Flammability, physiology and coexistence in fire prone environments

by

Peter David Cowan

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy in Integrative Biology in the Graduate Division of the University of California Berkeley

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Abstract

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Approximately 40% of the earth’s terrestrial surface is covered in fire-prone vegetation. Many of the plants in these habitats have evolved characteristics to avoid damage during wildfires, or to take advantage of the post-fire environment. As a consequence of being the fuel for wildfires, plants also possess characteristics that contribute to fire frequency and intensity. This dissertation considers both sides of the plant–fire interaction. The first chapter provides background information on our current understanding of plant trait and fire relationships and discusses the evolution of plant flammability.

The second chapter presents a model exploring coexistence among plant post-fire persistence strategies in fire-prone environments. In this model coexistence of more than two post-fire strategies is not stable on long time scales. The model also suggests that species with the ability to postpone seed germination until post-fire are favored at shorter fire intervals as long as variation in fire intervals is moderate.

The third chapter describes a non-destructive method for rapidly assessing fuel structure and load in shrubland systems like California chaparral. Results obtained by using this method correlate well with more time consuming destructive harvesting. In the fourth chapter this method is applied to four chaparral species that differ in their capacity for post-fire seed germination. The species differed in the amount of fine fuels, but not by post-fire strategy. Species with post-fire seeding did have significantly more dead branches than obligate post-fire resprouters.

The final chapter explores the effect on photosynthesis to plants which are not themselves burned by a wildfire, but exposed to its smoke. After smoke exposures as short as 15 minutes, tobacco plants show significantly reduced photosynthesis, stomatal conductance, and chlorophyll fluorescence. These reductions are short lived, after one day even plants exposed for 45 minutes no longer differ from controls. An appendix describes a method for assessing whole plant flammability characteristics, presents preliminary results, and discusses shortcomings of the method.

This dissertation adds to a growing body of research demonstrating the interdependence of plant flammability traits and fire response characteristics.
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Chapter One

Background

Fire is a major structuring force for much of the world's vegetation (Bond et al. 2005, Bond and Keeley 2005). Wildfires in fire-prone regions have significant effects on global processes such as carbon cycling and nitrogen deposition (Crutzen and Andreae 1990). It is well known that climate, topography, and vegetation type affect the nature and distribution of wildfires (Rothermel 1972, Krawchuk et al. 2009). Increasingly research has begun to focus on the role that the distribution of individual species can have of on wildfire conditions. Species specific combustion properties have been noted for several groups (e.g Montgomery 1976, Scarff and Westoby 2006, Kane et al. 2008). In the case of the Hawaiian invasion by Bromus tectorum, changing distribution has altered fire the regime by increasing frequency of burning (D'Antonio and Vitousek 1992).

In addition to its important for understanding plant ecology, there are substantial economic impacts of wildfire. In the United States alone, an average of 66,000 wildfires have burned nearly 2.4 million hectares annually over the last ten years (http://www.nifc.gov/nicc/sitreprt.pdf). Wildfire related costs in the United States are billions of dollars annually (USDA 2002). Forecasts indicate that the frequency, intensity, and extent of wildfires will increase as climate changes (Torn and Fried 1992, Fried et al. 2004, Westerling et al. 2006, Krawchuk et al. 2009). The already large impact of wildfires on human populations is likely to increase due to a combination of factors: greater human proximity to wildfire-prone vegetation, increased ignitions from human activity, and global warming.

In addition to loss of life and infrastructure destruction, fires also have significant effects on ecosystem services, such as natural water filtration, ground stabilization, and air quality. Smoke has widespread effects because it is transported by wind to an area much greater than the fire and can persist for well after. Persistent smoke is
related to a number of health concerns as well as issues of visibility which are closely
monitored in National parks. These issues are particularly relevant in the fire-prone
California chaparral ecosystem where the urban–wildland interface is extensive and
have been shown to produce high levels of smoke compared to other systems (Clinton
et al. 2006). Surprisingly little research has addressed the effects that smoke has on
vegetation neighboring a wildfire.

My dissertation focuses on how characteristics of species contribute to, and are
affected by fire regimes. I explore the traits of chaparral shrubs that may alter fire
regimes and how they can be quantified (Chapters 3 and 4). I present a model of how
different plant strategies succeed under various fire regimes (Chapter 2). Finally, I
address the physiological impacts on plants adjacent to wildfires (Chapter 5). In an
appendix I describe a project intended to address the magnitude and relative impor-
tance of plant flammability traits. Here, I provide context for these ideas.

1.1 Chaparral: A perfectly flammable system

The ideal systems to study the questions about plant traits and fire responses are
Mediterranean-type shrubland, such as California chaparral. Summer droughts lead
to intense, regular crown fires, at intervals of every 20–80 years, that exert a strong
selective force (Bond and van Wilgen 1996). These unique climatic conditions occur
in five geographically distinct regions: the Mediterranean basin, southwestern Aus-
tralia, South Africa, the west coast of the United States, and Chile. In contrast to the
other regions, Chile has a much less frequent fire regime, and may be especially use-
ful for disentangling the influence of climate and fire in trait evolution (Fuentes et al.
1994). In other respects all Mediterranean-type regions are notable for their strongly
convergent communities and physiology (Mooney and Dunn 1970, Cody and Mooney
1978). Mediterranean shrubland communities range from low to moderate diversity
(Cowling et al. 1996, Dallman 1998), and include species with a variety of post-fire re-
generation strategies (see Chapter 2 and Figure 2.1).

Fire regimes are also largely convergent among Mediterranean-climate regions.
Typically fires occur every 20-80 years and are almost always crown fires (some regions
are more similar than others, see Cowling et al. 2005). The interpretation of fire as a
selective force is much simpler in crown fire systems than ground fires that experi-
ence occasional crown fires. In Mediterranean shrublands every fire results in com-
plete death of above ground plant portions. This makes the analysis of plant charac-
teristics straight forward compared to ground fire systems where ground fires may be
beneficial for a species, but increase the risk of devastating crown fires.
Reproductive timing for many species Mediterranean-climate regions is directly tied to fire events. In particular, populations survive fires either by individuals re-sprouting from below ground roots or germination of new individuals from seed banks that persist through fires or by dispersal from unburned areas. In some cases, fire is a prerequisite for seed germination.

1.2 Flammability traits

The tight coupling of reproduction and wildfire events have lead some researchers to speculate whether flammability traits are adaptive, and how they may have evolved (Mutch 1970, Schwilk 2003, Schwilk and Kerr 2002, see also Chapter 4 for more discussion of these theories). Improved understanding of how fire prone communities are structured and the evolutionary implications of altered fire regimes is especially important for protecting species that are sensitive to fire frequency (Odion and Tyler 2002, Burgman and Lamont 1992). In Mediterranean-type shrublands theory suggests that traits increasing plant flammability would be more prominent in post-fire seeding species than resprouting species, as more frequent fire regimes may favor seeding species (see Chapters 2 and 4).

What is plant flammability

Wildland fires are shaped by three fundamental factors: weather, topography and fuel characteristics. The role of landscape-scale variables, such as slope and wind speed, on fire behavior is well understood. However, few studies have addressed the influence that plant traits have on fire behavior. Fuels (i.e., living and dead plants and plant parts) play an obvious role in the severity of wildfires; increased fuel loads allow greater potential total heat release. In chaparral, fuel load and structure have been shown to influence local fire severity (Schwilk 2003), but the link is not as well understood compared to extensively studied forested systems (Keeley et al. 1999).

Various definitions of flammability have been employed in discussing plant traits. The definition proposed by Anderson (1970) describes three elements of plant flammability: ignitability, the delay before flaming combustion; combustibility, the rapidity of consumption by fire; and sustainability, the capacity for continued burning after the heat source is removed (discussed in greater detail in Chapter 4). Ignitability may be particularly important because ignition events are thought to limit chaparral fire frequency historically (Keeley 2002). Table 1.1 lists traits known or expected to
influence flammability and includes hypotheses for the effect on each component of flammability and smoke production as the trait value increases.

Moisture content has long been known to be negatively correlated with fire intensity across all scales, and thus positively with smoke production (Weise et al. 1991), from individual leaves to the global weather cycles that shape continental fire patterns (Swetnam and Betancourt 1990). In addition to its importance as a primary driver of intensity, moisture content also varies greatly in natural populations. It is of particular interest in chaparral as every summer there is seasonal drought and plant moisture levels decline leading into the peak fire season in fall. Moisture content of leaves is well correlated with the time taken for them to ignite; however, Dimitrakopoulos and Papaioannou (2001) found that the slope of this relationship varied greatly ranging from 0.15–0.72, suggesting a strong species by moisture interaction.

A related flammability trait is the propensity of a plant to retain dead tissues. Moisture levels in dead plant material track relative humidity and are typically lower than in living plant material. Because of this, dead tissue can be much more flammable than live tissues (but see Rothermel 1976). Not all plants retain large amounts of dead material; many conifers, for instance, are known to ‘self prune’, and by shedding dead tissue, may prevent ground fires from spreading to crown fires. Indeed, Schwilk and Ackerly (2001) found that self pruning was associated with a suite of other ‘fire avoidance’ traits such as thicker bark.

Several studies have demonstrated that plant traits related to surface area to volume ratio are also important determinants of plant ignitability (Brown 1970, Montgomery and Cheo 1971, Engstrom et al. 2004) and combustibility (Scarff and Westoby 2006). Surface area to volume ratio determines the amount of oxygen available for combustion. Small twigs and thin leaves also allow a greater amount of the fuel to undergo pyrolysis and heat up more quickly.

Bulk density, a measure of biomass in a volume of space, is correlated with radiant heat transfer. The closer leaves and branches are to one another, the greater the heat radiated into adjacent fuels instead of the air. Radiative heat transfer is important in the spread of flames from one canopy to adjacent plants. If bulk density is extremely high, it is possible that combustion could be oxygen limited due to low diffusion. This has been demonstrated in constructed litter beds from Australian shrublands where rates of litter accumulation are high and an important factor in fire spread between plants (Scarff and Westoby 2006). In contrast, chaparral has low rates of litter accumulation and typically experiences crown fires that spread directly from canopy to canopy. Hardy et al. (1996) were unable to find evidence of diffusion limitation in mechanically crushed chaparral. In contrast, by manipulating the dead canopy fuel loads and arrangement in Adenostoma fasciculatum, Schwilk (2003) demonstrated that both
Table 1.1: The arrows indicate the expected trajectory of the flammability component or smoke production if the trait value increases. The ‘drought’ column indicates the expected impact of low water availability on the trait value. Smoke predictions are based on the expected effect of trait changes on fire efficiency (Urbanski et al. 2009). Particle density refers to the density of wood while bulk density is the mass of plant tissue in a volume of space. Branch retention is dead branch retention, leaf mass fraction is the proportion of plant mass made up by leaves, and ramification is the degree of branching or bushiness. Ignite: ignitability, Combust: combustibility, Sustain: sustainability, Smoke: smoke production, and Drought: the expected trait change in response to low water availability.

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fuel quantity and arrangement effects on maximum temperature and heat output of a prescribed fire. The spatial arrangement of plant parts has received very little attention, but is likely important in most wildfire systems (Bond and van Wilgen 1996). Because fuel quantity and arrangement also affect the mixing of oxygen during combustion they are likely to be determinants of smoke production in natural systems.

A number of studies have emphasized the importance of the chemical composition of plant tissue for combustion (Montgomery and Cheo 1969, Rothermel and Philpot 1973, Montgomery 1976, Rundel 1981). Volatile oils have also been identified by some investigators as contributors to flammability in chaparral species (Rothermel 1976, Rundel 1981). However, the only study to test the role of leaf volatiles on either whole plant peak or total heat release was unable to find any effect (Etlinger and Beall 2004).

Factors influencing flammability have been studied by a number of researchers over the last 30 years. However, most research has focused on a limited set of traits at either very large (landscape) (Rothermel and Philpot 1973) or very small (plant tissue and organ) scales (Brown 1970, Montgomery and Cheo 1971). Work to date has found that a number of traits influence plant flammability, and the effects vary greatly between species; sometimes a species is more flammable than a different species in one trait but less in another (Dimitrakopoulos 2001, Dimitrakopoulos and Papaioannou 2001, Etlinger and Beall 2004). Unfortunately, because most studies focus on only one or two traits and use different metrics for quantifying flammability, weighting the relative influence of different traits on flammability is infeasible, and predictions of relative flammability among species are not currently possible. Chapter 3 describes a method for producing comparable measurements of flammability traits across a range of taxa, and the method is applied to four species in Chapter 4. Appendix A describes an experimental approach to quantifying and ranking the plant flammability traits themselves.

1.3 Plant physiology in fire-prone environments

Because shrub fires are well known to produce more smoke than fires in other woodland systems several studies have sought pollution correlates at the landscape and whole stand level (Ward 1990, Hardy et al. 1996, Clinton et al. 2006). Hardy et al. (1996) found differences in the smoke production of stands that varied in age and species composition. However, due to the limited number of the fires in this study the authors were unable to differentiate the effects of age alone from those of species composition. Weise et al. (1991), by burning plants in constructed fuel beds, found that
species identity and time of year (presumably related to plant water status) had significant effect on smoke production. Table 1.1 summarizes some other flammability traits and their effects on flammability and pollution. More research on the influence of these traits on smoke release is necessary. The methods described by Appendix A could be easily modified to include a smoke production by trait component.

Smoke is produced in large quantities in both wild and prescribed fires (Ward and Hardy 1991, Hardy et al. 1996). The length or intensity of exposure by neighboring unburned vegetation is unknown, but it is widely assumed to be transitory. However, smoke may accumulate in valleys or other topographic features and remain for extended periods. For massive fires like those that burned in Indonesia during 1997 smoke may remain for weeks (Davies and Unam 1999).

The physiological effects of long term chronic smoke exposure on plants have been well known for a century (Knight and Crocker 1913, Bakke 1914). However, for the last several decades, despite many significant advances in plant physiology, essentially no work has been done to identify the mechanisms by which smoke affects plants. Moreover, only two studies have looked at the effects of wildfire smoke exposure on adult plant physiology (Davies and Unam 1999, Gilbert and Ripley 2003). This is surprising both because of the wide spread production of smoke and known effects on seed germination rates. Chapter 5 reports on the magnitude and duration of photosynthesis reduction resulting from acute smoke exposure in Nicotiana tobaccum.

Even as our understanding of flammability traits and their evolution deepens, several large gaps still exist. The most important of these is refining what constitutes a flammability trait and quantifying individual trait contributions to overall plant flammability. My approach to this question (Appendix A) has yet to be successful, but holds promise. Studies in the vein of Schwilk (2003) would also be welcome. The lack of an integrated understanding of flammability traits has left researchers to either focus on a single features such as litter beds (Brown 1970, Montgomery and Cheo 1971, Fonda 2001, Scarff and Westoby 2006, Kane et al. 2008) or assume equivalence of flammability traits (Dimitrakopoulos and Panov 2001, Saura-Mas et al. 2010, see also Chapter 4). In ground fire systems differences in litter flammability may be the primary determinant of fire regimes, yet only limited efforts to connect differences in litter flammability to fire regime variation and its ecological consequences have been made (e.g. Schwilk 2007). Additional research is also needed to separate the evolution of traits in response to physiological constraints from those as a result of fire regime shifts. This is particularly important in semi-arid shrubland systems where many of the adaptations to low water availability may mirror those of fire-embracing strategies (see Table 1.1). Approaches could include comparisons of similar areas that have differing fire regimes, like California and Chile, or regions of topographic fire refugia and
surrounding areas. Research could also focus on traits where the predicted evolutionary change in a fire-embracer differs from the change expected due solely to climatic drivers (see Table 1.1).

The following chapters explore the expected patterns in chaparral post-fire regeneration strategies and flammability traits. As predicted, high frequency fire regimes favor post-fire seeders (Chapter 2). Post-fire seeders also have higher rates of dead branch retention, a flammability trait (Chapter 4). Complementing this work I present an improved method for measuring and reporting shrub flammability characteristics (Chapter 3) and propose a method for quantifying the influence traits have on flammability (Appendix A). These tools lay a framework for a common approach to studying flammability traits and their evolution.
Chapter Two

Coexistence and post-fire regeneration strategies

2.1 Introduction

Fires are a major cause of natural disturbance and have shaped patterns of vegetation globally (Bond et al. 2005). Some ecosystems are more prone wildfires than others and characteristic fire regimes differ between systems. Mediterranean-type shrublands have high fuels loads and dry summers resulting in crown fires on 20-50 year intervals (Bond and van Wilgen 1996, Keeley and Davis 2007). To cope with this intense fire regime, shrubs have evolved characteristics for resisting the disturbance or persisting through of a particular regime (Gill 1981). However, fire regimes vary geographically and in response to land development by humans, climatic change, and other factors (Krawchuk et al. 2009). Life history adaptation to a specific fire regime leads to shifts in species abundance and community composition as aspects of the regime, such as frequency, change. We present a model exploring the effects of changes in fire frequency and predictability on post-fire regeneration strategy landscape-scale coexistence and success. In particular we are interested in assessing the long-term equilibrium state. By equilibrium state we mean stability over many fire cycles in the strategy abundance (averaged over all years of the fire cycle).

Post-fire regeneration strategies

All of the mediterranean-climate regions, aside from Chile which is less fire prone, contain habitats dominated by shrubs with similar post-fire regeneration strategies (PFRS) (see Table 2.1). Four recognized PFRS can be described by two non-exclusive
syndromes; resprouting ability and post-fire seed germination (see Figure 2.1 and Keeley 1991, Pausas et al. 2004). Resprouting species recover from fire injuries by resprouting from a below-ground burl or lignotuber (Keeley and Zedler 1978). Wells (1969) has suggested that this is the ancestral state for taxa in California, but phylogenetic analysis of Australian and South African groups is ambiguous on the ancestral state (Bond and Midgley 2003).

Post-fire seed germination, as defined here, refers to any means by which seed dormancy is maintained until after a wildfire, including serotiny and physical or chemicals cues that release dormancy in soil seed banks. Models presented by Enright et al. (1998a,b) show that stronger serotiny is favored in both resprouting and non-resprouting species of Banksia when the post-fire recruitment probability exceeds non-fire year recruitment probability and fires are frequent. Perry and Lotan (1979) present a model indicating that lodgepole pine, which has serotinous and non-serotinous cone types, is polymorphic in cone type because of variations in fire intensity.

The post-fire seeding and post-fire resprouting syndromes can be combined to produce four PFRS: obligate post-fire seeding (OS), obligate post-fire resprouting (OR), facultative post-fire seeding (FS), and opportunists (Figure 2.1). Timing of reproduction differs between PFRS. We model OR species as those that recruit in-between fire events and OS species recruit only immediately post-fire. In our model FS species may recruit exclusively after a fire (type I) or both during the free-free period or post-fire (type II). These PFRS combined with other demographic factors (life span, age of first reproduction, &c.), make the temporal spacing of fires important. Because of the time scales needed to address how PFRS and fire frequency interact to influence population and community dynamics, computer simulations have been increasingly employed (Hilbert 1987, Bond and van Wilgen 1996, Groeneveld et al. 2002).

Existing models

Models of PFRS demographics and coexistence fall into two categories. 1) Spatially explicit landscape models that incorporate many environmental factors aside from fire including shade, drought, and substrate conditions. 2) Demographic models that compare the coexistence of interacting PFRS, but omit environmental factors aside from fire.

Spatially explicit landscape simulations have been developed for shrublands in Spain (Pausas 1999), California (Franklin et al. 2001, Syphard et al. 2006) and Australia (Groeneveld et al. 2002). These models seek to be as realistic as possible and include several species or functional types with specific parameter estimates. In addition to demographic parameters Pausas (1999), Franklin et al. (2001), and Syphard
Figure 2.1: Post-fire regeneration strategy is determined by the extent to which seed germination is partitioned between non-fire years and fire-years and also the rate of post-fire resprouting. The facultative seeder strategy can indicate a species with high rates of non-fire year dormancy or some intermediate level. The I and II indicate the approximate parameter values used for the type I and type II FS strategies we examine.
et al. (2006) all consider seedling drought, seedling shade tolerance, differences in seed dispersal, and other factors. These models are typically used to predict vegetation changes over periods of 50-500 years, and thus do not assess landscape equilibrium conditions. In the periods that are simulated these models successfully capture coexistence of several species including all three PFRS strategies at the landscape scale. Groeneveld et al. (2002) used a simpler spatially explicit model to examine the the parameters necessary to mimic natural patterns of coexistence among three shrubs in the genus Banksia. One Banksia is an OR while the other two are OS with different levels of serotiny, the specificity for post-fire seed release. Stable coexistence among species was not obtained in the simulation until dispersal, stochastic fire intervals, stochastic seedling environments, and topographic gradients were included.

A complementary approach using the simpler demographic models of two strategy systems has illustrated mechanisms for coexistence. Hilbert (1987) calculated fitness responses of OS and OR strategies using estimated demographic characteristics for each strategy. In his model the OS strategy is most fit only at intermediate fire intervals and is excluded at short fire intervals, whereas the OR strategy is tolerant of short intervals and is dominant at long intervals. Recent model have incorporated local and regional processes to examine the role of dispersal in OS/OR or OS/FS systems (Miller and Chesson 2009, Higgins et al. 2008, respectively). Miller and Chesson (2009) found coexistence between OS and OR strategies was dependent upon high rates of locally retained seeds and intermediate local fire probability. Higgins et al. (2008) also found OS and FS strategies coexisted at a wider range of parameters when dispersal was local, though local dispersal was not a prerequisite for coexistence.

Landscape process simulations that incorporate seedling responses to shade, drought, and other environmental conditions important to plants do a reasonable job of matching the patterns of species coexistence observed in nature. However, because of their complexity it is difficult to infer mechanisms of species coexistence as multiple factors could be at work. Furthermore they are difficult to accurately parametrize which may lead to incorrect inference regarding model sensitivity or results. Demographic models, on the other hand, are more appropriate for understanding the importance of a single mechanism or process. While recent work has taken this approach, existing models have focused on only two PFRS at a time.

The simulations presented here consider the dynamics of each pairwise interaction among the fire persisting strategies (OS, OR, and FS) and for the first time, the three way interaction in a common framework. We explore similarities and differences between the sets of pairwise strategies and examine how they form a composite when all three strategies are considered together. In particular we focus on the importance of fire interval length and stochasticity. The expectation is that as the variance in fire
frequency increases obligate resprouters are favored; resprouting species are buffered against very short fire return intervals, and also recruit during long fire-free intervals. By applying the same model to all three strategies we gain insight into the different dynamics of pairwise coexistence and the minimum conditions required for all three strategies to coexist.

2.2 Model Description

We used a numerical simulation model to explore demographic dynamics in three PFRS strategies. All strategies are simulated at the same time and the proportion of strategy \( j \) in the landscape is dependent on its demographic parameters, in a lottery competition with other strategies, and the environmental conditions. In lottery competition the amount of available space captured by a strategy is proportional to its seed bank size and germination rate for the current environmental state. There are two possible environmental states: fire year and non-fire year. For each strategy the proportion of the landscape it occupies and its seed bank size are tracked and simulated year by year, with a varying number of non-fire years preceding a fire year.

In the case that the population of strategy \( j \) has no seed bank or zero germination its size \( N \) can only decline from one year to the next following

\[
N_{j(t+1)} = N_{j(t)}(1 - \delta_j),
\]

where \( \delta \) is annual non-fire mortality. In the more usual case where a seed bank is present, the proportion of available landscape captured by that seed bank when it germinates is determined by weighted lottery competition.

\[
\frac{S_j G_j}{\sum_l S_l G_l}
\]

(2.1)

where \( S \) is the seed bank size and \( G \) the non-fire year germination rate. Thus the proportion of landscape captured by strategy \( j \) is the product of strategy specific germination rate \( G_j \) and seed bank size \( S_j \) over the cumulative germination rates and seed banks of all strategies. Available space for which competition occurs is calculated as the landscape proportion unoccupied due to annual non-fire mortality \( \sum_l N_l \delta_l \). Combining this with Equation 2.1 we get the proportion of available space captured by strategy \( j \) and the total proportion at the next time step \( t+1 \) in a non-fire year can be calculated as

\[
N_{j(t+1)} = \sum_l N_{l(t)} \delta_l \frac{S_j G_j}{\sum_l S_l G_l} + N_{j(t)}(1 - \delta_j)
\]

(2.2)
The seed bank for each strategy is calculated by incrementing the current seed bank with a strategy specific reproduction rate $R_j$ multiplied by the population size.

$$S_{j(t+1)} = N_j R_j + (S_{j(t)}(1 - G_j))$$  \hspace{1cm} (2.3)

During a fire year plant mortality and seed germination differ from non-fire year values, most notably for obligate seeding species which experience high mortality and released dormancy for their seeds. This is incorporated by replacing the mortality term with $1 - P_j$ where $P$ is the fire survival (resprouting) rate. A specific fire year germination rate $F$ is used, but otherwise the equation is the same as Equation 2.2. All fires are assumed to be of equal intensity. The resprouting and germination rates are held constant for each simulation.

$$N_{j(t+1)} = \sum_l N_{l(t)}(1 - P_l) \frac{S_j F_j}{\sum_l S_l F_l} + N_{j(t)} P_j$$  \hspace{1cm} (2.4)

We also assume that plants do not produce seeds during a fire year, so the seed bank declines according to its germination rate.

$$S_{j(t+1)} = S_{j(t)}(1 - F_j)$$  \hspace{1cm} (2.5)

Table 2.2 lists the default parameter values for each strategy. In this manuscript we use a strict parameter set for each strategy, e.g. the OS strategy, has no ability to resprout and none of its seeds germinate between fires. However, we investigate the dynamics of two different types of facultative seeder, one where there is no between fire recruitment (type I) and another where germination is divided between both non-fire years and post-fire (type II). For simplicity we do not model a juvenile stage for new recruits so all individuals regardless of age contribute equally to reproduction.

### 2.3 Results

**Obligate seeders and obligate resprouters**

The simplest and most common strategy combination studied is OS and OR (e.g. Hilbert 1987, Miller and Chesson 2009). In the strict definition OS have no inter-fire germination and no adult fire survival. OR, on the other hand, have no post-fire seed germination. Because the non-fire germination rate for OS is 0 the population growth described in Equation 2.2 simplifies to...
Table 2.1: The percent of woody taxa in four Mediterranean-climate region that are obligate resprouters (OR), obligate seeders (OS), facultative seeders (FS), or opportunists (OP). Recreated from Pausas et al. (2004).

<table>
<thead>
<tr>
<th>Region</th>
<th>Post-fire strategy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OR</td>
</tr>
<tr>
<td>Australia</td>
<td>4</td>
</tr>
<tr>
<td>Mediterranean basin</td>
<td>57.5</td>
</tr>
<tr>
<td>California</td>
<td>51</td>
</tr>
<tr>
<td>South Africa</td>
<td>7</td>
</tr>
</tbody>
</table>

Table 2.2: Default simulation parameters for each strategy. In all simulations the strategies were initiated with equal $S$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>OS</th>
<th>OR</th>
<th>FS (Type I)</th>
<th>FS (Type II)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R$</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>$G$</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0.95</td>
</tr>
<tr>
<td>$\delta$</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>$P$</td>
<td>0</td>
<td>0.95</td>
<td>0.70</td>
<td>0.5</td>
</tr>
<tr>
<td>$F$</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Fire interval: 30
Fire cycles: 50,000
\[ N_{S(t+1)} = N_{S(t)}(1 - \delta_S) \]  
(2.6)

for obligate seeders and

\[ N_{R(t+1)} = N_{S(t)}\delta_S + N_{R(t)} \]  
(2.7)

for obligate resprouters. Likewise as there is no post-fire germination for OR, OS get 100% of the available space so the fire year population growth described by Equation 2.4 simplifies to

\[ N_{S(t+1)} = N_{R(t)}(1 - P_R) + N_{S(t)} \]  
(2.8)

for obligate seeders and

\[ N_{R(t+1)} = N_{R(t)}P_R \]  
(2.9)

for obligate resprouters. The seed bank dynamics described by Equation 2.3, 2.5 are unimportant in this special case because no lottery competition occurs and neither limiting reproduction nor dispersal are incorporated in these simulations. The resulting pattern at equilibrium is that OS proportion declines steadily between fires and rebounds in the fire year (see Figure 2.2).

It is clear from Equations 2.7-2.9 that during a non-fire year the OR capture all the space resulting from OS mortality, whereas during a fire year the OS strategy captures all space where OR does not resprout. Thus the populations will be in equilibrium when the cumulative mortality of OS during the non-fire interval equals the proportion of OR that do not resprout

\[ N_{S} - N_{S}(1 - \delta_S)^y = N_{R}(1 - P_R) \]  
(2.10)

where \( y \) is the length of the non-fire interval in years. Solving for the OS proportion we get

\[ N_{S} = \frac{P_R - 1}{(1 - \delta_S)^y + P_R - 2} \]  
(2.11)

and \( N_{R} = 1 - N_{S} \). This solution conforms closely to simulated results. The OS strategy is more successful at low \( \delta_S \), low \( P_R \), and shorter fire intervals (see Figure 2.3 and upper panel Figure 2.4).
Figure 2.2: Three fire cycles of a seeder and a resprouter at their default parameter values and a fire interval of 30 years. An initial 4000 fire cycles were simulated before sampling. At the end of each fire cycle the state before and after the fire year are plotted.

Figure 2.3: Simulated landscape proportions for an OS and OR at default \( \delta_S \) and \( P_R \) values over a range of fire interval lengths.
Figure 2.4: Simulations of OS (upper panel) and Type II FS (lower panel) competition with OR. OS and Type II FS annual mortality are varied against OR post-fire resprouting at three fire intervals. Tile colors for parameter values resulting in fixation of one PFRS are indicated by the legend. Intermediate colors indicate coexistence of strategies. Strips above each plot indicate the length of the fire interval in years. All other parameters were set to the default parameter set.
Facultative seeders

Facultative seeders and obligate resprouters

For a landscape starting with only the OR and type I FS strategies, the outcome is the same as the OS/OR landscape. In that case the OS strategy is the only one with positive population growth during the fire year, when it captures all the available empty space. In the FS/OR case the same pattern occurs where the FS strategy proportion declines in between fires, but takes all available space in a fire year. Substituting FS specific parameters into Equation 2.11 the proportions can be modeled as above. The $P_F$ parameter is unimportant in this case, because regardless of the resprouting rate the FS strategy takes all free space available in the fire year.

Models with type II FS and OR, or either type of FS strategy and OS, do not simplify as the above examples. This is because lottery competition occurs requiring the incorporation of the seed bank dynamics (Equations 2.3 and/or 2.5), which are dependent on the population sizes of each strategy, the resulting equations do not simplify in a useful fashion. Instead, for these comparisons we rely on simulations to understand the dynamics.

When in competition with OR alone type II FS has the same success in the fire year that the type I FS has. Even though the type II strategy has a smaller seed bank relative to the type I strategy due to non-fire year germination, it is assumed that it still saturates the available sites, for which the OR strategy does not compete. Furthermore, owing to non-fire year germination the type II strategy competes with the OR strategy when it is recruiting, resulting in greater success of the type II strategy compared to the type I FS and OS strategies (compare upper and lower panels Figure 2.4).

Facultative seeders and obligate seeders

Obligate seeders and type I facultative seeders cannot coexist because both strategies only recruit following a fire. The available space is divided by the proportion of the total seed bank that each respective strategy holds. Each fire cycle the strategy with the larger seed bank takes a larger proportion of the landscape, resulting in a positive feedback, as a larger proportion of the landscape means greater reproduction and a still larger proportion of the seed bank. After several fire cycles, as simulated here, one strategy goes to fixation (see Figure 2.5). Because resprouting after a fire gives the FS strategy an advantage during the critical post-fire stage, an OS must have either higher reproductive rate or lower non-fire annual mortality to outcompete FS (see Figure 2.6).

The type II FS and OS strategies can coexist because non-fire year germination allows the FS populations to recruit when the OS strategy cannot. In cases where the FS
Figure 2.5: OS proportion when simulated with FS as a function of fire interval after a range of fire cycles. At longer fire intervals the OS approaches an asymptote at the threshold fire interval for a given FS annual mortality (0.99 in this simulation) that separates intervals at which OS goes to fixation from those where it goes extinct.
Figure 2.6: OS and FS interactions at varying levels of OS mortality and yield against fire interval. Legend indicates the tile color when occupied entirely by one PFRS.
seed bank exceeds that of OS in the fire-year, either because of higher FS reproduction or lower mortality, the OS strategy will be excluded.

Three strategy interaction

We have been unable to find a region of parameter space where three strategies coexist at the same time in this model. In the case of OS, OR, and type I FS this is because type I FS and OS cannot coexist as described above. Even when type II FS is substituted only two strategies can coexist at a given set of parameters. FS either is out competed in both the non-fire and fire year by the obligate strategies resulting in it being excluded, or FS excludes one of the two obligate strategies. The dominance of strategies changes across parameter space (see Figure 2.7), and the outcome of simulations with all three strategies is a composite of the various two strategy simulations.

Stochastic fire interval

The above simulations all assume a fixed fire interval which, of course, is not the case. Fire interval was randomized by drawing from a normal distribution truncated at 1 and standard deviation equal to the mean fire interval multiplied by a coefficient of variation (cv). Where there are few fire cycles stochasticity has a larger role because cycle to cycle changes are larger than at equilibrium. As the number of fire cycles increases to where strategies approach equilibrium the outcomes at a given set of parameters converges on the non-stochastic simulation (see Figure 2.8). High levels of variation in fire interval can result in one year fire cycles which exclude the OS strategy.

2.4 Discussion

This simple, one patch model captures many of the dynamics observed in more complex models. The important dynamics result from the existence of two environmental states when recruitment can occur, immediately post-fire or during non-fire years. This is analogous to the the temporal storage effect described by Chesson (1985), Pacala (1997). For a PFRS to survive it must be competitively superior during one of these periods. As a strategy becomes more abundant, losses during the unfavorable environmental state exceed gains made during the favorable state. This phenomena stabilizes the proportion of the landscape a strategy can hold and allows invasion even when rare (Chesson 2000). Contrary to expectation, stochastic fire intervals do not ex-
Figure 2.7: Three strategy simulations are a composite of two strategy interactions. Each panel shows the results simulations across varying the non-fire year mortality for both the FS and OS strategies. Starting conditions are indicated by the panel above each plot, and the simulations were initiated with equal sized seed banks for all strategies included. Legend indicates the tile color when occupied entirely by one PFRS, color gradations indicate regions of strategy coexistence.
Figure 2.8: The number of fire cycles simulated and the variability the fire interval effect model outcomes. Even low variability can cause very short fire interval that exclude OS if run for many fire cycles. All parameters, aside from number of fire cycles and fire interval coefficient of variation (cv) are the same as the lower right panel in Figure 2.7. The fire interval was drawn every cycle for a normal distribution truncated at 1 with a mean of 30 years and a cv 0.1-0.3. The plot tiles indicate the final state of the simulation, and the legend indicates the extreme possibilities for each tile. The strip above each panel indicates the number of fire cycles and the cv used in the simulation.
pand the parameter space supporting PFRS coexistence, but can lead to OS extinction when fire interval variance is high.

OS and OR competition simulations resulted in patterns similar to Hilbert (1987), except at short fire intervals, where his model excluded OS plants (see upper panel Figure 2.4). This behavior occurs because Hilbert assigns a minimum age of reproduction for seedlings that is older than for resprouts; if a fire occurs before that period those plants have no seed bank and are excluded. Empirical evidence supports the finding that short fire interval can result in immediate local extirpation of OS species (Zedler et al. 1983, Jacobsen et al. 2004). For simplicity we do not include an explicit juvenile stage in our model. However, a similar pattern is still observed in simulations of OS and FS (see Figure 2.6) where the OS strategy is excluded at short intervals even at high FS non-fire mortality. The multi-patch model of OS and OR strategies, presented by Miller and Chesson (2009), indicates coexistence would not occur in the absence of stochastic disturbance and was most likely at intermediate fire frequencies. In contrast our finding suggest that patterns of coexistence are largely unaffected by stochasticity (except as discussed above) and more dependent on parameters other than fire interval for OS/OR simulations. In the upper panel of Figure 2.4, the parameter values where coexistence occurs shift as interval changes, but the relative breadth of the coexistence region is consistent. The lower panel shows a different pattern in which longer fire intervals lead to a shorter gradient between the FS and OR dominated simulations.

The Higgins et al. (2008) model of the OS and type I FS strategies indicates a region of coexistence dependent on OS fecundity and FS resprouting rate. The parameter space supporting coexistence was larger when local dispersal was incorporated, but not dependent upon it. A comparable result was only found in our model with type II FS, but not type I (results not shown). This may be due to different parameterizations of dispersal in the respective models, in particular that our model assumes dispersal is global and uniform. Another possibility is that the Higgins et al. (2008) model does not approach equilibrium, as they simulated only 50 fire cycles. Our simulations suggest doesn’t yet approach equilibrium for many parameters sets.

Unlike the multi-factor landscape models, we did not find regions of long-term coexistence for three PFRS. Again this could be due to the much longer time period that we are able to simulate, which increases the probability that one strategy will be eliminated. Another explanation is that these models incorporate several other environmental factors, whereas our model has only two states for seedling recruitment, post-fire or between fires. Strong resprouting may allow a population to remain through several fire cycles even if its seedlings are not competitive, but eventually it will be excluded. This explains why no coexistence was observed between OS and type I FS or
between two strategies that both recruit solely during the fire-free interval (results not show). The multi-factor models (e.g. Pausas 1999, Syphard et al. 2006) include multiple dimensions for specialization which allow otherwise similar strategies to co-exist (Hutchinson 1959). There is ample evidence to suggest that gradients in water and light availability do exist and are important in structuring communities (Davis and Mooney 1986, Ackerly et al. 2002, Cornwell and Ackerly 2009, but see Lamont and Bergl 1991). However, other aspects of disturbance regimes alone may accommodate multiple PFRS.

Four key features of disturbance regimes are the frequency, predictability, areal extent, and magnitude of disturbance (Sousa 1984). Frequency and predictability are explicitly included in our model and most of the models discussed here. We assume that the areal extent of fires encompasses entire local communities (Keeley et al. 1999) and do not attempt to model regional patterns. However, patch dynamics are commonly incorporated into other models and at regional scales may be important (Minnich and Chou 1997). Fire magnitude, or intensity, has received less attention in models of strategy coexistence. Syphard et al. (2006) vary intensity by making it dependent on stand age, but the effects of intensity variation are difficult to separate from other factors. Miller and Chesson (2009) hint in their discussion that simulations incorporating intensity as a parameter support coexistence among three strategies, but do not describe those simulations. Empirical evidence suggests that variation in fire intensity can have important impacts on both post-fire seeding and resprouting rates within a PFRS (Moreno and Oechel 1993, Schwilk 2003). Additionally, PFRS may differ in fire intensities response in a predictably (Reyes and Casal 2008).

Modifying our model so resprouting success was dependent on stand age as proxy for intensity (see Minnich and Chou 1997), did not result in three PFRS coexistence. This specific approach doesn't significantly change the model outcome at fixed fire intervals because the end result is the same resprouting rate every fire cycle as the vegetation is always the same age.

Coexistence among PFRS occurs because two different environmental states occur resulting in a temporal storage effect (sensu Chesson 1985). Post-fire seeding species survive a competitively inferior stage by directing seed germination to the post-fire environment, whereas post-fire resprouters survive that unfavorable period below ground. Because only two temporal states exist in our model, only two PFRS can be supported (Pacala 1997). Modeling the widely observed pattern of three PRFS coexistence requires models that consider additional factors such as competitive hierarchies or gradients in fire regimes characteristics like intensity.
Chapter Three

Rapid quantification of flammability traits in woody plants

Abstract

Accurate estimation of plant biomass and fuel structure in shrublands typically requires time consuming destructive methods, posing a challenge for comparative studies of flammability and large scale fuel estimation. We propose a non-destructive method for rapidly estimating various canopy fuel characteristics and above ground biomass in shrubs. We recorded the diameter of each twig touching a pole that was placed vertically through the upper shrub canopy to the ground multiple times. We then harvested the biomass within the cylinder surrounding those regions and sorted it by size and whether it was living or dead. The cumulative summed diameter (log transformed) of twigs touched by the poles provides an accurate estimate of the log biomass contained within that cylinder. Comparison of AIC scores for models predicting dry mass based on contact measurements indicates that models incorporating twig diameter are better predictors of total biomass than those which do not. In addition, the pole-contact technique is effective at capturing plant traits of interest for comparing species functional strategies, such as the distribution of twig diameters and dead branch retention.

3.1 Introduction

Traits that contribute to plant flammability have long been recognized (Brown 1970, Philpot 1970) and researchers continue to suggest more potential traits (Dimitrakopoulos and Panov 2001, Schwilk 2003). Comparative studies of these flamma-
bility traits are becoming increasingly common as researchers try to elucidate how community ecology and evolution influence landscape flammability (Montgomery 1976, Dimitrakopoulos and Panov 2001, Schwikl and Ackerly 2001, Cowan and Ackerly 2010). Yet, methods for assessing most plant flammability traits are not standardized (see Cornelissen et al. 2003) or calibrated to commonly used metrics, like fuel load (g/m²). While methods for assessing chemical flammability characteristics have been established (Philpot 1969, Montgomery 1976, Etlinger and Beall 2004), corresponding methods for comparing the physical aspects of whole plant flammability are less developed. Typically these traits require collecting entire plants (Countryman and Philpot 1970) or rely on metrics that require species specific calibration (Murray and Jacobson 1982, Pearcy and Yang 1996). Better information about fuel structure may also improve fire behavior model accuracy (Rothermel 1972). We present a method for rapidly assessing fuel load and physical flammability traits, such as proportions of fine or dead fuels, and describe the method's effectiveness in four chaparral species.

Two widely used non-destructive methods for estimating fuel structure and loads are dimension analysis (Murray and Jacobson 1982), and point intercept (Jonasson 1988, Clark et al. 2008). Dimension analysis relies on allometric relationships between plant size and biomass, whereas point intercept methods estimate biomass based on counts of branches intersecting a vertical line to the ground from a particular point. Both methods can provide accurate estimates of total biomass. However, for measurements of fuel elements like fine fuels and dead branches both methods require species and/or site specific calibration.

Planar intercept transects are an effective method for cross site and species estimates of coarse woody debris also known as “dead and down” fuels (van Wagner 1968, Brown 1974). These transects are useful, because they provide estimates of not only the mass, but also the distribution of fuel sizes. The method used most commonly in the United States is the one described by Brown (1974). In this method all dead material intersecting a vertical plane extending for 6 feet (1.83 m) from sampling point is tallied by size class. Larger size classes (>25 mm) are tallied up to 50 feet (15.24 m) from the sampling point. The height of the fuel above the ground and the depth of the duff layer are also measured along the sampling plane. However, Brown’s transect method is intended for quantifying dead material on the forest floor. It is not well suited to shrub environments where much of the dead fuels are retained in plant canopies and live fuels are important, or where species specific information is desired.

The methodology we describe is an elaboration of the point intercept method that applies concepts of Brown’s transects. By recording the fuel status (living or dead) and size at each intercept point, fuel structure and load of shrub canopies is better estimated. In accordance with our methodology we refer to this type of point-intercept
as the pole-contact method. We compare the results of species and site analyses done with both destructive sampling and pole-contact methods to assess the value of pole-contact for comparative studies (see Cowan and Ackerly 2010).

### 3.2 Methods

#### Site description

Jasper Ridge Biological Preserve (JRBP) located on 641 ha of the Stanford University campus, in the foothills of the Santa Cruz mountains, has received an average annual rainfall of 652 millimeters between 1975 and 2004. The majority of rain comes during the cool winter months, while summers are hot and dry. The preserve is dominated by mediterranean-type chaparral shrublands, evergreen oak woodlands and annual grasslands. The woodlands near the JRBP chaparral have historically experienced regular wildfires (Stephens and Fry 2005); however, the current chaparral stands have not burned for at least 100 years (P. Cohen, personal communication).

#### Sampling method

We established five plots in chaparral shrublands selected with the following criteria: each plot must contain at least one individual of all focal species within 10 m of each other and all study plants must be more than 5 m from any roads or trails. The focal species were the post fire seeders *Adenostoma fasciculatum* and *Ceanothus cuneatus* and the obligate resprouters *Heteromeles arbutifolia* and *Prunus ilicifolia*.

The longest axis of the plant canopy, measured as the length and the width, was recorded as the furthest extent of the plant perpendicular to this axis. The two dimensional canopy cover of the individual was estimated as an ellipse, and a computer script was then used to pick a random location in the canopy with respect to the southwest corner of the plant, no less than 15 cm from the edge (see Figure 3.1). This location served as the center point for two types of measurements, a non-destructive pole-contact measurement and a complete vertical sampling of a 15 cm radius cylinder. If, in the field, more than half of the cylinder diameter fell outside the individual plant canopy (due to departure of the canopy from the ellipse shape) another random canopy location using the same criterion was selected.

To quantify how well our pole-contact measure estimated the true biomass and structure of the canopy we sampled canopy vegetation within a single 15 cm radius vertical cylinder. Considering only tissues from the focal individual, one cylinder (7
pole measurements, one biomass sample) was measured from each individual (n = 20 plants). To ensure adequate sampling of the vegetation inside the cylinder seven pole measurements were made, one in the middle, and six more at a 10 cm radius from that point, spaced at 60° angles from one another (see Figure 3.1). After all pole measurements were made, all tissue from that individual within the cylinder was harvested to measure actual biomass.

**Pole-contact measurements**

Pole-contact measurements were made by placing a piece of steel electrical conduit 18 mm in diameter vertically into the plant canopy. The diameter of every twig that touched the pole was measured using digital calipers from the ground to the top of the canopy. Each twig was scored as either alive, or if brittle with no green tissue distal of the contact point, dead. If a single branch touched the pole multiple times, or touched the pole at two or more of the seven placements, each contact was recorded as an independent measurement.

**Destructive biomass measurements**

After pole-contact measurements were made, all vegetation from the focal individual within 15 cm of the center point was collected by raising an aluminum ring through the canopy and clipping all plant material. Samples were then sorted into either living or dead using the criterion above and further divided into five different diameter classes using calipers, 0–2.5 mm, 2.5–6 mm, 6–25 mm, 25–70 mm, and greater than 70 mm. Branch segments were subdivided until the resulting segments fell entirely into one size class. The largest two sizes classes were combined and leaves, fruits, and flowers were excluded for the purposes of these analyses. Leaves, fruits and flowers were excluded because it is difficult to formulate cross-species count-to-mass relationships for these tissues and their quantities vary seasonally. Once separated, samples were dried at 60°C for no less than 48 hours, then weighed.

**Statistical analyses**

Analysis of covariance (ANCOVA) as implemented in R was used to test the relationship between pole-contact and biomass measures and to test for differences among species in the slopes and intercepts of these relationships (R Development Core Team 2010). To compare different models of how well twigs diameters predict dry mass
Figure 3.1: The shrub canopy (solid line, seen from above) was estimated as an ellipse (dashed line), based on the maximum width and length of the plant (straight solid lines). The dotted lines indicate the southwest corner of the individual from which the sampling coordinates were measured. At these coordinates we located the pole-contact points (dots) and the destructive sampling (dashed circle) that surrounded them.
we calculated the Akaike Information Criterion (AIC) for each of five models (see Table 3.2). We investigated two general forms of models, illustrated by equations 3.1 and 3.2 where $\beta_0$ and $b$ indicate the intercept and error term respectively; $\beta$ and $X$ 1-4 are the model coefficients and trait means respectively. The equations describe a simplified model where all size classes were considered together as a single sample $X_{1}$ (see Equation 3.1, Table 3.2 models A, B, and C) and a full model where each size class ($X_{1-4}$) is added as a factor (see Equation 3.2, Table 3.2 models D and E). In all tests, except model A, the biomass and diameter data were summed by individual and then log plus one transformed to meet the assumptions of ANCOVA and linear regression. The log plus one transformation was used to account for cases with no diameter measurements, which sum to zero. In all analyses presented here data were summed across all height increments to produce one value per individual.

$y = \beta_0 + \beta_1 X_1 + b \quad (3.1)$

$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + b \quad (3.2)$

To assess the viability of the pole-contact method as a replacement for destructive sampling we contrast the results of analyses using either contact or destructive data. Specifically we compare total biomass between site and report nested two factor ANOVAs of total biomass, dead branch proportion, and fine fuel proportion. In each two way ANOVA the species term is nested within a post fire regeneration strategy term (seeders vs. non-seeders).

3.3 Results

A total of 140 poles were placed through the 20 plant canopies resulting in 536 touches averaging 26.8 contacts per plant (range 6–65). The number of contacts was distributed evenly among species (ANOVA $F = 0.9$, $p = 0.46$), but skewed heavily toward the size classes 6 mm and smaller. Destructive sampling yielded a total of 7,601 g of plant material over half of which was from the largest size class, 25+ mm (see Chapter 4, for details on the destructive samples). Fuel loads ranged from 963–8189 g/m$^2$, similar to other reported chaparral and Mediterranean shrubland fuel loads (see Table 4.3).

The ANCOVA of log sum diameter and log individual total biomass with species as a factor shows a significant relationship between diameter and mass ($F = 165.68$, $p < 0.001$) as well as an effect of species ($F = 3.78$, $p = 0.04$). The ANCOVA also indicates
Figure 3.2: Regression of log dry mass by log sum diameter for each of A. fasciculatum (panel a), C. cuneatus (panel b), H. arbutifolia (panel c), and P. ilicifolia (panel d) individual species regressions layered on one another in the same panel (panel f) and the pooled regression (panel e). Dashed lines indicate 95% confidence intervals.
a trend in the interaction between species identity and log twig diameter \((F = 2.94, p = 0.08)\) reflecting nearly-significant differences in slopes. Correlations within species were also robust, \((r^2 = 0.91, 0.95, 0.98, 0.97)\) for \(A. fasciculatum, C. cuneatus, H. arbutifolia,\) and \(P. ilicifolia\) respectively, see also Figure 3.2).

Across all species and size classes, log diameter was a good predictor of log dry biomass (see Figure 3.2). We also investigated the effectiveness of predicting biomass in a particular size class using the diameter measures or counts at that size class (see Table 3.1). Correlations at the smallest size class were strong \((r^2 = 0.7)\) regardless of the measure used. However, as the number of contacts decreases so does the quality of the fit; in particular, diameter predicted dry mass poorly for size classes 2.5–25 mm (results not shown).

Among the models of total biomass pole-contact measurements all had similar \(r^2\) values, except for model C which does not incorporate diameters (see Table 3.2). Model C also had a high AIC score, indicating a poor fit to the data, as did model A, the only model where biomass measurements are not log transformed. The model that fit the data best was D, which has a separate parameter for each size class.

In most of the comparative analyses of pole-contact data, the statistical outcome was the same as analyses of destructive samples (see Table 3.3 and Cowan and Ackery 2010). Specifically, results that were significant in the ANOVAs using destructive data were also significant using pole-contact data, with the exception of the fine fuel proportion analysis. Fine fuel proportion differed significantly between strategies and among species in the destructive sampling data; however, those patterns were not observed in the pole-contact data (see Table 3.1).

### 3.4 Discussion

For short (<10 m) multi-stemmed vegetation, like chaparral, the pole-contact method is much faster and easier to employ than destructive techniques. Across species and within species the log of the twig diameters summed together was a reasonable predictor of the log dry mass recovered from the corresponding destructive sample of the individual (see Figure 3.2). However, we did detect a significant effect of species on the intercept of the relationship and a trend in the slope of the relationship. This may be caused by the sparse biomass in \(P. ilicifolia\) compared to the other species (340 g total compared to 1572–2894 g). Comparison of nested models using ANOVA did not indicate that a model with a “\(P. ilicifolia\) factor” was significantly better (results not shown). However, when \(P. ilicifolia\) was excluded from the ANCOVA there was no longer a significant species effect nor a trend in the species by diameter interaction.
Table 3.1: Species means ± standard deviation for both pole-contact (PC) and destructive (D) sampling types. Dead fraction refers to the proportion of the total biomass that was classified as dead. Similarly fine fraction is the proportion smaller than 6 mm in diameter. Species columns are denoted by the first letter of the genus, *A. fasciculatum*, *C. cuneatus*, *H. arbutifolia*, and *P. ilicifolia*, respectively. The 'seeder' and 'species' columns are the ANOVA p-values, in all cases the species term is nested inside the seeder term.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Type</th>
<th>A</th>
<th>C</th>
<th>H</th>
<th>P</th>
<th>p-value Seeder</th>
<th>p-value Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total (log g)</td>
<td>D</td>
<td>5.31±1.09</td>
<td>5.55±1.07</td>
<td>5.34±1.84</td>
<td>3.95±0.933</td>
<td>0.192</td>
<td>0.250</td>
</tr>
<tr>
<td>Total (log mm)</td>
<td>PC</td>
<td>4.75±0.816</td>
<td>4.98±0.483</td>
<td>4.47±1.16</td>
<td>4.09±0.999</td>
<td>0.167</td>
<td>0.746</td>
</tr>
<tr>
<td>Dead fraction</td>
<td>D</td>
<td>0.685±0.218</td>
<td>0.67±0.312</td>
<td>0.193±0.259</td>
<td>0.214±0.257</td>
<td>0.001</td>
<td>0.989</td>
</tr>
<tr>
<td>Dead fraction</td>
<td>PC</td>
<td>0.612±0.254</td>
<td>0.644±0.339</td>
<td>0.245±0.145</td>
<td>0.22±0.277</td>
<td>0.004</td>
<td>0.970</td>
</tr>
<tr>
<td>Fine fraction</td>
<td>D</td>
<td>0.544±0.274</td>
<td>0.57±0.355</td>
<td>0.549±0.411</td>
<td>1.27±0.358</td>
<td>0.040</td>
<td>0.018</td>
</tr>
<tr>
<td>Fine fraction</td>
<td>PC</td>
<td>0.417±0.271</td>
<td>0.383±0.301</td>
<td>0.649±0.418</td>
<td>0.69±0.215</td>
<td>0.070</td>
<td>0.964</td>
</tr>
</tbody>
</table>
Table 3.2: Akaike Information Criterion and $r^2$ for models of chaparral dry mass. Letter indicates each model as described in the methods. Regression terms indicated by the ‘dependent’ and ‘independent’ columns. Data were natural logged after being summed by individual (or size class, if indicated).

<table>
<thead>
<tr>
<th>Model</th>
<th>Dependent</th>
<th>Independent</th>
<th>$r^2$</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>dry</td>
<td>dia</td>
<td>0.85</td>
<td>277</td>
</tr>
<tr>
<td>B</td>
<td>log dry</td>
<td>log dia</td>
<td>0.80</td>
<td>34.5</td>
</tr>
<tr>
<td>C</td>
<td>log dry</td>
<td>number of contacts</td>
<td>0.01</td>
<td>67.1</td>
</tr>
<tr>
<td>D</td>
<td>log dry</td>
<td>log of each size class</td>
<td>0.86</td>
<td>33.5</td>
</tr>
<tr>
<td>E</td>
<td>log dry</td>
<td>number of each size class</td>
<td>0.83</td>
<td>37.9</td>
</tr>
</tbody>
</table>

Table 3.3: Comparison of destructive and pole-contact methods for comparative analysis. The F and p values from ANOVA of strategy (two species nested within each strategy) or sites (first comparison only) for four fuel characteristics. Tests were repeated with data from both destructive (D) and pole-contact (P) samples from the same individuals.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Response</th>
<th>Method</th>
<th>F value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>total biomass</td>
<td>D</td>
<td>0.43</td>
<td>0.785</td>
</tr>
<tr>
<td></td>
<td>total biomass</td>
<td>P</td>
<td>0.62</td>
<td>0.653</td>
</tr>
<tr>
<td>Strategy</td>
<td>total biomass</td>
<td>D</td>
<td>1.86</td>
<td>0.192</td>
</tr>
<tr>
<td></td>
<td>total biomass</td>
<td>P</td>
<td>2.10</td>
<td>0.167</td>
</tr>
<tr>
<td></td>
<td>Proportion dead</td>
<td>D</td>
<td>16.19</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Proportion dead</td>
<td>P</td>
<td>11.31</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Proportion &lt; 6mm</td>
<td>D</td>
<td>5.02</td>
<td>0.040</td>
</tr>
<tr>
<td></td>
<td>Proportion &lt; 6mm</td>
<td>P</td>
<td>3.78</td>
<td>0.070</td>
</tr>
</tbody>
</table>
This does suggest that if high accuracy fuel load estimates within species are needed, specific models should be developed. It is also unknown how site specific variation may affect the relationship between twig mass and diameter, further study on these factors is needed.

Incorporating twig diameter into our point intercept model of overall biomass improved the regression fit and model AIC score. This is because large branches have a disproportionate effect on the overall biomass. Across all samples only 16 branches greater than 25 mm were contacted by the pole, yet branches in those size classes made up more than half of the dried material (3,781 g out of 7,601 g total). The best performing models, B and D, incorporate all of the individual branch diameters (see Table 3.2). Within size classes, the diameter measurements themselves were less important and the fits less robust (see Table 3.1). Because the data are already binned by size class the larger twigs and branches no longer have a disproportionate effect.

Despite the differences of the diameter–mass relationships among species the pole-contact measurements may be useful without being converted into mass values and this would reduce the necessity for calibrating different species. This was assessed using the raw pole-contact measurements, from the same canopy locations, to recalculate the comparisons of Cowan and Ackerly (2010). Both measurements resulted in identical conclusions for site and strategy differences in total biomass and strategy difference is proportion of dead aerial fuels. For these plant characteristics the pole-contact method is a faster less destructive alternative to plant harvesting. A reduction in power was found in comparisons of fine fuel proportion, which would be offset by the larger samples sizes possible with pole-contact methods.

The pole-contact method has promise for easing and speeding chaparral fuel load and structure estimates. It will be especially useful in comparative studies where detailed fuel structure is need and comparison of several sites and/or species are desired.
Abstract

Fire behavior is strongly influenced by fuel load and structure; however, efforts to describe fuel patterns have largely ignored differences among species or post-fire regeneration strategies. In California chaparral, evergreen shrubs can be grouped into three post-fire regeneration strategies that correlate with a wide variety of physiological and demographic characteristics including seasonal water status and the timing of reproduction in response to fire. To test if regeneration strategy is also associated with flammability, we compared the fuel loads and structure of two post-fire seeders, Adenostoma fasciculatum and Ceanothus cuneatus, and two obligate resprouters, Heteromeles arbutifolia and Prunus ilicifolia. Species and post-fire regeneration strategies did not differ in total fuel per area, or bulk density. The proportion of fuels smaller than 6 mm in diameter differed among species, but not consistently with regeneration strategy. However, species with a post-fire seeding regeneration strategy had higher proportions of dead branches. We discuss how this difference could have arisen from evolutionary, demographic, or physiological processes.
4.1 Introduction

Wildfire magnitude is determined by climatic, topographic, and fuel conditions. These factors are also the basic parameters for all fire spread and risk models (Fujioka et al. 2009). Initially the fuels component of these models only differentiated between major vegetation types, such as grasslands, shrublands, conifer forests and deciduous forests (e.g., Anderson 1982). Recently research in the Mediterranean basin has shifted toward predicting landscape flammability properties, like fuel loads and structure, from species traits (Papió and Trabaud 1991, Dimitrakopoulos and Panov 2001). However, flammability research on California chaparral has focused on *Adenostoma fasciculatum* because of its dominant role throughout its range (Dell and Philpot 1965, Rundel and Parsons 1979, Schwilk 2003). The few comparative studies of chaparral flammability have been limited to leaf tissues (Montgomery 1976, Engstrom et al. 2004) or plants of horticultural interest (Etlinger and Beall 2004, Weise et al. 2005). To our knowledge no study of Mediterranean shrublands has tested for a relationship between post-fire regeneration strategy (PFRS) and plant flammability.

Post-fire regeneration strategies

Populations of woody plants persist through fire events by sprouting from protected organs, such as a lignotuber, through post-fire germination of a persistent seedbank, or both (Hanes 1971, Pausas et al. 2004). Obligate resprouters are species that rely primarily on post-fire sprouting; likewise, obligate seeders are species that rely solely on persistent seedbanks. Facultative seeders are species with both persistent seedbanks and the capacity for sprouting. These differing responses to fires lead to reproductive consequences as fire frequency changes. Because obligate resprouters typically only recruit during the fire free interval, they are favored at low fire frequencies, whereas higher frequencies favor post-fire seeders (Groeneveld et al. 2002). However, if fire intervals are too short for plants to reach reproductive age, obligate seeders can be rapidly excluded (Zedler et al. 1983, Jacobsen et al. 2004).

Mutch (1970), Bond and Midgley (1995), Kerr et al. (1999), and Schwilk and Kerr (2002) describe scenarios where plant flammability could be under positive selection in fire-prone environments. After observing that fire-prone plant assemblages, such as *Eucalyptus* forests, were resistant to invasion and that species in these areas tended to be more flammable than non-fire-prone species, Mutch (1970) hypothesized that: “Fire-dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favored development of characteristics that make them more flammable.” Critics of the Mutch hypothesis have argued that natu-
ral selection does not operate on communities, that flammability could have evolved as a side effect of other adaptations, and it would be paradoxical for a species to evolve characteristics, such as increased flammability, that would reduce individual survival and lifetime reproduction (Troumbis and Trabaud 1989, Snyder 1984). However, others have proposed models to address these critiques (Bond and Midgley 1995, Kerr et al. 1999, Schwilk and Kerr 2002). The Bond and Midgley (1995) model assumes that flammability traits are genetically linked to others traits with positive effects on fitness and increase when they do. Kerr et al. (1999) also found that invasion of flammability alleles was more stable when they were linked to other adaptations such as a fitness advantage in gap regeneration. They also suggest that “Mutch’s converse”, where the presence of flammability characters intensify selection for fire-regime adaptations in the same and other species, may be a more important process and does not require flammability traits to be directly selected for. Schwilk and Kerr (2002) relaxed the assumption of genetic linkage and showed that fire induced mortality can increase fitness by allowing a species to track environmental conditions.

Plant Flammability

Anderson (1970) describes three primary components of plant flammability: ignitability, the delay before flaming combustion; combustibility, the rapidity of consumption by fire; and sustainability, the continued burning after the igniting heat source is removed. Subsequent studies have identified both chemical and structural traits associated with ignitability (influences wildfire frequency) and combustibility (affects rate of spread and intensity) (Philpot 1970, Rundel 1981, Etlinger and Beall 2004). In turn, these components of flammability are ultimately controlled by the chemical composition, moisture content, and physical arrangement of the plants themselves. In this paper, we examine how physical arrangement, total fuels, and proportions of dead and fine fuels vary between regeneration strategies, and in relation to their expected effects on flammability.

Physical structure encompasses several facets of fuels including particle density, surface area-to-volume ratio, fuel shape, orientation, and bulk density. We use bulk density to refer to the amount of fuel in a volume of airspace (in this study, a vertical cylinder through the plant canopy). Bulk density, or the compactness of branches and leaves in space, controls the rate that oxygen can flow through the fuels as well as the heat transfer between fuel elements. In the case of litter beds, contrary to the expectation for canopy leaves, larger leaves may increase flammability by reducing overall packing of fuels, increasing airflow (Scarff and Westoby 2006).
In addition to variation in fuel structure, plants vary in the flammability of specific tissues. The high latent heat of evaporation for water means large amounts of energy are required to drive it off before most other compounds can pyrolyze. In Mediterranean-type regions, plant water status varies among PFRS and seasons, with non-resprouting species showing larger declines in minimum water potential, which may influence tissue water content, during the summer drought season (Ackerly 2004). Within individuals, plant tissues vary widely in their moisture content, from young tissues where it can exceed 200% of dry mass in Adenostoma (Countryman and Philpot 1970), to dead branches that equilibrate with atmospheric humidity (Dell and Philpot 1965 report dead fuel moistures no higher than 9% of dry mass in southern California). Because the water content in dead wood is so low, differences in the proportions of live and dead tissues have a larger effect on total plant water content than differences resulting from physiology. Thus, quantifying the degree to which species retain dead branches and leaves is critical for understanding overall fuel moisture content and flammability.

Evidence for the evolutionary coordination of post-fire reproduction with traits related to flammability has been demonstrated in the genus Pinus (Schwil and Ackerly 2001). Across all pines, including those occurring in Mediterranean climates, self-pruning (a trait that reduces flammability by limiting aerial dead fuels) is negatively correlated with serotiny, yet positively correlated with bark thickness, a fire survival trait.

In the present study, we quantify the physical structure of canopy fuels and proportion of dead biomass in two obligate resprouters, Heteromeles arbutifolia and Prunus ilicifolia; and two species with post-fire seeding, Ceanothus cuneatus, an obligate seeder, and Adenostoma fasciculatum, a facultative seeder. We test the hypothesis that species with post-fire seeding will have higher absolute amounts and proportions of dead biomass and fine fuels.

4.2 Methods

Our study took place at the Stanford University Jasper Ridge Biological Preserve (JRBP) located in the foothills of the Santa Cruz mountains. JRBP has a Mediterranean-type climate with an average annual rainfall of 652 millimeters (1973–2004), that falls primarily during the winter months. The preserve covers 481 ha and chaparral is the dominant woody vegetation. There have been no wildfires in the chaparral at JRBP for at least 100 years (P. Cohen, personal communication), though adjacent woodlands do show evidence of regular wildfires historically (Stephens and Fry 2005). Within
the chaparral shrubland we selected five sites (A–E) where we sampled one individual each of the post-fire seeders *Adenostoma fasciculatum* and *Ceanothus cuneatus* and the obligate resprouters *Heteromeles arbutifolia* and *Prunus ilicifolia* ($N = 5$ per species). Sites were selected such that all individuals were at least 5 meters from any road or trail and within 10 meters of each other. Sites had aspects ranging from southerly to westerly, but were selected to have minimal slope ($< 15\%$) to facilitate sample collection. Within a site, individuals were selected haphazardly and the length and width of each plant was measured to estimate the two dimensional canopy cover as an ellipse. A computer script was then used to pick a random location in the canopy at least 15 cm from the edge. In cases where more than half of the cylinder fell outside the individual plant canopy (owing to departure of the canopy from the ellipse shape) this point was rejected and another random canopy location selected for sampling. This location served as the center point for a complete vertical sampling of a cylinder (30 cm diameter) from the ground to the canopy top.

Sampling was accomplished by raising an aluminum ring through the canopy and clipping all plant material inside the ring. These foliage and stem samples were categorized as either living or dead and further divided into six different fuel size classes using calipers: leaves, and stems with diameters: 0–2·5 mm, 2·5–6 mm, 6–25 mm, 25–70 mm and greater than 70 mm. These size classes were chosen to correspond roughly with the recommendations of Cornelissen et al. (2003). Owing to the small number of branches sampled in the largest size class, these were combined with the 25–70 mm branches to create a 25+ mm size class. Fuels classified as leaves or smaller than 6 mm in diameter were considered fine fuels. Fruits and flowers were excluded because interpretation of their flammability is unclear and they comprised a minor contribution of the total fuels. Tissues were categorized as dead if no green leaves could be found on any distal branch. Sorted samples were dried at 60°C for no less than 48 hours and weighed (select samples were reweighed to confirm they were dry) (Cornelissen et al. 2003). In cases where no plant matter was collected for a size class and category it was treated as a zero value. Bulk density was calculated by dividing the biomass collected by the volume of the sampling cylinder.

We used analysis of variance (ANOVA) to compare the total biomass, bulk density, proportion of dead biomass, and fine fuels (total, proportional and bulk density) among PFRS. Biomass data were natural log transformed and proportion data were arcsin-root transformed to meet the assumptions of ANOVA. To facilitate comparison of PFRS, we used a nested design where species is nested within PFRS for all analyses. All statistics were conducted using the R programming environment (R Development Core Team 2010).
### 4.3 Results

A total of 7,628 g of plant material was collected, averaging 332, 483, 612, and 99 g per individual from *Adenostoma*, *Ceanothus*, *Heteromeles*, and *Prunus*, respectively. Table 4.1 shows the mean biomass for each species by fuel class. Both *Heteromeles* and *Ceanothus* are dominated by the largest fuel class; however, across all individuals, sampling for this size class was uneven (see Table 4.1). The larger size classes are notably lighter in the *Prunus* samples, reflecting the smaller size of some of the individuals sampled (data not shown) and the more tree-like stature (one primary vertical stem as opposed to multiple horizontally oriented stems) of the species. Biomass in the leaf size class also differs between strategies with more found on the larger-leaved, non-seeding *Prunus* and *Heteromeles*.

We did not find a difference in mean fuel load among the sites (ANOVA p = 0.85). Nor did the residuals of analyses excluding the site term (e.g. Table 4.2) differ among sites (ANOVA results not shown). The largest sample from a single individual was 2057 g from the *Heteromeles* at site D, whereas the smallest was 20 g from the *Prunus* at site E. Differences in total biomass, across all individuals, were driven primarily by the largest two stem size classes. Variation in these size classes, rather than variation in fine fuel mass, is the main contributor to differences in fine fuel proportion (see Table 4.2). The proportion of dead plant material ranged from 2% for the *Prunus* at site D to 95% for the *Ceanothus* at site C (species means ranged from 16% in *Prunus* to 65% in *Adenostoma*; Fig. 4.1 and Table 4.1). The variation in proportion of dead material among species was significantly different between PFRS (Table 4.2) with the proportion of dead material in the two species with post-fire seeding (*Adenostoma* and *Ceanothus*) over 3.5 times that of the obligate resprouters (Fig. 4.1).

### 4.4 Discussion

Our objective was to compare the flammability traits of shrubs with two contrasting post-fire regeneration strategies. We found significantly higher dead branch proportion in species with post-fire seeding compared to obligate resprouters. Total fuel load and bulk densities, however, did not differ between PFRS or species. The proportion of fine fuels did differ between species, but not consistently with PFRS. Non-significant results should be interpreted with caution due to the small sample size and large variance.

Rundel and Parsons (1979) found that total fuel loads for *Adenostoma* peaked after 16 years reaching 1436 g m$^{-2}$ and were no higher in individuals 60 years old,
Table 4.1: Fuel load (g/m² ± standard error for live and dead tissues across species and size classes. For several categories, particularly the larger fuel classes, no material was encountered in a replicate, these were treated as zeros for calculating the mean and standard error.

<table>
<thead>
<tr>
<th>Species</th>
<th>Fuel type</th>
<th>Leaves</th>
<th>0.0-2.5 mm</th>
<th>2.5-6.0 mm</th>
<th>6.0-25 mm</th>
<th>25+ mm</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adenostoma</td>
<td>Alive</td>
<td>208.1±113.1</td>
<td>133.6±70.1</td>
<td>182.1±89.7</td>
<td>1030.6±490.3</td>
<td>0</td>
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<tr>
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<td>Dead</td>
<td>29.4±21.8</td>
<td>189.0±81.6</td>
<td>200.1±55.0</td>
<td>2416.2±1492.1</td>
<td>297.2±297.2</td>
<td>3132±841.3</td>
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<tr>
<td>Ceanothus</td>
<td>Alive</td>
<td>145.3±29.5</td>
<td>117.7±27.5</td>
<td>249.0±61.6</td>
<td>421.1±327.1</td>
<td>3763.1±3763.1</td>
<td>4696±1864.6</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>0.3±0.2</td>
<td>204.0±88.0</td>
<td>353.9±117.6</td>
<td>497.0±222.6</td>
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<td>Heteromeles</td>
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<td>26.4±26.4</td>
<td>0</td>
<td>257±55.7</td>
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Figure 4.1: Proportion of dead biomass by species. Bars show the mean proportion of dead biomass in each of the four study species. Error bars indicate ±1 standard error.
Table 4.2: Summary of ANOVA results. For each test, species was treated as a factor nested within post-fire regeneration strategy (PFRS), totals and bulk densities were natural log-transformed while proportional data were arcsin-root transformed. Untransformed species means are shown for each trait, (A, C, H, P correspond to *Adenostoma fasciculatum*, *Ceanothus cuneatus*, *Heteromeles arbutifolia*, and *Prunus ilicifolia* respectively.) The $R^2$ column shows the total $R^2$ of the model (strategy plus the within-species nested effect). For standard errors and full p-values, see 'destructive' models in Table 3.1. The 'Strategy' column indicates the significance of the PFRS term in the model. Likewise, the 'Species' column indicates the significance of the species within PFRS nested effect. NS indicates p-value > 0.05; * indicates p-value < 0.05; *** indicates p-value < 0.001.

<table>
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<tr>
<th>Test</th>
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<th></th>
<th></th>
<th></th>
<th>$R^2$</th>
<th>Strategy</th>
<th>Species</th>
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<td>612</td>
<td>99</td>
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<td>NS</td>
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<tr>
<td>Bulk density</td>
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<td>0.18</td>
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<td>NS</td>
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<tr>
<td>Dead dry mass</td>
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<td>0.64</td>
<td>0.18</td>
<td>0.16</td>
<td></td>
<td>0.54</td>
<td>***</td>
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<td>67</td>
<td>76</td>
<td>67</td>
<td>80</td>
<td></td>
<td>0.03</td>
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<td>NS</td>
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<td>Fine fuel bulk density</td>
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<td>0.38</td>
<td>0.30</td>
<td>0.45</td>
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<td>NS</td>
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<tr>
<td>Fine fuels</td>
<td>proportion</td>
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<td>0.36</td>
<td>0.39</td>
<td>0.88</td>
<td></td>
<td>0.47</td>
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<td>*</td>
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</table>
whereas our findings were over three times greater (Table 4.3). Other reports for *Adenostoma*, also found lower proportions of dead branches, 0.32 for 21-year-old plants and 0.22–0.29 for plants aged 31–55 years (Paysen and Cohen 1990, Riggan et al. 1988) compared with the 0.33–0.93 we found. We were unable to find similar measurements for the other three species presented here, though Riggan et al. (1988) report dead branch proportions of 0.12 and 0.06 for *Ceanothus crassifolius* and *Ceanothus oliganthus*, respectively. Increased total fuel load and the proportion of dead fuels we report for *Adenostoma* and *Ceanothus cuneatus* compared to these studies may be a result of differences in site productivity. Each of the cited studies took place in southern California, and though Rundel and Parsons and Riggan et al. report similar annual rainfall, (~700 mm) the temperature regime at JRPB is likely more moderate. JRPB also differs from the above studies in the extreme age of the chaparral, as no fires have been recorded in the last century, allowing fuels to accumulate (Stephens and Fry 2005; Philippe Cohen, personal communication). Such an age-dependent pattern is supported by Papió and Trabaud (1991) who found, in five species of Mediterranean shrubs, that smaller, and presumably younger, plants had lower portions of dead material in size classes 5 mm and smaller. The average fuel loads they report are similar to our findings (Table 4.3).

The contrast among reproductive strategies in the proportion of dead branches is consistent with Schwilk and Ackerly (2001), who found that branch retention correlates with serotiny and minimum reproductive age in the genus *Pinus*. It also conforms with Mutch’s 1970 hypothesis, that selection may favor increased flammability in species with fire-cued reproduction. The difference in dead-branch retention between seeding and non-seeding shrubs may also be related to the age of JRPB chaparral. Because non-seeders tend to recruit between fire events, whereas seeders tend to recruit immediately after a fire event, non-seeding species have an uneven age structure compared to seeding species. Some non-seeding individuals may be much younger than the time since the last fire, and consequently have had less time to add biomass, or collect dead material. The *Prunus* individuals in this study, in particular, appeared to span a larger range of sizes and ages.

Differences in rooting depth may also lead to less dead fuel in obligate resprouting species. Several authors have noted that resprouting species have greater energetic investment in their roots, in the form of increased root-to-shoot ratio or greater starch content, than non-resprouting species (Pate et al. 1990, Schwilk and Ackerly 2005). This means that non-resprouters are supporting more above-ground biomass with less root biomass, perhaps making non-resprouters more prone to dieback during the summer drought season. Presumably increased allocation above ground would also lead to increased growth rate (however, see Schwilk and Ackerly 2005). The combined
Table 4.3: Mean fuel load (g/m²) by species with standard errors. Data from the present study are indicated, while other values were recalculated from additional studies as indicated. Data from Papió and Trabaud are for species in southern France, Countryman and Philpot report *Adenostoma* fuel loads in southern California, and the present study for species in northern California.

<table>
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<tr>
<th>Species</th>
<th>g/m²</th>
<th>Source</th>
</tr>
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<td>Present study</td>
</tr>
<tr>
<td><em>Ceanothus</em></td>
<td>6678±4396</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Heteromeles</em></td>
<td>8189±5298</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Prunus</em></td>
<td>963±281</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Adenostoma</em></td>
<td>2209±299</td>
<td>Countryman and Philpot (1970)</td>
</tr>
<tr>
<td><em>Cistus salviolius</em></td>
<td>1217±244</td>
<td>Papió and Trabaud (1991)</td>
</tr>
<tr>
<td><em>Genista scorpius</em></td>
<td>5250±1753</td>
<td>Papió and Trabaud (1991)</td>
</tr>
<tr>
<td><em>Phillyrea angustifolia</em></td>
<td>4583±1246</td>
<td>Papió and Trabaud (1991)</td>
</tr>
<tr>
<td><em>Pistacia lentiscus</em></td>
<td>3500±295</td>
<td>Papió and Trabaud (1991)</td>
</tr>
<tr>
<td><em>Rosmarinus officinalis</em></td>
<td>2700±507</td>
<td>Papió and Trabaud (1991)</td>
</tr>
</tbody>
</table>
effect of increased growth rate and dieback, over time, may drive differences in dead material production, as opposed to differences in retention.

Future tests of the Mutch hypothesis should focus on groups where PFRS evolved independently in multiple lineages, such as the California genera *Ceanothus* and *Arctostaphylos*, the Australia genus *Banksia* or South Africa genus *Protea* (see Bond and Midgley 2003, Pausas et al. 2004).

4.5 Conclusion

Our comparison of four co-occurring chaparral species found no differences in the total fuel load or bulk density. The proportion of fuels smaller than 6 mm in diameter differed among species but not consistently between post-fire regeneration strategies. However, the proportion of dead branches did differ significantly between strategies. Previous studies of California chaparral, focused on *Adenostoma*, have found significantly lower total and dead fuel loads; these differences are likely attributed to the old age of the chaparral at JRBP. These results suggest that post-fire regeneration strategy may be a useful contribution to a framework for predicting fuel properties.
Chapter Five

Physiology of Nicotiana tobaccum after smoke fumigation

5.1 Introduction

Studies dating back over a century have reported deleterious effects of industrial smoke on plant life (Cohen and Ruston 1909, Knight and Crocker 1913, Bakke 1914). More recently, research has focused on how plants take advantage of naturally occurring smoke as a germination cue (Keeley 1991, Baldwin et al. 1994, Flematti et al. 2004) and on how smoke affects the light response in seedlings (Nelson et al. 2010). To date comparatively little is known about the physiological effects of natural fire smoke on adult plants.

Work by Cohen and Ruston (1909), Bakke (1914), and many others (see McClelland 1913) nearly a century ago documented the effects that coal and steel plant smoke and soot have on plant health. At the time, negative impacts were readily documented, but mechanisms by which smoke caused damage were unclear (e.g. Rhine 1924). Followup research focused primarily on individual environmental pollutants, including CO₂, CO, SO₂, and NOₓ (Wilcox 1911, Bakke 1914).

Wildfire smoke, in contrast to industrial smoke, has been primarily studied for its role in germination in some species, especially those in fire prone environments such as Mediterranean-type shrublands (Keeley 1991, Flematti et al. 2004). A broad survey of coastal sage and chaparral species found germination enhanced in several families when seeds were exposed to charred wood (Keeley 1991). For at least one species with strong smoke released dormancy, NO₂, a smoke constituent, induced germination as effectively as smoke (Keeley and Fotheringham 1997). Butenolides, another group of compounds in smoke, also induce germination in several species as effectively as full
smoke (Flematti et al. 2004). This latter class of compounds also upregulates genes in *Arabidopsis thaliana* associated with seedling light responses, suggesting they may be important beyond germination (Nelson et al. 2010).

Many of these studies have been done in the context of plant responses to direct disturbance by fire. However, the spatial extent of wildfire smoke is much greater than the region of combustion alone. When inversions, still air, or topography prevent dispersion, smoke and the pollutants it contains can spread and linger for days, lengthening the temporal extent as well (Sandberg et al. 2002). Smoke from Indonesian wildfires in 1994 reportedly impacted an area greater than 3 million square km and lingered for weeks (Nichol 1997). Clinton et al. (2006) estimated that southern California fires in 2003 alone released over 80,000, 400,000, and 70,000 metric tons of particulate matter, carbon monoxide and other pollutants (including SO₂, NOₓ, and methane), respectively. Prehistoric emissions in California were likely many times these amounts (Stephens et al. 2007).

Dozens of chemicals have been detected in the smoke of wildland fires and others, notably ozone, are produced within smoke plumes via photochemistry and reactions with the atmosphere (Urbanski et al. 2009). The proportion of gases and compounds in smoke varies by fuel source and combustion efficiency (Ward and Hardy 1991). Studies of how these gases affect plant physiology exist only for a subset of these compounds. Carbon monoxide, the second most abundant chemical in smoke, has long been known to be toxic at high concentrations (Richards and MacDougal 1904). Wilks (1959), Siegel et al. (1962), Tarr et al. (1995), and others have demonstrated that plants produce small amounts of the gas as seeds, when exposed to light, and during senescence. Carbon monoxide may also induce small reductions in stomatal aperture (She and Song 2008), but other effects of low and moderate concentrations are unknown.

The physiological effects of sulfur dioxide, a significant constituent in industrial coal smoke, have been studied extensively. These effects are complex, varying among species, temperatures, and vapor pressure deficits (vpd) (Mansfield 1999, Kropff et al. 1990). In long term fumigation, low doses of SO₂ increased above-ground dry mass, but high SO₂ concentration decreased above-ground biomass in a dose dependent manner (Mansfield 1999). In *Nicotiana tabacum* SO₂ concentrations of 35–350 parts per billion (ppb) caused irreversible increases in stomatal conductance (gₛ) at low vpd, and reversibly reduced gₛ at high vpd (Black and Black 1979). Photosynthesis responses to SO₂ vary, some species showing no response and others a rapid reduction in photosynthesis that recovers quickly after exposure (Darrall 1986).

The effects of nitrogen oxide and nitrogen dioxide on plants are extensively reviewed by Darrall (1989) and Wellburn (1990). In general concentrations below 0.5 ppm result in increased stomatal conductance or growth while higher concentrations
reduce photosynthesis, transpiration, and growth. NO may more strongly damage plants than NO₂, reducing photosynthesis at lower concentrations. Studies of chlorophyll fluorescence after NO₂ fumigation found no effect except at high concentrations (4-5 ppm) (Schmidt et al. 1990).

During the 1997 Indonesian wildfires Davies and Unam (1999) found photosynthesis ($A_{max}$) and conductance were reduced during the days of heavy smoke cover. They associate this reduction with decreased light levels and increased pollutant levels, but in field conditions these factors are confounded. *Chrysanthemoides monilifera*, a South African shrub, has a strong response to very short periods of smoke exposure with $A_{max}$ and $g_s$ reduced for up to five hours after 1 minute of smoke exposure and leaf necrosis observed after 5 minutes of exposure (Gilbert and Ripley 2003). Gilbert and Ripley (2003) attribute the short exposure response to stomatal closure and reductions in carboxylation or rubisco regeneration. Calder et al. (2010), using a different smoke exposure method, found that both broadleaf and conifer tree seedlings were able to survive up to 20 minutes of smoke exposure with no visible necrosis, but $A_{max}$ and $g_s$ were reduced post-exposure in most species.

In the present study, we report the effect of non-lethal levels of smoke exposure on tobacco *Nicotiana tabacum* var. *glurk* a model plant system that has congeners with a range of seed responses to smoke (Baldwin et al. 1994). Specifically we are interested in how photosynthesis, conductance, and photosystem II are affected by leaf litter smoke. We investigate the duration and dose dependency of the response. Photosynthesis is dependent on the rate at which CO₂ can enter the leaf (stomatal conductance), the plant chemistry that fixes CO₂ once inside the leaf, and the photochemistry that uses light energy to transform CO₂ into sugars. Stomatal conductance can be calculated from gas exchange measurements and chlorophyll fluorescence provides information about the health of the photosystem II photochemistry. Using these techniques we assess the effect of smoke on photosynthesis and whether it acts by affecting stomatal conductance or photochemistry.

5.2 Methods

Plant material

Forty *N. tabacum* var. *glurk* were germinated in a glasshouse on April 30th 2010 and transferred to an indoor growth room and paired by size on June 25th. One member of each pair was treated with smoke (see below) and the other served as a control. While in the glasshouse plants were top watered twice a day, once with Hoagland’s solution.
After transferring the plants indoors they were rotated and bottom watered with a solution of 1 ml 15 l⁻¹ Liquid Grow™ complete fertilizer (Dyna-Gro, Richmond CA) three times a week. To control aphids all plants were sprayed with Safer™ Brand insecticidal soap (Woodstream Corporation Lititz PA) as needed, every other day at most. To prevent biasing results, when insecticide was used it was applied to all plants regardless of the presence of aphids.

Smoke exposure protocol

Smoke was generated from coast live oak (Quercus agrifolia) litter collected around the University of California Berkeley campus. To produce a consistent fuel bed, litter was sorted to remove twigs and acorns, then ground in a blade style coffee grinder. Ground litter was then sifted using soils sieves to obtain particles between 1 and 2 mm in size.

Plants were individually exposed to smoke inside a chamber constructed from a 94 x 37 x 37 cm (128 l) marine cooler (see Figure 5.1). An inlet at the top of the chamber allowed smoke to enter through a pipe with several holes in it. An outlet at the bottom of the chamber was attached to a vacuum line which drew air through the smoke apparatus attached to the inlet hose and into the chamber when a valve was opened. A small fan for mixing the air sat below the plant at the bottom of the chamber. The inlet hose was connected to an Erlenmeyer flask sitting in a cool water bath. In the mouth of the flask was a glass funnel with a piece of wire mesh to prevent the litter from falling through.

Each 15 minute smoke exposure was produced by burning 0.4 g of sieved litter in the glass funnel. Two wooden matches were struck and allowed to burn until the sulfur tips had been completely consumed. They were then placed over the glass funnel while the vacuum valve was opened for 30 seconds, igniting the litter. The valve was then closed and the fan run for 10 seconds. The fan was run again for 10 seconds after 5 and 10 minutes. Forty-five minute smoke exposures were produced by repeating the above 15 minute protocol three times (a total of 1.2 g of litter burned).

Control plants were used as procedural controls and given the same handling and light treatment as the treatment plants. Specifically, they were moved to and from the room with the smoke chamber and placed inside a box for the duration of the smoke exposure to mimic the light levels inside the smoke chamber.

Experimental design and plant physiology

A preliminary study indicated that 15 minutes of exposure produced long-term responses. However, during the course of the present study differences were not as large
Figure 5.1: Diagram of the chamber used for exposing plants to smoke. The chamber consists of a large cooler turn on end, with a fan and stand at the bottom, and two tubes through the casing. One tube is attached to a vacuum line and the other to a glass funnel where litter is combusted. Arrows indicate the direction of air or smoke flow.
as suspected so the pairs were evenly divided into low (15 minute exposure) and high (45 minute exposure) treatment levels. As a result all the low treatments occurred before the high treatments with low on day 1 and 3, and high on day 5 and 7. Because one cohort of plants was used, plant age and exposure level are confounded, though we have no a priori reason to suspect a plant age by exposure dose interaction. Physiological measurements were made relative to the day of exposure and occurred immediately before and after exposure, as well as, one, three, and five days post-exposure. All measurements were made on the eighth leaf from the top, as marked at the beginning of the study. The eighth leaf was chosen because it was mature and expanded at the beginning of the experiment and presumably of similar age across individuals.

To assess the effect of smoke on the leaf physiology and its duration, the value of the smoke response is subtracted from the value of the paired control plant. This controls for differences in the day that the pair was exposed to smoke, and in particular, the steady decline in leaf function over the course of the experiment. This decline and the sequential order of treatments mean both the control and treatment plants start at lower functional levels in the 45 minute trials. Statistical significance was assessed using ANOVA as implemented in the R package nlme (Pinheiro et al. 2009). Exposure length and time relative to smoke exposure were treated as fixed factors and plant pair was included as a random variable to account for repeated measures. Planned contrasts were used to compare pre-smoke exposure values to the average of both treatment levels at each post-exposure time point. The effect of exposure length was tested by the contrast between treatment levels at time points showing significant differences from pre-exposure values.

Leaf gas exchange was measured using two LI-6400 portable infrared gas analyzers (LI-COR Biosciences Lincoln Nebraska). To ensure that values were as comparable as possible across times and days, chamber conditions were held constant at 400 µmol CO₂, 20 mmol H₂O, 29·3°C, and 250 µmol m⁻² s⁻¹ photosynthetically active radiation. This light level was chosen to be slightly higher than the light level at which the plants were growing, to minimize the amount of time required for plant gas exchange to reach steady state. Gas exchange values are averages of 4-5 instantaneous measurements taken 1 min apart after 16-18 minutes of instrument chamber acclimation. In all cases both plants in a pair were measured using the same gas analyzer throughout the experiment to minimize the influence of machine specific differences.

Chlorophyll fluorescence was assessed using a pulse-modulated fluorometer (Hansatech Instruments Ltd., Norfolk England). Two different chlorophyll fluorescence parameters were recorded, Fv/Fm and quantum yield. Fv/Fm, a measure of the function of photosystem II (PSII), was measured before the growth lamps were turned on in the morning because this measurement requires leaves to be at steady state in
the absence of light. Thus, Fv/Fm was measured the morning before exposure as well as one, three and five days after exposure. Quantum yield, a light adapted measurement, was recorded immediately before, 10 minutes, approximately 35 minutes, one day, three days, and 5 days after smoke exposure.

5.3 Results

Both the smoke and procedural control treatments reduced A₂₅₀ immediately after treatment (see Figure 5.2). The difference between controls and treatments (control–smoke delta) was only significant the same day of exposure (p<0.001). The one day followup measurement exhibited no difference between smoke and control treatments. No differences were detected three or five days later, though there appears to be a steady decline in leaf A₂₅₀ throughout the followup period in both controls and smoke treatment plants. Control–smoke deltas did not differ between the low and high treatments on the day of exposure indicating no smoke dose effect (see Table 5.1 for ANOVA tables).

Stomatal conductance had a similar pattern to photosynthesis with lower conductance post exposure in both procedural control and treatment plants (see Figure 5.3). The mean difference was significantly different immediately after exposure (p<0.001). Again, no significant contrast, or dose effect, was found between low and high treatment levels in the control–treatment difference (p=0.2).

The specific timing of the two chlorophyll fluorescence measurements differed from the gas exchange schedule. Fv/Fm was measured only ‘predawn’ meaning that the first followup measure occurred the morning after smoke exposure. Quantum efficiency in contrast was measured 10 and ∼35 minutes after smoke exposure in addition to the following day. Fv/Fm did not differ between any of the measurement days in either treatment level. The quantum efficiency control–treatment delta did increase immediately post-exposure (p=0.25), but recovered rapidly and was no longer significantly different from pre-exposure at 35 minutes (p=0.15; see Figure 5.4). There was a significant contrast between exposure levels at the 10 minute measurement, but after 35 minutes the contrast was not significant (p=0.007 and p=0.91, respectively), suggesting a short term dose effect.

Quantum efficiency is calculated from Fs, fluorescence under ambient light, and Fm’, the maximum light adapted fluorescence, using the equation Fm’ − Fs/Fm’. We compared these individual parameters at each measurement to determine how they change as quantum yield changes. The difference in Fs between controls and treatment plants did not differ throughout the experiment. The control–smoke delta Fm’
Figure 5.2: Boxplot of leaf photosynthesis ($A_{250}$) before, after, and up to five days following smoke exposure of 15 minutes (upper panel) or 45 minutes (lower panel). Blue boxes represent control plants while red boxes are smoke treated plants.
Table 5.1: ANOVA tables for physiological measurements. The time relative to smoke exposure is indicated by the 'Time' term and the 'Treatment' term indicates the length of the smoke exposure.

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<td>Time:Treatment</td>
<td>5</td>
<td>89</td>
<td>2·6</td>
</tr>
</tbody>
</table>
Figure 5.3: Boxplot of leaf conductance ($g_s$) before, after, and up to five days following smoke exposure of 15 minutes (upper panel) or 45 minutes (lower panel). Blue boxes represent control plants while red boxes are smoke treated plants.
Figure 5.4: Boxplot of quantum efficiency before, after, and up to five days following smoke exposure of 15 minutes (upper panel) or 45 minutes (lower panel). Blue boxes represent control plants while red boxes are smoke treated plants.
also was not significantly different from the pre-exposure measurements (10 minutes after p=0.24, 35 minutes after p=0.51, see also Figure 5.5). However, there is a significant contrast between the two levels at 10 minutes after exposure which was not found after 35 minutes (p=0.007 and p=0.28, respectively).

5.4 Discussion

Though extended exposure has been reported to cause leaf necrosis in some species in as little as five minutes (Gilbert and Ripley 2003, Moritz unpublished data), we did not observe any leaf damage in tobacco after 45 minutes of smoke exposure. Smoke exposure did significantly reduce leaf photosynthesis. This appears to be caused by both stomatal closure, and chemical responses that reduce PSII capacity. In all cases the duration of leaf function depression was less than 24 hours and in the case of PSII, recovery appears to occur rapidly.

The complex chemical and physical parameters of smoke make it difficult to isolate a single constituent impacting leaf function. Moreover the characteristics of combustion such as fuel moisture and oxygen supply can greatly alter the smoke composition. In the present study we attempted to control these factors, but some trials did combust more quickly than others due to differences in fuel packing or vacuum line strength. In general the primary constituents of smoke include CO₂, carbon monoxide, methane, ethene, nitrogen oxides, ammonia, sulfur dioxide, and dozens of other trace gases and particulate matter (Urbanski et al. 2009).

While we were unable to measure the concentrations of gases directly, we can estimate the concentrations using published emissions factors. Emission factors are conversion factors from the mass of fuel burned to the mass of gas produced. Chen et al. (2007) used laboratory burn experiments to determine emissions factors for several fuels including pine needles, sagebrush, and two grass species. These are separated into emissions during the flaming and smoldering phases of combustion, the former having much higher efficiency and producing the bulk of the emissions (Chen et al. 2007, Urbanski et al. 2009). In the present experiment, we assume that 100% of the smoke is generated in the flaming stage; this is reasonable because of the short time the sample was burned (30 sec.), and the high level of aeration generated by the vacuum line. The molar fraction of gas X resulting from burning F kg of fuel can be calculated using

$$\frac{E_x F}{M_x} \times \frac{V_c}{22.4} = \text{molar fraction of } X$$
Figure 5.5: Boxplot of $F_s$ a component of quantum efficiency before, after, and up to five days following smoke exposure of 15 minutes (upper panel) or 45 minutes (lower panel). Blue boxes represent control plants while red boxes are smoke treated plants. pairs.
Where $E_x$ is the emission factor (g kg$^{-1}$) of $X$, and $M$ is the molecular mass (g mole$^{-1}$). This is multiplied by $V_c$, the chamber volume, over 22.4, the moles l$^{-1}$ of an ideal gas at standard temperature and pressure. Table 5.2 gives estimated gas concentrations during the 15 minute smoke exposures and the emission factors used to calculate them.

There are caveats with this approach, in particular differences in fuel and burn characteristics between wildfires and our litter combustions. The laboratory experiments of Chen et al. (2007) use woody plant foliage and twigs, but not fallen litter as we used in the present experiment. The SO$_2$ emissions factor comes from reports by Sinha et al. (2003) based on savannah fires sampled by airplane at $\sim$500 m altitude. The combustion characteristics of the present study may also differ as the vacuum line ensured high oxygen availability and probably more efficient combustion. The vacuum line itself is another source of error as some gases may be drawn off before the valve is shut at the beginning of the exposure. For this reason we don’t attempt to estimate the concentrations during the 45 minute exposures.

Given the rapid recovery it is unlikely that smoke particulates are directly blocking the stomata, which concurs with analyses of coal soot damage (Rhine 1924). As summarized in the introduction several of the trace gases that occur in smoke are known to adversely affect plant function.

Increased CO$_2$ is well known to reduce $g_s$ under a variety of conditions (Pallas 1965, Farquhar and Sharkey 1982, Mansfield et al. 1990). The majority of studies have assessed the effects of CO$_2$ concentration doubling rather than the greater than seven fold increase estimated here. However, Jones and Mansfield (1970) exposed Lactuca sativa and Xanthium pennsylvanicum to 2400 ppm CO$_2$ for 4 hours and noted significantly reduced $g_s$. It is unknown how CO$_2$ concentrations of these magnitude affect chlorophyll florescence.

Little is known about the effects of low carbon monoxide concentrations on plant physiology. The estimated CO exposure of 50 ppm is greater than maximum production by rye seeds that Siegel et al. (1962) reported, but two orders of magnitude lower than Knight and Crocker (1913) needed to produce effects in pea seedlings. Recent work on leaf tissues in solution suggests CO may induce stomatal closure at low concentrations (She and Song 2008). However, aqueous concentrations are not easily converted to gaseous concentrations.

Concentrations of NO and NO$_2$ below the levels we estimate have been shown to reduce photosynthesis in tomato (Capron and Mansfield 1976), but have mixed effects on photosynthesis, and biomass in a wider range of species (Saxe 1994, Wellburn 1990). At half of our estimated concentration, NO$_2$ had no effect on tomato chlorophyll fluorescence, but slightly higher levels did reduce peak fluorescence in Spinacia oleracea.
Additive and synergistic effects of the two gases when mixed are reported by a number of authors and are reviewed by Darrall (1989) and Wellburn (1990).

The only emissions factor we found for SO₂ is from savannah fires which are likely dominated by grass fuels (Urbanski et al. 2009). Using that emission factor we estimate a maximum concentration for SO₂ of ~43 ppb, well below the levels used by Schmidt et al. (1990) that caused strong reductions in chlorophyll fluorescence, or those that showed reduced photosynthesis and gs (Darrall 1986). They are within the range (20–200 ppb) reported to induce stomatal dilation in *Vicia faba* (Black and Unsworth 1979). At the levels estimated here, it seems unlikely that SO₂ by itself caused the physiological responses we report; however, several experiments demonstrate synergistic reductions in leaf function in mixtures of SO₂ and NO or NO₂ (reviewed in Darrall 1989, Mansfield 1999).

While the response to the smoke exposures reported here are transitory they do suggest that wildfires may affect vegetation beyond their flames. It is well known that large wildfires reduce the amount of solar radiation that reaches vegetation (Nichol 1997, Davies and Unam 1999). Our findings and others suggest that smoke may further reduce stomatal conductance as well as disrupt leaf chemistry (Gilbert and Ripley 2003, Calder et al. 2010). A number of candidate pollutants have been identified and may be acting in concert to reduce stomatal conductance and photosynthesis, while also disrupting PSII.

These candidates could be winnowed by a series of experiments with treatment levels that include fumigations with pure gas at expected concentrations, or by selectively filtering out particular gases. For example, passing the smoke through a column of soda lime to remove the CO₂ before it enters the chamber would allow a researcher to study the effect of smoke in the absence of the carbon dioxide pulse associated with combustion.

**Conclusion**

Immediately after short term exposure to smoke tobacco plants exhibited significantly reduced photosynthesis, stomatal conductance, and quantum efficiency. Within 24 hours the difference between controls and treatment plants was no different than it was prior to smoke exposure. The mechanism by which smoke acts on leaves remains unknown and should be assessed by comparing smoke fumigations to fumigations with specific pollutants at similar concentrations, or to smoke scrubbed of pollutants. Effects of sustained smoke exposures similar to those occurring around major wildfires needs further attention.
Table 5.2: Estimated concentrations of compounds in smoke chamber for 15 minute exposure (burning of 0.4 g litter). Estimates are calculated using literature emissions factors from either laboratory tests on Ponderosa Pine needles (Chen et al. 2007) or wildfire smoke plume sampling Sinha et al. (2003), converted to emission factors Urbanski et al. (2009).

<table>
<thead>
<tr>
<th>Gas [\text{conc. (µl l}^{-1})</th>
<th>Reference</th>
<th>[\text{conc. (µl l}^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>[\text{CO}_2]</td>
<td>1763 [\text{F (g kg}^{-1})</td>
<td>2800 [\text{conc. (µl l}^{-1})</td>
</tr>
<tr>
<td>[\text{CO}]</td>
<td>19.9 [\text{F (g kg}^{-1})</td>
<td>50 [\text{conc. (µl l}^{-1})</td>
</tr>
<tr>
<td>[\text{NO}]</td>
<td>2.9 [\text{F (g kg}^{-1})</td>
<td>6.8 [\text{conc. (µl l}^{-1})</td>
</tr>
<tr>
<td>[\text{NO}_2]</td>
<td>0.9 [\text{F (g kg}^{-1})</td>
<td>1.4 [\text{conc. (µl l}^{-1})</td>
</tr>
<tr>
<td>[\text{SO}_2]</td>
<td>0.043 [\text{F (g kg}^{-1})</td>
<td>0.047 [\text{conc. (µl l}^{-1})</td>
</tr>
</tbody>
</table>
Appendix A

Quantification of plant flammability

Few studies bridge the understanding of individual flammability traits with community-scale fire behavior. The reasons for this gap are twofold: first, current landscape models have focused on climatic and topographic factors that structure the behavior of fires at large scales, particularly when fire intensity is high. Second, while we know whole plant flammability is a composite of several plant characteristics, there is as of yet no framework for partitioning their contribution.

Despite the poor understanding of the suite of flammability traits, several researchers have begun to document the variation in traits found in plant communities. Efforts at broad-scale measurement of traits leading to flammability rankings based on hypothesized trait–flammability relationships have been attempted in the Mediterranean and Florida (Dimitrakopoulos 2001, Dimitrakopoulos and Panov 2001, Behm et al. 2004). These studies produced lists of species ranked as high, moderate, or low flammability, but did not validate those findings experimentally. Below I describe a project intended to provide greater insights into how traits affect plant flammability by manipulating one trait at a time, thus avoiding the confounding factors such as plant identity and multiple covarying traits that are present in most previous studies. Unfortunately, due to limited facilities access and sample size it was completed successfully. It may serve as a useful template for future projects seeking to address this question. The two questions this experiment was designed to address are:

1. Which flammability traits have the greatest effect on peak heat release, total heat release, and rate of fire spread?

2. How do we scale from individual trait measurements to community-level flammability?
These questions can be answered by manipulating flammability traits of whole plants and burning them under the controlled conditions of a calorimeter. The precise measurements a calorimeter is capable of allow evaluation of differences in several combustion characteristics.

Combustion of woody plants progresses through three stages: heat absorption, pyrolysis (flaming combustion), and glowing combustion (smoldering) (Philpot 1970). Heat absorption is an endothermic stage during which plant matter gives up its water and chemical compounds begin to volatilize. The first exothermic stage is when the temperature rises sufficiently for those compounds that have volatilized to be ignited. This is the flaming stage that is most obvious and dramatic, it is also the stage at which heat is produced most rapidly. Smoldering occurs after pyrolysis and is the oxidation of carbon monoxide occurring at the surface of the embers. While this stage produces heat more slowly it does so for a longer period of time and is inefficient compared to flaming combustion resulting in the majority of the carbon monoxide and particulate production. In general the amount of smoke produced is inversely proportional to the efficiency of combustion, pyrolysis being far more efficient that smoldering.

We are only beginning to understand how plant fuel characteristics affect these stages of combustion. The goal of this project was to quantify the contribution of flammability traits to rates of fire spread, total heat release, and peak heat released from experimental plant ignitions.

A.1 Which flammability traits have the greatest effect on peak heat release, total heat release, and rate of fire spread?

To assess the influence that each trait had on plant flammability each plant was manipulated to enhance or reduce its flammability. Then whole plants were burned in the large scale calorimeter located at the California Bureau of Home Furnishings and Thermal Insulation (CBHFTI). This calorimeter facility is equipped with an oxygen-depletion calorimeter providing accurate measurement of both peak and total heat release, which cannot be measured accurately in natural fires. Plants were ignited in the calorimeter by exposing them to an open propane flame until the plant material was capable of carrying the flame itself. This stage ended up being more difficult than expected. In many cases plants failed to catch on fire, even after multiple attempts.
The calorimeter consists of a large insulated room with a hood to capture gases released by the burning plant. These gases are then passed by sensors which determine the oxygen, carbon dioxide, and carbon monoxide concentrations of the smoke. Using established stoichiometric equations and the rate of mass loss, the heat released by the burning object can be determined at five-second intervals (Etlinger and Beall 2004). The peak heat release is the highest energy release reached while the total heat release is the integral of instantaneous heat release for the entire period of combustion. While the material is burning, load cells beneath the burning platform determine the instantaneous mass loss, which can be used to determine heat release per unit mass lost; see Damant and Nurbakhsh (1994) for a full description.

For each trait I manipulated three individuals to have a high trait values and three individuals to have a low trait value as summarized in Table A.1. The original design called for the magnitude of the manipulation will be quantified using non-destructive methods developed in Chapter 3. However, it proved difficult to apply manipulations in the field before harvesting the plants for burning. Furthermore, because the number of trials I was able to run was limited I opted for full removal of dead branches or leaves as the treatment. Each manipulated plant was then be burned individually to determine peak and total heat release.

Few studies have attempted to apply our understanding of flammability traits to whole plant flammability and resulting fire behaviors such as smoke production. Those that have were primary concerned with comparing species as opposed to carefully manipulating plant characteristics. By taking a trait based approach and limiting the scope to a narrow set of traits, it may be possible to determine the explanatory power that each has for key fire metrics. These metrics could then be directly correlated with proven field methods for assessing plant flammability traits. This approach still holds promise and future attempt could utilize the following trait manipulations to increase their probability of success.

Moisture content could be manipulated by harvesting shrubs in late summer, when plant water status is naturally low and can be lowered further by cutting and drying samples. Other individuals could meanwhile be experimentally watered to increase moisture content. Because moisture content may vary in trials of other traits, it is important to characterize the species-specific effect of moisture on our flammability measures. These trials should probably be conducted first, and regression statistics can be used to correct later trials where moisture content is not of primary interest. Moisture content is easily measured by taking a small subsample of leaves and twigs which are oven dried at 60°C. The prediction is that as the moisture content of both foliage and woody material increases, the rate of spread and heat release will decrease. Species will differ in moisture contents in the field due to differential access to wa-
ter; however species identity is not expected to affect the relationship between heat release and moisture content.

Dead branch retention has been shown by Schwilk (2003) to have significant effects on the peak temperature reached in a prescribed fire, though Schwilk’s treatments also altered the bulk density. Bulk density can be held constant while modifying branch retention by changing only the proportion of live to dead fuels, but not the total amount. Dead material removed from plants in the trait reduction treatments can be physically wired into the the plant’s canopies in the increased dead branch treatment. Live material could then be added or removed in order to keep the bulk density and total biomass constant across replicates. As the proportion of dead material increases all metrics of fire intensity are expected to increase. Adding dead material is similar to decreasing the moisture content of the plant, as dead wood quickly equilibrates with the humidity of air. There is no expectation for a species by treatment interaction.

Surface area to volume ratio was one of the first plant characters determined to influence plant flammability (Brown 1970). Numerous bench-scale studies have confirmed its importance (Montgomery and Cheo 1971, Engstrom et al. 2004). This trait can be easily manipulated by progressively pruning away small fuel classes. Starting with all the foliage and proceeding on to twigs less than 2.5 mm, 5.0 mm, and 7.5 mm or similar. The main concern is accounting for the changes in biomass and bulk density that are associated with each of these treatments. Two possible solutions are 1) to start with larger plants for treatments that remove more plant material, or 2) to use only the heat-release measurement standardized to mass-loss terms. The predicted result is that as finer fuels (leaves, and small twigs) are removed, the peak rate of heat release and the rate of spread will decrease. The total heat release, however, will be less affected as it is more a function of available biomass as opposed to combustibility and ignitability of the material.

Bulk density can be manipulated in a similar fashion to branch retention: plants are either be pruned or have material added so that the amount of biomass in a cubic meter is altered across a range of values. The overall plant mass should be maintained across replicates. One approach is to construct some plants that take up more space than others by having a similar number and size of branches that spread out further. Schwilk (2003) achieved a similar effect by lashing on branches using wire. Conversely, at the high end of the treatment, the plants could be manipulated to have shorter, more densely packed branches. The expectation is that as bulk density increases, peak heat, total heat release, and rate of spread will increase as the amount of radiant heat impinging on nearby branches is enhanced.
A.2 How do we scale from individual trait measurements to community-level flammability?

Individual flammability traits are now identified well enough to warrant a study integrating several traits at once. By taking a trait-based approach and limiting the scope to a narrow set of traits, it will be possible to determine the effect of each trait on components of flammability. The predictive ability of this approach can be tested by comparing the flammability of unmanipulated individuals from two different species, in relation to the trait difference between the two species.

Future studies could use these trait correlations to predict species flammability and validate those predictions using a standard methodology (see Etlinger and Beall 2004). Differences in fire severity have been linked to changes in fuel structure (J.E. Keeley personal communication). We are approaching an understanding of how plant traits impact natural fire regimes. Because fire is important for structuring communities and the traits of species in the community influence fire intensity and frequency, both positive and negative feedbacks will exist between communities and fire regime. Some communities will be favored at high intensity or frequency fires and others at lower intensity or frequency (Schwik 2003, Keeley et al. 2005). These feedbacks will structure shrub communities on short time scales and drive evolution on longer time scales, particularly if differences in flammability are associated with post–fire regeneration as indicated in Chapter 4.

A.3 Example tests

Plant material was collected at the University of California Davis Quail Ridge Reserve, located a 1 hour drive from the CBHFTI testing facility in Sacramento. Twelve Adenostoma fasciculatum individuals were collected from a single stand that had burned 13 years prior to the study. This was chosen because the plants were smaller, less tangled with their neighbors, and more upright than older stands of A. fasciculatum. It is unknown what proportion of the plants were resprouts after the fire, but no charred skeletons were present on or immediately around any of the individuals. Only individuals with exposed burls were harvested; the burl served to hold the plant stems in place making it possible to replicate the approximate stem arrangement in the calorimeter. Plants were collected several days before the burn date, as preliminary burns suggested that freshly cut plants did not ignite even though the study took place at the end of the summer drought (late October). After plants were cut, they were paired by mass and randomly assigned to either a branch removal or control treat-
Table A.1: The trait manipulations for each focal trait. The 'low value' column lists how the magnitude of each trait was manipulated downward (see text for details). The next column shows the reverse. No experimental burns were done on plants with manipulated bulk density.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Low value</th>
<th>High value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture content</td>
<td>Plant harvested one week before</td>
<td>Plant harvested three days before</td>
</tr>
<tr>
<td>Branch retention</td>
<td>Removal of all dead branches</td>
<td>No manipulation</td>
</tr>
<tr>
<td>Surface area/vol</td>
<td>Removal of all leaves</td>
<td>No manipulation</td>
</tr>
<tr>
<td>Bulk density</td>
<td>Removal of branches</td>
<td>Addition of branches</td>
</tr>
</tbody>
</table>

Figure A.1: An example of a control plant on the burn platform. The upright shape is a result of tying branches in for transportation.
Figure A.2: An example of a relatively successful test. Note the unburned portion on the left and the propane gas torch (still lit) on the right.
ment. Dead branches were considered any tissue distal of green foliage and were removed from the experimental treatment.

Figure A.1 shows an example of a control plant ready for ignition in the calorimeter. For each test the ignition torch was lit for 30 sec, in some cases this was more than sufficient to start self-sustaining combustion (see Figure A.2). In other cases almost no plant material combusted. Due to limits on access to the calorimeter, I was only able to run tests on six branch removal–control pairs. The heat release curves for these tests are shown in Figure A.3. Three shrubs did not start a self-sustaining fire, even after multiple attempts to ignite them. As a result of this difficulty, the low sample size, and the high variability in the other tests, neither the peak nor total heat release differed between treatments (paired t-test, p > 0.2 in both cases).

While this particular experiment did not yield a robust dataset, efforts with greater sampling and more homogeneous source material could be successful. Etlinger and Beall (2004) had success in a similar experiment using potted plants and a kiln to dry the plants before experimental burns. Another factor that may improve on the method presented here, is a more substantial ignition system. We used a T-shaped propane torch to light one side of the plant, sometimes resulting in uneven plant burning (see Figure A.2). A wider flame front would result in more even combustion and less variation in the initial heat release between samples. An important consideration is that burning one plant at a time will never fully replicate the true nature of a wildfire where a flame front passes from one canopy to another directly. It would be useful to test the differences in combustion characteristics when plants burned in groups or individually.

Using whole plant combustion studies it will be possible to integrate flammability traits at the level of the individual. This will lead to a much greater understanding of how individual traits contribute to whole plant flammability. Additionally the ability to compare whole plant flammability between species and post-fire regeneration strategies will allow researchers to address many of the questions discussed in Chapter 1 and 4 more directly. These applications alone, justify continued effort to hone the methods described here.
Figure A.3: Heat release during experimental burns. Plants were paired (letters in side panel) to control for the effects of plant size and time of day. One plant of each pair had all of the dead branches removed and the other served as the control. Time 0 indicates the time at which the ignition burner was lit, and relative heat release was sample every 3 seconds. Curves with multiple peaks indicate instances where a second ignition was attempted. The highest point is the peak heat release and the area under the curve is the total heat release.
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