size, the distribution of burned and unburned patches, and the spatial pattern of fire severity) influence the potential for establishment from unburned areas. Burn season also influences nonnative plant response, especially as it interacts with plant phenology and vulnerability to heat damage.

Influence of Fire on Resource Availability and Interactions Between Plant Species

Superior competitive ability is often used to explain postfire invasions by nonnative species. Explanations for spread of invasives based on competition theory include the natural enemies hypothesis (Elton 1958; Mack and others 2000), the evolution of increased competitive ability hypothesis (Blossey and Notzold 1995), and the novel weapons hypothesis (Callaway and Ridenour 2004). These hypotheses are supported by examples of particular species, but their relevance to fire has not been demonstrated. We focus here on theoretical concepts leading to the expectation that fire will alter the competitive balance between native and nonnative species, and empirical evidence of such impacts.

A review of nonfire competition experiments from world literature suggests that at least some nonnatives are better competitors than native species, with the caveat that “Invaded communities are not random assemblages, and researchers tend to study the most competitive alien plants” (Vilà and Weiner 2004). Reduction of nonnatives can lead to increases in native species, as demonstrated in the Mojave Desert (Brooks 2000). These results are consistent with the hypothesis that nonnatives can outcompete natives for limited resources in early successional environments (MacDougall and Turkington 2004).

If fire increases resource availability on an invaded site, the relative competitive abilities of the species present should theoretically determine which will benefit most from the increased resources. However, competitive interactions between native and nonnative species are poorly understood and difficult to measure in the field. Studies conclusively demonstrating postfire competition between native and nonnative species for a specific resource are lacking. This is not surprising when one considers the scale and methodological differences between fire research and competition research. Most fire research addresses plant communities with high spatial variability and variation in fire severity, many native and sometimes many nonnative species, and several resources altered by fire. In contrast, most

competition studies are comparisons of paired species under carefully controlled conditions (Vilà and Weiner 2004).

Availability of Specific Resources—Many disturbances increase the availability of resources for plant growth and thus have the potential to increase a community’s susceptibility to invasion (Davis and others 2000). Fire can increase light availability by reducing cover. It can increase water availability by killing vegetation and thus the demand for moisture. It can increase nutrient availability by killing vegetation and also by converting nutrients from storage in biomass to forms that can be absorbed by plants. By consuming surface organic layers, fire increases exposed mineral soil; while not a resource itself, mineral soil exposure affects postfire germination and establishment (reviewed in Miller 2000).

Postfire increases in the availability of specific resources are likely to be interrelated and subtle. For example, by reducing the quantity and vigor of existing vegetation, a canopy fire may increase not only light levels but also moisture availability; however, increased exposure to light and wind and decreased albedo may dry the surface layer of the soil. A surface fire that causes lethal crown scorch may initially increase moisture availability and mineral soil exposure but have little effect on light availability; then, as foliage is cast, light levels will increase and exposed mineral soil will decrease. Most surface and ground fires increase mineral soil exposure, but they may increase or decrease nutrient availability depending on fire severity. Correlations between levels of different resources make it difficult, if not impossible, to isolate plant response to fire-caused changes in a particular resource.

The light available to understory species after fire in forests, woodlands, and some shrublands increases as canopy cover and woody basal area decrease (for example, Keyser and others 2006). Increased light in the understory is generally associated with increased cover and biomass of understory species and sometimes with increased species richness (for example, Battles and others 2001; Messier and others 1998; Son and others 2004). This pattern has been well documented following fire (Miller 2000, review). Nonnative invasive species that are shade-intolerant—the majority (Sutherland 2004)—are likely to benefit from increased light if they survive or establish in forests, woodlands, or shrublands after fire. If the canopy closes with time after fire, decreased light levels may then reduce the abundance of shade-intolerant nonnative species (see “Question 4” page 25). However, nonnative species that persist at low abundance or maintain a viable soil seed bank when the canopy closes may increase rapidly when fire or another disturbance opens the canopy and again increases available light.

Growing-season fires reduce aboveground vegetation, so they are likely to reduce moisture uptake by plants, at least temporarily (Knoepp and others 2005; Neary and Ffolliot 2005). These changes can increase the moisture available to sprouting plants and seedlings, although the increase may be offset by runoff and evaporation from exposed mineral soil (DeBano and others 1998). In shrub-steppe ecosystems of the Great Basin, soil moisture patterns on burned sites differ both spatially and temporally between burned and unburned sites; these differences may affect the success of nonnative species relative to native species (Prater and others 2006). However, research to date has not isolated soil moisture as the cause of postfire spread of nonnative species. The effect can be inferred in a grassland study in which the effect of late spring prescribed fire on Kentucky bluegrass (*Poa pratensis*) was related to postfire moisture. Burning reduced this nonnative grass significantly on sites that experienced subsequent dry growing conditions but not on sites that had abundant postfire moisture (Blankespoor and Bich 1991). Conversely, smooth brome (*Bromus inermis*) decreases when postfire moisture availability is high and increases when available moisture is low. The authors suggest that when soil moisture is high, native warm-season grasses are able to outcompete fire-injured smooth brome for water; and when less soil moisture is available, native grasses are less competitive (Blankespoor and Larson 1994).

Fire mineralizes several plant nutrients, including nitrogen, potassium, and phosphorus, releasing them from complex molecules in tissues and either volatilizing them or depositing them in forms that are more available for plant uptake (Anderson and others 2004; Bauhus and others 1993; Keeley and others 2003; White and Zak 2004). We focus here on nitrogen, since fire research on this plant nutrient is somewhat more complete than on others. Nitrogen often limits plant growth because it is used in many organic molecules essential for life, including proteins and DNA. When plants and litter are burned, some of the nitrogen from organic compounds is volatilized, and the rest remains on site as ammonium and nitrate—small ions that plants can readily absorb with soil water (Knoepp and others 2005). Subsequent changes in soil biota also affect availability of these ions to plants (Blank and others 1996). A meta-analysis of the effect of fire on nitrogen in forests, shrublands, and grasslands (Wan and others 2001) found no significant effect on total nitrogen but a significant short-term increase in available soil nitrogen (ammonium and nitrate). Ammonium usually peaked immediately after fire, while nitrate peaked 7 to 12 months after fire. Fire-caused increases in available nitrogen were transitory. In the 22 studies analyzed, ammonium and nitrate returned to prefire levels within 3 to 5 years after fire.

Increases in available nitrogen generally favor nonnative annual species over native perennials (McClendon and Redente 1992). Cheatgrass (*Bromus tectorum*), for example, effectively uses both patches and early pulses of nitrogen, which may contribute to its successful competition with perennials for available nitrogen (Duke and Caldwell 2001). No studies elaborate on nitrogen's influence on annual-perennial relationships in the postfire environment, though a similar relationship might be assumed with the post-fire flush of available nitrogen. Several reviews link postfire increases in nitrogen to increased nonnative plant biomass (for example, Brooks 1998; 2002; Floyd and others 2006; Hobbs and others 1988; Huenneke and others 1990). However, none has demonstrated a link between increased nitrogen and increased nonnative abundance at the expense of native species. Research in Hawai'i demonstrated that nonnative grasses, which convert native Hawaiian woodlands to fire-maintained grasslands, alter the seasonal pattern of nitrogen availability to plants (Mack and D'Antonio 2003); however, this change was described as a likely result of the invasion rather than the cause of it.

Fires consume litter and organic layers, exposing mineral soil, a condition that may favor nonnative invasive species. A meta-analysis of the impact of litter on understory vegetation indicated a generally inhibiting effect on germination, establishment, and productivity (Xiong and Nilsson 1999), though the analysis did not differentiate between nonnative and native plants. Postfire research in northern Arizona ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests suggested that sites with bare mineral soil and little litter favored nonnative plants, whereas native herbs were more tolerant of litter cover (Crawford and others 2001). In contrast, abundance of nonnative grasses Japanese brome (*Bromus japonicus*), soft chess (*Bromus hordeaceus*), and Italian ryegrass (*Lolium multiflorum*) may be reduced by fire when litter is removed because they rely on the moisture retained in the litter layers for germination and establishment (see "Influence of Weather Patterns on Postfire Invasions" page 19).

A small body of research focuses on establishment of nonnative species on burned versus unburned soil or effects of ash on establishment. Research in piñon-juniper woodlands suggests that some nonnative species have an affinity for burned microsites within larger harvested units (for example, prickly lettuce (*Lactuca serriola*), Japanese brome, and London rocket (*Sisymbrium irio*)). Other species, Dalmatian toadflax (*Linaria dalmatica*), white sweetclover (*Melilotus album*), and red brome (*Bromus rubens*), showed no preference for burned soil (Haskins and Gehring 2004). Scotch broom (*Cytisus scoparius*) establishment may even be reduced by exposure to ash (Regan 2001).

Several nonnative invasives occur on harvested forest sites following broadcast burning and appear to prefer burned microsites (chapter 10). Maret and Wilson (2000) found that several nonnative species in western Oregon prairies showed similar emergence but better survival on burned than unburned plots.

Influence of Fire Severity on Postfire Invasions

Fire severity is a measure of a fire's effects on an ecosystem. Specifically, it is the degree to which a site has been altered by fire (National Wildfire Coordinating Group 1996; chapter 1). Fire severity is complex, difficult to measure and predict, and not directly linked to the difficulty of controlling fire, so it is not monitored or reported as regularly as fire behavior descriptors. Nevertheless, an understanding of fire severity is crucial to understanding differential effects of fire on different plant species.

Fire severity is often described as the result of both an upward heat pulse and a downward heat pulse, which are not necessarily correlated (Neary and others 2005b; Ryan and Noste 1985). The upward heat pulse is formed by the flaming front and described by rate of spread, fireline intensity, and flame length. The downward heat pulse is influenced to some extent by the flaming front, especially flaming zone depth, residence time, and reaction intensity. It is influenced more strongly by total heat production and duration, including smoldering and glowing combustion. Upward and downward heat pulses depend to some extent on fire type. Ground fires may heat the soil substantially without producing a strong upward heat pulse. In contrast, surface and crown fires can produce long flames and strong upward heating but may move too fast to ignite ground fuels or heat the soil appreciably.

Upward Heat Pulse—The upward heat pulse from a fire largely determines survival of aboveground plant tissues. Just as for native plants (Miller 2000), nonnatives with aboveground parts that most often survive surface or crown fire are trees with a high canopy, protected buds, and/or thick bark. For example, a single fire results in little mortality of mature, nonnative melaleuca (*Melaleuca quinquenervia*) trees despite a high occurrence of torching and crown fire. Additionally, melaleuca has an aerial seed bank consisting of canopy-stored seed that survives even severe fire. It is one of the first species to germinate after fire in many habitats in southern Florida and can subsequently establish large seedling populations (Munger 2005b, FEIS review). Herbaceous species that retain mature seeds in inflorescences such as nonnative annuals in the Mojave Desert (Brooks 2002), medusahead (*Taeniatherum caput-medusae*) (Pyke 1994), and diffuse knapweed (*Centaurea diffusa*) (Watson and Renney 1974) may be more susceptible to seed mortality from fire than species with soil-stored seed. Of course,

this depends on timing of fire relative to eventual seed dispersal.

Seedlings and saplings of woody plants are more susceptible to mortality from fire than larger individuals because their buds are closer to the ground, and their bark—which can protect the cambium from heat damage—is generally thinner (Morgan and Neuenschwander 1988). For example, while mature common buckthorn (*Rhamnus cathartica*) (Boudreau and Willson 1992), Chinese tallow (*Triadica sebifera*) (Grace and others 2005), and Brazilian pepper (*Schinus terebinthifolius*) (Meyer 2005a, FEIS review) often survive and/or sprout from underground parts after fire, their seedlings and saplings are typically killed by fire.

Downward Heat Pulse—The downward heat pulse from fire influences survival of belowground plant tissue, survival and potential heat scarification of buried seed, consumption of soil organic matter, changes in soil texture and water-holding capacity, and changes in soil nutrient availability—all of which influence the potential for nonnative species to establish, persist, and spread on burned sites, possibly at the expense of native species. An understanding of this aspect of fire severity is crucial for understanding mortality and survival of plants and seeds that are present on a site when it burns. Research investigating the relationship between the downward heat pulse and abundance of nonnative invasive species is discussed below (see “Question 2” page 22). Fundamental aspects of the downward heat pulse are summarized here; more detailed discussion is provided by DeBano and Neary (2005) and Knoepp and others (2005).

The peak temperature reached in soils during fire usually declines rapidly with depth (for example, Beadle 1940; DeBano and others 1979; Neal and others 1965; Ryan and Frandsen 1991). Sites with dry soils that are without heavy fuel loads may burn with no change in temperature 1 to 2 inches (2 to 5 cm) beneath the soil surface (DeBano and others 2005; Whelan 1995). Surface and crown fires may heat the soil relatively little if it is insulated by thick surface organic horizons (“duff”) that do not burn (DeBano and others 2005; Hartford and Frandsen 1992). Duff in forests of western Montana and northern Idaho was unlikely to burn if its moisture content exceeded 60 percent, though it burned even without continued heat from surface fire if its moisture content was less than 30 percent (Hartford and Frandsen 1992).

Duff moisture changes in response to long-term weather patterns (Alexander 1982). When duff becomes dry enough and is subjected to sufficient heat to ignite, seeds and plant parts within it are consumed, its insulating value decreases, and it begins to contribute to the fire's downward heat pulse. Because of its high bulk density, duff burns slowly, usually

with smoldering rather than flaming combustion, and produces an ash layer that can provide a new form of insulation—preventing heat from dispersing upward (DeBano and others 2005).

The heat produced by fire interacts with soil moisture and soil physical properties in complex ways to influence soil heating. Following are some of the principles governing heat transfer into the soil:

1. More heat input is needed to increase the temperature of moist soils than dry soils (DeBano and others 1998; 2005).
2. The thermal conductivity of moist soils may increase with increasing temperature (Campbell and others 1994).
3. When soil water is heated to vaporization, it absorbs substantial heat from its surroundings. When the resulting steam moves to an area of low temperature, it condenses and releases substantial heat to its surroundings (DeBano and others 1998; 2005).

If managers want to minimize soil heating from prescribed burns, the planning process should address both fuel load and the desired soil moisture range. Frandsen and Ryan (1986) found that increasing soil moisture reduced the maximum temperature and duration of soil heating beneath burning fuel piles. Busse and others (2006) measured temperature regimes in soils under approximately 60 tons/acre of masticated fuels and found that soil moisture greater than 20 percent (by volume) kept mineral soil temperatures below 140 °F (60 °C) at depths greater than 2 inches (5 cm); lower soil moisture allowed for greater soil heating. For a review of soil heating models and heat transfer in soil, see Albini and others (1996).

The effects of soil heating on survival of underground plant parts depend on both temperature and duration of heating (Hare 1961). Lethal temperatures for plant tissues generally range from about 104 to 158 °F (40 to 70 °C); some seeds can survive exposure to much higher temperatures (Hungerford and others 1991; Levitt 1980; Volland and Dell 1981). Fire effects studies sometimes use maximum temperature to describe fire severity, but elevated temperatures lasting only seconds are much less likely to kill or damage living tissue than the same temperatures sustained for minutes or hours. Species differ in their susceptibility to heat, and the time needed to kill plants of a given species decreases exponentially as temperature increases (fig. 2-2). Therefore, a time-temperature profile of the soil is a better indicator of fire effects on underground plant parts than a maximum temperature profile. Time-temperature profiles generally show the surface layers reaching higher temperatures than deeper layers, which is consistent with maximum temperature profiles; in addition, they often show shorter duration of elevated temperatures at the soil surface than in deeper layers (for example, Hartford and Frandsen 1992; Ryan and Frandsen 1991). Figure 2-3 shows time-temperature profiles measured during an August prescribed fire under two mature ponderosa pines in northwestern Montana. Maximum temperatures in litter and duff were higher than in deeper layers, but the duration of elevated temperatures increased with depth.

Fire effects on plant tissues also vary with the moisture content and metabolic state of the tissues, a topic addressed in more detail under “Influence of Fire Season and Plant Phenology on Postfire Invasions” page 18.

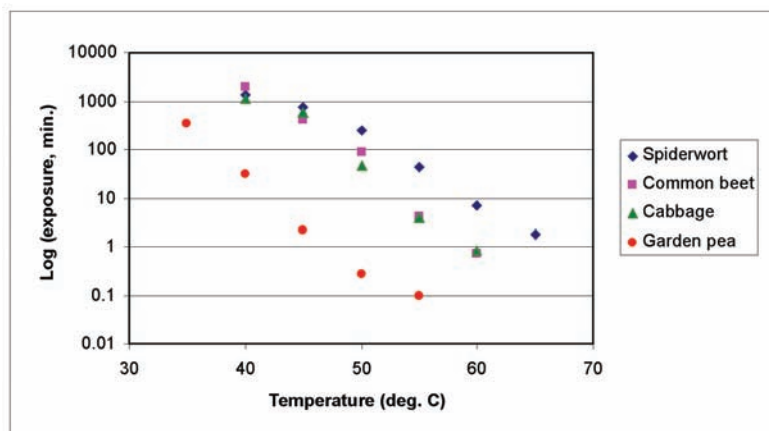


Figure 2-2—Time required to kill four species of plants (spiderwort (*Tradescantia* sp.), common beet (*Beta vulgaris*), cabbage (*Brassica oleracea*), and garden pea (*Pisum sativum*)) at a range of temperatures, adapted from Levitt (1980), from laboratory research conducted in Germany. Note that the y axis is a logarithmic scale. Highest time values for spiderwort, beet, and pea are approximate or the midpoint of a range.

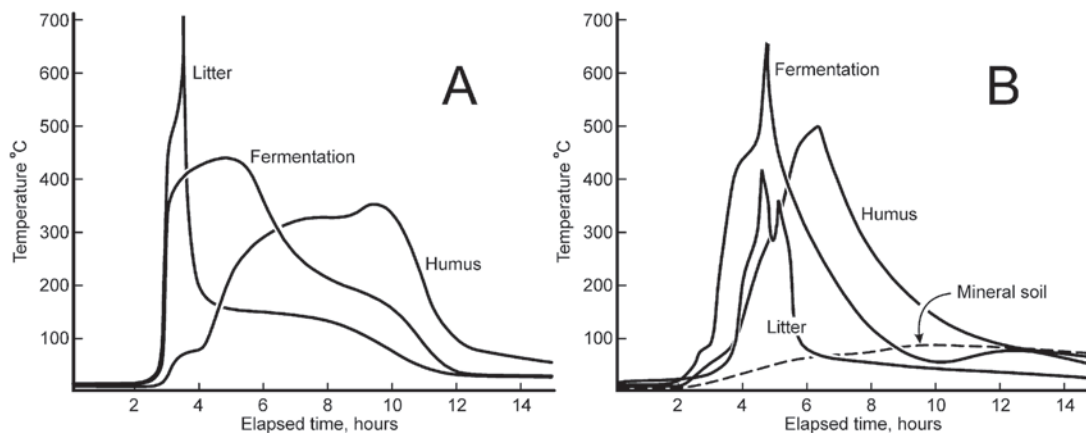


Figure 2-3—Time-temperature profiles under mature ponderosa pine canopy in northwestern Montana (Ryan and Frandsen 1991). (A) Downward-spreading ground fire in litter and fermentation layer (duff) 7 cm deep. (B) Laterally spreading ground fire in litter/duff 17 cm deep. (Adapted with permission from *International Journal of Wildland Fire*, CSIRO Publishing, Melbourne Australia.)

Downward heat pulse effects on plant survival—

The ability of individual plants to survive fire depends on the temperature regime at the location of their perennating tissues (Miller 2000) and is thus related to fire severity. Raunkiaer (1934) classified plants according to their means of surviving freezing temperatures, by noting the vertical position of their perennating tissues, or buds, above and below the

soil surface (table 2-2). This classification can be adapted to explain plant response to fire by considering not only dormant buds that survive fire but also adventitious buds that sprout after the plant is top-killed. Many plants survive lethal heating of aboveground tissues because their underground parts are capable of producing new stems, roots, and leaves (Smith 2000).

Table 2-2—Effects of fire on Raunkiaer (1934) plant life forms.

Raunkiaer life form	Example	Perennating tissue	Potential injury from fire
Therophytes	Annuals	Seeds that reside on or under the soil surface, or on senesced plants	Depends on where seeds are located during fire
Chamaephytes	Some shrubs & herbs	Perennial tissue and/or adventitious buds just above the soil surface	Often killed by fire due to position within the flaming zone
Hemicryptophytes	Rhizomatous plants, root sprouters	Perennial tissue and/or adventitious buds just above or below the soil surface	Depends on their location in organic or mineral soil; combustion of litter and duff; amount of soil heating from smoldering combustion; can be as well protected as bulbs or corms
Cryptophytes	Plants with bulbs or corms	Perennial tissue and/or adventitious buds well below the soil surface	Protected from all but severe fires due to insulation from soil
Phanerophytes	Trees & tall shrubs	Perennial tissue and/or epicormic buds well above the soil surface	Can be killed by crown fires, which consume the canopy, or by surface fires if severe enough to kill the cambium or perennating buds

Plants with buds located in the combustible organic layers of soil can survive if the organic matter does not burn. Plants with buds in mineral soil have greater potential to survive; the deeper the perennating tissue, the more likely their survival. Dormant and adventitious buds can occur on stolons, root crowns, rhizomes, roots, caudices, bulbs, and corms (fig. 2-4). Stoloniferous plants have stems or branches that grow on the surface and can sprout from buds along their length. Because of their position, stolons are likely to be damaged by fire. In contrast, buds in the root crown, the transition area between stem and root, are somewhat better protected from fire because of their position at or beneath the surface, possible insulation from bark, and thermal mass. Rhizomes (usually horizontal) and caudices (vertical) are plant stems growing within the organic or mineral soil, and roots also grow in these layers (fig. 2-5). Duff and mineral soil may insulate their buds from heat damage, especially when they are located in mineral soil, well below the surface. Bulbs and corms—underground plant storage organs bearing roots on their lower surfaces—usually grow below the organic layer in mineral soil and are well protected from all but severe ground fires.

Several species of nonnative invasive trees sprout after fire. Examples include melaleuca (Munger 2005b), Chinese tallow (Meyer 2005b, FEIS review), and tamarisk (*Tamarix* spp.) (Zouhar 2003c, FEIS review). However, severe fire can kill both Chinese

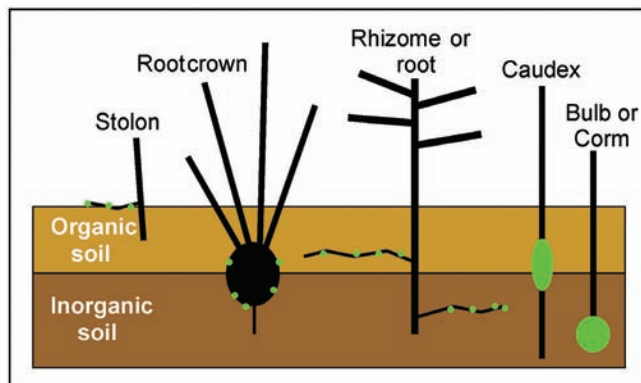


Figure 2-4—Organs that may enable perennial plant species to survive fire. Green circles indicate meristem tissues. Native species may have any of these organs; none of the nonnative species discussed in this volume have bulbs or corms. Organic soil horizons are not always distinct, as suggested by this diagram; they often intergrade with top layer of mineral soil. For more discussion of plant organs in relation to fire, see Miller (2000).



Figure 2-5—Sulfur cinquefoil sprouting, probably from surviving caudex, within a month after September wildfire in a western Montana mountain grassland. (Photo by Peter Rice.)

tallow (Grace and others 2005) and tamarisk (Ellis 2001). Fire can top-kill most nonnative invasive shrubs, but many persist via underground tissues, with survival depending on fire severity. For example, gorse (*Ulex europaeus*) occurs in heathlands in its native range, where it responds to low-severity surface fire by sprouting from the basal stem region. Under these circumstances, postfire vegetative regeneration of gorse can be prolific and rapid. However, severe ground fire, which consumes most or all of a deep organic surface horizon, typically kills gorse (Zouhar 2005d, FEIS review). Mortality of Scotch broom in Australia (Downey 2000) and Washington (Tveten and Fonda 1999), and French broom (*Genista monspessulana*) in California (Boyd 1995; 1998) also appears to be related to fire severity. Gorse and brooms also establish prolifically from on-site seed in the postfire environment, with abundance dependent on fire severity (see “Downward heat pulse effects on seed” page 16).

Most grasses are top-killed by fire. However, perennial grasses sprout seasonally, so removal of aboveground biomass in itself is not a factor affecting postfire survival. Rhizomatous grasses have an extensive underground network of rhizomes that are likely to survive and sprout after fire. There are many examples of invasive perennial grasses that sprout after fire, especially in the Central (chapter 7), Interior West (chapter 8), and Hawaiian Islands (chapter 11) bioregions. These species typically respond with rapid sprouting and high fecundity in the postfire

environment (see “Question 1” page 20). However, some nonnative perennial grasses may be killed by high-severity fire. Redtop (*Agrostis gigantea*), for example, a rhizomatous grass introduced from Europe, generally survives fire (Carey 1995, FEIS review) but may be killed by ground fires in peat (Frolik 1941). Crested wheatgrass (*Agropyron cristatum*) and desert wheatgrass (*Agropyron desertorum*) are nonnative bunchgrasses that generally burn quickly, transferring little heat into the soil. However, fires that smolder in the dense clusters of stems in these bunchgrasses, burning for extended periods after the fire front has passed, are likely to kill them (Skinner and Wakimoto 1989).

Fires may kill seedlings and top-kill adult nonnative perennial forbs, but adult plants typically survive and sprout from perennial underground parts after fire. This is probably because even the most severe fires rarely damage plant tissues below 2 inches (10 cm) in the soil, while perennial rhizomes and roots with dormant or adventitious buds on some plants can penetrate the soil to a depth of several feet. Information on differential effects of fire severity was found for several invasive perennial forbs, but results from these studies are inconclusive due to incomplete information. A study from Australia suggests that St. Johnswort (*Hypericum perforatum*) mortality increases with increased fire severity (Briese 1996); and two studies from central Illinois suggest that garlic mustard (*Alliaria petiolata*) may be sensitive to severe fire (Nuzzo 1996; Nuzzo and others 1996).

Where information on response to fire is lacking for most nonnative species, cautious inferences can be made based on plant morphological traits. Species with subterranean dormant and adventitious buds are likely to survive and sprout following fire (Goodwin and others 2002). Perennial woody and herbaceous species known to sprout following mechanical damage or top-kill by means other than fire may be capable of similar responses to fire if their perennating tissues are protected from the downward heat pulse. However, fires and mechanical disturbances alter a site in different ways, so biological responses cannot be assumed to be equivalent.

Downward heat pulse effects on seed—Like plants that survive a fire onsite, residual colonizers (species that leave viable seed onsite even if mature plants are killed by fire) have early access to resources in the postfire environment. Seed survival depends on seed location relative to the occurrence of lethal temperature regimes. Because grasses produce fine fuels with high surface-to-volume ratios, fuel consumption in grassland communities is often rapid, residence times are short, and lethal temperatures may not occur at the soil surface (Daubenmire 1968a). Invasive grasses and grassland invaders with seed that frequently survives

fire include medusahead (Blank and others 1996), cheatgrass (Evans and Young 1987), yellow starthistle (*Centaurea solstitialis*) (Hastings and DiTomaso 1996), and filaree (*Erodium* spp.) (chapter 9). Seeds in soil organic layers may be killed or consumed by fire if the organic material burns, but seed at the mineral soil surface may survive even where litter is burned (for example, Japanese brome (Whisenant 1985)). It should be noted that grassland fires do not always produce mild temperature regimes. For example, in prescribed fires on the Texas plains, the maximum temperature recorded at the soil surface was 1260 °F (682 °C), and temperatures exceeded 150 °F (66 °C) for as long as 8.5 minutes (Stinson and Wright 1969).

Buried seeds are most likely to survive fire. For example, tumble mustard (*Sisymbrium altissimum*) has tiny seeds that fall into fire-safe microsites such as soil crevices (Howard 2003b, FEIS review), and cutleaf filaree (*Erodium cicutarium*) seed is driven into the soil by the styles (Felger 1990)—traits that may protect these seeds from fire. However, seeds buried too deep in the soil may fail to establish if they require light for germination (for example, bull thistle (*Cirsium vulgare*) and Lehmann lovegrass (*Eragrostis lehmanniana*)) or if endosperm resources are depleted before the seedlings emerge from the soil. The effect of seed burial depth on germination is demonstrated by several nonnative invasives. Rattail sixweeks grass (*Vulpia myuros*), a nonnative annual grass, germinated more successfully from 0.5-inch (1-cm) depth than from 2-inch (5-cm) depth in a greenhouse study; seedlings emerging from 5 cm weighed significantly less than seedlings from 1 cm (Dillon and Forcella 1984). Optimum germination of spotted knapweed (*Centaurea biebersteinii*) seed occurs with the seeds at the soil surface and decreases with depth, with little germination below 2 inches (5 cm) (Spears and others 1980; Watson and Renney 1974). Scotch broom germination rates are highest in the top inch (2 cm) of soil, and seedlings do not emerge from below 3 inches (8 cm) (Bossard 1993). St. Johnswort seed germination is limited in the dark, and seedlings emerging from seed buried as little as 0.5 inch (1 cm) rarely survive (Zouhar 2004, FEIS review).

Seed bank formation is complex and depends on many factors, including (1) seed rain, dormancy, predation, longevity, and size; (2) soil texture, structure, deposition, and compaction; and (3) movement of seeds by wind, earthworms, insects, and animals (Baskin and Baskin 2001). Because of this complexity, seed longevity under field conditions is rarely known accurately and is often estimated from field observations and laboratory studies. Several nonnative forbs have been reported to regenerate from a soil seed bank, including bull thistle (Doucet and Cavers 1996), St. Johnswort (Zouhar 2004), tansy ragwort (*Senecio jacobaea*) (chapter 10),

and common groundsel (*S. vulgaris*) (Zammit and Zedler 1994). Establishment and spread of these species is triggered by disturbances that remove existing vegetation. Gorse, Scotch broom, and French broom all form seed banks (Zouhar 2005a,c,d). The ability of these shrubs to establish large numbers of seedlings after fire is related to prolific seed production, longevity of viable seed, and a scarification requirement for germination.

Seeds of several nonnative species are stimulated to germinate by exposure to heat or fire. Brooms and gorse seed germination is stimulated by heat scarification (Zouhar 2005a,c,d). Mimosa (*Albizia julibrissin*) seeds exposed to flame in the laboratory had higher germination rates than unheated seeds (Gogue and Emimo 1979). Lehmann lovegrass seeds are dormant at maturity, but seed on the soil surface can be scarified either by fire or by high summertime seedbed temperatures (Sumrall and others 1991). Field observations (Briese 1996; Sampson and Parker 1930; Walker 2000) and laboratory tests (Sampson and Parker 1930) suggest that fire stimulates germination of St. Johnswort seed. Most yellow sweetclover (*Melilotus officinalis*) and white sweetclover seeds can remain viable in the seed bank for 20 to 40 years (Smith and Gorz 1965; Smoliak and others 1981; Turkington and others 1978) and have hard seed coats that require scarification for germination (Smith and Gorz 1965). Fire aids establishment of sweetclover in grasslands, probably because it scarifies seed and simultaneously creates openings in which sweetclover can establish (Heitlinger 1975). Soil heating by fire may promote kudzu (*Pueraria montana* var. *lobata*) germination by scarifying the seedcoat, allowing water to penetrate (Munger 2002b, FEIS review).

While heat stimulates seed of some nonnative invasives to germinate, it inhibits others. Examples from laboratory tests include spotted knapweed (Abella and MacDonald 2000), bull thistle, woodland groundsel (*Senecio sylvaticus*) (Clark and Wilson 1994), common velvetgrass (*Holcus lanatus*) (Rivas and others 2006), and Johnson grass (*Sorghum halepense*) (Mitchell and Dabbert 2000). Other species show reduced establishment following fire in the field. Menvielle and Scopel (1999, abstract) report that the surface seed bank of chinaberry (*Melia azedarach*) is completely killed by fire, although there was "some" emergence from buried seed. Brooks (2002) found that nonnative annuals (red brome, Mediterranean grass (*Schismus* spp.), and cutleaf filaree) in the Mojave Desert responded to different temperature regimes in different microsites. The highest temperatures occurred under the canopies of creosotebush (*Larrea tridentata*) shrubs (where the most fuel was consumed), and these microsites had reduced biomass of the nonnative annuals for 4 years after fire. At the canopy dripline, where temperatures

were lower, annual plant biomass was reduced for 1 year, while negligible postfire changes occurred in interspace microsites, where fire produced little soil heating (Brooks 2002).

Influence of Fire Frequency on Postfire Invasions

The relationship between nonnative species and fire frequency has received little attention outside the context of control efforts (chapter 4). A plant's response to fire frequency should theoretically be related to its life history, morphology, and maturity. Many annuals can persist under a regime of frequent, even annual, burning if their seeds are protected from heat and subsequent growing conditions are favorable (see table 2-2). Examples among nonnative species that persist under a regime of frequent fire include many annual grasses and forbs in the Great Basin and California (chapters 8 and 9). Exceptions include medusahead and rippgut brome (*Bromus diandrus*), which showed a significant decrease in abundance after two consecutive burns (DiTomaso and others 2006b), probably because their seeds are not protected from heat. Another exception is prickly lettuce in Central bioregion tallgrass prairie (Towne and Kemp 2003). In fact, native prairie species tend to be adapted to frequent fire and can often resist invasion by nonnatives under a regime of frequent fire (chapter 7). This is especially evident in large, intact ecosystems with low propagule pressure, as compared to fragmented landscapes with large pools of nonnatives present (Smith and Knapp 2001).

The ability of perennial species to persist through repeated fires depends on protection of their meristem, buds, and seed from heat and their ability to replenish energy stores and buds after fire (Whelan 1995). Most perennial herbs are vulnerable to fire as seedlings, so repeated fires at short intervals are likely to reduce establishment. Ability to withstand fire is likely to increase with maturity if underground structures expand (Gill 1995). Unfortunately, literature describing responses of nonnative plants to differing fire intervals is rarely available (chapter 12). Results of studies in different locations can be compared, but it is difficult to ascertain whether differing results are caused by different fire frequencies or by other variables, such as community properties and fire severity and seasonality. For example, spotted knapweed abundance tends to increase after single fires in ponderosa pine communities in the Interior West bioregion (chapter 8), while in Michigan, annual spring prescribed burning under severe conditions (when humidity and dead fine fuel moisture are as low as possible) reduces spotted knapweed populations and increases the competitiveness of the native prairie vegetation (J. McGowan-Stinski, personal communication 2001).

Woody species seedlings also tend to be susceptible to fire, though fire resistance for many increases with age as bark thickens, underground structures expand, and bud-bearing stems become taller. Even though mature melaleuca trees are very resistant to damage from repeated fires (Geary and Woodall 1990), most seedlings (up to 12 inches (30 cm) tall) are killed by fire (Timmer and Teague 1991). Similarly, Grace and others (2005) describe prescribed fires that killed all Chinese tallow less than 4 inches (10 cm) tall and 40 percent of those 4 inches to 3 feet (10 cm to 1 m) tall (Grace and others 2005). It is not surprising that research is lacking on the effects of varying fire frequencies on invasive trees, since this information can only be obtained from long-term studies. Considering the potential for interactions among carbohydrate reserve patterns, fluctuating resources in the ecosystem due to fire, heat damage to plants and secondary damage from insects and pathogens, and competitive interactions among species, it is difficult to accurately predict the effects of varying fire frequencies on long-lived woody species without field research, and even then results are likely to be specific to the plant community studied. Long-term research is needed on how varying fire intervals and their interactions with fire severity and seasonality affect nonnative plants.

Influence of Spatial Extent and Uniformity of Fire on Postfire Invasions

The availability of propagules within a burn and from nearby unburned sites depends on fire size, patchiness, and uniformity of fire severity. Giessow and Zedler (1996) found that rates of establishment of nonnative species declined with distance from source populations. If a burned area is large, species establishing from off-site are likely to be represented by long-distance seed dispersers. Several nonnative species with small, wind-dispersed seed are reported in early postfire communities (see “Question 1” page 20). Animal dispersal of invasive plant seeds after fire has not been documented in the literature, but this mode of establishment seems likely for many nonnative invasives, such as Brazilian pepper in the Southeast (Ewel and others 1982) and numerous shrubs and vines in the Northeast (chapter 5).

When burned areas occur in patchy vegetation or a highly fragmented landscape, rates of postfire establishment of nonnative species can be high (Allen 1998; Minnich and Dezzani 1998). After comparing the establishment of nonnative invasive species from small and large species pools in Kansas tallgrass prairie, Smith and Knapp (2001) suggest that increasing fragmentation of ecosystems will increase invasibility. Cole (1991) notes that sweetclover may persist despite repeated burns to control it if the fires are patchy,

leaving some of the seed bank intact and enabling second-year shoots to survive. Keeley and others (2003) found that nonnatives were uncommon in unburned chaparral but persistent in adjacent blue oak (*Quercus douglasii*) savannas. Because these two communities occurred in a mosaic, nonnatives rapidly established in patches of burned chaparral from the savanna. Nonnatives in chaparral constituted 8 percent of the plant species present 1 year after fire, 23 percent the second year, and 32 percent the third year.

Variation in fire severity (which may result from patchy vegetation, variation in fuel structure and moisture, or other factors) may also increase the susceptibility of a site to spread of invasives (see “Question 2” page 22).

Influence of Fire Season and Plant Phenology on Postfire Invasions

Fire effects on plant tissues vary with the moisture content and metabolic state of the tissues themselves (Hare 1961; Volland and Dell 1981). More heat is required to raise the temperature of large, thick tissues than fine ones (Hungerford and others 1991; Levitt 1980; Whelan 1995), so lignotubers and thick rhizomes are generally less susceptible to fire damage than root hairs and mycorrhizae at the same depth in the soil. In addition, actively growing plants generally suffer damage at lower temperatures than seeds or dormant plants of the same species (Volland and Dell 1981). Kentucky bluegrass, for example, flowers early and is dormant by mid-summer. The species is not usually damaged by late-summer fire unless it occurs during drought (Uchytel 1993, FEIS review). This variation in fire response may be related to the higher water content of growing than dormant plants (Zwolinski 1990) or the lack of stored carbohydrates available for regrowth if plants are burned during the growing season (Whelan 1995). Phenological patterns may interact with soil moisture patterns to influence a species' susceptibility to heat damage, since plant and soil moisture may vary together through the seasons.

Influence of fire season on invasions by nonnative species is not often described in the scientific literature (chapter 12). Since temperate herbs die back to the ground at the end of the growing season, dormant season fires usually have little impact on their survival. Growing season fires are more likely to cause direct mortality, damage actively growing tissues, deplete resources, and increase postfire recovery time (Miller 2000) in herbaceous plants and woody species as well. A review by Richburg and others (2001) suggests that prescribed burns conducted in the Northeast bioregion during the dormant season ultimately increase the density of invasive woody species. Similarly, dormant season and growing season burns do not differ in

immediate damage to Chinese tallow, but growing season fires result in weaker recovery and greater long-term impacts to this species (Grace and others 2005). Additionally, season of burning may indirectly affect postfire response of a particular species due to its relationship to fire severity. For example, higher severity of fall fires versus spring fires may account for the significantly higher mortality and lower basal sprouting of Scotch broom following fall burning (Tveten and Fonda 1999). Managers can take advantage of differences in phenology between nonnative invasives and desired native species in planning burns to increase dominance of desired species (chapter 4).

Influence of Weather Patterns on Postfire Invasions

Weather patterns, especially timing and amount of precipitation, may be decisive in determining the ability of nonnative invasive species to establish, persist, and spread. This may be particularly evident in arid and semiarid communities. Abundance of nonnative annuals in desert shrublands, for example, is strongly affected by precipitation patterns (chapter 8). Increased fuel loads and continuity in years with above-average precipitation can increase the probability that an area supporting nonnative annual grasses will burn in the following dry season (Knapp 1995, 1998). When these annual grasses persist and spread after fire, creating conditions favorable for more fire, a grass/fire cycle may result (chapter 3).

Postfire weather conditions affect the ability of nonnative invasive species to persist and spread after fire (D'Antonio 2000). *Melaleuca* seedling establishment, for example, is affected by timing and amount of precipitation relative to burning (Munger 2005b; chapter 6). In a central Utah sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) community, postfire abundance of cheatgrass over a 20-year period seems closely tied to precipitation patterns—declining during drought and increasing during wet periods (Hosten and West 1994; West and Hassan 1985; West and Yorks 2002).

Species exhibiting a reduced abundance after fire coincident with lower than average postfire precipitation include yellow starthistle, sulfur cinquefoil (*Potentilla recta*), and Japanese brome. A single burn typically increases germination and density of yellow starthistle, but fire eliminated yellow starthistle on a site that experienced drought after fire (DiTomaso and others 2006b). For 2 years following an August wildfire in grasslands dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*) and Sandberg bluegrass (*Poa secunda*) in Idaho, yellow starthistle canopy cover increased significantly—probably aided by substantial precipitation the month after the fire

(Gucker 2004). In a northwestern Montana rough fescue (*Festuca altaica*) grassland, small prescribed burn treatments were followed by increased density of small sulfur cinquefoil plants, but the population then decreased under the drought conditions that prevailed during the 5-year study (Lesica and Martin 2003). The current view of fire effects on Japanese brome is based on its requirement for sufficient moisture to establish and the role of plant litter in retaining soil moisture (Whisenant 1989). Fire kills the majority of Japanese brome plants and much of the seed retained by the plant and also removes the litter layer, so populations of Japanese brome are often substantially reduced following fire (for example, Ewing and others 2005; Whisenant and Uresk 1990). When fall precipitation is plentiful, however, litter is not required for successful establishment and populations can rebound immediately (Whisenant 1990b). Moisture availability may influence Japanese brome population dynamics more than fire (chapter 7).

In contrast to the above examples, burned perennial Lehmann lovegrass may increase under postfire drought conditions. This species exhibited no reduction in biomass production during an experimental drought (Fernandez and Reynolds 2000) and had greater reproductive output on burned versus unburned plots during 2 years of lower than average precipitation after fire in the High Plains of Texas (McFarland and Mitchell 2000).

Generalizations About Fire Effects on Nonnative Invasives

In the previous sections, we applied concepts of invasion ecology, fire behavior, fire regimes, and competition to the potential effects of fire on nonnative invasive species. In this section, we use that conceptual basis to examine several generalizations about postfire invasion that are often suggested. We treat these generalizations as questions and explore their applicability and scope using examples from the scientific literature. While several of the generalizations are supported by examples from the literature, each one also has exceptions. The take-home message of this analysis is that, while generalizations are useful for *describing and explaining* fire's relationship to nonnative invasive species, they have limited usefulness for *predicting* what will happen on a given site after a given burn. Generalizations can alert the manager to what might happen after fire; but local knowledge of plant communities, the status of nonnative species, and the burn itself (especially severity and uniformity) are essential for managers to select and prioritize management actions that will minimize ecosystem impacts from nonnative species after fire and to avoid

management actions that are unnecessary and could themselves cause environmental damage.

One problem with most scientific literature on nonnative species is that the species considered have been selected for study because they are problematic. They are usually among the ~1 percent of nonnative species that become invasive (causing ecological or economic harm) or are otherwise considered pest species (Williamson 1993; Williamson and Brown 1986). Because researchers tend to study the most invasive nonnative species (for example, see Vilà and Weiner 2004), it is worthwhile to keep in mind that (1) not all nonnative species are invasive, (2) no invasive species causes harm in every native plant community in which it occurs, and (3) some nonnatives currently considered innocuous may eventually cause ecological damage to a native community. As mentioned frequently in this volume, local knowledge is as important as an understanding of general concepts relating to nonnative species and fire.

Question 1. Does Fire Generally Favor Nonnatives Over Natives?

Generally speaking, if a fire occurs in a plant community where nonnative propagules are abundant and/or the native species are stressed, then nonnative species are likely to establish and/or spread in the postfire environment. To what degree they will dominate, and for how long, is less clear. Chapter 12 points out the lack of long-term studies on nonnative species after fire.

The interaction between fire and nonnative species is complex and research results are limited and variable. A review of recent research on fire and nonnative species (D'Antonio 2000) supports the contention that accidental and natural fires often result in increases in some nonnative species. However, the scope of the review is limited with regard to North American plant communities: It includes studies from five habitats in California, two in the Great Basin Desert, three in the Sonoran Desert, one in Canada, and one in Hawai'i (D'Antonio 2000). The bioregional discussions in this volume provide a more comprehensive review of nonnative-fire interactions in North American plant communities. Community-level information supporting postfire increases in nonnatives is available for California grasslands and shrublands (chapter 9), desert shrublands (chapter 8), wet grasslands invaded by melaleuca (chapter 6), and closed-canopy forests (chapter 10). In addition, a growing body of literature describes postfire increases of nonnatives in other communities, including forests dominated by ponderosa pine (for example, Cooper and Jean 2001; Phillips and Crisp 2001; Sackett and Haase 1998; Sieg and others 2003); piñon-juniper (*Pinus* spp. –

Juniperus spp.) woodlands (chapters 8 and 9), and Hawaiian shrublands and grasslands (chapter 11). These bioregional discussions also present exceptions. Fires in grasslands and prairies, which have evolved with frequent fire, often favor native species over nonnatives (chapters 6, 7, 8, 10). In other plant communities (for example, Oregon white oak (*Quercus garryana*) woodlands) and other bioregions (for example, the Northeast and Alaska), information on interactions between fire and invasives does not follow a consistent pattern. Because research is limited and results are variable, the generalization that fire favors nonnatives over natives cannot be applied to all nonnative species or all ecosystems. A breakdown based on postfire regeneration strategies of the nonnative species may be more helpful.

Survivors—Most nonnative perennial species studied have the ability to sprout from root crowns, roots, or rhizomes following top-kill or damage. For several of these species, the literature reports postfire sprouting. Some reports also note that these species spread in the postfire environment, although information regarding their effects on native communities, especially over the long term, tends to be sparse.

Nonnative invasive woody species are most common in the Northeast, Southeast, and Northwest Coastal bioregions, and in riparian communities in the Interior West and Central bioregions. Melaleuca (Munger 2005b; chapter 6) and tamarisk (Busch 1995; Ellis 2001) are known to sprout after fire with greater vigor than associated native species and tend to dominate postfire communities. The woody vine kudzu, known to dominate plant communities in the Southeast bioregion to the detriment of native species, sprouts from the root crown after fire and may return to previous levels of dominance by the second postfire growing season (Munger 2002b). For other woody species, however, such as tree-of-heaven (Gibson and others 2003), Russian-olive (USDA Forest Service 2004), and autumn-olive (chapter 5), reports of postfire sprouting tend to be anecdotal, and postfire consequences to ecosystems are not described.

Nonnative shrubs such as chinaberry, bush honeysuckles (*Lonicera* spp.), and glossy buckthorn (*Frangula alnus*) are known to sprout after fire, but information on postfire response in invaded communities is limited and sometimes conflicting. For example, chinaberry exhibited vigorous crown and root sprouting from adventitious buds after fire in Argentina (Menvielle and Scopel 1999, abstract). It is speculated that postfire sprouting of this type can lead to spread of chinaberry (Tourn and others 1999), but to date, no fire research on this species has been published from North America. Several studies indicate limited mortality and basal sprouting in bush honeysuckles after fires in spring, summer, and fall (for example, Barnes 1972; Kline

and McClintock 1994; Mitchell and Malecki 2003), but none provide information beyond the first postfire year. Glossy buckthorn was reported to increase after fire in a calcareous fen in Michigan (chapter 5) and in an alvar woodland in Ontario (Catling and others 2001), but this species was also strongly associated with unburned alvar woodland (Catling and others 2002), so the specific effects of fire are unclear. In the Northwest Coastal bioregion, several nonnative woody species including blackberries (*Rubus* spp.), Scotch broom, sweetbriar rose (*Rosa eglanteria*), and common pear (*Pyrus communis*) sprout from underground parts after fire, often with increased stem density; however, effects of these species on the native community after fire are not well described. Additionally, these species also spread with fire exclusion in some communities (chapter 10).

Nonnative perennial herbs such as Canada thistle (*Cirsium arvense*) (Zouhar 2001d, FEIS review), spotted knapweed (MacDonald and others 2001; Zouhar 2001c, FEIS review), Dalmatian toadflax (*Linaria dalmatica*) (Jacobs and Sheley 2003a), St. Johnswort (Zouhar 2004), and sulfur cinquefoil (Lesica and Martin 2003) tend to survive fire and may spread in postfire communities (see “Downward heat pulse effects on plant survival” page 14). But postfire dominance is likely to vary with plant community, fire frequency, and fire severity. For example, spotted knapweed and Canada thistle may increase in abundance in ponderosa pine and closed-canopy forests after fire, while in native prairies, where the dominant native species are well adapted to frequent fire, their abundance may be reduced by fire (see “Influence of Fire Frequency on Postfire Invasions” page 17, and “Question 5” page 27).

In Hawai‘i, nonnative perennial grasses and nonnative Asian sword fern (*Nephrolepis multiflora*) survive fire and can respond with increased cover at the expense of native species (chapter 11). For example, fountain grass (*Pennisetum setaceum*) can sprout rapidly following top-kill and set seed within a few weeks (Goergen and Daehler 2001). In another study, total nonnative grass cover was about 30 percent higher and total native species cover lower in burned than unburned transects 2 to 5 years after fire (D’Antonio and others 2000; Tunison and others 1995). Asian sword fern is observed to sprout shortly after fire and quickly dominate the understory in mesic ōhi‘a forest (Ainsworth and others 2005; Tunison and others 1995).

Seed Bankers—Residual colonizers with surviving viable seed in the soil after fire have early access to resources and may dominate the postfire environment, at least in the short term. Several examples are presented above (see “Downward heat pulse effects on seed” page 16).

Flushes of seedlings from heat-scarified seed in the soil seed bank can be dramatic, so these species tend

to dominate immediately after fire. Examples include brooms (Zouhar 2005a,c), St. Johnswort (Sampson and Parker 1930; Walker 2000), and lovegrasses (*Eragrostis* spp.) (Ruyle and others 1988; Sumrall and others 1991). Dense populations of these species can persist in some communities. For example, Scotch and French broom form dense thickets in California grasslands. Flushes of broom seedlings after fire (for example, see Haubensak and others 2004) are likely to maintain populations of these species indefinitely (for example, Boyd 1995, 1998).

Other species that establish from the soil seed bank include annual grasses and forbs, though they may not dominate until the second or third postfire season, and may or may not persist. Density and timing of postfire dominance by these species may depend on precipitation (see “Influence of Weather Patterns on Postfire Invasions” page 19). Once established, populations can persist for many years. For example, in a Wyoming big sagebrush shrub-steppe community on the Snake River Plain south of Boise, Idaho, cover of nonnative annual grasses was sparse in control plots, which were dominated by predominantly native species, while nonnative annuals dominated burned plots 10 years after fire (Hilty and others 2004).

Seed Dispersers—Dramatic postfire increases in nonnative species with wind-dispersed seed are commonly described in the literature, although the seed source is rarely indicated so establishment may be from the soil seed bank in some cases. Nonnative species with small, wind-dispersed seed often occur and sometimes dominate burned forest sites in the early postfire environment in the Interior West and Northwest Coastal bioregions. Examples include Canada thistle (Floyd and others 2006; MacDougall 2005; Turner and others 1997; Zouhar 2001d), bull thistle (MacDougall 2005; Zouhar 2002b, FEIS review), musk thistle (*Carduus nutans*) (Floyd and others 2006), wild lettuces (*Lactuca* spp. and *Mycelis* spp.) (Agee and Huff 1980; Sutherland, unpublished data 2008; Turner and others 1997), tansy ragwort (Agee and Huff 1980), hairy catsear (*Hypochaeris radicata*) (Agee and Huff 1980), common velvetgrass (Agee 1996a,b), and dandelion (*Taraxacum officinale*) (Wein and others 1992). These species tend to be absent from adjacent undisturbed forest. Their abundance usually peaks 2 to 4 years after fire, after which their numbers decline (see “Question 4” page 25). However, there are exceptions to this pattern. For example, piñon-juniper communities have supported populations of Canada and musk thistle for over 13 postfire years (Floyd and others 2006), and many species can survive on site through viable seed in the soil seed bank from which seedlings can establish after another disturbance (Clark and Wilson 1994; Doucet and Cavers 1996). Other invasives that establish after fire via long-distance seed dispersal

include princess tree (*Paulownia tomentosa*) in the Northeast bioregion (Reilly and others 2006), cogon grass (*Imperata cylindrica*) (Mishra and Ramakrishnan 1983) in the Southeast bioregion, and fountain grass in Hawai'i (Nonner 2006).

Species With Increased Fecundity After Fire—Several species produce unusually large seed crops in the postfire environment. For instance, the August following a stand-replacing fire at Lees Ferry, Arizona, 69 percent of burned tamarisk plants were blooming heavily, while on adjacent unburned sites 11 percent of tamarisk plants were blooming (Stevens 1989). Other perennials showing an increase in flowering and seed production after fire include Dalmatian toadflax (Jacobs and Sheley 2003a) and St. Johnswort (Briese 1996). Annual species often produce more seed in burned than unburned sites, allowing the annuals to spread rapidly during the time when resource availability may be high (Brooks and Pyke 2001). Examples include cheatgrass in diverse habitats (Mojave desert, sagebrush (*Artemisia* spp.) grasslands, and dry ponderosa pine and grassland in Idaho) (Zouhar 2003a, FEIS review), yellow starthistle in California grasslands (Hastings and DiTomaso 1996), and annual vernal grass (*Anthoxanthum aristatum*) in Oregon white oak woodlands (Clark and Wilson 2001).

Exceptions—While many studies support the generalization that nonnatives increase after fire, the above discussion illustrates substantial variation. Additionally, impacts from postfire invasions are not well documented, especially over the long term.

Some species can be reduced by fire (chapter 4), and some research demonstrates that fire exclusion contributes to invasion of native plant communities that have evolved with frequent fire. For example, native prairies are invaded by woody species and cool-season grasses in the Central bioregion (chapter 7). Oregon white oak woodlands and Idaho fescue (*Festuca idahoensis*) prairies are invaded by nonnatives Scotch broom and Himalayan blackberry (*Rubus discolor*) in the Northwest Coastal bioregion (chapter 10). Wet grasslands and pine habitats are invaded by nonnative woody species in the Southeast (chapter 6), and oak forests and savannas are invaded by nonnative shrubs and vines in the Northeast (chapter 5).

Question 2. Do Invasions Increase With Increasing Fire Severity?

Several researchers report greater abundance of nonnative species following high-severity fire compared with unburned or low-severity burned sites. Definitions of fire severity vary in these accounts, with some relating severity to canopy removal and others relating it to litter or fuel consumption and/or

ground char. On conifer sites in California, abundance of nonnative species was low in virtually all burned sites, but was greatest in areas with high-severity fire (Keeley and others 2003). Similarly, nonnative species cover in ponderosa pine forests of Colorado, New Mexico, and Arizona was positively correlated with fire severity and reduction of tree cover (Crawford and others 2001; Hunter and others 2006). High-severity burn patches were associated with establishment of nonnative invasive species such as tansy ragwort and common velvetgrass in closed-canopy forests in the Northwest Coastal bioregion (Agee 1996a,b). Establishment of prickly lettuce was greatest in high-severity burn patches in forests of Yellowstone National Park (Turner and others 1997) and ponderosa pine forests in Idaho (Armour and others 1984). Much of the literature on burning of slash piles, which produces high-severity patches in an otherwise unburned site, indicates that ruderal species (native and nonnative) establish readily in burned patches, but persistence is variable (see Question 3 below).

Although several studies support the generalization that severe fire leads to increased establishment and spread of nonnative species, fire obviously has the potential to consume all living tissue if it is severe enough, and high fire severity has also been associated with decreases in nonnative species abundance. For example, seed banking species may show lower establishment in microsites that experience high temperatures for long durations (for example, see Brooks 2002) (also see “Downward heat pulse effects on seed” page 16). Similarly, sprouting species may have greater mortality after high-severity fires (see “Downward heat pulse effects on plant survival” page 14). Where burning is severe enough to kill both sprouters and seed bankers, postfire invasion depends on propagule pressure from outside the burned area.

Question 3. Does Additional Disturbance Favor Invasions?

Postfire establishment of nonnative species may be exacerbated by other types of disturbance. This is related to the observations that postfire species composition is strongly related to prefire composition, and disturbance tends to increase nonnative abundance in communities that are already severely invaded (Harrison and others 2003). This section first demonstrates that nonnative species are often associated with nonfire disturbances, then examines the evidence that fire exacerbates establishment and spread of nonnatives—whether nonfire disturbances occur before, during, or after fire. Postfire establishment of nonnative species may also be enhanced in areas subjected to postfire rehabilitation activities (see chapter 14).

The scientific literature is rich with examples of relationships between site disturbance and nonnative species richness and abundance. At regional or landscape scales, richness and abundance of nonnative invasive plants tend to be lower in protected or undeveloped areas than in human-dominated landscapes or landscapes fragmented by human use (Barton and others 2004; Ervin and others 2006; Forcella and Harvey 1983; Huenneke 1997; McKinney 2002; Pauchard and Alaback 2004), although exceptions to this pattern are noted in some locations (for example, Fornwalt and others 2003; also see chapter 13). High nonnative species abundance and richness often occur in areas of high road density (for example, see Dark 2004), large human populations, a history of human occupation, and agricultural use of surrounding areas (Johnson and others 2006; McKinney 2002; Moffat and others 2004). Regional variation in the number of nonnative plant species is positively correlated with human population density ($R^2 = 0.58$, $P = 0.01$) (fig. 2-6). An analysis of nonnative species richness using broad geographic regions (the Geographic Area Command Centers for fire management) shows a 10-fold difference in the number of nonnative species between the South (1,981) and Alaska (193), with areas of highest human population density (California, the South, and the East) having the most nonnative species (data from Kartesz and Meacham 1999).

At local scales, nonnative invasive species richness and abundance are generally highest in and around disturbed patches, corridors, and edges such as small animal disturbances (for example, Larson 2003), riparian corridors (for example, DeFerrari and Naiman

1994), and transportation corridors (roadsides, old road beds, and/or trails) (Benninger-Truax and others 1992; Flory and Clay 2006; Frenkel 1970; Gelbard and Belnap 2003; Gelbard and Harrison 2003; Harrison and others 2002; Larson 2003; Parendes and Jones 2000; Parker and others 1993; Reed and others 1996; Tyser and Worley 1992; Watkins and others 2003; Weaver and others 1990). Forest edges typically have higher nonnative plant abundance than forest interiors (Ambrose and Bratton 1990; Brothers and Spingarn 1992; Fraver 1994; Hunter and Mattice 2002; Ranney and others 1981; Robertson and others 1994; Saunders and others 1991; Williams 1993). Features common in logged areas such as skid trails are also likely to support populations and propagules of nonnative plants (Buckley and others 2003; Lundgren and others 2004; Marsh and others 2005; Parendes and Jones 2000). Similarly, areas with fuel treatments, including forest thinning (chapter 13) (fig. 2-7), fuel breaks (Giessow and Zedler 1996; Keeley 2006b; Merriam and others 2006), and firelines (for example, Benson and Kurth 1995; Sutherland, unpublished data 2008), often support higher abundance of nonnatives than nearby untreated areas.

While there is concern regarding the effects of livestock grazing on changes in community composition including effects on the abundance of nonnative plants, relatively few quantitative studies are available on this topic. In a review of the literature on disturbance and biological invasions, D'Antonio and others (1999) found that a majority of the available studies suggest a correlation between livestock grazing and nonnative species abundance. A small number of case studies from

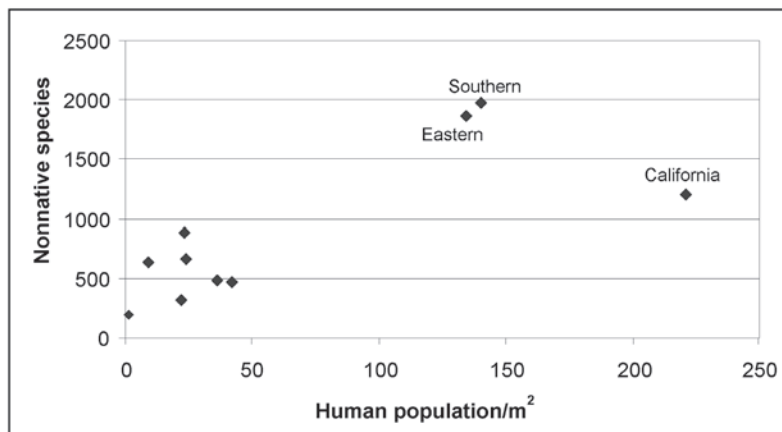


Figure 2-6—Relationship between number of nonnative species in various regions of the United States and human population density. The three most populous areas are labeled. The remaining areas are the Northern and Central Rocky Mountains/plains, East and West Great Basin, Northwest, Southwest, and Alaska (which has the lowest population density). Hawaii is not included. Regions used here are based on the national Geographic Area Coordination Centers for managing wildland fire and other incidents (information available at <http://www.nifc.gov/fireinfo/geomap.html>).



Figure 2-7—Effects of fuel reduction treatment on a closed-canopy ponderosa pine-Douglas-fir forest, western Montana. (A) Before treatment, understory is comprised of sparse clumps of native grasses and limited spotted knapweed. (B) Same photo point 3 years after thinning to reduce canopy fuels, followed by prescribed fire. Spotted knapweed (forb with gray-green foliage) and flannel mullein (forb with tall brown inflorescence) dominate understory. (Photo by Mick Harrington.)

western North America suggests that grazing plays an important role in the decrease of native perennial grasses and an increase in dominance by nonnative annual species; however, invasion has been found to occur with and without grazing in some areas. While it is difficult to discern the relative importance of grazing, climate, and fire on nonnative plant abundance (D’Antonio and others 1999), areas with a history of livestock grazing often support a variety of nonnative species, especially in areas where nonnatives have been

introduced to increase forage value of rangelands or pastures (see, for example, chapters 7, 8).

When fire occurs in an area with a large number of nonnative plants in and around the burned area, one might expect establishment and spread of nonnatives within that burned area because (1) resources become more available after fire, and (2) nonnative propagules are available to establish and spread on that site. Research demonstrating this pattern is available from several areas in the central and western United States. Nonnative species abundance often increases, sometimes dramatically, in postfire plant communities in southwestern ponderosa pine forests with a history of anthropogenic disturbance (for example, see Crawford and others 2001; Griffis and others 2001). This contrasts with postfire dominance by native species and occurrence of very few nonnative species in relatively undisturbed mixed conifer and ponderosa pine communities at Grand Canyon National Park, Arizona, and Bandelier National Monument, New Mexico (Foxy 1996; Huisinga and others 2005; Laughlin and others 2004). This is likely due to lower nonnative propagule pressure in less disturbed landscapes. A seed bank study conducted in northern Arizona ponderosa pine communities representing “a historical land use disturbance gradient” found that the soil seed bank on sites with high and intermediate disturbance had many nonnatives, while sites with low levels of disturbance had only two nonnative species in the seed bank: cheatgrass and annual canarygrass (*Phalaris canariensis*) (Korb and others 2005). In high elevation Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) forests in West Yellowstone, establishment and spread of nonnatives in forests was significantly enhanced along roadsides (where nonnative species richness was highest) but not along the edges of burns or clearcuts (Pauchard and Alaback 2006). Christensen and Muller (1975) also noted that nonnative plants were most common after fire in heavily disturbed parts of their California chaparral study area, such as along roadsides. In tallgrass prairie, postfire increases in nonnatives were greater in areas where the landscape is fragmented and nonnative propagule pressure is higher than in less fragmented areas with fewer nonnatives (Smith and Knapp 2001).

Fuel reduction efforts using fire may enhance the invasibility of treated forests, although long-term studies are needed to determine if established nonnatives will persist (Keeley 2006b, review) (also see chapter 13). Several studies have found that a combination of thinning and burning resulted in greater abundance of nonnatives than either thinning or burning alone in ponderosa pine forests of Arizona (Fulé and others 2005; Moore and others 2006; Wienk and others 2004) and western Montana (Dodson and Fiedler 2006; Metlen and Fiedler 2006). Similarly, cheatgrass, Japanese brome, North Africa grass (*Ventenata dubia*), and prickly lettuce were more strongly associated with plots that were thinned and burned than plots that were only burned or thinned in low-elevation forests of northeastern Oregon (Youngblood and others 2006).

Fire suppression activities (including construction of fire lines, temporary roads, fire camps, and helicopter pads) may increase nonnative species in the postfire environment by disturbing soil, dispersing propagules (Backer and others 2004, review), and altering plant nutrient availability (chapter 14). For example, following wildfire in a mixed conifer forest in Glacier National Park, nonnative species were more diverse in bulldozed (23 species) than burned (5 species) or undisturbed plots (3 species) (Benson and Kurth 1995). One year after wildfire in dense ponderosa pine/Douglas-fir forest in western Montana/northern Idaho, nonnative species richness was 7 on bulldozed plots and 1.7 on adjacent burned and unburned plots (Sutherland, unpublished data 2008). In an eastern Ontario alvar woodland dominated by northern white-cedar (*Thuja occidentalis*), many nonnative species were associated exclusively with bulldozed tracks and did not occur on sites that were undisturbed or burned within the previous year (Catling and others 2002). Nonnatives in areas disturbed during fire suppression may provide propagules for spread into adjacent native communities (see “Nonnative Propagule Pressure” page 9). Although no studies are available, there is concern that because fire retardant supplies nitrogen and phosphorus to the soil, the establishment and spread of invasive species may increase in the nutrient-rich environment where it is applied.

Livestock grazing before or after fire is another disturbance that can influence nonnative species establishment, persistence, and spread. Interactions of grazing with invasive species and fire, however, are complex (Collins and others 1995, 1998; Fuhlendorf and Engle 2004; Stohlgren and others 1999b), and studies that incorporate all three topics are rare. Plant communities that are in poor condition due to prolonged or excessive grazing may be more susceptible to nonnative plant invasions (chapters 7, 8, 9). Similarly, when livestock grazing occurs soon after a fire, the potential for animals to disperse nonnative propagules while

possibly stressing desirable species must be considered. On the other hand, grazing has occasionally been used in conjunction with prescribed fire to reduce invasive species (see “Treatments That Increase Effectiveness of Prescribed Fire,” chapter 4).

Question 4. Do Invasions Become Less Severe With Increasing Time After Fire?

Traits that allow nonnative species to exploit disturbed sites may also make them dependent on disturbance in some plant communities. As vegetation recovers after fire, canopy cover increases and sunlight reaching the soil surface decreases. Nutrients and soil moisture are taken up by the dominant vegetation. Nonnative species that are not adapted to these new conditions are likely to decline. This pattern is demonstrated to some extent in plant communities where fires are infrequent and postfire communities succeed to forest (for example, closed-canopy forests in the Northwest, Southwest Coastal, and Interior West bioregion) or shrubland (for example, chaparral in the Southwest Coastal bioregion). However, it is not consistent among all studies reviewed, and the duration of most studies on postfire succession is too short to demonstrate or refute this generalization. This generalization is usually examined using chronosequence studies, which assume that conditions on a site are consistent through time. This assumption is unlikely to hold true in regard to nonnative species. The nonnative portion of a plant community is unlikely to be constant in species or abundance over many decades. For example, in 1959, there were fewer than 800 nonnative species in California (Munz and Keck 1959), but by 1999 there were 1,200 nonnative species (Kartesz 1999). If most invasives establish soon after disturbance, a plant community burned in 1959 in California would not have been exposed to the same suite of species or the same degree of nonnative propagule pressure as a plant community burned in 1999.

In coniferous forests of the Northwest Coastal bioregion, information on postfire persistence of nonnative species comes primarily from studies on the effects of timber harvest and associated slash burning. Ruderal herbs, mostly native but including some nonnatives, are the dominant vegetation during the first few years after slash burning. Nonnative species in this group include woodland groundsel, tansy ragwort, bull thistle, Canada thistle, St. Johnswort, and wild lettuces. Non-ruderal native species typically regain dominance within about 4 to 5 years after slash burning (chapter 10). A wildfire chronosequence from this bioregion supports this pattern for woodland groundsel and wall-lettuce (*Mycelis muralis*). These two species dominated the herb layer 3 years after fire and are

not mentioned in any other postfire year by this study, which covered stands 1 to 515 years after fire (Agee and Huff 1987). Conversely, St. Johnswort was present in mature (80 to 95 years old) and old growth (200 to 730 years old) stands in Oregon and California (Ruggiero and others 1991), indicating that it can establish and persist in closed-canopy forests. Woody nonnatives such as Scotch broom and Himalayan blackberry typically invade disturbed forests and sometimes form dense thickets. While these species are not shade-tolerant, and therefore may not persist after canopy closure, they may prevent or delay reforestation (chapter 10).

In closed-canopy forests of the Interior West bioregion that have burned, postfire invasion of nonnative species is not well studied or well documented, although two studies provide some support for this generalization, and a third demonstrates this pattern in ponderosa pine forest. Doyle and others (1998) observed an initial increase in Canada thistle abundance followed by a steady decline after fire in a mixed conifer forest in Grand Teton National Park. Turner and others (1997) document prickly lettuce densities of around 100 stems/ha 3 years after fire in Yellowstone National Park, followed by a 50 percent decrease in density by the fifth postfire year; however, Canada thistle density increased from 2 to 5 years after fire. Similarly, in ponderosa pine forest in western Montana, prickly lettuce reached nearly 4 percent average cover the second year after stand-replacing fire (fig. 2-8) but declined substantially in the next 2 years to near preburn levels (Sutherland, unpublished data 2008).



Figure 2-8—Dense prickly lettuce establishment the second year after stand-replacing fire in ponderosa pine forest in western Montana. Red-stemmed plants are native fireweed (*Chamerion angustifolium*). (Photo by Steve Sutherland.)

Stands of chaparral and coastal scrub with intact canopies are relatively resistant to invasion by nonnative plants, and postfire succession by resprouting dominants follows a relatively predictable but highly dynamic pattern in these communities when fire-return intervals occur within the range of 20 to 50 years (chapter 9; Keeley and Keeley 1981; Keeley and others 2005). Herbaceous species, including some nonnatives, dominate in the first few years after fire, then gradually diminish as succession proceeds, shrub cover increases, and the canopy closes (for example, Guo 2001; Horton and Kraebel 1955; Keeley and others 1981, 2005; Klinger and others 2006a). However, when fire intervals decline to 15 years or less, shrub dominance declines, and nonnative annual grasses and forbs are more likely to dominate and initiate a grass/fire cycle in which it is extremely difficult for woody and herbaceous native species to establish and regenerate (chapter 9).

Resprouting dominants in mountain shrub communities of Mesa Verde National Park reduce invasibility. Dominants in these communities include Gambel oak (*Quercus gambelii*) and Utah serviceberry (*Amelanchier utahensis*), which sprout rapidly after fire, apparently utilizing available resources so efficiently that nonnative species have limited opportunity to become established. Dominants in adjacent piñon-juniper communities do not resprout; consequently, these communities recover their prefire structure slowly, which provides open conditions favoring nonnative species after fire. Eight and 13 years after fire in Mesa Verde National Park, mountain shrub communities were less invaded than adjacent piñon-juniper communities, based on density and species richness measures (Floyd and others 2006); comparisons to unburned sites were not provided.

Research on nonnative species in piñon-juniper woodlands is not clear in regard to this generalization. A study of six fires over 15 years indicates that musk thistle, Canada thistle, and cheatgrass have persisted for at least 13 years after wildfire in piñon-juniper communities in Mesa Verde National Park. Conversely, prickly lettuce and prickly Russian-thistle (*Salsola tragus*) were common 3 years after fire but were not recorded 8 and 13 years after fire (Floyd and others 2006). Chronosequence studies from piñon-juniper woodlands in Mesa Verde, Colorado (Erdman 1970), Nevada and California (Koniak 1985),

and west-central Utah (Barney and Frischknecht 1974) suggest that nonnative annuals are most abundant in early postfire years and decline in later successional stages.

Even if long-term research eventually demonstrates that nonnative invasive species decline during succession as native species increase and a closed canopy develops, one cannot assume that the invasives have disappeared from the site. Seeds of many nonnative invasives can remain viable in the soil seed bank for many years or decades, and nonnative perennials may persist in suppressed, nonflowering form at low densities under closed canopies. Another fire is likely to again produce conditions favoring their development and dominance, but the long-term successional outcome may be different. Many factors, such as reduced abundance and vigor of native species, different postfire precipitation patterns, or presence of additional nonnative species, could alter successional trends and make it more difficult for native species to regain dominance. Unfortunately, research on the influence of multiple burns is lacking for most nonnative invasive species (chapter 12).

Question 5. Do Invasions Increase With Disruption of the Presettlement Fire Regime?

If ecological processes that have shaped a plant community are altered, the vigor and abundance of native plants may decline, theoretically making the community more invasible. Application of this concept to fire regimes leads to the generalization that disruption of a plant community's fire regime increases its invasibility (Huenneke 1997). This generalization may apply to changes in any aspect of the fire regime, but the primary aspects treated in the literature to date are fire severity and fire frequency. Examples include ecosystems where fire exclusion or, conversely, increased fire frequency have stressed native species adapted to fire regimes of different frequencies and severities. Fire exclusion from grasslands, for example, may stress native species adapted to frequent fire and favor nonnative species that are intolerant of frequent fire. Exclusion of fire from open-canopy forests, on the other hand, has led to increased surface and ladder fuels and subsequent increases in fire severity in some areas, when the forests eventually burn. Native plant communities are likely to be adversely impacted by fire under these fuel conditions, so nonnative species may be favored in the postfire environment. Ecosystems where fire frequency has increased, either due to increases in anthropogenic ignitions or changes in fuel structure brought about by invasive species themselves, also support this generalization (chapter 3).

Fire exclusion from grasslands and savannas adapted to frequent fires may favor nonnative invasive grasses, forbs, or woody species. Tallgrass prairie ecosystems, for example, tend to support more nonnative grasses and forbs under a regime of infrequent fire than with frequent burning (chapter 7). Many ecosystems are invaded by woody plants when fire is excluded: honeysuckles, buckthorns (*Rhamnus cathartica* and *Frangula alnus*) and barberries (*Berberis* spp.) occur in oak savannas of the Northeast and Central bioregions (chapters 5 and 7); melaleuca, Chinese tallow, Brazilian pepper and chinaberry invade wet grasslands of the Southeast bioregion (chapter 6); Chinese tallow increases in southern tallgrass prairie (chapter 7); and brooms and gorse may spread in oak savannas and grasslands in the Northwest and Southwest Coastal bioregions (chapters 9 and 10). Most of these woody invasives are fire-tolerant and continue to reproduce and thrive even after fire is reintroduced. In some cases, they shade herbaceous species, reducing the cover and continuity of fine fuels such that they are difficult to burn. Chinese tallow, Brazilian peppertree, and common buckthorn are examples of invasive species for which this pattern has been suggested.

In open-canopy forests, such as ponderosa pine forests in the Interior West bioregion, fire exclusion has led to changes in structure, species composition, and fuel accumulation such that, when wildfire occurs, it may be more severe than was common in presettlement times. Several nonnative forbs and grasses increase after fire in these successionaly altered plant communities. Canada thistle, bull thistle, and knapweeds are the most frequently recorded nonnative forbs during the early postfire years (Cooper and Jean 2001; Crawford and others 2001; Griffis and others 2001; Phillips and Crisp 2001; Sackett and Haase 1998; Sieg and others 2003). This is in contrast to conifer forests where fire intervals and fire severity have not increased substantially (Foxy 1996; Huisinga and others 2005; Laughlin and others 2004). For example, few nonnative species were present at any site (burned or unburned) after a low-severity fire in remote ponderosa pine forests on the North Rim of Grand Canyon National Park, Arizona, where fire regimes have not been disrupted, grazing has been minimal, and logging has not occurred (Laughlin and others 2004).

Interactions between fire exclusion and grazing have influenced invasion of piñon-juniper woodlands and sagebrush grasslands by nonnative species. At many contemporary piñon-juniper sites, perennial grass cover has declined and tree cover has increased following decades of livestock grazing and fire exclusion (for example, Laycock 1991; Ott and others 2001). In sagebrush grasslands, livestock grazing has reduced native grasses while fire exclusion has allowed trees,

especially juniper, to spread (M. Miller, personal communication 2007). As piñon-juniper stands increase in density and approach crown closure, native herbaceous cover (Tausch and West 1995), seed production, and seed bank density decline (Everett and Sharrow 1983; Koniak and Everett 1982). Nonnative species, especially cheatgrass, are typically present in and around these sites and are likely to establish and dominate early successional stages after fire under these conditions. Dominance of cheatgrass, in turn, may lead to increases in fire size and frequency, thus initiating an annual grass/fire cycle (chapter 3). Successional trajectories in piñon-juniper stands are further complicated by recent widespread tree mortality caused by extended, severe drought interacting with insects, root fungi, and piñon dwarf mistletoe (*Arceuthobium divericatum*) (Breshears and others 2005; Shaw and others 2005) (see chapter 8 for more information).

In some ecosystems, fire frequency has increased and favors nonnative species. These increases may be due to increases in anthropogenic ignitions or changes in fuel structure brought about by the invasive species themselves. The latter case is best exemplified by invasions of nonnative grasses in Hawai'i and in southwestern and Great Basin desert shrublands and the resulting grass/fire cycle (chapter 3). An example of invasive species' response to increased fire frequency due to anthropogenic ignitions is found in Fort Lewis, Washington, on a 2,500 to 3,000 acre (1,000 to 1,200 ha) area called Artillery Prairie. Here broadcast burns ignited by artillery fire have occurred nearly annually for about 50 years, resulting in a plant community dominated by nonnative forbs and annual grasses. The natural fire cycle is less frequent, and a prescribed fire regime of burning every 3 to 5 years maintains native prairies and oak woodlands (Tveten and Fonda 1999).

Question 6. Are Postfire Invasions Less Common in High Elevation Ecosystems?

Several studies indicate a negative correlation between elevation and nonnative species richness or abundance; this pattern has been observed in California (Dark 2004; Frenkel 1970; Randall and others 1998; Keeley and others 2003), the northern Rocky Mountains (Forcella and Harvey 1983; Sutherland, unpublished data 2008; Weaver and others 1990), and the Southwest (Bashkin and others 2003; Fisher and Fulé 2004). Only a few of these studies relate to fire, and no research has illuminated the reasons for these correlations. Here we discuss possible explanations for and management implications of this generalization.

Invasive species richness may decline with increasing elevation because fewer species (native as well as nonnative) thrive in the shorter growing seasons,

cooler temperatures, and generally more stressful environment of subalpine and alpine ecosystems than at lower elevations. Fire would further limit the number of invasives to species that can survive a burn or disperse into burned sites.

Nonnative species that can persist at high elevations may show relatively low abundance because, like native species, they grow and spread more slowly in severe conditions. This factor suggests that, while high-elevation ecosystems may currently be less invaded than lower-elevation sites, they have no intrinsic immunity to invasion and could be impacted as severely as any other community type in time. Insofar as fire increases resource availability and mineral soil exposure and reduces native species dominance and vigor, it could accelerate invasions; however, the ruderal species most favored in recent burns are unlikely to persist in high-elevation environments, which favor slow-growing, perennial species with persistent underground structures.

Another explanation for lower invasion levels at high elevations is that human-caused disturbance is generally less and propagules are less likely to be introduced in large numbers in high-elevation ecosystems (Klinger and others 2006b). This is supported by observations that, with increased disturbance such as roads and clearcuts, nonnative species occurrence extended to higher elevations (Forcella and Harvey 1983; Weaver and others 1990). Thus increases in accessibility, use, and mechanical disturbance of high-elevation plant communities—including activities related to fire management or fire suppression—have potential to increase propagule pressure from nonnative invasive species and invasibility of these sites.

Climate change, expressed at high elevations by longer growing seasons and milder temperature regimes, is likely to simultaneously increase stress on native plants and favor more nonnative invasive species. Fire frequency may increase at high (as at low) elevations, occurring at intervals shorter than the regeneration time for some native plants and creating more disturbed sites for establishment of nonnatives. See “Changing Atmosphere and Climate” page 29.

Conclusions

Generalizations that explain patterns across a wide range of systems are elusive in invasion ecology in general (for example, see review by Rejmánek and others 2005), a principle that certainly applies to fire. Nonnative invasive species show some patterns in their responses to wildland fire. The generalization that fire favors nonnatives over natives is supported by the literature for some nonnative species in some plant communities under some conditions. Postfire invasions can be intense and lead to severe impacts on native

communities, so vigilance is warranted. However, invasions also vary with numerous site and climatic factors, depend on the nonnative propagules within and near the burn, and can be short-lived. Information about fire effects on specific plant communities with specific invasive species is the best knowledge base for making management decisions. Second best is knowledge of nonnative species in similar environments. The more conditions in the area of concern diverge from conditions in published research or other known areas, the less reliable predictions will be.

Examination of the literature provides insights regarding other common assumptions about fire and nonnative species:

- Nonnative species establishment increases with increasing fire severity. This pattern depends on fire resistance of onsite species, propagule pressure, and the uniformity and size of high-severity burn patches.
- Additional disturbance favors invasions in most circumstances, though the influence of grazing-fire interactions on nonnative species are complex and may not follow this pattern consistently.
- Invasions become less severe with increasing time since fire in some plant communities, particularly where ruderal species invade closed-canopy forests and chaparral after fire. However, there are few long-term studies investigating this pattern and there are many exceptions. Without local, long-term knowledge, this generalization may not be reliable as a predictive tool.
- Invasions increase in some plant communities with disrupted fire regimes, whether the disruption relates to fire regime characteristics that increase or decrease relative to baseline conditions. Communities that have developed an invasive grass/fire cycle support this generalization (chapter 3), as do native grasslands from which fire has been excluded (chapter 6, 7, 8, 10). However, a “disrupted fire regime” may be too complex an ecological property to use as a predictive tool. Specific stresses on the native plant community arising from disrupted fire regimes may be more helpful.
- Postfire invasion is currently less likely to occur and persist in high-elevation than low-elevation ecosystems, but elevation *per se* does not provide the only explanation for this pattern. Differences in human-caused disturbance, resource availability, and propagule pressure should also be considered; where these influences are increasing, high-elevation ecosystems are likely to become more vulnerable to postfire invasions.

It is important to keep in mind that exceptions to these patterns are common. Our knowledge about fire and nonnative plants is not extensive enough in space and time for use in widely applicable predictive tools. Site-specific knowledge is essential for management to successfully meet objectives.

Variation

There are many reasons for variation in nonnative species’ responses to fire. The invasive potential of nonnative species varies throughout their range (Klinger and others 2006a). For the majority of nonnative plants in the United States, the distribution of the species is much larger than the states that have declared it a noxious species (Kartesz 1999). Fire itself also varies tremendously in severity, size, spatial complexity, frequency, and seasonality. Finally, invasibility of a community is also influenced by site history, the condition of native plant populations, and postfire precipitation patterns, so postfire spread of nonnatives may be inconsistent even within a plant community.

Site-specific knowledge about fire effects on nonnative plants depends to some extent on the monitoring techniques used and the length of time monitored (chapter 15). Data collected only within the first 2 or 3 postfire years usually cannot be used to project long-term patterns; this is particularly true of forests and woodlands where tree regeneration occurs over many decades, changing stand structure and the availability of resources. Research has not been particularly helpful with this problem. Despite the need for long-term studies, 70 percent of recent literature reviews covering fire effects on nonnative invasive species in the Fire Effects Information System contain no postfire response information beyond the first 2 postfire years (chapter 12).

Changing Atmosphere and Climate

Our understanding of the responses of nonnative species to fire is based on the premise that the community of native species occurring on a site has been shaped by natural selection to be well suited to local site conditions and climate. Confidence in the robustness of the native community is part of the rationale for using “natural” conditions as a baseline for management. Past conditions are useful as a reference for desired future conditions, not because of a hope to return to the past, but because past conditions capture a range of variability that was sustained over long periods (Klinger and others 2006a). This rationale may not apply in a world where the climate is changing substantially from historic patterns, as is currently occurring. Earth’s air and oceans are warming to levels not seen in the past 1,300 years, possibly in the past 10,000 years. According to the International Panel on Climate Change, this

warming is now unequivocal and could continue for centuries. Global climate change is expressed in many areas as earlier snowmelt, longer warm seasons, and changes in extreme weather; however, these effects vary geographically, and some areas are likely to be colder or more moist than in past centuries (Alley and others 2007). In the Western United States, climate change appears to be contributing to longer fire seasons and more frequent, more extensive fires (McKenzie and others 2004; Westerling and others 2006), which may increase the vulnerability of many ecosystems to invasion and spread of nonnative plants.

An example of potential impact of climate change is the die-off of piñon over 4,600 square miles (12,000 km²) in the southwestern United States. On an intensively studied site in northern New Mexico, Breshears and others (2005) found that greater than 90 percent of the dominant overstory tree, Colorado piñon (*Pinus edulis*), and greater than 50 percent of the dominant understory herb, blue grama (*Bouteloua gracilis*), died after a 4-year drought with unusually high temperatures. These results were supported by four regional studies in Arizona, Colorado, New Mexico, and Utah, reporting piñon die-off ranging from 40 to 80 percent. Not only is the die-off a major ecosystem disturbance in its own right, but also the increase in dead fuel loading increases wildfire hazard in this area. Although the study does not address invasives, the disturbance resulting from die-off and the possibility of subsequent high-severity wildfires may increase this area's susceptibility to invasion and spread of nonnative species.

Increased atmospheric carbon dioxide alters not only climate but also plant properties and the balance between species (Huenneke 1997). Laboratory research on cheatgrass biology demonstrates changes in plant properties. Cheatgrass grown at carbon dioxide levels representative of current conditions matures more quickly, produces more seed and greater biomass, and produces significantly more heat per unit biomass when burned (associated with reduced mineral and lignin concentrations) than cheatgrass grown at "pre-industrial" carbon dioxide levels (fig. 2-9). These responses to increasing carbon dioxide may have increased flammability in cheatgrass communities during the past century (Blank and others 2006; Ziska and others 2005). Research on cheatgrass has not addressed the possibility that native species biomass has increased along with that of cheatgrass in response to increasing carbon dioxide, but a study in the Mojave Desert has addressed that possibility in regard to red brome, another nonnative annual grass. In an environment with elevated carbon dioxide, red brome density increased while density of four native annuals decreased. Red brome showed greater increases in biomass and seed production in response to elevated carbon dioxide than did the four native species (Smith and others 2000). At the community level, nonnative species that respond favorably to increased carbon dioxide may thrive at the expense of native species with lower nutrient requirements; this change in the balance between species favors many fast-growing plants, including nonnative invasives (Huenneke 1997).

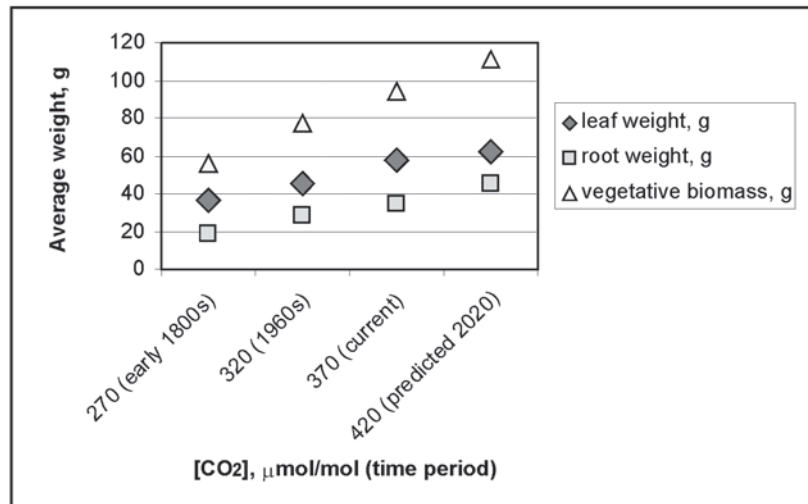


Figure 2-9—Average weight of cheatgrass seedlings grown for 87 days under varying concentrations of carbon dioxide. Carbon dioxide level was a significant predictor of leaf weight, root weight, and total vegetative biomass. In addition, increasing CO₂ reduced the time from germination to flowering. (Graphed from data in Ziska and others 2005, table 1.)

Increased carbon dioxide is not the only atmospheric change affecting wildland ecosystems and, potentially, fire regimes. Nitrogen deposited from air pollution can increase available soil nitrogen (for example, see Baez and others 2007; Padgett and others 1999), altering the relative abundance of native and nonnative species. In the Mojave Desert, artificial nitrogen addition significantly increased the density and biomass of nonnative annual herbs and, in 1 of 2 years, significantly reduced the density and biomass of native species. Increased biomass is likely to increase fire frequency on these desert sites (Brooks 2003). In more mesic areas, greater depletion of surface soil moisture by invading C_3 grasses may favor deep-rooted shrubs, and the increase in nitrogen fixation that occurs with the increased metabolic activity triggered by increased carbon dioxide could favor leguminous shrubs (Dukes 2000).

Not all nonnative species will benefit more than native species from atmospheric changes (Dukes 2000). However, the dispersal capability of many nonnatives, plus their rapid growth in disturbed areas, makes them well suited to the conditions accompanying climate change. Climate change will be expressed as local changes in growing conditions and fire regimes, which may interact synergistically to increase invasions (Barrett 2000). Local knowledge regarding nonnative invasive species, monitoring, and adaptive use of the knowledge gained will be increasingly important for successful management.

Management in a Changing World

The relationships between nonnative invasive species and fire described here are based on information from the past century or two, and they hold true only to the extent that conditions that shaped this relationship continue. Management of wildlands must be

based on current conditions and likely future conditions (Klinger and others 2006a). How can managers prepare and respond? A decision framework such as that presented by Pyke and others (in review) can be a useful tool. To use a decision framework or model effectively, knowledge about local patterns of invasion, problematic nonnative species, and highly invasible sites is critical. This information should be readily available to fire managers and postfire rehabilitation specialists. Communication between local fire managers and local botanists is important. Careful monitoring of burned areas is crucial, and the monitoring must extend over decades rather than years. Knowledge gained from monitoring prescribed burns may be helpful for projecting effects of wildfires, although wildfires are likely to be larger, more severe, and occur in a different season than prescribed fires.

Prevention and early eradication are daunting tasks. The number of native species within a particular plant community on a specific site is finite, whereas the number of species from around the world that could potentially grow on the site may be greater by orders of magnitude (Randall and others 1998; Williamson 1993). Prevention of invasion is always the best strategy, since control and eradication are costly and may never be complete (Klinger and others 2006a). Even if a nonnative species is eradicated, any invasion leaves a legacy of subtle alterations in the site and gene pool of the remaining species.

Control of invasives already present on a burn, combined with early detection and treatment of new invasives and regular monitoring after treatment will be essential for preventing dominance of postfire habitats by nonnative invasive species. And continued research is needed, especially long-term studies addressing effects of various fire severities, frequencies, intervals, and seasons.

