Fire Intensity and Vegetation Recovery in Chaparral: A Review

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Abstract. Chaparral wildfires can generate enormous amounts of energy from flaming and glowing combustion. Fire intensity can heavily influence the direction and rate of vegetation recovery but intensity interacts with a complex of factors that affect postfire recovery. Fire intensity has been measured by several different descriptors in chaparral studies: temperature and duration of heating, average maximum temperatures and total heat release. Conspicuously absent from the list of descriptors is fireline intensity. In order to compare results among fire effects studies in chaparral, we recommend one or a set of tested fire behavior descriptors be used in future studies.

Recovery of chaparral depends on the survival of the soil-seed bank and belowground resprouting organs (bulbs, lignotubers etc.). Studies indicate that lignotuber mortality and postfire resprouting of Adenostoma fasciculatum are directly determined by fire intensity. A high proportion of chaparral species resprout to some degree after fire but only a small number have been studied in fire intensity studies.

Considerable seed mortality can take place in chaparral burns, but high heat tolerances of chaparral seeds, insulating capacity of soil, variation in soil heating, and vertical (depth of burial) and horizontal (canopy vs. gaps) distribution of seeds in the soil ensures that abundant postfire seedling regeneration will occur, even after high-intensity wildfires. Evaluation of soil seed banks before and after fire has demonstrated that variable soil heating can strongly modify small-scale patterns of germinable seeds and seedlings.

Keywords: Chaparral; fire intensity; fire severity; vegetation recovery; resprouting; seed germination; seed patterns.

Introduction

Anyone who has observed a wildfire in chaparral on a hot, windy day is immediately impressed by the tremendously high temperatures and flame lengths produced by the fire. Equally impressive is the blackened, barren landscape left in its wake. The enormous energy generated by the fire plays a significant role in the postfire recovery of chaparral; that is, sites vary in the direction and rate of vegetation recovery depending on the total amount and duration of energy input into the site. Craddock (1929) and Sampson (1944) were among the first to measure temperatures and duration of heating in chaparral fires. In time other investigators turned their attention to the effects of the fire on the environment, including the vegetation.

In most fire effects studies the term "fire intensity" has been used to describe the relative strength of fire, e.g. high, moderate or low intensity. Intensity has been measured by several different descriptors: total heat release, maximum temperatures and duration of heating (time-temperature curves, Table 1).

Following publication of equations to describe energy release by flaming combustion (Byram 1959), forest and grassland ecologists began to use "fire intensity" synonymously with fireline intensity, which quantifies the energy released by the flaming front (discussed below). More recently, the term "fire severity" has been introduced to distinguish between the physical descriptors of fire (maximum temperature, fireline intensity etc.) and the effects of fire on the biophysical environment (Ryan and Noste 1985). In chaparral, for example, severity is expressed as lignotuber mortality, nitrogen volatilization, changes in microbial populations etc. Thus, a fire in *A. fasciculatum* that burns in early spring with a low average maximum temperature at the soil surface (i.e. a low intensity fire) may be categorized as high severity in terms of lignotuber mortality since resprout reserves are low at this time of year (Jones and Laude 1960). Because the ultimate goal of all these studies is to assess quantitative and qualitative changes in the biophysical environment that result from fire, we will use "fire intensity" to describe relative differences in the strength of the fire, "fireline intensity" as a physical descriptor of fire, and fire severity to describe the effects of fire on the biophysical environment.

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Phases of fire

To understand how fire changes the environment, we distinguish between the two primary phases of the combustion process, the relative importance of each in chaparral, and how each is measured. There are two primary phases of fire: active and glowing combustion (Alexander 1982). In the active combustion phase energy is released by the flaming front and is described by the equation for fireline intensity (Byram 1959):

$$I = HWR$$

where I is energy per length of fire front (kilowatts/meter), H is the heat yield per unit mass of fuel (Joules/gram), W is the weight of fuel consumed by the flaming front (grams/m²) and R the rate of spread of the fire (meters/second). Fireline intensity (I) is allometrically related to flame length (L in meters) by the equation $I = 259.83L^{2.174}$.

Fireline intensity was first used to describe fire behavior in prescribed burns of eucalypt and *Pinus radiata* stands in Australia (McArthur 1962; McArthur and Cheney 1966). McArthur and Cheney (1966) created three classes of fireline intensity to predict effects on eucalypt forests. Subsequently, Van Wagner (1973, 1977) extensively used fireline intensity to assess damage to pine and oak stands and to develop models to predict the start and spread of crown fires in conifer forests. It is now used routinely in studies of fire effects on forest and grassland ecosystems (e.g.Trollope and Tainton 1986, Vose and White 1987, Roberts et al. 1988, Swezy and Agee 1991, Finney and Martin 1993).

In chaparral research fireline intensity has been adopted for modeling fire behavior and fuels (Albini 1976, Salazar 1985) but it has not been used in any study of fire effects. Fireline intensity has proven valuable for studying the effects of fire on aboveground plant parts (e.g. crown scorch, cambium damage etc.), but its relationship to soil heating in chaparral and belowground damage to plant parts (e.g. seed banks, lignotubers etc.) has not been investigated. As Figure 1 demonstrates, there is an inverse relationship between energy released per unit area (fuel consumption) by the fire and rate of spread. Thus, the same fireline intensity can be achieved by a fast-moving fire that consumes a low quantity of fuel or by a slow-moving, high-fuel consumption fire. Although the two types of fires have the same fireline intensity, the slow moving, high-fuel consumption fire would cause much higher soil heating than the fast-moving fire. Because the same fireline intensity is produced by very different types of fires, it is necessary to know both flame length and rate of spread. Salazar (1985) defined four fire severity classes for chaparral and other fuel types using rate-of-spread and fireline intensity.

Fireline intensity has the advantages that it can be measured without instrumentation and represents a universally accepted descriptor that can be compared among fires. For example, Hodgkinson (1991) found that shrub recruitment in a semi-arid Australian woodland was positively correlated with fireline intensity. Clearly, this descriptor merits greater consideration in chaparral fire effects studies.

The second phase of fire is glowing combustion or combustion that continues after the passage of the

Table 1. Chaparral vegetation studies that have related fire effects to fire descriptors.

| Fire Effects	Fire Descriptor	Technique for Measurement	Source
Herbaceous production	Maximum temperatures in the soil	Temperature-sensitive paints	Bentley and Fenner 1958
Lignotuber mortality and resprouting	Maximum soil surface temperature	Temperature-sensitive paints	Anfuso 1982
Shrub size and height	Total heat release	Fire behavior model	Malanson and O'Leary 1985
Lignotuber mortality and resprouting	Total heat release	Minimum branch diameters	Rundel et al. 1987
Patterns in seed bank mortality and seedling	Maximum temperatures in the soil	Temperature-sensitive paints	Davis et al. 1989
Postfire seedling establishment	Total heat release	Minimum branch diameters	Moreno and Oechel 1991a
Lignotuber mortality and resprouting	Maximum soil surface temperatures and total heat release	Temperature-sensitive paints and water loss from cans	Moreno and Oechel 1991b, Moreno and Oechel 1993
Patterns in seedling establishment	Total heat release	Minimum branch diameters	Rice 1993
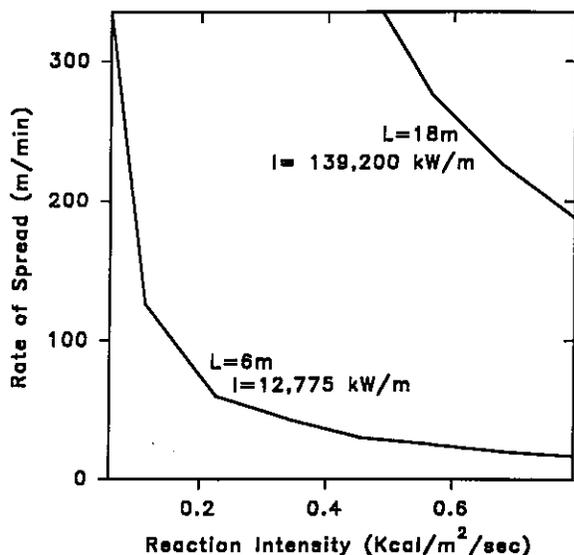
Figure 1. Relationship between fireline intensity, rate of spread, and rate of heat released per unit area (reaction intensity) for chaparral. L is the flame length (m) and I is fireline intensity (kW/m). Heat content of the fuels is assumed to be 8415 kJ/kg. (Adapted from Albini (1976), page 33).

flaming front. Glowing combustion typically occurs without a flame and is an important source of soil heating in chaparral. After the flaming front passes, litter and embers of the collapsed canopy may continue to burn for an extended period of time on the ground, often at high temperatures. To quote Craddock (1929) who studied fire behavior in chaparral with thermocouples:

"Fire may burn rapidly through the crowns of brush, causing leaves and small stems to fall in flames to the ground where they ignite the litter to produce maximum surface soil temperatures in 2-9 minutes, after which the temperature decreases. Should the spacing of branches in the brush crowns be close, intense radiation is induced, which causes the burning through of heavy branches. These fall to the ground as additional fuel."

It is noteworthy that two points in the same fire (in maritime *A. fasciculatum* chaparral) can have very different time-temperature curves (Fig. 2). At the first point temperature quickly peaks with the passing flame front and drops steadily to a low level. At the other
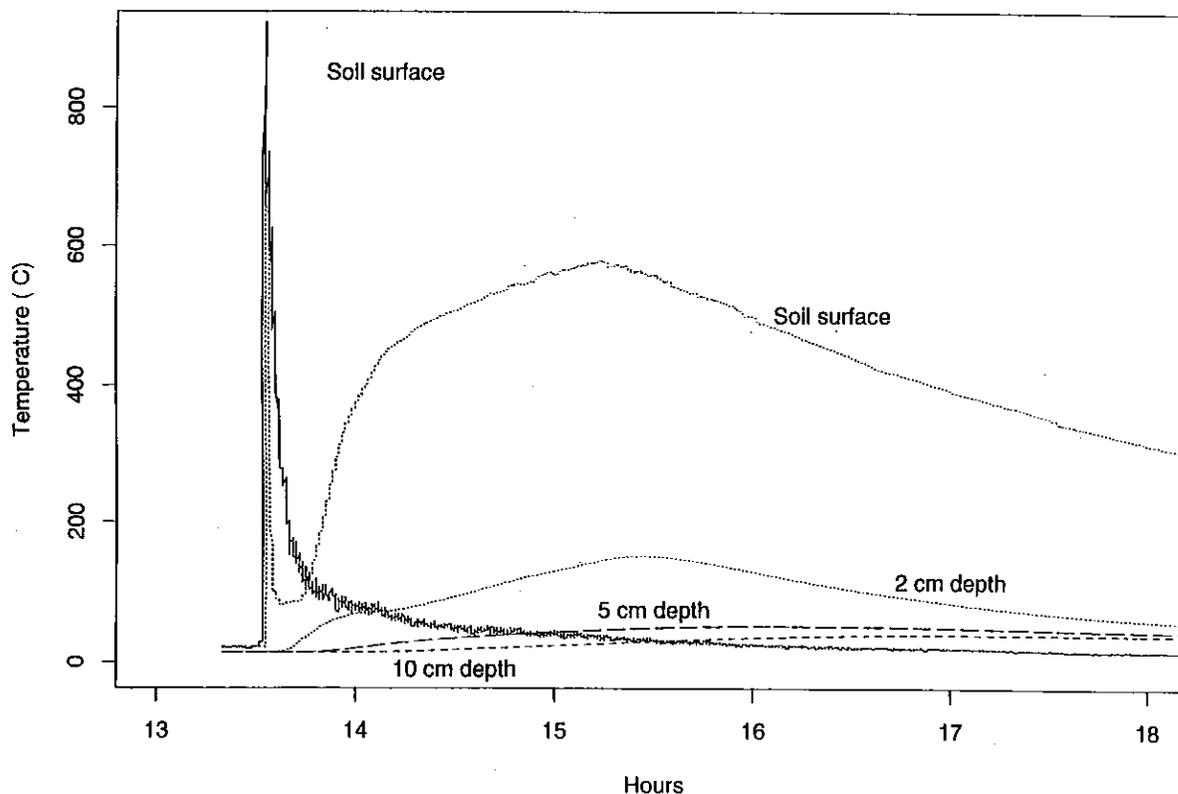

Figure 2. Time-temperature curves for two points in a fire in maritime chaparral. Temperatures at the soil surface are measured for one point (solid line). At the other point, temperature curves are presented for the soil surface and at depths of 2 cm, 5 cm and 10 cm (dotted and dashed lines).

point, however, the initial temperature spike is followed by an extended period of heating at high temperatures, presumably because of embers burning on the soil surface. Heat conducted downward during this phase of combustion may exceed that transmitted to the soil during flaming combustion so this phase can have an especially important effect on belowground plant parts.

Time-temperature curves from thermocouples (Fig. 2) provide the most accurate information about both fire front temperatures and glowing combustion in contact with the soil surface (Wright and Bailey 1982, Engle et al. 1989). The disadvantages of thermocouple measurements are that they are point samples and cannot easily be applied to large areas. Moreover, instrumentation is relatively expensive and the number of samples monitored by a data logger is limited.

Fire descriptors

If effects of fire on chaparral are to be compared among studies, standardization of terminology and techniques for describing fire are needed. So far, maximum temperatures in the soil and at its surface are the only parameters that can be readily compared among chaparral studies. Using thermocouple measurements and data from Sampson (1944) and Bentley and Fenner (1958), DeBano et al. (1979) divided maximum temperature into three fire intensity classes (Table 2). Although there are gaps in temperatures between classes, they provide a rough index of fire intensity.

Maximum temperature, however, has its limitations as a descriptor. Although temperatures are easily measured using temperature-sensitive paints and crayons, Hobbs et al. (1984) found summary statistics like mean maximum or minimum temperatures to be of little value for the evaluation of fire intensity because they neglect within- stand variability in heating. Furthermore, they found that uniformly high temperatures in the shrub canopy but highly variable temperatures in the soil (Hobbs and Atkins 1988).

A number of recent studies have estimated total heat release from fire by measuring evaporative water loss from cans painted black with a hole in them (Beaufait 1966). This technique provides an integrated measure of heat release per unit area by both flaming and glowing combustion. Moreno and Oechel (1989) found that water loss was a good predictor of both maximum temperature at the soil surface and minimum branch diameter of dead *A. fasciculatum* (r=0.83, P<0.05) plants remaining after the fire. On the other hand, Odion, Davis and Weirich (in preparation) noted a weaker relationship between water loss and maximum soil surface temperatures (r=0.56, P<0.05) and minimum branch diameter (r=0.57, P<0.05). They suggest that when fires consume much fuel, remaining branch diameters will be less useful for the detection of heat patterns. Furthermore, minimum branch diameters can be affected by species-specific differences in wood characteristics (specific density) and fuel moisture at the time of burning. Nevertheless, minimum branch diameter offers an inexpensive and relatively accurate method for establishing severity classes in low and moderate intensity fires but the technique needs further testing in other shrub types and in conditions of low fuel moisture.

In conclusion, a number of fire descriptors have potential for use in monitoring fire severity for research and management studies: fireline intensity, water loss from cans, maximum soil temperatures and minimum branch diameters. These techniques need testing to find one or a set of descriptors that can routinely be used in most studies. Once fires are described using similar

Table 2. Fire intensity classes of DeBano et al. 1979 (based on maximum temperatures in °C at the surface and 2.5 cm in the soil) and average maximum temperatures measured in other fire effects studies.

Temperature (°C)						
High Intensity		Moderate Intensity		Low Intensity		
Surface	Soil	Surface	Soil	Surface	Soil	
538-691	199-288	177-429	166-202	177-249	71-93	Source
529,588	—	—	—	—	—	Anfuso 1982
—	—	—	—	—	122	Davis et al. 1985
800-900	—	—	—	—	—	Odion et al. 1992
575,625	—	455	—	—	—	Moreno and Oechel 1993

terminology and methodology, fire effects can more effectively be compared across chaparral types, geographic areas, seasons and years.

Fire Intensity and Resprouting

Of the 78 common woody chaparral species, 34 (44%) resprout from lignotubers (Hanes 1971), semiburied woody structures that contain dormant buds, nutrients, and carbohydrate reserves. Barro and Conard (1991) point out that broadleaf evergreen shrubs like *Rhus* spp. and *Heteromeles arbutifolia*, that primarily sprout after fire, have high survival (70-100%) even in the most intense fires. On the other hand, *A. fasciculatum*, a seeder-sprouter, has highly variable postfire survival (15-85%). Despite the high proportion of sprouting chaparral species, research on fire intensity and resprout demography has focused exclusively on *A. fasciculatum*.

Anfuso (1982) measured maximum fire temperatures at the bases of *A. fasciculatum* plants in two July prescribed burns. Using shrub height as an index of plant size, we reanalyzed his data from the site east of Santa Maria, California. Multiple regression showed a weak but significant relationship between mean resprouting twig length in April of the following year and maximum basal temperature and plant height ($r2= 0.084$, $P<0.04$, $n=45$). There was no indication, however, that larger plants survived better or resprouted earlier than smaller ones.

Rundel et al. (1987) examined survival of *A. fasciculatum* after spring and fall prescribed burns. They classified burns into low, moderate and high intensity classes based on the minimum diameter of *A. fasciculatum* branches remaining after fire. They found that small shrubs suffered higher mortality than large shrubs and that resprout biomass increased with the preburn biomass of the plant. Season of burn and intensity strongly interacted to affect A. fasciculatum mortality. For the same intensity class, *A. fasciculatum* burned in late spring suffered higher mortality than plants burned in late summer, possibly because in late spring or early summer, *A. fasciculatum* plants have limited root and lignotuber reserves for resprouting.

Moreno and Oechel (1991b, 1993) have conducted the most detailed studies on fire intensity and resprouting in *A. fasciculatum*. They measured maximum fire temperature and evaporative water loss from cans in an experimental winter burn and monitored three treatments: normal fuel loading (approximately 4 kg/m², see Riggan et al. 1988), normal loading plus 4 kg/m² of cut and stacked brush, and normal loading plus 8 kg/m². Some of their major conclusions are as follows:

1. Increasing fire intensity increased plant mortality, reduced the number of resprouts per plant, and delayed time until resprouting. For the same intensity class, smaller plants suffered higher mortality than larger plants.

2. The ability of a plant to survive the fire and resprout improved with size of the lignotuber. Lignotuber size and depth of burial increased with increasing plant size and the effects of increasing intensity diminished with increasing plant size.

3. Post-resprouting mortality increased with fire intensity.

4. For a given intensity class, large plants resprouted earlier than small ones.

5. Herbivory was higher on plants with delayed resprouting.

Fire Intensity and Seed Survival and Germination

Germination behavior of chaparral seeds in relation to heat

Since the early studies of Wright (1931), considerable research has focused on the effect of heat on seeds of chaparral species, mostly utilizing freshly collected seeds. Not surprisingly, high heat tolerance and heat-induced germination is widespread among species with high seedling production following fire (Keeley 1991). In addition to heat, some species (e.g. fire annuals) require byproducts of combustion present in charred wood for germination. Still others (e.g. A. fasciculatum) have high germination if charate is added with heat (Keeley 1991) but do not necessarily require charate treatment for germination. A number of species (e.g. *A. fasciculatum*) produce seeds that are polymorphic in germination behavior, i.e. some germinate with no treatment while others remain dormant (Stone and Juhren 1953).

Seeds of many chaparral herb species that regenerate from seed after fire have maximum germination after exposure to temperatures ranging from about 70 to 120° C for five minutes (Sweeney 1956). Although duration of heating determines the total heat incident upon seeds, they appear to be relatively more sensitive to maximum temperature than duration. For instance, seeds of many species can tolerate 2-4 hours of 80-100° C (Wright 1931, Keeley et al. 1985). This is 20-40 times the total heat produced in 5 minutes at 170° C,

which is almost always lethal. Seeds of some species require exposure to 70-80° C for two hours to produce a germination response equal to that obtained from exposure to 100° C for five minutes (Keeley et al. 1985).

Figure 3 shows the relative heat tolerance and germination responses of selected shrub species that commonly establish seedlings after fire (Sampson 1944). Unmoistened seeds of these species germinate over a wide range of temperatures. Given the high spatial variability in soil heating that occurs during fires, it is likely soil temperatures will span the temperature range necessary to induce germination of most of the fire-following flora. The combination of broad heat tolerances and high variability in soil heating likely promotes coexistence of many species rather than selects for particular species. This in part explains the variety of species and regeneration modes present in a given area after fire (Davis 1991).

Beadle (1940) was one of the first researchers to observe that seeds which readily imbibe moisture also have reduced resistance to high temperatures. Seeds of several fire-following herbs that imbibe water like *Emmenanthe penduliflora* and *Camissonia micrantha* also have greatly reduced heat tolerances (Sweeney 1956) (Fig. 4). Parker and Rogers (1988) found a similar reduction in heat tolerances of the herbs *E. penduliflora, Chaenactis artemisfolia, Phacelia grandiflora,* and *P. parryi* and the shrubs *A. fasciculatum, Arctostaphylos canescens* and *A. glandulosa* (Parker 1987).

Figure 4. Germination comparison of moistened and dry scarified seed after 5-minute exposures to each temperature for *Emmenanthe penduliflora* and *Camissonia micrantha*. Curves for *E. penduliflora* are: moistened (dashes) and dry (solid) and curves for *C. micrantha* are: moistened (dot-dash) and dry (dots). (Data from Sweeney 1956).
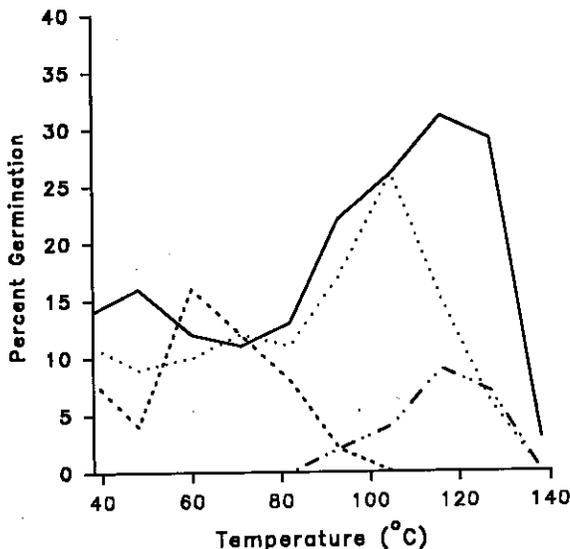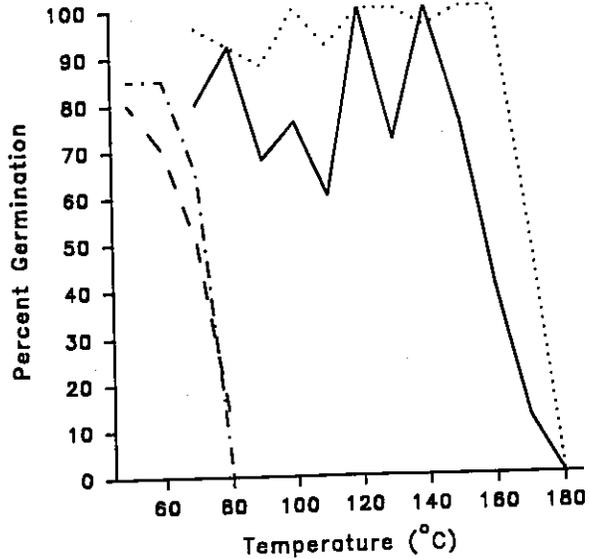

Figure 3. Germination of dry, scarified seeds after a 5-minute exposure to each temperature. Shrub species are: *Adenostoma fasciculatum* (solid; *Ceanothus megacarpus* (dots); *Ceanothus crassifolius* (short dashes; and *Arctostaphylos parryi* (dot-dash) (from Sampson 1944).

In contrast, Sweeney found that the heat tolerance of *Ceanothus cuneatus* was unaffected by soaking in water because its hard seed coat does not absorb water. A similar response has been observed for the herb *Calystegia macrostegia* (Parker 1987). In fact, seed germination of hard-seeded species can be increased by submerging them in boiling water, a technique recommended for propagation of *Ceanothus* spp., *Fremontia* spp., *Lepechinia* spp., *Lotus* spp., *Lupinus* spp., *Malosma laurina, Pickeringia montana, Rhus* spp., and *Thermopsis macrophylla* (Emery 1988). Little is known, however, about moisture uptake and heat tolerances of many other species that are abundant after fire.

This differential sensitivity to heat caused by the moisture absorption has important management implications. Since prescription burning typically occurs over moist soils, species with seeds that imbibe water may suffer disproportionately higher mortality than hard-seeded species, even in low-intensity fires. On the other hand, it is possible that the same high variability in soil heating that occurs in both prescribed burns and in wildfires reduces or compensates for the impact of high soil moisture on sensitive seeds. Soil moisture has rarely been measured in studies on prescribed burns, but if it is as spatially variable as soil heating, its relative effect on sensitive seeds would be less predictable.

Soil heating, seed burial and seed survival

Considering the tremendous radiant energy produced by chaparral wildfires, the amount of soil heating is surprisingly low. This is because soils are a porous media with low thermal diffusivity, only a small portion of the energy released during burning is transferred into the soil (DeBano et al. 1979). Sweeney (1956) heated the soil surface by direct flame from an air gas burner for 20 minutes and found that at a depth of 1.25 cm maximum temperature was 190° C, and at 2.5 cm only about 100° C (for reference, flame temperatures are about 1200° C in the yellow zone, and about 600° C in the blue zone). A similar heat and soil-depth pattern emerged when a 7.5 cm layer of excelsior was burned on the soil surface. Field studies using themocouples in the soil also have confirmed that maximum temperature of the fire-induced heat pulse into the soil attenuates dramatically with depth (Fig. 2) (Sampson 1944, Bentley and Fenner 1958, review by Debano et al. 1979, Odion, Davis, and Weirich, in preparation).

The capacity of soils to insulate seeds from high surface temperatures is critical to their survival. Because of the enormous temperature gradient that develops in the upper soil layer in chaparral fires, vertical distribution of seeds, rather than heat tolerances, is probably the most important factor determining total seed survival and subsequent germination. Seeds on or at the soil surface in a chaparral fire usually experience high mortality (Keeley 1977, Bullock 1982, D'Antonio et al. 1993), but refractory seeds covered by 2-3 cm of soil may be sufficiently insulated to survive extremely high temperatures at the surface. In a fire study of maritime chaparral, Odion and Davis (in preparation) found that *Adenostoma fasciculatum* had a high proportion (91%) of seed in the top 2.5 cm of soil compared to *Arctostaphylos purissima* (36%) (Table 3). Where shrub canopy cover was high and, as a result, soil heating also was high, *A. fasciculatum* suffered higher seed mortality than *A. purissima* (Table 3). They

Table 3. Seed burial and seed survival of *Adenostoma fasciculatum* and *Arctostaphylos purissima* after fire at two sites in maritime chaparral.

Species	Percentage of seed below 2.5 cm of soil	Percentage of seed surviving the fire		
		Dense canopy, Site 1	Dense canopy, Site 2	Canopy gaps
Adenostoma fasciculatum	10	2.3	2.8	49.6
Arctostaphylos purissima	56	16.7	not present	56.3

attributed the higher postfire survival of *A. purissima* seeds to greater depth of burial rather than to interspecific differences in heat tolerances of the seeds. Poor regeneration may still occur locally where prolonged combustion (mostly glowing) causes essentially complete seed kill, such as under wood rat (*Neotoma fuscipes*) nests, or in areas where fuels are piled (Bently and Fenner 1958, Green 1970, Odion and Davis, in preparation).

Spatial patterns of seeds and seedlings in relation to soil heating during fire

Variability in soil heating during chaparral fires can dramatically alter both seed and seedling spatial patterns. A field study by Davis et al. (1989) found striking patterns in the distribution of seed and seedlings following fire in maritime *A. fasciculatum* chaparral. Seed and seedling densities were higher in 1-2 m diameter gaps where soil heating was lower compared to adjacent 4-6 m areas of continuous shrub canopy where soil heating was relatively higher. Germination of soil samples collected before the burn indicated that non-refractory seed was much more abundant in gaps than under the shrub canopy. Refractory seed probably had the same pattern, but this was not determined. Unfortunately, because the burn was carried out in early December, 8 days after a light rain, mortality of seeds that imbibe water may have been elevated, magnifying postfire seed and seedling patterns. Conditions for combustion at the time of the burn also were sub-optimal. Maximum flame lengths were only around 5-6 m, so heating patterns may not have been representative of most chaparral fires.

In a more recent study, Rice (1993) investigated small-scale seedling patterns after a dry-season wildfire in the Sierra foothills. The magnitude and pattern of soil heating in this fire were probably more representative of wildfire conditions; that is, thermal diffusivity of the soil and the heat tolerances of seed were less influenced by soil moisture. Rice correlated patterns of seedling emergence with the minimum diameter of twigs remaining on *A. fasciculatum* snags and found that postfire seedling patterns were strongly related to total heat release at a block size of 4-5 m, the probable scale of prefire canopy gaps. In addition, she found that the distribution and depth of surface ash was positively correlated with total heat release. Ash is an important source of nutrients for seedlings (Nilson and Schlesinger 1981, Rundel and Parsons 1984) and total plant cover had a higher correlation with ash thickness than with twig diameter.

Odion and Davis (in preparation), studied autumn prescribed burns in which soil heating was very high.

Preburn seed bank samples were heated and treated with charate to inventory refractory seed. They found that the amount of preburn seed bank remaining after fire at sites with dense preburn shrub cover was only 2-3% of the original density for *A. fasciculatum* but 17% for *Arctostaphylos purissima* (Table 3). On the other hand, seed survival in gaps in the preburn canopy increased to 50% for *A. fasciculatum* and 60% for *A. purissima*.

In this study fire strongly modified patterns of germinable seed and seedlings in the field. Figure 5

shows how fire altered the distribution of *A. purissima* seeds along a 47 m transect. Seeds of *A. purissima* and other species were abundant over much of the transect prior to fire (Fig. 5a). In contrast, postburn seed and seedling distributions in the field were highly variable but strongly interrelated. Postburn viable seeds and seedlings were concentrated in areas where the preburn canopy was less dense i.e. where soil heating was relatively low. Other species had similar pre- and postburn patterns as a result of soil heating. Overall, the pattern of seedlings in the field was one of alternating
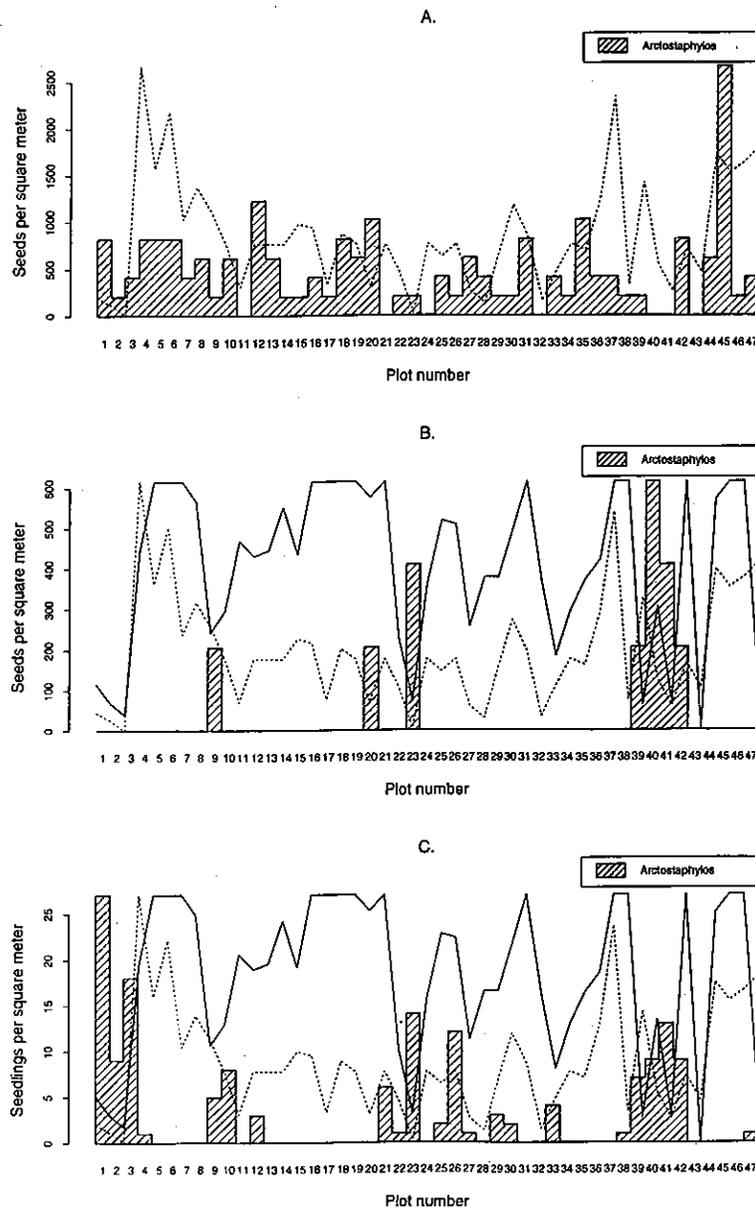

Figure 5. (a) Prefire seed densities of *Arctostaphylos purissima* on a transect of 47 contiguous 1-m² plots. (b) Postburn seed densities on the same transect. (c) Postburn seedling densities along the transect. Dotted line is preburn canopy cover of *Adenostoma fasciculatum* and the solid line is evaporative water loss from cans, a measure of heat release per unit area (data from Odion and Davis in preparation).

1-2 m diameter patches with high seedling densities, and 5-6 m diameter areas of low seedling densities. Where seedling densities were low, shrub resprout cover tended to be high. Because small-scale fuel arrays in chaparral are typically heterogeneous, modification of seed bank patterns by fire is probably commonplace. However, the extent to which these patterns are further modified by hillslope processes like rill and sheet erosion is not known.

Conclusions

Chaparral fires are characterized by high phytomass consumption that is usually accompanied by high energy release in flaming and glowing combustion. Because aboveground plant parts invariably succumb to the fire, vegetation recovery is entirely dependent on survival of soil-stored seed and resprouting organs. The interaction between fire and vegetation is extremely complex which makes predictions about postfire recovery difficult at best. For example, spatial heterogeneity of fuels, fuel moisture content, species- specific differences in heat content of the fuels interact with microclimate, slope, aspect, elevation, soil characteristics and time of year to produce highly variable patterns of soil heating at many scales. Moreover, the effect of soil heating on the seed bank adds another layer of complexity because they differ in species composition, seed densities, and horizontal and vertical distribution of seeds in the soil. Similar complexities influence mortality of resprouting species.

To date most research on fire intensity and fire severity has focused on *Adenostoma fasciculatum* at the scale of the stand. Future research needs to address fire intensity and the response of other species of resprouting shrubs, subshrubs, lianas and herbs (e.g. geophytes). Moreover, the scale of fire severity studies needs to be expanded to larger landscape units, like the watershed.

Finally, additional studies of micro- and mesoscale patterns of seed mortality and seedling recruitment are needed in wildfire burning conditions if we are to develop models to predict postfire response of the vegetation.

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