

REVIEW ARTICLE

Fire as a Restoration Tool: A Decision Framework for Predicting the Control or Enhancement of Plants Using Fire

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Abstract

Wildfires change plant communities by reducing dominance of some species while enhancing the abundance of others. Detailed habitat-specific models have been developed to predict plant responses to fire, but these models generally ignore the breadth of fire regime characteristics that can influence plant survival such as the degree and duration of exposure to lethal temperatures. We provide a decision framework that integrates fire regime components, plant growth form, and survival attributes to predict how plants will respond to fires and how fires can be prescribed to enhance the likelihood of obtaining desired plant responses. Fires are driven by biotic and abiotic factors that dictate their temporal (seasonality and frequency), spatial (size and patchiness), and magnitude

(intensity, severity, and type) components. Plant resistance and resilience to fire can be categorized by a combination of life form, size, and ability to disperse or protect seeds. We use a combination of life form and vital plant attributes along with an understanding of fire regime components to suggest a straightforward way to approach the use of fire to either reduce or enhance particular species. A framework for aiding decisions is organized by life form and plant size. Questions regarding perennating bud and seed characteristics direct restoration practitioners to fire regimes that may achieve their management objectives of either increasing or decreasing plants with specific life form characteristics.

Key words: fire prescriptions, fire regime, life form, plant reproduction, resilience, vital attributes.

Introduction

Humans have a long history of using fire to manage vegetation. Aboriginal people used fire to maximize food production and hunting success and to improve pathways of travel (Nelson & England 1971; Nicholson 1981; Hall 1984; Lewis 1985; Pyne 1991). More recently, fire has become a common management tool to control undesirable plants and pathogens (Vallentine 1989; Storeheier 1994; Fujisaka et al. 1996; Young et al. 1999; Zimdahl 1999; Stolle et al. 2003; DiTomaso et al. 2006), create desired plant communities for livestock or wildlife (Wright & Bailey 1982; Bunting et al. 1987), reduce fuel loads (Williams et al. 1999; Fernandes & Botelho 2003), and restore historical disturbance regimes (Bonnicksen & Stone 1985; Baker 1994).

Effects of fire on wildlands are often difficult to predict because of the large numbers of coexisting species, high ecological complexity, heterogeneous fuel structure, and unpredictable weather after fire when species are regenerating or recruiting into burned sites. The complex assemblage of plant species in wildlands requires managers to conduct fires when their effects may be beneficial or neutral for desirable species, and detrimental for undesirable species.

Our knowledge of how plants respond to wildland fires is based on observations made after fires have burned and subsequent plant communities have developed. Managers have integrated years of experience into general guidelines that they follow. The greatest amount of information comes from fire-prone grasslands (Clarke & Knox 2001; Briggs et al. 2002), shrublands (Van Wilgen & Forsyth 1992; Bell et al. 1996; Keeley 2002), and forests (Schimmel & Granström 1996; Fule et al. 1997). A century or more of fire suppression in many ecosystems, in addition to an abundance of non-native species in some landscapes, now makes it difficult to predict successional trajectories of communities after fires. Citing controversy over the best approaches for restoring fire-suppressed ponderosa pine ecosystems, Allen et al. (2002) advocated a series of science-based studies to aid the process of determining appropriate uses of fire to accomplish specific objectives.

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Concerns about potential threats of fire to lives and livelihoods (e.g. urban or residential concerns), air quality, or other ecosystem processes (e.g. water quality) limit the use of fire as a management tool. However, when fire is deemed appropriate, managers need guidelines to help determine its effectiveness in achieving their objectives. We believe there are basic principles that determine effects of fire among differing plant life forms and that a reductionist approach focused on immediate effects of fire on individual plants (often referred to as first-order fire effects) would aid in predicting vegetation responses to fire. We recognize that plant community development after fire results from an intricate set of ecological processes that depend on complex timing of biotic and abiotic factors to form plant trajectories during years following fire (often referred to as second-order fire effects, or post-fire succession). However, first-order fire effects can set the stage of subsequent post-fire succession and as such are important to consider when predicting plant community response to fire. Specifically, we believe restoration science and management could benefit from a merging of two major topics: fire regimes and drivers that influence them, and plant morphology and survival mechanisms. This information is the foundation for most approaches used by experienced fire managers, but the majority of land managers who have little experience using fire may not recognize how plant species may respond individually to fire and its complexities. We therefore briefly discuss these two topics separately, but then combine them into a simple decision framework for use in predicting plant responses to fires in a restoration context. Although this framework simplifies a series of highly complex relationships, we believe it provides the necessary decision structure and ease of use and

understanding to allow restoration practitioners to communicate with fire managers in designing effective use of fire as a restoration tool.

Fire Regimes

Fire is a natural disturbance that can occur in any ecosystem (Sousa 1984). It is characterized by variability in space, time, and magnitude, the combinations of which can have differing effects on plant communities (Sugihara et al. 2006). Collectively, these components comprise the fire regime of a particular ecosystem. Each component is regulated by a combination of abiotic and biotic drivers (Fig. 1) of which only biotic drivers can be influenced easily by land managers. For example, various fuel bed and human ignition characteristics can be manipulated to promote particular fire behavior and fire regime characteristics. Variability among these drivers can produce a wide range of fire effects. Hence, it is not sufficient to ask whether fire affects a particular species, rather it is more useful to ask what combination of drivers produces the desired fire behavior and fire regime characteristics designed to illicit a specific response by a particular plant species.

Temporal Fire Regime Components

Fire regimes can vary among seasons and frequencies of recurrence (Fig. 1). Generally, fire seasons are defined by ignition sources and fuel moisture, the latter of which is driven by increases in temperatures and decreases in precipitation and humidity. In addition, continuity of fuels and their packing ratios (fuel-to-air ratio relative to fuel bed volume; Van

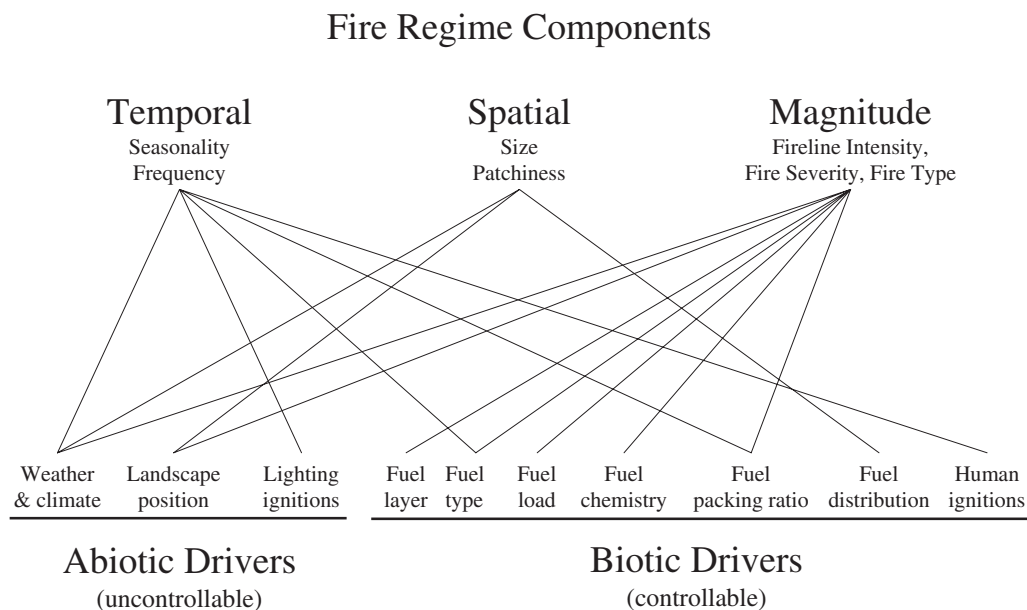


Figure 1. Fire regimes are the complexity of temporal and spatial effects of fires on ecosystems. These fire regimes are composed of a combination of fire regime components that are driven by a series of abiotic and biotic factors. Lines display those abiotic and biotic drivers that are associated with each fire regime component (after Sugihara et al. 2006).

Wagtendonk 2006) also influence seasonality of burning by influencing fuel production and distribution. Managers select the season of prescribed fires based on fuel moistures to create safe, yet effective fires with adequate heat to provide the desired fireline intensity and spread rate to meet management objectives of removing or favoring certain plant species.

Fire frequency is affected mostly by patterns of ignition from both lightning and human sources and by fuel type (Fig. 1); herbaceous fuels that regenerate, senesce, and dry quickly allow for a greater frequency of fire than woody fuels that regenerate, senesce, and dry slowly. Thus, fire frequency is driven by speed at which continuous fuel beds and fuel loads can reestablish after previous fires, speed at which fuel dries during periods of low moisture availability, and the frequency of ignitions during weather conducive for burning (Moritz 2003; Moritz et al. 2004).

Spatial Fire Regime Components

Fire size and spatial complexity (patchiness) (Sugihara et al. 2006) are driven primarily by combinations of weather and climate, landscape position, and distribution of fuels. Continuous fuels generally only need suitable weather conditions for ignition, after which a fire will consume fuels until it reaches an adequate break in fuels to halt further ignition. For example, managers can choose to ignite fires so they burn up or down slopes and thus modify the fire spread rate through the use of landscape positions. They do not actually manipulate the driver, so much as they select and use the driver to manipulate other fire regime components.

Magnitude Fire Regime Components

Fireline intensity, fire severity, and fire type contribute to fire magnitude and are affected more by biotic drivers than are either temporal or spatial components. Fireline intensity is the physical energy released by a fire, often measured as heat per unit area (J/m^2) combined with speed of fire spread (m/s) (Rothermel & Deeming 1980). Fireline intensity is regulated by all seven of the fire regime drivers associated with magnitude (Fig. 1). Weather and climate along with landscape position are abiotic drivers that are less controllable by managers. Specific components include wind speed and direction, humidity, air temperature, slope, and aspect. They contribute to fire spread rates, whereas moisture level of fuels controls fire heat. Fast-moving fires transfer less heat than slow-moving fires. Even though managers cannot control these abiotic components in a wildfire they may be able to use them for predicting where a fire might transfer more heat and thus have a greater likelihood of killing plants.

When managers reduce fuels as a fire prevention measure they are reducing biotic drivers that will reduce fire magnitude. Fuel load is mass of available fuel in a given locale. It includes distribution of materials into size classes with differing timelags to reach a standard moisture equilibrium with the environment. Larger size classes generally transfer more heat than smaller classes (e.g. heat from 100-hour fuel > heat

from 1-hour fuels) during total fuel consumption. Within size classes, species with higher specific stem density (Cornelissen et al. 2003) will have greater mass per volume of stem and will provide greater heat than species with lower specific stem density at the same fuel moisture. Fuel chemistry relates to the amount and type of combustible hydrocarbons that are available to burn and increase intensity. Fuel distribution is the spatial arrangement of vegetation that includes horizontal and vertical continuity of fuels.

Fuel type, fuel layer position, fuel distribution, and packing ratio of each layer in addition to drivers of fire magnitude via fireline intensity, also dictate fire types. Fire types range from surface fires to mixed fires and crown fires. Type of fuel indicates type of flammable material, such as peat, grassland, shrubland, woodland, or forest with subtypes available within each fuel type (e.g. Scott & Burgan 2005). Fuel types with greater woody fuels tend to produce greater fuel loads and more intense fires. Fuel layer position describes vertical structure of fuels and is typically divided into ground, surface, and crown categories. Packing ratio of fuel relates to small-scale bulk density of fuels, of which there is an ideal value for combustion that can vary among specific situations.

Fire severity is the remaining fire magnitude component and is related to the effects of fire on ecosystem properties (Keeley 2009). Ecosystem effects of fires are a combination of conditions during burning (especially fireline intensity, residency time, and biomass consumption) and resiliency of ecosystem components (typically soils and vegetation) to these conditions. Generally, fire severity is regulated by fireline intensity and fire type and its ramifications are expressed both immediately after a fire through losses of plants and animals in the communities and through longer term second-order fire effects.

Fire Regime Summary

Managers rarely regulate temporal or spatial regime components of wildfires because these components are mainly driven by abiotic factors that largely fall outside of the manager's control. In contrast, restoration projects can change fuel distributions by reducing fuel packing-ratios and disrupting fuel continuity. For example, within Mediterranean-like ecosystems dominated by invasive annual grasses, a goal in many locations (e.g. Great Basin, United States) is establishment of perennial tussock grasses to break the continuous fuel of *Bromus tectorum* (Brooks & Pyke 2001). In addition, managerial decisions regarding timing and placement of prescribed fires are made regularly in the fire planning process. Fires during the plant's growing season can produce differences in fire severity relative to dormant-season fires. In short-grass steppe ecosystems, dormant-season fires had little impact on perennial grasses while reducing some forms of biological soil crusts, but the reverse occurred if fires burned during the growing-season (Ford & Johnson 2006).

When prescribed fires are being considered for control or enhancement of a particular plant species, specific manipulations of appropriate drivers to achieve the necessary fire regime

to meet the management goal need to be understood. In many cases, these fire regime characteristics may not be possible or safe to achieve, in which case alternative tools must be selected.

In the remainder of this paper, we discuss options available for manipulating biotic drivers of fire regimes to achieve vegetation management goals with special emphasis on conditions where fire can be used to control or enhance species. We incorporate characteristics of individual species and plant communities into a management framework for projecting changes in plant populations (e.g. mortality, reproduction, dispersal, recruitment, or survival) and community composition.

Plant Responses to Fire

Responses of plants within a species to fire are determined at the individual level with individual responses translating into populations and with responses of populations of species translating into community responses. The Fire Effects Information System database provides literature on how plant species, particularly in the United States, typically respond to fires (USDA Forest Service 2007). Several recent reviews evaluate specifically how non-native plants respond to fire treatments designed to control them (D'Antonio 2000; DiTomaso et al. 2006). Other reviews have used plant traits, also known as vital attributes (as defined by Noble & Slatyer 1980), to predict plant responses to fire, but most lack a tractable framework for applying fire and predicting plant responses across ecosystems (Lavorel & Garnier 2002; Bradstock & Kenny 2003; Pausas et al. 2004). Noble and Gitay (1996) compared a number of plant classification systems and recommended a functional classification system based on the Noble and Slatyer (1980) system for predicting community responses with recurring disturbances. The system recommended by Noble and Gitay (1996) is thorough, but its use is limited by its complexity (e.g. the timing of disturbances relative to vital attribute timing; competitiveness of species in the form of tolerances to resource conditions as seedlings or adults). These complexities have also led to the development of a computer model to aid in predicting plant community responses (Moore & Noble 1990). Fire ecologists and restoration practitioners are in need of a simple and useable framework for making decisions regarding plant responses to fire. The framework proposed here uses elements of Noble and Slatyer's (1980) vital attributes and Raunkiaer's (1934) life forms classification to describe how plants will respond to fire. It relates these elements to the fate of individuals (survival or death) relative to fire characteristics that largely relate to the heat to which a plant individual is exposed. We discuss how restoration practitioners can manipulate fire regime drivers to attain management goals relative to a plant's likelihood to survive fire and how this response may translate into compositional changes in the community.

Plants can survive or resist fire through avoidance or tolerance (Levitt 1980; Lavorel & Garnier 2002) depending on the location of a plant's perennating buds relative to the soil surface (Raunkiaer 1934), extremes in temperature

caused by fire, and on a plant's vital attributes (Noble & Slatyer 1980). The latter explain a species' ability to persist through a fire or immigrate, establish, and mature between fires. Lethal temperature for a plant is related to exposure of vital tissues to elevated temperatures and duration of heating of vital tissues (Miller & Findley 2001). Heating durations that cause mortality tend to be shorter at higher temperatures. Lower lethal temperatures may occur when seeds or plant tissues are hydrated because water conducts heat better than air. Soil depth necessary to protect plant tissues from lethal temperatures depends on type of fuel (fine vs. coarse), its packing ratio and soil moisture. Coarse fuels or slow fire spread rates result in higher temperatures that transfer heat for longer periods of time deeper into soils (Clark 2001). Masticated woody vegetation can transmit lethal temperatures to at least 10 cm deep (Busse et al. 2005), whereas grasslands rarely transmit lethal temperatures below 2 cm (Wright & Clarke 2008). Moist soils conduct heat better than dry soils, but they also dissipate heat through evaporation; therefore, moist soils often do not heat as deeply as dry soils (DeBano et al. 2005). Although plants may vary in their lethal temperatures (Levitt 1980), most plants are thought to fall within a fairly narrow range of lethal temperatures close to 60°C (Wright & Bailey 1982; Whelan 1995). Plants avoid lethal temperatures more than they tolerate them. They avoid fire mortality by having perennating buds or seeds located adequate distances from lethal heat. Thus, parts of plants may experience lethal temperatures or even combust, but as long as some of the perennating tissue and critical vascular connections are protected from these temperatures the plant may survive.

There are three general mechanisms that plants may use to avoid lethal heat. First, buried buds are protected from lethal temperatures by soil insulation. Burial from 2 to 10 cm may be necessary depending on type of fuels. For example, grazed grasslands have little fuel that burns quickly yielding relatively little heat in comparison with forests with more fuel, especially in the form of woody debris that transfers more heat (Busse et al. 2005; Wright & Clarke 2008). Species that have buried buds include cryptophytes (Raunkiaer 1934) or species with vegetative persistence (V persistence; Noble & Slatyer 1980) (Table 1). Noble and Slatyer (1980) define plants without this persistence as unaffected (U persistence). A second mechanism is size-dependent and requires fire intervals to be sufficiently long for mature plants to grow tall enough for perennating buds to escape lethal temperatures of surface fires and for anatomical structures such as bark to become thick enough to insulate cambial tissues (Gill & Ashton 1968; Vines 1968; Gill 1981). Species utilizing this mechanism include phanerophytes or woody species with thick bark (W persistence; Noble & Slatyer 1980; Table 1). The third mechanism relies on long-distant seed dispersal (Disperser) or on adequate seed persistence in a long- (Storage) or short-lived (Germinating) seed bank to bring new recruits to recolonize or to reestablish species on sites (D, S, and G persistence class; Noble & Slatyer 1980). Species possessing these seed-dependent mechanisms are found in all life forms.

Table 1. Vascular plant life forms with Raunkiaer's (1934) life form names, Noble and Slatyer's (1980) vegetation persistence classes, descriptions of the locations of perennating buds and characteristics that describe the life form and the susceptibility of the life form to fire mortality.

<i>Raunkiaer Life Form Name</i>	<i>Noble and Slatyer Vegetative Persistence Names</i>	<i>Life Form or Vital Attribute Characteristics</i>	<i>Susceptibility to Fire Mortality</i>
Annuals Therophytes		Seeds perpetuate populations from one generation to the next and their lifecycles are complete in 1 year or less	Depends on thickness of seed coat and location (above, below, or at the soil surface) when fire occurs. Those in the soil are more insulated from the lethal temperatures
Perennials Cryptophytes	V: Vegetative U: Unaffected	Perennating buds are located below soil or water surface; these include aquatic and perennial wetland plants and terrestrial plants with rhizomes, bulbs, corms, and tubers	These plants are generally the most protected from fires because their buds are below the soil and insulated from lethal temperatures. Those with perennating buds or organs near the surface (<3 cm in grassland to <10 cm under thick woody debris) may be susceptible to high intensity fires with slow rates of spread
Hemicryptophytes	V: Vegetative U: Unaffected	Perennating buds are located at the soil surface and may form rosettes, partial rosettes, or tussocks	Survival of these plants often depends on the moisture content of the leaves and the concentration of buds. Densely packed buds that create a thatch of residual plant material may extend the fire residence time and increase susceptibility to fire mortality
Chamaephytes	None	Perennating buds are above the soil surface, but generally remain below a height of 30 cm; these include subshrubs cushion plants, and trailing vegetation that may have buds near or above the soil surface	This group is often susceptible fire mortality because all buds are located in the flame path of surface fires and would likely experience lethal temperatures
Phanerophytes	W: Woody with thick bark	Perennating buds are above the soil surface by at least 30 cm; these include shrubs and trees	Susceptibility to fire mortality depends on the combination of the fire type and the plant's ability to insulate the vascular tissues from lethal temperatures of surface fires if buds are safely located above the fire

Fire and Plant Decision Framework

Because locations of perennating buds or mechanisms for rapid seedling establishment are important for determining representation of a plant species in a community after a fire, then life forms and vital attributes in combination with fire regime components provide a structure on which to build a decision framework to evaluate a plant's susceptibility to fire (Fig. 2). For perennating buds, their position relative to the soil surface and their degree of protection from outer layers of insulating tissue, largely dictates survival. For seeds, their spatial orientation relative to the parent plant and soil can change during a growing season, most notably between predispersal and dispersal stages of growth. Fire prescriptions often regulate intensity by regulating ignition dates (seasonality of fires). Frequency of fire, another temporal fire regime component, may also aid in evaluating susceptibility or in proposing management options

to assist in using fire as a restoration tool to either increase or decrease plant species within a community. Use of frequent fire to control a particular species can be hampered by slow regrowth of fuel between fires. This situation could be improved by planting a dense sterile cover crop of annual plants between planned fire events or by adding dry fine fuels such as straw to increase fuel loads (Hodgkinson 1991). However, both these treatments might be cost prohibitive when compared with spot herbicide treatments, so managers should evaluate their cost-benefit ratio relative to their options available for achieving management goals.

Although fires may directly kill most individuals of a species, the species may be capable of quickly reestablishing from seeds. Seed coat thickness and insulation qualities, embryo longevity, and density and location of seeds relative to lethal temperatures influence fire survival. For example, seeds of *Pinus contorta* are long-lived and housed in thick, woody

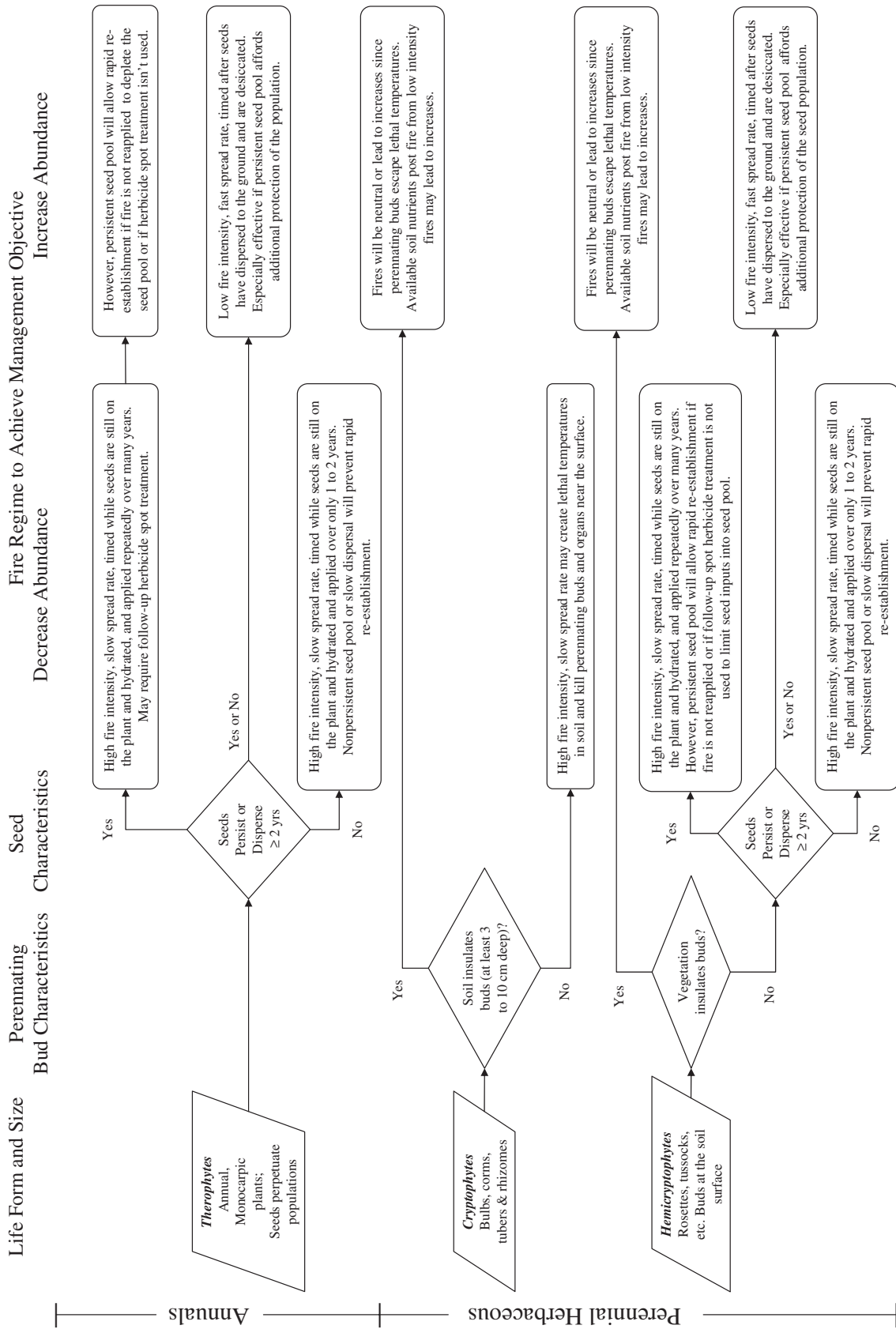


Figure 2. Decision framework for using fire to manipulate plant communities based on plant life forms (after Raunkiaer 1934), bud and seed persistence (after Noble & Slayter 1980), and fire regime components to either increase or decrease the abundance or dominance of plant species in a community through using fire with or without additional plant management tools. Users begin at the left side of the framework and select the appropriate plant life form and size of the species. Then moving to the right, they answer questions regarding perennating bud and seed characteristics that lead to management objectives that will either increase or decrease plant abundance.

Life Form and Size
 Bud Characteristics
 Perennating
 Characteristics
 Seed
 Characteristics
 Fire Regime to Achieve Management Objective
 Decrease Abundance
 Increase Abundance

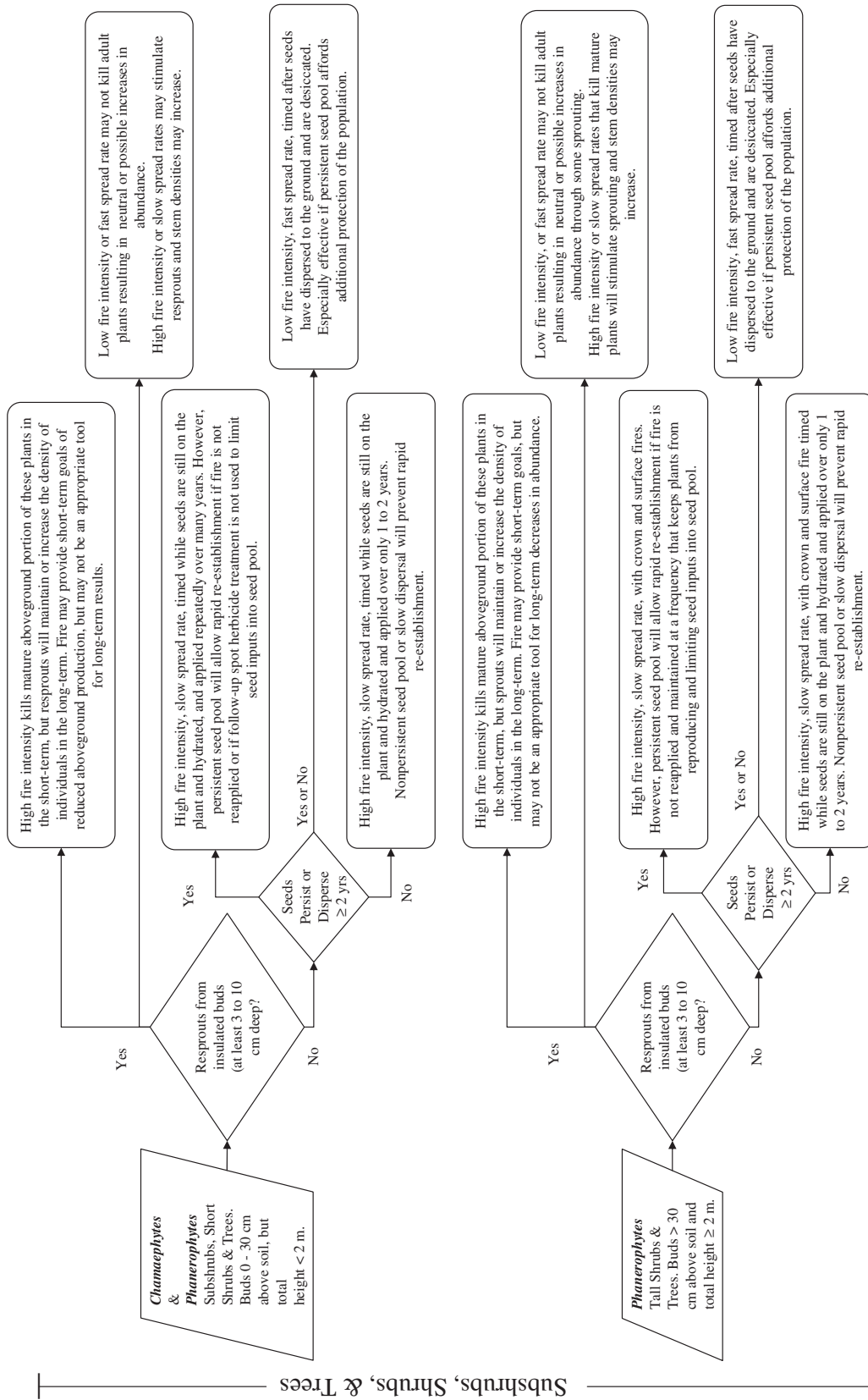


Figure 2. Continued

serotinous cones that require heat, such as that produced by fast-moving fires, to open cone bracts allowing seeds to disperse, germinate, and establish (Wheeler & Critchfield 1985).

Populations of species with short seed longevity (≤ 2 years) may be more susceptible to fire-induced population crashes than those with long-lived seeds. Populations with short-lived seeds may be reduced using fire alone (singly or repeated) or in combination with other control techniques (e.g. spot treatments of herbicide or physical removal) if adults are killed before reproduction can occur (e.g. *Centaurea solstitialis*, DiTomaso et al. 1999; *Melinis minutiflora* D'Antonio et al. 2001). The location of seeds in seed banks will also influence their susceptibility to surface fire. Those seeds in litter that contribute to fine surface fuels are more likely to be consumed than those below soil surface where soil can act as an insulator from lethal temperatures. Unfortunately, seed bank research often does not distinguish between seeds in the litter versus mineral soil and for most species it is not known what proportion of the seeds is in each horizon. This is important information that, if known, could improve predictability of plant responses to fires.

A combination of information on life form, seed longevity, perennating bud location and vulnerability provides ample information to predict how plants may respond to fires of varying types. Sometimes plants avoid fire mortality because they are dormant during normal fire seasons and perennating buds are positioned where they are protected from lethal temperatures. Alternatively, seeds may have already dispersed and found safe sites from lethal temperatures. For example, wildfires fueled by annual grasses generally burn after seeds disperse and these fires typically spread fast without heating soils to lethal temperatures for these seeds. Thus, these annuals are generally resilient to wildfires, but fires prescribed when seeds are still maturing on plants, which is often 1–2 months before typical wildfires seasons, can make them vulnerable to being consumed (DiTomaso et al. 2006). In these cases, prescribed fires could be conducted out of season using artificial accelerants (Ascard 1995).

Those plants that are capable of surviving fires or recruiting quickly into a burned site often reap benefits of post-fire environments. Depending on fireline intensity and whether the ecosystem has burned recently, soil nutrients may increase, decrease, or remain the same. High fireline intensity can result in nutrient volatilization or nutrient losses via runoff and soil erosion, but lower intensity fires can provide increases in plant available nutrients (Neary et al. 1999). Immediately after fires, there is a flush of soil nitrate and ammonium available for plant uptake (Wan et al. 2001; Stubbs & Pyke 2005). Surviving plants, especially those that were dormant and had protected buds, experience reduced competition at least initially because of death of fire sensitive species and reductions in size of many surviving species that were growing during the fire. Thus, fewer plants exist after the fire than before and these surviving plants are poised to capture resources and grow with less competitive interference from other plants.

The decision framework consists of three major divisions: annual plants; herbaceous and subshrub perennial plants; and shrubs and trees (Fig. 2). The susceptibility of annual plants (therophytes) to fires generally depends on fire season and intensity. Natural fires occur during dormant seasons for most herbaceous perennials, deciduous woody plants, and well beyond the lifecycle completion of annual plants. If prescribed fire is used to manipulate annual plant-dominated communities, then successful population reduction will rely on using fire before seed is dispersed or on achieving high intensity fires at the soil surface to obliterate the seed bed. The former situation might require using fire outside of the “normal” fire season or supplementing fuel within the prescribed fire area. Burning outside of the normal season could be accomplished through either using accelerants or treating the community with an herbicide that results in early senescence and therefore production of dead fine fuels. Fuel supplementation can be achieved for small scale burns by adding cut shrubs or branches throughout the proposed area. Thus, fires may reduce annual plant populations if they are used before seed dispersal and are intense enough to kill seeds on plants, in litter and soil seed banks. If seeds live less than 2 years in seed banks, then combinations of fires and normal seed mortality may significantly reduce population size. In California, DiTomaso et al. (2001) showed how 2 years of fire could control *Aegilops triuncialis* and enhance desirable species if fires occurred at *A. triuncialis* seed maturation. If the goal is to reduce an undesirable species, such as an invasive plant, a follow-up spot treatment with herbicide may be necessary to kill remaining plants.

The response of perennial herbaceous plants (cryptophytes and hemicryptophytes) and subshrubs (chamaephytes; Table 2; Fig. 2) to fire depends strongly on fire type and locations of perennating buds relative to soil surface. Because of their stature, these species are most susceptible to slow-moving surface fires, but may escape being burned if fires are elevated into strict crown fires in tall trees. For surface fires, life forms provide a convenient means of predicting a plant's tolerance to fire. Cryptophytes with buds protected by the soil and hemicryptophytes with leaves or plant structures that insulate perennating buds are likely to survive fires and may be able to take advantage of post-fire nutrient flushes in growing seasons following fires through rapid growth and reproduction. Hemicryptophytes with less-protected buds will be vulnerable to fires, especially backing fires with slow spread rates increasing the time buds are exposed to lethal temperatures. For all perennials, if population reduction is the goal, then follow-up treatments may be necessary to remove any residual surviving plants.

Plants that are capable of resprouting from basal or root buds after aboveground buds are burned will be favored by fires and will likely respond quickly to post-fire nutrient flushes by growth or coppicing. Seed production by resprouters may be limited initially after a fire, especially for species that require a year of growth to develop flowers and may only be important for population recovery if sprouting fails. If resprouters are undesirable, then use of fire for their control

is likely to be unsuccessful unless there is a threshold above which fire can be lethal. For example, many managers have attempted to use fire to reduce cover of *Tamarix* species; yet, they generally resprout vigorously after fire making fire a generally inappropriate tool without follow-up treatments (Ellis 2001). However, supplementing fuel at the base of *Tamarix* plants can cause greater mortality during fire, but that fire is effective only when *Tamarix* are highly stressed and have low nonstructural carbohydrates (G. Drus, T. Dudley & C. D'Antonio 2009, Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA, U.S.A. personal communication).

Survival of phanerophytes (woody plants) depends on type and intensity of fire in combination with total height of the plant, insulating capacity of bark, and resprouting or coppicing ability of the plant (Fig 2). This life form is too broad to provide adequate predictability of plant survival in response to fires of various types just based on its life form alone. It requires information on height and bark thickness. Attempts to gather bark thickness information are being encouraged as an important plant functional trait (Cornelissen et al. 2003). Woody plants taller than 2 m with thick bark are better able to insulate cambial tissue and survive surface fires while placing apical buds above lethal temperatures from surface fires. However, if these plants are nonsprouters, they are susceptible to crown fires. Those woody plants shorter than 2 m or with thin bark will be susceptible to any fire type except the rare crown fire without an accompanying surface fire.

As with other life forms, woody plants can sprout from protected meristems (usually basal or buried buds) thus avoiding mortality and reestablishing individuals quickly. If a management goal is to reduce the density of resprouting woody species, then follow-up control treatments, such as herbicides, may be required. If the goal is to temporarily modify aboveground dominance hierarchy or simply to reduce standing fuel, then fire alone may be useful. Resprouting shrubs and trees are generally favored by fires because they are capable of activating root buds once aboveground buds are removed. High intensity fires may be capable of reaching lethal temperatures for shallow-rooted species, but fire will not likely affect those plants with deeper roots where soils insulate roots from heat.

Perennial plants that are killed by fire must rely on seeds to sustain populations. If seeds do not maintain protective structures, such as a fruit wall that insulates the seed, then seed longevity or dispersal ability, similar to annual plants, will dictate the ultimate effect of fires on populations. If the management goal is to reduce a species population, then high intensity, slow-spreading fires will likely kill seeds and depending on seed longevity, follow-up treatments may be necessary to reduce or eliminate germinants.

Conclusions

This decision framework provides a simplified mechanism for predicting plant population responses to fires and should be applicable to both wildfires and prescriptive fires, although it

is designed primarily for the latter. When fire is used as a management tool it is important for managers to adjust temporal (seasonality), spatial (choose appropriate landscapes, such as upslope for fast spread rates or downslopes for slow spread rates to create necessary fire types), and magnitude (fireline intensity) fire regime components. Knowledge of the location of plant perennating buds relative to the soil surface and to fire types and knowledge of the species' seed longevity and dispersal potential of the desirable and undesirable species in the community are important a priori considerations. In some cases, it may be possible to anticipate that fire will have undesirable impacts on plants, warranting consideration of techniques other than fire. In particular, when fire favors a highly undesirable species, managers might consider using other techniques (e.g. herbicides or mechanical removal) to achieve management goals. Mechanical techniques may produce similar results to those of fire, especially in resprouting species because sprouts are normally activated hormonally through the removal of apical buds and reduction of auxin. Currently, land managers in the United States are using combinations of fire and fire surrogate techniques to manipulate fuel loads in communities where fires have been suppressed in hopes of restoring natural fire intervals and restoring native plant communities (Youngblood et al. 2005). Databases such as the Fire Effects Information System (USDA Forest Service 2007; <http://www.fs.fed.us/database/feis/>) (last accessed 4 December 2009) are extremely helpful in providing necessary information on plant survival and establishment as well as life form information for each species. Additional information on seed longevity and seed bank retention of both soil and litter-based seed banks will assist practitioners in making better-informed decisions using this framework, although this information is more difficult to attain. A restoration practitioner can use this simplified framework to decide when and where to use fire to sustain or favor desired species while reducing undesirable ones.

Implications for Practice

- Wildfires often cause restoration practitioners to consider implementing plant rehabilitation projects. Revegetation decision-makers might consider the fire's potential effects on the pre-existing vegetation before implementing revegetation. This framework can provide guidance in predicting post-fire communities and in deciding if a rehabilitation treatment is necessary.
- Predictions of how plants will resist, avoid, or succumb to fire depend on a combination of factors associated with the fire regime and on the plant's life form and vital attributes for establishment and survival. This framework will assist practitioners in considering potential outcomes to plant communities after fire.
- A decision framework with four steps leads practitioners through a process to determine whether fire will be

a useful tool to either reduce or enhance plant species. First, the plant's life form is determined. Second, determinations of whether the plant's perennating buds are protected from the fire are made. Third, seed persistence or ease of seed dispersal is determined. Finally, fire regimes are described that can either enhance or reduce the plant species' abundance based upon its life form and plant establishment or survival characteristics.

- Using this decision framework may aid in prescribing appropriate fire conditions for desired results and may aid in determining whether rehabilitation after wildfires might be necessary to maintain desired plant communities.
- The decision framework suggests situations where fire alone may not achieve desired restoration results, and alternative or follow-up procedures may be required.

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