

FIRST-ORDER FIRE EFFECTS ON HERBS AND SHRUBS: PRESENT KNOWLEDGE AND PROCESS MODELING NEEDS

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ABSTRACT

Herbaceous plants and shrubs have received little attention in terms of fire effects modeling despite their critical role in ecosystem integrity and resilience after wildfires and prescribed burns. In this paper, we summarize current knowledge of direct effects of fire on herb and shrub (including cacti) vegetative tissues and seed banks, propose key components for process-based modeling, and outline research needs. Most herbs and shrubs are likely to be killed or top-killed even in low intensity surface fires. Therefore, modeling efforts should focus on mortality of protected above and below ground meristematic tissue and seeds as well as the effects on seed germination. Further development of an organic and mineral soil heating model capable of describing heating patterns under a range of flaming and smoldering fire behaviors, validated heat transfer models for protected plant structures, standardized descriptions of tissue heat tolerance for a wider range of species, and a better understanding of the effects of soil heating on seed banks are required. The combination of these components would result in a comprehensive, process-based model predicting immediate herb, shrub, and seed mortality and post-fire responses. It would permit quantitative description of fire severity and a more accurate prediction of post-fire ecosystem recovery.

Keywords: cacti, heat tolerance, herbs, fire ecology, first-order fire effects, process modeling, research needs, review, shrubs

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INTRODUCTION

Shrubs, forbs, and grasses are important structural and functional components of ecosystems with critical roles in nutrient cycling (McClellan and Wein 1977, Harris and Covington 1983), erosion control (Meeuwig 1970, Robichaud and Waldrop 1994), and providing habitat and food for animals (Hobbs and Spowart 1984, DeByle *et al.* 1989). Furthermore, shrubs and herbs are central to ecosystem integrity as well as resilience after disturbances such as wildfire. Prediction of vegetation response to fire helps land managers evaluate the success of prescribed fires and to assess post-wildfire risk and the need for restoration (e.g., via BAER, Burned Area Emergency Response; Robichaud *et al.* 2007). However, models that predict post-fire survival of plants have focused on trees or other plants with high economic value (see Kavanagh *et al.* 2010 and Butler and Dickinson 2010). Understory vegetation in forests and the vegetation of shrublands (e.g., chaparral), grasslands, and deserts deserve equal attention, yet, with few exceptions (e.g., see Mercer *et al.* 1994, Choczynska and Johnson 2009), no process-based models currently exist to predict how fire affects their survival. Climate change and introduced species and their effects on fire regimes (Westerling *et al.* 2006) and, consequently, vegetation structure (Brooks 2008), lend a new urgency to understanding and modeling fire effects on these plant types.

We discuss components essential for predicting first-order fire effects (i.e., immediate and direct effects; see Dickinson and Ryan 2010) on herbs, shrubs, and cacti. The discussion is linked to a review of direct fire effects on vegetative structures and seeds. Our search for general principles is based on literature published in English and not limited to any particular geographic region. We include an assessment of the current status of process-based, predictive modeling of fire effects on herbs and shrubs and conclude by outlining research needs.

THE EFFECTS OF HEAT ON PLANT CELLS AND TISSUES: GENERAL PRINCIPLES

The most direct fire effects on plants are heating or combustion of whole organisms or their parts. Whereas combustion of the entire organism leads inevitably to its death, the effects on vegetation of partial combustion (above ground) or heating (above ground, below ground, or both) depend on the amount of meristematic (i.e., cambium, buds) and regenerative tissue that survives. A major determinant of tissue survival is its location and, thus, its heat exposure. Tissues may be directly exposed to heat from a fire, or shielded by plant material such as bark or leaves, or by litter and organic and mineral soil layers. Shielded plant material may resist injury simply because it is not exposed to large heat fluxes. This kind of resistance is termed heat avoidance. Directly heated tissue might resist injury due to the tissue's ability to prevent, reduce, or repair injury. This type of resistance is termed heat tolerance—the ability of organisms or tissue to survive heat stress (Levitt 1980).

Heat injury to cells is a consequence of protein denaturation and coagulation, membrane destabilization, and the accumulation of reactive oxygen species that damage proteins, membranes, and DNA (Leone *et al.* 2003). The exact mechanisms of heat-induced cell death, however, are unknown, but accumulation of lesions (injurious biochemical events) caused by reactive oxygen species has been suggested as the primary cause in yeast cells (Davidson *et al.* 1996). It has long been established that the biophysical rate processes that result in injury or necrosis of cells and tissues are characterized by approximately exponential relationships between temperature and exposure time (Levitt 1980). The exponential relationship implies that a longer exposure to lower temperatures might have the same effect as a much shorter exposure to higher temperatures; that is, small increases in temperature

can lead to large increases in the rates at which tissue impairment occurs.

Plant cells and tissues are capable of acclimation to heat wherein heat tolerances are increased by exposing plant parts to superoptimal but sublethal temperatures. The higher the temperature, the shorter the time required to produce a distinct increase in heat tolerance (Yarwood 1967, Precht *et al.* 1973, Levitt 1980). Heat tolerance of hydrated tissue is founded in the presence of heat-induced synthesis of heat-shock proteins that prevent protein coagulation, promote proper protein conformation (Iba 2002), and stabilize membranes (Tsvetkova *et al.* 2002). It is also reported that dehydrated plant tissues with more negative osmotic potentials have higher heat tolerance (Levitt 1980). Acclimation to drought might involve some of the same mechanisms as long-term acclimation to high ambient temperatures, so that a response to one environmental stress cross-protects against another (Leone *et al.* 2003). Such heat tolerance may be conferred by the accumulation of low-molecular-weight compounds (e.g., sucrose, betaine) known to protect proteins against heat denaturation (Lee and Timasheff 1981, Leone *et al.* 2003), changes in membrane lipid composition, and the production of enzymes that detoxify reactive oxygen species (Iba 2002, Leone *et al.* 2003). Factors involved in heat tolerance may play out differently in different species and seasons and, thus, contribute to the interspecific and seasonal differences.

The tissue necrosis models available for use in fire effects modeling are parameterized with data on either tissue functional impairment (e.g., Kayll 1963, Caldwell 1993, Dickinson *et al.* 2004) or mortality rates in populations of cells (Lorenz 1939) and, thus, describe the necrosis and subsequent wound response processes (e.g., Shigo 1984) only in the most approximate way. A review of tissue necrosis models is outside the purview of this paper. However, applications of heat tolerance models to tissue necrosis during fires may be found

in Martin (1963), Dickinson and Johnson (2004), and Jones *et al.* (2006). Uncertainty in predicting tissue temperatures from fire behavior (see Butler and Dickinson 2010) has been used to justify the use of a threshold temperature ($\sim 60^\circ\text{C}$) for necrosis of various tree components (e.g., Brown and DeByle 1987, Gutsell and Johnson 1996, Michaletz and Johnson 2008). Such a simplification is likely not appropriate for shielded tissues exposed to sub-threshold temperatures for extended periods of time (Dickinson and Johnson 2004), particularly where tissue acclimation occurs.

FIRE EFFECTS ON ABOVE GROUND STRUCTURES

Despite their different morphologies, most shrubs and herbs are similar in being thermally thin (i.e., they have small diameters and high surface area to volume ratios) and unshielded. Diffusion-limited wildland fire flames have temperatures near 1000°C regardless of size, with temperatures declining through the intermittent zone at the top of the flame and into the plume (i.e., the hot gases that rise from the flame; Depuy *et al.* 2003, Kremens *et al.* 2010). Therefore, even low intensity surface fires usually result in the top-killing of herbs and shrubs (Morgan and Neuenschwander 1988). The processes governing tissue heating during fires, that is, heat transfer from fires to vegetation and the heating of tissues that results, are discussed in Butler and Dickinson (2010).

Consumption of small diameter shrub fuels can occur during fires. For example, in a Rocky Mountain forest, a wildfire consumed live and dead shrub stems less than 0.6 cm in diameter (Anderson 1968). In many ecosystems, herbaceous plants are in or near a cured state during the fire season, and are consumed by flaming combustion. As the life cycle of herbs includes death of stems and leaves each year, the loss of above ground biomass *per se*, particularly if cured, is of little consequence to

the plant. In fire-prone ecosystems, plants have evolved strategies for persistence despite the loss of above ground parts. These strategies are resprouting, seed heat tolerance, and fire-stimulated germination (Paula and Pausas 2008).

Interspecific and seasonal differences in heat tolerance are commonly reported (Flinn and Pringle 1983, Smith *et al.* 1994). In the evergreen shrub, crossleaf heath (*Erica tetralix* L.), Lange (1961) observed that after 30 min of heating, 50% leaf mortality occurred at 6.5°C higher in summer than during spring. Wright (1970) demonstrated interspecific and seasonal differences in heat tolerance for two bunchgrass species native to North America. In May, squirreltail (*Elymus elymoides* [Raf.] Swezey ssp. *hordeoides* [Suksd.] Barkworth) and needle-and-thread (*Hesperostipa comata* [Trin. and Rupr.] Barkworth) culm bases could tolerate 60°C for several minutes before tissue death occurred. In September, when leaf mois-

ture content was low, both species could tolerate the same duration of exposure at temperatures 10°C higher. Wright's study demonstrates that near instantaneous death of tissues does not necessarily occur at 60°C.

Even where crown combustion does not occur, high surface-to-volume ratios of above ground organs, the short stature of herbaceous and shrub vegetation, and high rates of convective heating in and near flames mean that high temperatures will generally be reached by unshielded crown tissues. Thus, predicting necrosis of above ground plant components may generally be accomplished from knowledge of spatial burn patterns (Figure 1), and the details of tissue heating and heat tolerance can be ignored. As such, the importance for fire effects prediction of adequate fire behavior measurements (Kremens *et al.* 2010) and fire model predictions (Leonard 2009, Butler and Dickinson 2010) is underscored.

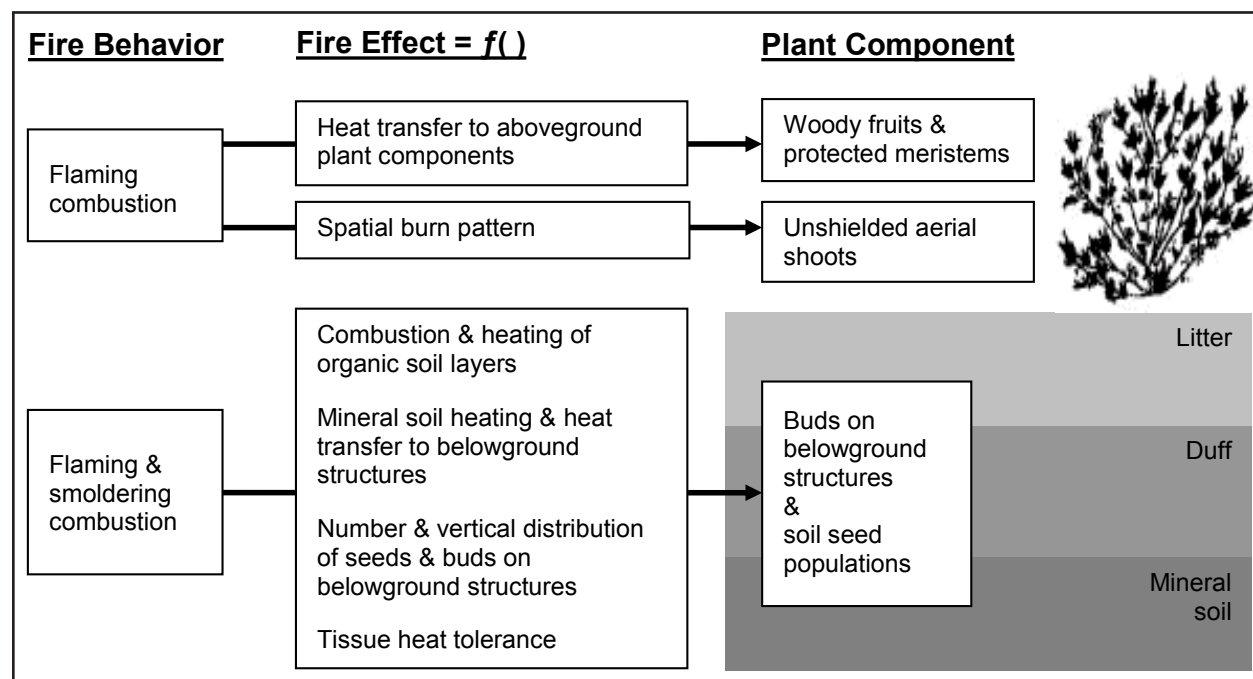


Figure 1. Conceptual model for predicting first-order fire effects on non-woody plants. Mortality of aerial shoots will generally be determined by the spatial pattern of combustion, while predicting fire effects on sheltered meristems and seeds within protective structures will also require knowledge of fire heat release patterns. The spatial pattern of heat output from flaming and smoldering combustion in combination with soil physical, plant organ, and seed properties will determine mortality of below ground buds, storage organs, and seeds and potential heat stimulation of germination.

There are a few exceptions to the general pattern of complete mortality of above ground shrub and herbaceous plant components in response to passage of a fire. Many arborescent monocotyledons, e.g., screwpine (*Pandanus* L. f.) in Hawaii, palms, and Australian grasstrees (*Xanthorrhoea* Sol. ex Sm.), protect their buds within moist, densely packed, tufted crowns, and vital stem tissues are shielded via closely packed leaf bases persisting long after the major photosynthetic part of the leaf is lost (Gill 1981). Thus, tissue temperatures do not rise to high enough levels for long enough for necrosis to occur. Cacti also present an interesting case of relatively high survivorship in fires.

Fire Effects on Cacti

Cacti can survive heat exposure from fire even though often less than 50% of individuals survive in burned areas (Thomas 1991). These succulents might survive fire due to some of their adaptations to dry, hot environments. Cacti have a thick, water-storing cortex that buffers the phloem and cambium from rapid heating. It has been suggested that fires toward the end of a dry season are more injurious since plants are most dehydrated then (Humphrey and Everson 1951). The apical meristem of cacti is well protected from heat due to an infolding of the apex and a covering of hairs and spines. Because of this protection, resumption of growth is common after fire, even if phloem and cambium have been killed and plant mortality is only delayed. The apical meristem is more likely to survive in taller (often older) individuals because the apex is raised above flames and because older plants have thicker cortical tissues (Thomas 1991). As cactus stems age, the tubercles and ribs at the base of the plant may develop a bark-like layer, increasing protection from heating by fire.

It is currently not known how cacti tissues react to heating during fires. Cacti exhibit some of the highest heat tolerances ever re-

ported for vascular plants and have high potential for acclimation, ensuring their survival during the summer months (Smith *et al.* 1984). These authors showed in heating experiments of photosynthetic tissue of several species and growth forms that 50% of the cells in chlorenchyma tissue can withstand 55°C for 1 h if the cacti had been grown at 30°C daytime and 20°C nighttime air temperatures. When cacti had been acclimated at 50°C daytime and 40°C nighttime air temperatures for 5 days prior to heat treatment, 50% cell mortality after the 1 h heat treatment occurred at about 65°C. However, the study also showed that 100% cell mortality occurred if tissues were heated for 1 h at a temperature of just 5°C higher than the temperature causing 50% cell death. This result might indicate that cacti operate near their maximum heat tolerance under ambient temperature regimes, and might not survive additional heating from fires.

Cacti and other succulents themselves do not usually combust (Thomas 1991). The source of heat is from associated fuels, particularly grasses, and cacti are thus more likely to be exposed to fire when dense stands of herbaceous growth have developed and cured after abundant rain. Fire risk to cacti has been increased by the invasion in Arizona and west Texas of the exotic grasses red brome (*Bromus rubens* L.) and buffelgrass (*Pennisetum ciliare* [L.] Link). These species produce much more biomass than is typical in desert communities, increasing the frequency and ecological effects of fires. Such fires have been lethal to giant saguaro (*Carnegiea gigantea* [Engelm.] Britton & Rose) in Arizona, and pose a threat to the endangered Chisos Mountains hedgehog cactus (*Echinocereus chisoensis* W.T. Marsh.) in west Texas (Esque *et al.* 2007).

Understanding injury and mortality of cacti during fires will require more work on the heating of basal sections of plants and the response of outer cortical, cambium, and phloem tissues to elevated temperatures. Apical meristems may be sufficiently well shielded to ig-

nore as are below ground organs, since resprouting is rare in cacti (Thomas 1991; for exceptions, see Bunting *et al.* 1980). Regardless, the distribution and abundance of herbaceous fuels may be the greatest determinant of cactus mortality during fire.

FIRE EFFECTS ON BELOW GROUND STRUCTURES

The death of above ground tissue does not necessarily lead to the death of the entire plant. In fact, many understory plants possess the ability to regenerate vegetatively from surviving buds on plant organs located at the surface (e.g., stolons) or below ground at various depths in litter or organic or mineral soil layers (e.g., roots, rhizomes, lignotubers, bulbs, corms) (Flinn and Pringle 1983, Miller 2000, Paula *et al.* 2009). The mortality of dormant buds on below ground organs during fire depends on 1) the amounts of surface litter and organic soil materials that are consumed (Miller 2000), soil and fuel moisture (Busse *et al.* 2007), and the resulting magnitude, duration, and depth distribution of subsurface heating; 2) the distribution of buds within the organic and mineral soil profile (McLean 1969, Flinn and Wein 1977); and 3) the heat tolerance of below ground organs (Flinn and Pringle 1983).

Vertical Distribution of Below Ground Structures

Depth below the surface and whether regenerative structures are located in organic layers or mineral soil directly affect the potential for lethal heating from the consumption of surface fuel (Miller 2000, Choczynska and Johnson 2009). Buried regenerative structures within duff or other organic soil layers are at greater risk from fire because these layers can be consumed by smoldering combustion. On sites that experienced higher soil temperatures at the mineral soil surface as a consequence of duff layer consumption, aspen (*Populus* sp. L.)

suckers (Brown and DeByle 1987) and huckleberry (*Vaccinium* L.) shoots from rhizomes (Miller 1977) originated from deeper within the soil because buds closer to the surface had been killed.

There are relatively few data on the vertical distribution of below ground organs in soil. For understory species in eastern Canadian boreal forest, Flinn and Wein (1977) found the depths of underground reproductive structures (root or rhizome) to be species-specific. Of 23 herb and shrub species, structures of six species were predominantly located in the top few centimeters of the litter layer, structures of five species were found within the F and H layer, and structures of 12 species were found from 3 cm to 15 cm depth in mineral soil (Flinn and Wein 1977). In Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests of southern interior British Columbia, Canada, McLean (1969) assessed depth of regenerative tissue and whether it was located within duff layers or mineral soil for 26 species. Based on depth and location, he classified species in terms of their relative fire resistance. Choczynska and Johnson (2009) found that most buds of three rhizomatous grasses occurred within a few centimeters of the soil surface, though the distribution had a long tail, with many buds occurring more deeply within the soil. Given that data on type and depths of reproductive structures are known, duff consumption and soil heating models are pivotal in predicting their mortality (e.g., Choczynska and Johnson 2009).

Bud Mortality in Bunchgrasses

Bunchgrasses have been found to be susceptible to injury from fires (e.g., Peláez *et al.* 1997) and, in a North American tallgrass prairie, bunchgrasses were found to be more negatively affected by increases in fire intensity than rhizomatous grasses (Ewing and Engle 1988). Important factors in bud mortality include 1) bud location, i.e., whether buds and

meristems are close to the surface of the crown (the basal part of a bunchgrass plant from which the leaves, stems, and roots arise), shielded by basal material within the crown, in the middle or near the outer edge of the crown, or located within mineral soil (Wright 1971, Zedler 2007, Choczynska and Johnson 2009), and 2) whether and how the bunchgrass combusts. Buds of fire-sensitive bunchgrass species in Argentina were located just above the soil surface (Peláez 1997). Bud heating is determined by the amount of flammable fuel that is present (primarily grass litter), how densely it is packed, and how close dead material is to buds and meristems (Conrad and Poulton 1966, Wright 1971, Zedler 2007). The amount and density of dead plant material influences fire residence time and the amount of heat transmitted to growing points (Wright 1971). The flaming phase of combustion is usually of short duration, yet sustained smoldering can occur in dense litter accumulations in long-unburned grasslands and in the center of bunchgrasses, causing mortality of growing points (Wright 1971, Zedler 2007). Species with buds within the crown can survive if the protective basal material does not ignite and smolder down to these growing points (Wright 1971). Buds within and shielded by mineral soil have the highest likelihood of survival, although they can be killed if a large amount of basal material is consumed (Wright 1971). In addition to developing an understanding of the combustion of individual plants, predicting fire effects in low-productivity bunchgrass-dominated systems, where plants form discrete fuel patches, requires data and modeling of the conditions required for fire spread (e.g., Burrows *et al.* 1991).

Heat Tolerance

Flinn and Pringle (1983) assessed heat tolerances of rhizomes for eight species: eastern teaberry (*Gaultheria procumbens* L.), Canada mayflower (*Maianthemum canadense* Desf.),

lowbush blueberry (*Vaccinium angustifolium* Aiton), bunchberry dogwood (*Cornus canadensis* L.), western brackenfern (*Pteridium aquilinum* [L.] Kuhn), sheep laurel (*Kalmia angustifolia* L.), leatherleaf (*Chamaedaphne calyculata* [L.] Moench), and rhodora (*Rhododendron canadense* [L.] Torr.). Rhizome sections were immersed in water baths set at 45°C, 50°C, 55°C, and 60°C for 5 min. The results indicated that heat tolerance is species-specific. Necrosis occurred for three species at 55°C and 60°C, and two species survived the 60°C treatment. Thus, heat tolerances appear similar to that of above ground tissue. Season of rhizome collection influenced heat tolerance, and differently so for different species (Flinn and Pringle 1983). This was manifested in the number of shoots growing from the rhizomes rather than a change in the maximum temperature at which buds still produced shoots. Heat tolerance did not appear to vary with rhizome depth in the soil (from the litter layer to >9 cm of mineral soil) or rhizome diameter (0.5 mm to 7.7 mm) and, thus, surface area to volume ratio (Flinn and Pringle 1983). The latter result may be due to rhizome buds being located at the surface. Rhizome buds in three tallgrass prairie species, big bluestem (*Andropogon gerardii* Vitman), Indiangrass (*Sorghastrum nutans* [L.] Nash), and switchgrass (*Panicum virgatum* L.), are less than 4 mm in size and have little resistance to heat flow from the surrounding soil (Choczynska and Johnson 2009). It might be speculated that interspecific or seasonal variation in moisture content plays a role in heat tolerance of below ground organs, but no data are currently available.

For modeling mortality under relatively rapid heating, the threshold temperature for near-instantaneous necrosis of below ground buds may be assumed to be similar to that of above ground tissue (Flinn and Pringle 1983). However, soil and the bark of roots, sheaths of rhizomes, or other shielding tissue layers would cause below ground organs to heat up gradually, and it has been shown for tree tis-

sues that acclimation to superoptimal though sublethal temperatures occurs over tens of minutes (e.g., Dickinson and Johnson 2004), a time scale relevant to soil heating during fires. It is not clear whether differences in thermal properties between soil and woody subsurface masses will protect buds from heating relative to buds at or near the surface of below ground organs.

Carbohydrate Reserves

Whether surviving below ground buds actually develop into new shoots depends on the availability of the nutrient and carbohydrate reserves that support initial growth. Carbohydrate levels are affected by the plants' seasonal growing cycles (Hare 1961, Harrington 1989, Zasada *et al.* 1994). Plants may resprout soon after fire or not until the following spring if they were seasonally dormant when the fire occurred (Miller 1978). Reserves can be a critical factor in plant recovery under regimes of annual (Waldrop and Lloyd 1991) or biennial growing season burns (Harrington 1989), and where grazing or browsing pressure are high before or after the fire (Miller 2000). Resprouting species can be eliminated from a site if subsequent burns or high levels of livestock or wildlife utilization occur before carbohydrate and nutrient stores are replenished. However, some species such as saw palmetto (*Serenoa repens* [Bartram] Small) and sabal palmetto (*Sabal* spp. Adans.), show remarkable resilience to repeated loss of foliage (Kalmbacher *et al.* 1983, Macpherson and Williams 1998). A reasonable assumption may be that plants capable of resprouting have sufficient carbohydrate stores to resprout after a single burn regardless of the point in the growing cycle. This is supported by Zasada *et al.* (1994), who showed that salmonberry (*Rubus spectabilis* Pursh) rhizome segments could grow new shoots throughout the year, although the number of shoots correlated closely with the stored carbohydrate levels. Post-fire soil moisture or competition between plants may also affect

plant survival. While post-fire growing conditions and utilization by wildlife and livestock can have significant effects on vegetation recovery, they will not be discussed further within this paper because they are not first-order fire effects.

EFFECTS OF HEAT ON AERIAL AND SOIL-STORED SEEDS

Fire can cause mortality of aerial or soil-stored seed, but it can also stimulate germination. The combined effects of these two processes will determine germination response from seed banks. Seed depths and heat tolerances will affect soil seed bank responses to fire, while the characteristics of seed capsules will have an important influence on aerial seed banks.

Seed Depth in Soil

Similarly to below ground buds, mortality of soil-stored seeds depends on the magnitude and duration of subsurface heating at a given depth, the distribution of seeds within the organic and mineral soil profile, and the heat tolerance of seeds. Most seeds are located in organic soil layers and the top 5 cm of mineral soil (Moore and Wein 1977, Roberts 1981, Schimmel and Granström 1996). Viable seeds found deeper in the soil profile likely belong to species with the greatest seed longevity (Moore and Wein 1977). In the case of seeds of annuals such as cheatgrass (*Bromus tectorum* L.) or medusahead (*Taeniatherum caput-medusae* [L.] Nevski) located on the soil surface at the time of burning, modeling will require knowledge of surface heat fluxes and conditions necessary to consume the surface litter layer in which these seeds often are found.

Heat Tolerance

Extreme heat tolerance has been found in seeds of desert succulents (Aizoaceae, Cacta-

ceae). A high proportion of seeds survived exposure to 103 °C for 17 h (Daws *et al.* 2007). In their study, survival rate of seeds correlated with maximum annual temperature, suggesting that heat tolerance has evolved, enabling these species to persist in a soil seed bank. In fire-prone southeastern Australia, Judd *et al.* (1993) found 90 °C to 100 °C to be a threshold temperature for 90% seed mortality if seeds of three myrtaceous shrub species were heated gradually over the course of 30 min to 60 min. In fire-prone shrublands of southern Spain, a proportion of hard-coated seeds of seven legume species (20% to 75%, depending on species) could survive 1 min exposures to dry heat at 150 °C (Herranz *et al.* 1998). These authors tested seed germination after exposures to 50 °C to 150 °C, temperatures commonly recorded during wildfire in the top 5 cm of mineral soil (DeBano *et al.* 1998).

Seed moisture content. Seed mortality also follows the generally exponential relationship of exposure time and temperature found in physiologically active tissue. However, it has long been known that tissue in the dehydrated state can tolerate higher temperatures for longer than active and fully hydrated tissue. Robbins and Petsch (1932) found a curvilinear relationship between moisture content of corn and wheat grains and the ability to survive a 2 h heat treatment. At grain moisture contents of 35%, 20%, and 5%, one quarter of the grains survived exposures to 53 °C, 60 °C, and 80 °C, respectively. Imbibed grains of barley and wheat died after brief exposure to 60 °C to 65 °C (Levitt 1980), which indicates that fully hydrated seed tissue seems to respond to heat exposure in a similar fashion as other hydrated tissue.

Seed moisture content depends on the seed coat's permeability to water and on the moisture content of the surrounding soil. LeFer and Parker (2005) conducted two experiments on 13 California chaparral species to test for effects of heating and moisture on seed germina-

tion. Little to no germination of chamise seeds (*Adenostoma fasciculatum* Hook. & Arn.) occurred in moist soil at temperatures of 90 °C, 100 °C, and 110 °C, while germination of dry chamise seeds increased after exposure to temperatures of up to 90 °C. Species negatively impacted by burning under moist soil conditions typical of spring fires lacked dormancy induced by the seed coat and seeds readily imbibed water. Thus, seeds that are protected from imbibing water by hard seed coats, such as seeds of buckbrush (*Ceanothus cuneatus* [Hook.] Nutt.) (LaFer and Parker 2005) and hollyhock (*Iliamna* spp. Greene) (Brown and DeByle 1989) can have high tolerance to external heat.

Seed oxygen environment. Ambient oxygen concentration can also influence seed heat tolerance. Ben-Zeev and Zamenhof (1962) found that dry radish (*Raphanus sativus* L.) and rape seeds (*Brassica napus* L.) in a vacuum could survive 20 °C to 35 °C higher temperatures than dry seeds heated under atmospheric pressure. However, dry seeds desiccated further while under vacuum, so that the increased heat tolerance might have resulted from the lowered moisture content or the low oxygen environment. Siegel (1953) found that when air dry (7% to 10% water content) embryonic axis of kidney beans (*Phaseolus vulgaris* L.) were exposed to 100 °C for 25 min under 20%, 10% and 0.002% oxygen, 90% of the embryos survived under the lowest oxygen concentration, while only 12% survived at 20% and 10% oxygen. This is relevant as low oxygen conditions in soil are likely to occur during fire (Bryant *et al.* 2005). Thus, seed temperature and moisture content might not be sufficient in predicting seed survival during fire.

Seed size and species identity. Little is known about the influence of seed size or species identity on heat tolerance. In Ben-Zeev and Zamenhof (1962), 50% and 90% of rad-

ish (2 mm to 3 mm seed diameter) and rape seed (1.5 mm to 2 mm) survived 16 min at 120 °C in vacuum, respectively, whereas only 3 % of seeds of Aztec tobacco (*Nicotiana rustica* L.; 1 mm seed diameter), 33 % of Joseph's coat (*Amaranthus tricolor* L.; 1 mm), 10 % to 32 % of white mustard (*Sinapis hirta* L.; 2 mm), and 11 % of tomato (*Lycopersicon esculentum* L.; 2 mm) survived under the same conditions. This indicates large variability amongst species even if seed size is similar. Only the seed moisture content of rape and radish was given at the beginning of the experiment (~5 % for either species) so that the role of seed moisture in the above results cannot be assessed. Hanley *et al.* (2003) studied heat stimulated seeds of eight species, ranging in mass from 1.1 mg to 29.5 mg, from the Darling Range of western Australia. Contrary to expectations, smaller seeded species had greater germination after exposure to higher temperatures than the larger seeded species in the study.

The temperature of the soil in which a small seed is being heated may generally be sufficient as a boundary condition for modeling seed heating because heat transfer to the surface of the seed and through the seed coat and into the embryo would be rapid. As seeds become larger (e.g., seeds of recumbent oaks or shrub oaks; Abrahamson 1984, Paula *et al.* 2009), the center of the seed will heat much more slowly than the outer tissues (see Butler and Dickinson 2010). However, even in large seeds, vital tissue is located just under the seed coat, so seed surface temperatures may be a good indicator of injury.

Aerial Woody Fruit

An interesting situation arises if seeds are contained within woody fruits. This is the case in *Hakea* (*Hakea* Schrad. & J.C. Wendl), a genus of shrubs common to the southern hemisphere. *Hakea* has fruit (follicle) walls of up to 20 mm and it thus was hypothesized and

confirmed by Bradstock *et al.* (1994) that fruit wall thickness (analogous to bark thickness in trees) plays a role in seed survival. *Hakea* (Proteaceae) and some other shrubs in the Proteaceae and Myrtaceae have aerial seed banks that are common in trees of both hemispheres but are not typical in shrubs of the northern hemisphere. Mercer *et al.* (1994) predict the survival of seeds in aerial woody fruits using heat-conduction equations with time-dependent temperature inputs. Thermal death of the seeds correlated with thermal diffusivity of the fruit and fruit diameter. Seed death was assumed to occur when the inner 20 % of the fruit radius reached a temperature of 70 °C. This threshold was derived from Judd *et al.* (1993); it is the lowest temperature at which any seed mortality occurred. Variation in seed survival in capsules has been found to be related to seed capsule size and fire intensity in Australian shrublands (e.g., Bradstock *et al.* 1994); as such, further development of a predictive model is warranted.

Germination after Fire

Fire cannot only cause mortality of aerial or soil-stored seed, but germination of dormant seeds surviving fire can be stimulated by various factors related to fire. Fire-mediated germination cues can be moist or dry heat (Martin *et al.* 1975, Herranz *et al.* 1998), smoke (Brown and Van Staden 1997; Keeley and Fotheringham 1998), soluble chemicals of charred wood (charate) (Keeley and Nitzberg 1984), light (Baskin and Baskin 1988), and the availability of nitrogen (Thanos and Rundel 1995). These stimuli break dormancy by removing a physical barrier to germination, such as by cracking the seed coat of hard seeded species or rupturing seed coat fissures, that allow moisture to enter (Keeley 1987, Rasmussen and Wright 1988), or by triggering physiological processes associated with germination. Some species require a specific combination of cues to induce germination (Thanos and Run-

del 1995, Brown and Van Staden. 1997, Moreira *et al.* 2010). It has been hypothesized that two sets of traits allow for persistence under crown-fire regimes in Mediterranean habitats: plants with poor resprouting ability tended to have seeds with a higher probability of heat-tolerance and higher probability of heat stimulation than plants with good resprouting ability and heat tolerant below ground organs (Paula and Pausas 2008). Grouping plants into obligate or facultative seeders and resprouters might simplify model development. A seed-survival model could potentially be combined with a seed-germination model (second-order effect), once species-specific seed longevity and germination requirements are known. Again, predicting soil heating will be a critical component of any effort to model fire effects on soil seed banks.

For many species of plants that have seeds dispersed by gravity or wind after fire, the highest likelihood of establishment is from those seeds that land on bare mineral soil (Miller 2000). Reasons for this include improved moisture and nutrient availability, decreased competition, and destruction of allelopathic chemicals in plant litter that inhibit germination. Schimmel and Granström (1996) reported that aerial seeders are favored by seed beds with a high degree of organic matter consumption, while the results of Zasada *et al.* (1983) are more extreme. They described the results of artificial seeding on experimentally burned sites in interior Alaska upland black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb.) and feathermoss (Hypnaceae) stands. In three burn units with differing burn severity (and, thus, duff consumption levels), a fixed number of seeds of eight native woody species were sown onto 1 m² plots in October or June, depending on the timing of their natural dispersal date. Seeded species included paper birch (*Betula papyrifera* Marsh.), alder (*Alnus viridis* [Chaix] DC ssp. *crispa* [Aiton] Turrill), black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb.), aspen (*Populus*

tremuloides Michx.), balsam poplar (*P. balsamifera* L.), feltleaf willow (*Salix alaxensis* [Andersson] Coville), Scouler willow (*S. scouleriana* Barratt ex Hook.), and Bebb willow (*S. bebbiana* Sarg.). By the third year, of the 1322 seedlings still alive on experimental blocks, 1316 were growing on the heavily burned seed beds. Improved models of organic layer consumption that include bare mineral soil seed bed creation would enhance our ability to model the establishment from seeds (e.g., Miyawishi and Johnson 2002).

DATA AND MODELING NEEDS

Proposed components of a more complete model of first-order fire effects on shrubs and herbs are summarized in Figure 1. As pointed out previously, with exceptions including a model of aerial seed capsule heating (Mercer *et al.* 1994) and one describing the heating of rhizomatous grass buds (Choczynska and Johnson 2009), most process-based modeling efforts have focused on trees (see Butler and Dickinson 2010, Kavanagh *et al.* 2010). Based on current understanding, it appears that efforts to develop process models for herb and shrub response to fires may be most fruitfully focused on reproductive structures partially exposed at the surface, below ground organs and seed banks, and aerial seeds stored in protective structures.

Soil Heating

A major obstacle to modeling heat-induced mortality of below ground plant organs and seeds and effects on seed germination is the lack of accurate predictions of organic and mineral soil heating with sufficient horizontal, vertical, and temporal resolution (see Massman *et al.* 2010). Heat is generated by smoldering combustion (Hungerford *et al.* 1991) of woody fuels, especially coarse woody debris (Monsanto and Agee 2008), duff (Hartford and Frandsen 1992), and deep beds of masticated

fuels (Busse *et al.* 2005). Soil heating from radiation during crown fires on sites where there can be extensive areas with thin or nonexistent organic soil layers (in chaparral, desert shrub, sagebrush, and pinyon-juniper habitat) may also be important (e.g., Odion and Davis 2000, Butler and Dickinson 2010). The key factors regulating heat transfer into the soil are the total amount of heat generated at the surface (Steward *et al.* 1990), the duration of heating (Steward *et al.* 1990, Hungerford *et al.* 1991), and the soil moisture content (e.g., Aston and Gill 1976, Hartford and Frandsen 1992, Campbell *et al.* 1995, Busse *et al.* 2005). All of these factors vary at a range of spatial scales.

While heat is transported more quickly in moist soil than in dry soil at temperatures below which substantial moisture vaporization occurs ($\sim 100^{\circ}\text{C}$; Campbell *et al.* 1995), dry soils are more readily heated to higher temperatures than moist soils because of the lack of a substantial vaporization heat sink (e.g., Aston and Gill 1976, Hartford and Frandsen 1992, Campbell *et al.* 1995, Busse *et al.* 2005). Once the soil layer dries, a rapid rise in temperature can occur if a heat source is still present (Campbell *et al.* 1995). Frandsen and Ryan (1986) found that the total heat flux into wet mineral soil was 20 % of that of dry mineral soil during a pile burn. Busse *et al.* (2007) burned constructed and natural masticated shrub fuels over soils of different moisture and texture in northern California. Temperatures exceeded the threshold for near-instantaneous necrosis of 60°C to a depth of 2.5 cm to 5.0 cm in moist soil regardless of the fuel load, while in dry soils temperatures exceeded 60°C to a depth of 10 cm to 15 cm.

Existing Models

First Order Fire Effects Model. The soil heating module within the First Order Fire Effects Model (FOFEM) (Reinhardt 2003, based on the work of Campbell *et al.* 1995) is the only well-developed model for predicting soil

heating under a range of burning conditions and fuel types (e.g., Choczynska and Johnson 2009). Using user-selected inputs or default values, it predicts mineral soil heating in two situations: when there is no surface duff layer, and when a surface duff layer is present (D.M. Jimenez, Forest Service, unpublished report). When there is no duff layer, the heat source is calculated from the consumption of coarse woody debris. For soil covered by a duff layer, the heat source is the burning duff layer, modified by the amount of heat absorbed by unburned duff. However, FOFEM currently does not model the insulating effects of a thick, unconsumed duff layer or the heating caused by a combination of duff and woody debris consumption. The weakest link in making accurate predictions of soil heating is uncertainty in predictions of the extent and spatial variability in fuel consumption, particularly duff (Butler and Dickinson 2010). Furthermore, FOFEM is a stand-level model. Its ability to resolve fine spatial detail related to the heating of highly variable soils and surface fuel conditions, such as open stands of ponderosa pine or juniper resulting from encroachment into shrub and grasslands with discontinuous litter and duff layers, is limited (Massman *et al.* 2010). It is also not known if the FOFEM soil heating model will apply in arid and semi-arid shrub communities.

Understory Response Model. The only existing model tailored for predicting understory response to fire is the Understory Response Model (URM) (Sutherland and Miller 2005). The URM is a species-specific computer model that qualitatively predicts change in total species biomass based on resprouting and seedling establishment. The model predicts the response of grasses, forbs, and shrubs after thinning, prescribed fire, or wildfire one, five, and ten years post-treatment. The model takes into account individual life history traits and changes in the site caused by thinning and fire. The URM would be significantly enhanced if

it could be coupled with improved models for fuel consumption and subsurface heat transfer. Since the URM uses FOFEM to estimate mineral soil heating and mineral soil exposure, mortality of plant structures and seeds within litter and duff layers cannot be described, and mineral soil exposure is only coarsely estimated. The model outputs are also limited by lack of information on life history, below ground structural characteristics, and post-fire recovery mechanisms for most plant species.

Summary of Data and Modeling Needs

Because most herbs and shrubs are likely to be killed or top-killed even in low intensity surface fires, modeling efforts should focus on mortality of protected above ground and below ground meristematic tissue and seeds, as well as the effects on seed germination. To enhance the Understory Response Model or build a new model to predict initial recovery for vegetatively regenerating species, information is needed on the type and heat tolerance of buried structures from which new shoots develop; the size, number, and density of buds; the vertical distribution of buds and buried structures; any age specific limits on sprouting ability; heat transfer through protective tissue (such as in Mercer *et al.* [1994]); and whether buds or buried structures occur in duff, mineral soil, or both. Examination and modeling of bunchgrass survival will require investigation of threshold conditions for ignition of dense basal material. For species that reproduce from seed, data are needed on the number, vertical distribution, longevity, viability, presence of hard coats (and thus, heat tolerance), and details on any specific germination requirements, such as heat or smoke. Heat tolerance data are currently reported differently across studies, though a dose-response index has been developed that allows comparison (Paula and Pausas 2008).

Modeling mortality of below ground buds and seeds is critically linked to subsurface heat-

ing, and currently hampered by lack of a site-specific soil heating model that predicts temperature profiles through surface organic layers and mineral soil at a resolution relevant for plants. Data are also needed on heat transfer rates through tissue that shields buried meristems, regenerative structures, and roots. Improved fuel and duff consumption metrics and models, and enhanced knowledge and modeling of radiant and subsurface heat transfer, are necessary precursors for a soil heating model that links to vegetation recovery processes in both forested and non-forested plant communities.

To develop many of the suggested model components and validate final models, field research is required. Much could be learned from studies that replicate fire treatments under a range of burning and fuel conditions on the same site. Statistically sound, replicated experiments, rather than unreplicated observational studies, are needed. It is suggested that field and associated laboratory experiments be undertaken first in a few ecosystems that represent a range of ecological conditions (including both forested and non-forested ecosystems). While some of the required information can be developed through literature review, regional, local, or site specific experiments will be needed because of variability among sites in environmental conditions and vegetation.

CONCLUSION

Land managers would benefit from the development of a process-based model of fire effects on herbs and shrubs and its inclusion in an appropriate software system (see Reinhardt and Dickinson 2010). This model should allow them to: 1) predict initial understory response at local scales (given that vegetation distribution and composition, fuel loads, and fire behavior information were available on the same scale), 2) determine the necessity of post-burn rehabilitation measures, 3) assess fire effects over large areas for which on-the-ground investigations are not feasible given limited

personnel, 4) use the model in planning prescribed burns in order to achieve a desired effect on herbs and shrubs, and 5) determine the best management strategy for wildfires. As demonstrated in this paper, components of a comprehensive model of fire effects on herbs and shrubs exist (e.g., Mercer *et al.* 1994, Re-

inhardt 2003, Sutherland and Miller 2005, Choczynska and Johnson 2009), yet considerable gaps remain in our understanding of fire effects on herbs, shrubs, and seed banks, in our ability to model those processes, and in the datasets on which models would be based.

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