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By

Benjamin Sean Ramage

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Committee in charge:

Professor Kevin L. O’Hara, Chair
Professor John J. Battles
Professor David D. Ackerly

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Abstract

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Several different disturbances affect forests dominated by coast redwood (*Sequoia sempervirens*). Among the most important disturbances are fire, which has occurred historically, and sudden oak death (SOD), an emerging disease caused by the exotic pathogen *Phytophthora ramorum*. Both of these disturbances affect redwood forest ecosystems in critical ways; some effects are similar across these two disturbance types, while others are dramatically different. In this dissertation, I present three original field studies designed to further scientific understanding of the effects of fire and sudden oak death in isolation. In addition, I integrate these findings to develop comprehensive insights into the disturbance ecology of redwood forests.

Fire was frequent and ubiquitous in redwood forests prior to European settlement, but fires have been exceedingly small and rare over the last 70-80 years because of aggressive fire prevention and suppression policies. As a result, many aspects of redwood fire ecology remain poorly understood. Sudden oak death, a novel disturbance that was first discovered in the 1990s, is currently affecting redwood forests throughout coastal California. The most severely affected species, tanoak (*Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*), is still widespread and abundant in the redwood ecosystem, but diseased areas have begun to experience considerable mortality. Tanoak is extremely valuable as a food source to numerous wildlife species and thus its decline could have major impacts on redwood forest communities. Despite substantial public concern and a great deal of research attention, many effects of this devastating disease have yet to be studied.

Chapter 1 presents an investigation of tree regeneration in second-growth redwood forests experiencing sudden oak death-induced tanoak mortality, including a discussion of the factors that may be limiting seedling recruitment. I studied heavily impacted stands in Marin County (CA) and found the following: (1) despite reductions in canopy cover, there is no evidence that any species other than tanoak has exhibited a regenerative response to tanoak mortality, (2) the regeneration stratum was dominated by redwood and tanoak (other tree species were patchy and/or scarce), and (3) some severely affected areas lacked sufficient regeneration to fully re-occupy available growing space. These results indicate that redwood is likely to initially re-occupy the majority of the ground relinquished by tanoak, but also provide evidence that longer-term trajectories have yet to be determined and may be highly responsive to management interventions.

Chapter 2 presents an assessment of how sudden oak death has affected – and may eventually affect – stand structure in redwood forests. I utilized a stratified plot design and a stand reconstruction technique to assess structural impacts, at present and in the future, of this emerging disease. I found that residual trees in diseased plots were more aggregated than trees in unaffected plots, and my models predicted that the loss of tanoak will lead to the following short-term changes: (1) greater average diameter, height, height-to-live-crown, and crown length, (2) higher standard deviations of diameter, height, and crown length, and (3) larger average nearest neighbor differences for diameter, height, and crown length. In addition, plots lacking tanoak (living or dead) – as compared to plots with tanoak – exhibited (1) greater average diameter, (2) higher standard deviations of diameter and crown length, and (3) increased nearest neighbor differences with regard to diameter, height, and crown length. This chapter also includes preliminary explorations of how sudden oak death-induced structural changes compare with typical old-growth characteristics and how this disease may affect the structure of old-growth forests.

Chapter 3 presents an examination of the role of fire in the stand-level competitive dynamics of forests dominated by coast redwood, with a particular focus on post-fire survival rates and basal sprouting responses of redwood and tanoak. This study was initiated in response to a storm event in 2008 that ignited numerous fires throughout the redwood region and provided a rare opportunity to conduct replicated fire effects research. One year post-fire, bole survival and basal sprouting were quantified, for redwood and associated species, at four field sites that spanned much of the latitudinal range of redwood and encompassed second-growth and old-growth stands, burned and unburned areas, and a wide range of fire severities. I employed a mixed effects analytical framework and found that: (1) the probability of bole survival was greater for redwood than for tanoak, (2) this divergence was much more pronounced at higher fire severities, and (3) tanoak exhibited a slight advantage in terms of post-fire basal sprouting, but the dominance of tanoak basal sprouts in burned areas was reduced relative to unburned areas. In summary, fires of all severities increased the abundance of redwood relative to tanoak, but higher severity fires more strongly favored redwood.

In chapter 4, findings from all three chapters are integrated to facilitate a detailed comparison of SOD and fire, as well as a discussion of several other aspects of redwood ecology and management. Major points include the following: (1) the effects of SOD and fire are similar in some ways (both favor redwood and remove understory/subcanopy trees), but very different in others (e.g. SOD may lead to the complete extirpation of tanoak from redwood forests), (2) the low levels of regeneration in many SOD-impacted areas may be a result, at least in part, of key differences between SOD and historical disturbances, and (3) interactions between SOD and fire may have more profound effects than either of these disturbances in isolation. Redwood forests are currently undergoing dramatic changes, many of which represent challenges to forest health and ecological integrity; some of these problems are effectively insurmountable, but others may be amenable to management interventions. Researchers and land managers must acknowledge that redwood forests are transitioning to a novel state, and recognize that successful stewardship of the redwood forest ecosystem will require sustained inquiry and considerable experimentation.

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TABLE OF CONTENTS

Introduction

Overview of disturbance

All ecosystems experience natural disturbances and these perturbations often have profound effects on physiognomic structure and species composition, as well as a wide range of other ecological factors. Precise definitions of "disturbance" vary, but all those in common use describe a relatively discrete event that kills, displaces, or damages pre-existing individuals or colonies, and alters resource availability (Sousa 1984, White and Jentsch 2001, Pickett and White 1985). Changes in resource availability often occur via a reduction in competition following the loss of living biomass, but also may result from numerous other mechanisms (e.g. post-fire ash inputs, sedimentation resulting from floods, altered consumer populations and communities; Sousa 1984, White and Jentsch 2001, Pickett and White 1985). Disturbances, which can result from biotic or abiotic agents, are generally distinguished from "stressors": phenomena that are gradual (e.g. climate change) and/or that do not directly affect ecosystem structure (e.g. diseases that slow growth rates but do not cause significant mortality; White and Jentsch 2001).

Disturbances often produce patchy heterogeneous landscapes, as well as variable micro-site and micro-climatic conditions, and thus tend to increase structural diversity and provide a wide range of substrates and habitats (Pickett and White 1985). However, the specific effects of any particular disturbance event are difficult to predict and will depend upon the traits of the species in and adjacent to disturbed areas, as well as characteristics of the disturbed patch and surrounding landscape (e.g. severity of damage, size, shape, isolation, internal heterogeneity, nature of and time since previous disturbances, seasonality and other temporal factors; White and Jentsch 2001, Pickett and White 1985). The likelihood that the species present in a given area will be able to endure a given disturbance will depend in large part upon the extent to which these species are adapted to the disturbance; these adaptations are in turn a function of the disturbances experienced throughout the evolutionary history of the species. Similarly, any species that have persisted within a given region must be able to endure or escape the disturbances that have historically occurred within that region (Sousa 1984, White and Jentsch 2001, Pickett and White 1985). Ecologically important characteristics of historical disturbances include disturbance type, frequency, scale/size, intensity, severity, predictability, distribution (e.g. spatial, topographic), specificity (e.g. species, age/size classes), and synergism (e.g. one disturbance increasing the probability of another disturbance); these characteristics are collectively referred to as the "disturbance regime" (White and Jentsch 2001). In summary, disturbance has been – and will continue to be – a strong force in the evolution of species, the assembly of communities, and the development of physiognomic structures.

Ecosystems throughout the globe are currently experiencing dramatic departures from their historical disturbance regimes (White and Jentsch 2001). These altered disturbance regimes may be composed of historical disturbance types that differ only in quantitative attributes (e.g. frequency, intensity), or they may result from entirely new disturbance agents (i.e. "novel disturbances"). A plethora of mechanisms are responsible for the appearance of altered disturbance regimes, including direct anthropogenic manipulations (e.g. timber harvest, damming and flood control), indirect anthropogenic effects (e.g. increased ignition sources, landscape fragmentation), climate-mediated effects, and introduction of exotic species (Dale et al. 2001, Mack and D'Antonio 1998, White and Jentsch 2001). Exotic species can influence disturbance regimes directly (e.g. mortality caused by exotic animals or pathogens; Lovett et al. 2006, Mack and D'Antonio 1998) or indirectly (e.g. increased fire frequency owing to highly flammable exotic plants; Keeley 2005).

Following disturbances that have occurred historically, the affected species generally maintain the capacity to return to similar structures and relative abundances (Oliver and Larson 1996, Pickett and White 1985). However, these trajectories often do not materialize in the aftermath of novel disturbances, especially those caused by exotic organisms that have become permanent residents of the invaded ecosystem (Lovett et al. 2006). An example of such a situation is provided by chestnut blight, a disease caused by *Cryphonectria parasitica* that was introduced to the eastern United States approximately one hundred years ago (Ellison et al. 2005). The American chestnut (*Castanea dentata*), which exhibits very little resistance to the pathogen, has avoided absolute extirpation from eastern forests but has been entirely removed from the forest canopy as a result of frequent episodic sprout dieback. This dramatic physiognomic change, which represents a form of "functional extinction" (*sensu* Ellison et al. 2005), has produced forest structures and relative abundances that did not exist prior to the introduction of chestnut blight; as such, this devastating disease has created a "novel ecosystem" (*sensu* Hobbs et al. 2006). Although departures from historical disturbance regimes will not necessarily lead to profound ecological changes, major transitions are possible; if altered disturbance regimes include novel disturbance types (i.e. those caused by disturbance agents that were not historically present), permanent transitions to novel ecosystem states will be much more likely (Lovett et al. 2006; Hobbs et al. 2006).

Disturbance in redwood forests

With ages that frequently exceed 1,000 years, coast redwood (*Sequoia sempervirens*), the tallest tree species in the world, must be able to endure a wide range of disturbances, including those that recur only on centennial time scales (Noss 2000). Similarly, common associates of redwood must be well-adapted to the historical disturbance regime of redwood forests. However, smaller and shorter-lived tree species need not necessarily be as resistant as redwood; on the contrary, species-specific differences in disturbance resistance may help to explain the dominance of redwood in certain areas (Lorimer et al. 2009). Disturbances affect redwood forest stand structure via size- and species-specific mortality rates as well as spatial variations in severity, and also influence regeneration through numerous mechanisms (Noss 2000, Lorimer et al. 2009).

Knowledge of disturbance effects is essential for a complete understanding of redwood forest composition, physiognomy, and dynamics. These attributes are not independent of each other (e.g. species often have characteristic structures, growth rates, and regeneration patterns), but distinctions sometimes have tremendous ecological importance. For instance, tanoak (*Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*; the most abundant broadleaf associate of redwood) may not be structurally distinct from young redwood trees in some stands, but these two species are highly divergent as wildlife food sources; tanoak regularly produces large nutritious acorns that are utilized by many animal species (e.g. bear, deer, and several rodent and bird species), while redwood yields unpredictable crops of small and light seeds with limited food value (Burns and Honkala 1990). In other contexts, structural attributes may be more important than species composition. In forests dominated by redwood and/or other conifers, marbled murrelets (*Brachyramphus marmoratus*) nest exclusively in tall trees with large limbs, but do not appear to discriminate between redwood and other conifers capable of achieving very large sizes, such as Douglas-fir (*Pseudotsuga menziesii*; Noss 2000).

The historical disturbance regime of redwood forests was dominated by fire, windstorms, floods, and landslides; there is little evidence that any biotic agents (e.g. pathogens, insects, mammals) were major sources of disturbance in forests dominated by redwood. Strong wind events, which are more common in northerly parts of the redwood range, may snap or uproot isolated trees (typically redwood or other tall conifers), but large contiguous tracts are rarely if ever toppled. Severe floods, which generally occur during the winter and exhibit return intervals of approximately a century, can deposit 1.5 m or more of sediment on alluvial sites; these deposits rarely damage large existing redwood trees, but often displace or kill most other vegetation. It is possible that land-use practices and channel modifications have altered flood frequencies or magnitudes, but any such changes have not been definitively identified. Isolated landslide events occur occasionally, particularly on steeper slopes, and there is some evidence that activities associated with timber harvest (e.g. road construction) have increased their probability of occurrence (Lorimer et al. 2009).

Fire was perhaps the most consequential component of the historical disturbance regime in redwood forests, especially on upland sites that are not susceptible to flooding. Fires were frequent and ubiquitous for at least several centuries prior to European settlement; mean return intervals of 6-25 years have been estimated throughout the entire redwood range (Lorimer et al. 2009). However, there is evidence that the majority of fires that occurred prior to European settlement were of Native American origin. Thus, while it is clear that redwood has thrived throughout its recent fire-prone history, the question of whether redwood experienced frequent fire in its distant evolutionary past continues to be debated (Lorimer et al. 2009). Progress towards the resolution of this debate has been hindered in recent decades by the scarcity of opportunities to study redwood fire ecology; fires have been relatively rare and small over the last 70-80 years as a result of successful fire suppression efforts (Oneal et al. 2006, Donovan and Brown 2007). Redwood forests appear to be persisting in the absence of fire, but eight decades is a relatively short interval for a species that often survives for more than a millennium, and thus the long-term role of fire remains unresolved (Lorimer et al. 2009).

In addition to the quantitative shifts discussed above (i.e. altered fire frequencies), the twentieth century exposed redwood forests to fundamentally new disturbance types. First and foremost among these novel disturbances is timber harvest, which has converted more than 90% of old-growth stands to second-growth stands stocked largely by basal sprouts that emerged from the tops and bases of cut stumps (Noss 2000). Although some trees were undoubtedly harvested by Native Americans, the intensive logging that began after European settlement, which utilizes advanced technology and often removes all standing trees from large areas, is a fundamentally different phenomenon (Noss 2000, Lorimer et al. 2009). Despite the novelty of this disturbance, redwood and associated species have proven resilient to timber harvest; second-growth redwood forests usually retain similar tree species compositions and stands that are not re-harvested generally begin to slowly acquire old-growth structures.

Sudden oak death (SOD), a devastating disease caused by the recently introduced exotic pathogen *Phytophthora ramorum*, is currently impacting redwood forests throughout coastal California (Rizzo et al. 2005). Although much remains unknown about this emerging novel disturbance, it is clear that the effects will be quite distinct from all other redwood forest disturbances (both historical and novel). Mature redwood trees are not vulnerable to SOD, but tanoak, which is currently widespread and abundant in redwood forests (Burns and Honkala 1990), is extremely susceptible. Tanoak is experiencing drastic population declines, and mounting evidence (e.g. field studies, genetic resistance trials, disease progression models) suggests that SOD could eventually drive tanoak to extinction in redwood forests (Maloney et al. 2005, Meentemeyer et al. 2004, McPherson et al. 2010, Rizzo et al. 2005, Ramage et al. 2010). Furthermore, because many native species support sub-lethal foliar infections, including redwood (Davidson et al. 2008), *P. ramorum* has almost certainly become a permanent resident of infested areas and future attempts to re-introduce tanoak to areas from which it has been extirpated are likely to fail. As a result, diseased redwood forest ecosystems appear to be undergoing a process of lasting and profound transformation.

Objectives

The core of this dissertation consists of three original field studies designed to enhance scientific understanding of the effects of a novel disturbance (sudden oak death) and a historical disturbance (fire) in coast redwood forests. Specifically, chapters are arranged as follows:

Chapter 1: An investigation of tree regeneration in second-growth coast redwood forests experiencing sudden oak death-induced tanoak mortality, including a discussion of the factors that may be limiting seedling recruitment.

Chapter 2: An assessment of how sudden oak death has affected – and may eventually affect – stand structure in coast redwood forests, including a preliminary exploration of SOD impacts in old-growth forests, as well as a comparison between SOD-induced second-growth structures and typical old-growth structures.

Chapter 3: An examination of the role of fire in the stand-level competitive dynamics of forests dominated by coast redwood, with a particular focus on post-fire survival rates and basal sprouting responses of redwood and tanoak.

In the concluding section (“Chapter 4: Synthesis and Conclusions”), findings from all three data chapters are integrated to develop comprehensive insights into the disturbance ecology of redwood forests.

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Chapter 1

Forest transformation resulting from an exotic pathogen: Regeneration and tanoak mortality in coast redwood stands affected by sudden oak death

Benjamin S. Ramage

Sudden oak death, an emerging disease caused by the exotic pathogen *Phytophthora ramorum*, is impacting coast redwood (*Sequoia sempervirens*) forests throughout coastal California. The most severely affected species, tanoak (*Notholithocarpus densiflorus*), is currently widespread and abundant in the redwood ecosystem, but diseased areas have begun to experience considerable mortality. Tanoak, which is extremely valuable as food source to numerous wildlife species, is unlikely to successfully regenerate in these areas, and thus affected redwood forests are transitioning to a novel state. In this study, to predict which species might replace tanoak, I investigated regeneration patterns in heavily impacted stands in Marin County, California. My main findings were: (1) despite reductions in canopy cover, there is no evidence that any species other than tanoak has exhibited a regenerative response to tanoak mortality, (2) the regeneration stratum was dominated by redwood and tanoak (other tree species were patchy and/or scarce), and (3) some severely affected areas lacked sufficient regeneration to fully re-occupy available growing space. My results indicate that redwood is likely to initially re-occupy the majority of the ground relinquished by tanoak, but also provide evidence that longer-term trajectories have yet to be determined and may be highly responsive to management interventions.

Introduction

Forest ecosystems throughout the globe are currently experiencing invasion by exotic insects and/or pathogens. In many instances, pest-induced mortality is occurring at extremely high rates and rapidly altering the structure and composition of affected forests, causing great concern about the future of impacted areas (Lovett et al. 2006, Liebhold et al. 1995). Following disturbances that have occurred historically (biotic and abiotic, natural and anthropogenic), the affected species generally maintain the capacity to return to similar structures and relative abundances (Oliver and Larson 1996, Pickett and White 1985). However, such trajectories often do not materialize in the aftermath of novel disturbances, especially those caused by exotic organisms that have become permanent residents of the invaded ecosystem (Lovett et al. 2006). Thus, competitive interactions may be fundamentally altered and pre-invasion models of community assembly and forest development might no longer apply, elevating the need for direct measurements of regeneration and stand development in affected areas.

Tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H.Oh syn. *Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), a broadleaf evergreen in the Fagaceae family, is currently widespread and abundant in coast redwood (*Sequoia sempervirens* (D.Don) Endl.) forests and is believed to be an integral component of the structure and function of these unique ecosystems (Burns and Honkala 1990, Hunter et al. 1999, Noss 2000). However, the close association between redwood and tanoak may be relegated to history if sudden oak death (SOD), an emerging disease caused by the exotic pathogen *Phytophthora ramorum* (S. Werres, A.W.A.M. de Cock) continues to spread throughout coastal California. Current research demonstrates drastic declines in tanoak populations and mounting evidence (e.g. field studies, genetic resistance trials, disease progression models) suggests that SOD could eventually drive tanoak to extinction in redwood forests (Maloney et al. 2005, Meentemeyer et al. 2004, McPherson et al. 2010, Rizzo et al. 2005, Ramage et al. 2010).

Several tree species succumb to SOD, but tanoak is the most severely affected tree and the most abundant SOD-susceptible species in redwood forests (Rizzo et al. 2005, Burns and Honkala 1990). The extreme susceptibility of tanoak results from a combination of factors: (a) little or no genetic resistance (mortality levels are approaching 100% in some areas and seedling trials have failed to detect any individuals immune to infection), (b) susceptibility at all ages and size classes, and (c) ability of tanoak foliage and twigs to support pathogen sporulation, facilitating eventual lethal infection of the bole (all other species that are killed by SOD require the presence of a secondary foliar host for infection of the bole; Maloney et al. 2005, McPherson et al. 2010, Meentemeyer et al. 2004, Ramage et al. 2010, Rizzo et al. 2005). Furthermore, because many native species support sub-lethal foliar infections, including redwood (Davidson et al. 2008), *P. ramorum* has almost certainly become a permanent resident of infested areas. Tanoak also occurs in other community types (e.g. mixed evergreen forest, Douglas-fir forest; Burns and Honkala 1990), but the moist, mild climate that characterizes redwood forests appears to be especially conducive to pathogen spread and infection (Meentemeyer et al. 2004).

Considered collectively, the specific properties of this pathosystem suggest it is unlikely that tanoak will ever return to pre-SOD abundances in diseased redwood forests. Tanoak stumps often sprout prolifically following death of the main bole (Cobb et al. 2010, Ramage et al. 2010), and it is feasible that root systems could be maintained indefinitely if adequate amounts of photosynthate are consistently produced prior to episodic SOD-induced sprout dieback; a similar situation has been occurring for approximately a century with the American chestnut, *Castanea dentata* (Marsh.) Borkh., and the exotic disease chestnut blight, caused by *Cryphonectria parasitica* (Murrill) Barr. (Ellison et al. 2005). However, even if this scenario was to manifest and tanoak were to avoid absolute extirpation from redwood forests, such an outcome would still represent a form of *functional extinction* (sensu Ellison et al. 2005).

It is often assumed that redwood forests are relatively poor in tree species diversity because of the strong competitive effects of redwood, but there is surprisingly little evidence to support this conjecture. Given that tanoak is a nearly ubiquitous associate of redwood (Burns and Honkala 1990, Noss 2000), we cannot discount the possibility that tanoak is competitively excluding one or more species otherwise capable of persisting in redwood forests. Of particular concern is the question of whether functionally similar native tree species will be able to colonize and persist in areas previously occupied by tanoak. Tanoak regularly produces large nutritious acorns that are utilized by many wildlife species (e.g. bear, deer, and several rodent and bird species), in contrast to redwood's unpredictable crops of small and light seeds with limited wildlife value (Burns and Honkala 1990). If tanoak is not replaced by one or more functionally similar tree species (e.g. a true oak species), its loss could result in serious cascading impacts. For instance, acorns are a primary food source for the dusky footed woodrat (*Neotoma fuscipes* Baird), which is in turn a primary food source for the northern spotted owl (*Strix occidentalis caurina* Xantus de Vesey; Courtney et al. 2004).

Tree regeneration represents the next cohort of canopy trees and its composition is thus an important predictor of future forest conditions (Oliver and Larson 1996, Smith et al. 1997). There is strong evidence, from a wide range of ecosystems, that dispersal and recruitment limitation greatly affect species composition, and accordingly, that seedling establishment is a critical factor in the post-disturbance community assembly (Clark et al. 2007). Regeneration in SOD-induced mortality gaps is likely to differ from regeneration in areas not experiencing mortality, and – because SOD gaps represent a novel occurrence – unexpected patterns may emerge. Features such as standing dead trees and debris piles may attract birds and thereby increase the input of bird-dispersed seeds into disturbed areas (Rost et al. 2009). Seedling and sprout survival and growth rates may increase following the death of mature trees via: a) improved photosynthetic capacity, which can occur with even small reductions in canopy cover, and/or b) a reduction in the intensity of competition for water and soil nutrients (Oliver and Larson 1996, Smith et al. 1997); increased basal sprouting incidence could also occur due to bole damage from falling trees. These mechanisms vary among species (Grubb et al. 1977), and thus relative abundances of regeneration in mortality gaps are likely to differ from that of the surrounding matrix. In the case of redwood, studies have shown that basal sprout survival and growth rates were greater in higher light environments (O'Hara & Berrill 2010, O'Hara et al. 2007), and that a greater proportion of established redwood stems had basal sprouts in an area experiencing SOD-induced tanoak mortality than in an unaffected area (Waring and O'Hara 2008).

This is the first publication to comprehensively examine tree regeneration in coast redwood forests experiencing SOD-induced tanoak mortality. My specific objectives were to: (1) test the hypothesis that regeneration is positively associated with tanoak mortality, (2) identify the species that are regenerating in the greatest numbers in areas severely affected by sudden oak death, and (3) consider the potential implications of the observed patterns.

Methods

Study area and plot selection

Fieldwork was conducted at the Marin Municipal Water District (MMWD), which occupies approximately 8500 ha of protected land on the northern slope of Mount Tamalpais in Marin County, California. Redwood forest, primarily second-growth stands that originated at the end of the 19th century or beginning of the 20th century, is scattered throughout the watershed, covering a wide range of slopes, slope positions, and aspects. Unusual levels of tanoak mortality were first observed in Marin County in 1994, and SOD has been causing extensive tanoak mortality at MMWD since at least 2000 (Rizzo et al. 2002, McPherson et al. 2010, Waring et al. 2008).

The plot placement protocol consisted of two distinct regimes: random and stratified. Under the random sampling scheme, I used a GIS to generate random coordinates, separated by a minimum of 500 meters, within areas identified as redwood forest by the California GAP Analysis (Davis et al. 1998). The stratified sampling scheme was used to ensure adequate sampling of two conditions that are relatively uncommon at MMWD, but that I deemed essential for detecting patterns associated with SOD-induced tanoak mortality: (a) areas with high tanoak abundance but little or no tanoak mortality, and (b) areas with very high levels of tanoak mortality. In order to sample these extreme conditions, I selected representative *stands* (each approx. one to three ha in size) and then randomly located plots within these stands. In addition, I installed three plots in areas where previous SOD-related research had been conducted and where *P. ramorum* presence was verified (Spencer 2004), so that some historical records would be available for comparison. Spencer (2004) used a similar sampling scheme (representative stand selection and randomized plot location) to locate these plots in areas with abundant tanoak, and thus, for the purposes of analysis, I have grouped these three plots with the stratified plots.

All random and stratified plots consisted of a 1/20 ha (12.62 m radius) inner plot, as well as a buffer, which extended to a 1/4 ha area (28.21 m radius); these two elements are collectively referred to as an extended plot. Plots were located in second-growth redwood forest satisfying the following criteria: (a) sufficient redwood coverage (at least 25% redwood canopy cover in all four quadrants of the extended plot, estimated visually); (b) between 50 and 200 meters from trails or roads (the lower limit imposed to avoid edge effects, and the upper limit to aid accessibility in areas with rugged terrain); and (c) on slopes less than 60% (31 degrees) for worker safety and minimization of erosion. If any of these conditions were not met at the initial random (or stratified and randomized) location, the plot was relocated at 50 meter intervals along a randomly selected azimuth until all criteria were satisfied.

Data collection and sampling

Data for *mature* trees ($\geq$ 10 cm diameter at breast height; 1.37 m; DBH) were collected during the summer of 2008. Within each plot, I recorded species and DBH for all tree species, as well as health and deterioration status for all tanoaks. Stems of species other than tanoak were not recorded if broken below breast height, but to ensure that I captured the majority of SOD-induced tanoak mortality, tanoak stems that were broken below breast height were also recorded if the fallen bole wood was relatively intact. Multi-stemmed trees that were split below breast height were counted as separate trees. Health status of living tanoak trees was characterized with SOD symptoms (bleeding, bole cankers, *Hypoxylon* fungi, beetle holes and/or frass, and canopy dieback; Swiecki and Bernhardt 2006; McPherson et al. 2010), and post-mortality deterioration was characterized with the percentage of dead leaves still clinging to dead trees as well as the height and stem diameter of bole breakage. In 2008, I also collected symptomatic samples of tanoak (leaves and twigs) and/or California bay (*Umbellularia californica* (Hook. & Arn.) Nutt; leaves only) in all plots, to test for the presence of *P. ramorum* via polymerase chain reaction (PCR); methods are described in Hayden et al. (2006).

Regeneration and canopy cover data were collected during the summer of 2010. Counts of all seedlings (< 1.37 m height), basal sprouts (< 1.37 m height), saplings (seed or sprout origin stems $\geq$ 1.37 m height and < 3 cm DBH), and juvenile trees (3 - 10 cm DBH) were conducted for all tree species in two randomly selected quadrants per plot (e.g. NW and SE). Dead regeneration was ignored in all size categories. Canopy cover was measured with a spherical densiometer at five points per plot (plot center and 3m in each cardinal direction) and values were averaged.

Data analysis

To limit any potentially confounding effects of tanoak abundance, all plots with less than the median basal area (BA) of total tanoak (living and dead trees combined, calculated with the randomly located plots only; 14.4 m^2 per ha) were excluded from all analyses. Using this dataset (n = 16 plots), I tested the effects of tanoak mortality on canopy cover and tree regeneration with generalized linear models. For each response variable, I fit models in which either dead tanoak BA (in 2008) or the number of dead tanoak stems (in 2008) was specified as the sole predictor variable (with and without squared terms). Response variables, data for all of which were collected in 2010, consisted of canopy cover and all measures of regeneration (seedlings, basal sprouts, saplings, and juvenile trees) for several species groups (all species combined, all non-tanoak species, non-tanoak hardwoods, and non-redwood conifers), as well as each tree species individually: tanoak, redwood, pacific madrone (*Arbutus menziesii* Pursh), California bay, bigleaf maple (*Acer macrophyllum* Pursh), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and California nutmeg (*Torreya californica* Torr.*)*. All species groups and individual species exhibited over-dispersed poisson distributions and thus I specified quasi-poisson error distributions with logarithmic link functions. For canopy cover, I applied a logit transformation (because predicted values had to bounded by 0 and 1) and then specified a gaussian error distribution (because errors were approximately normal on the logit scale).

To determine which species are beginning to replace tanoak, I examined tanoak mortality and species-specific regeneration patterns in areas heavily impacted by SOD (plots with $\geq$ 300 dead stems per ha and/or $\geq$ 15 m^2 dead BA per ha), i.e. "severe" plots (n=8; Fig. 1.1), and I present relevant data for these plots. I also re-executed all of the models described above using only the "severe" plots. Finally, I identified three plots in which the total density of non-tanoak seedlings (in 2010) was less than the density of dead tanoak stems (in 2008), i.e. "regen-deficient" plots (Fig. 1.1); these plots were examined in greater detail and used to facilitate a discussion of potential constraints on regeneration in diseased areas. Throughout the entirety of the paper, all values (except proportional metrics) are provided as densities per ha.

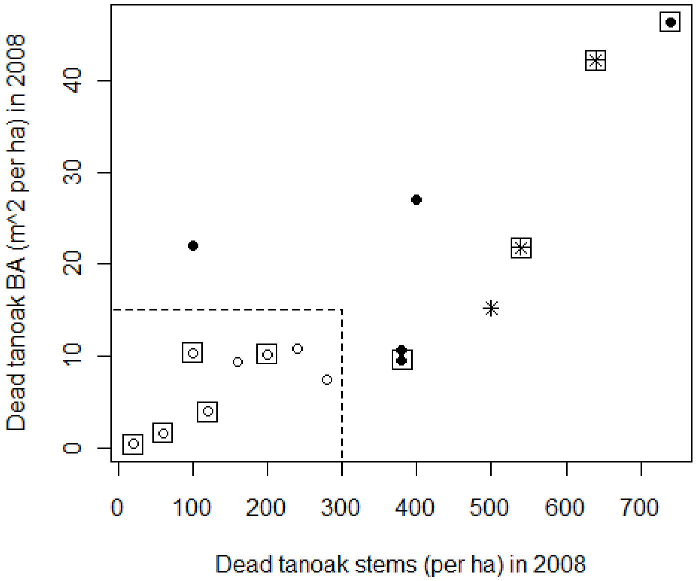

Fig. 1.1. Study plots by tanoak mortality, analytical grouping, and placement protocol. All plots above and to the right of the dashed lines (solid circles and asterisks) were considered severely impacted ("severe" plots). Asterisks indicate "regen-deficient" plots. Plots surrounded by squares resulted from the stratified plot placement protocol; some of the stratified plots exhibited intermediate mortality levels because precise plot locations were always randomized.

Results

Effects of tanoak mortality on canopy cover and regeneration

Canopy cover in 2010 was significantly affected by tanoak mortality in 2008 (BA: $p < 0.0001$; stems: $p = 0.0014$). Squared terms were not significant in either model; predicted values are curved because of the logit transformation prior to model fitting and subsequent back-transformation prior to plotting (Fig. 1.2). In the plots with the greatest mortality, canopy cover was below 60%, while canopy cover was generally above 90% in plots with little or no mortality.

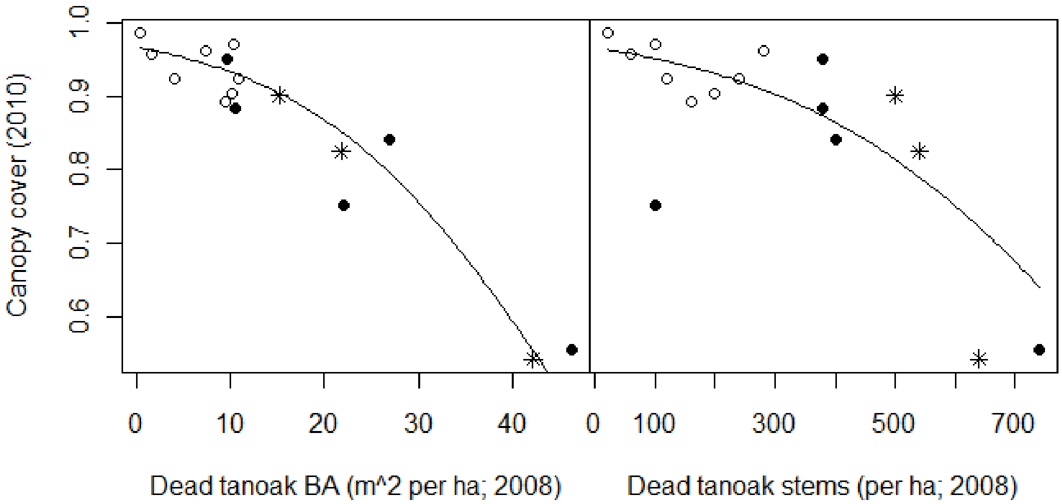

Fig. 1.2. Canopy cover (2010) as a function of tanoak mortality (2008). Solid circles and asterisks were deemed severely impacted ("severe" plots); asterisks indicate "regen-deficient" plots.

Dead tanoak BA (in 2008) did not affect the density of tanoak seedlings, basal sprouts, or juvenile trees (in 2010), but the density of tanoak saplings was positively related to dead tanoak BA (p = 0.0105; Fig. 1.3). The density of dead tanoak stems (in 2008) did not affect the density of tanoak seedlings, basal sprouts, or saplings (in 2010), but the density of tanoak juvenile trees was negatively related to dead tanoak stems (p = 0.0007; Fig. 1.3). Squared terms were not significant in either model; predicted values are curved because of the log transformation prior to model fitting and subsequent back-transformation prior to plotting.

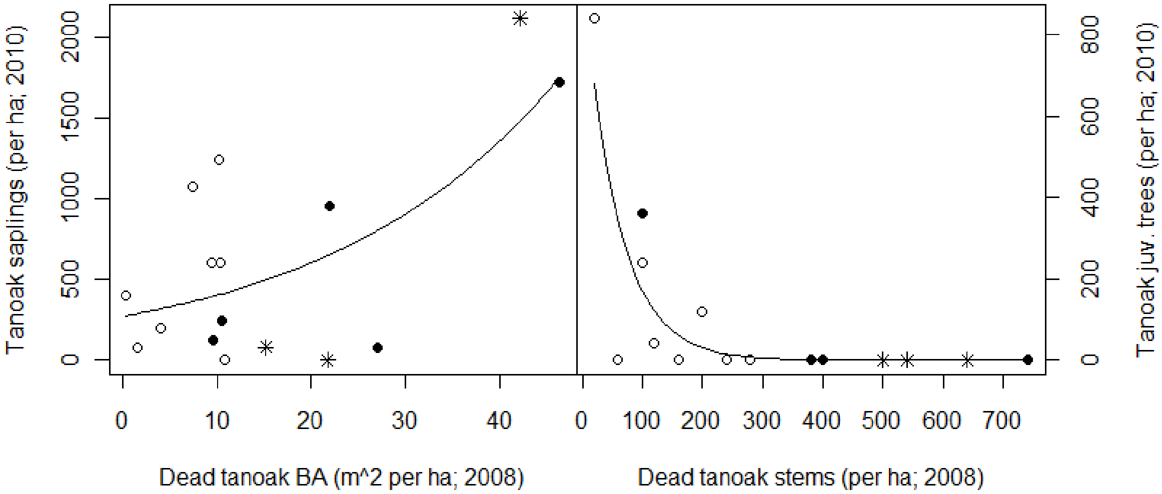

Fig. 1.3. Tanoak saplings and juvenile trees (2010) as a function of tanoak mortality (2008). Solid circles and asterisks were deemed severely impacted ("severe" plots); asterisks indicate "regen-deficient" plots.

Tanoak mortality (in 2008) was entirely unrelated to regeneration (in 2010) of all species other than tanoak, including redwood. This was true across both tanoak mortality metrics (BA and stem counts) and all regeneration categories (seedlings, basal sprouts, saplings, and juvenile trees), and regardless of whether each species was analyzed individually or pooled into functional groups (non-tanoak hardwoods, non-redwood conifers). Similarly, tanoak mortality was unrelated to total regeneration (all species including tanoak and redwood), as well as all non-tanoak species (Fig. 1.4). I also re-executed all these analyses using only the eight "severe" plots; all results were qualitatively identical, except for the relationship between tanoak juvenile trees and dead tanoak stems, which was insignificant in the "severe" analysis.

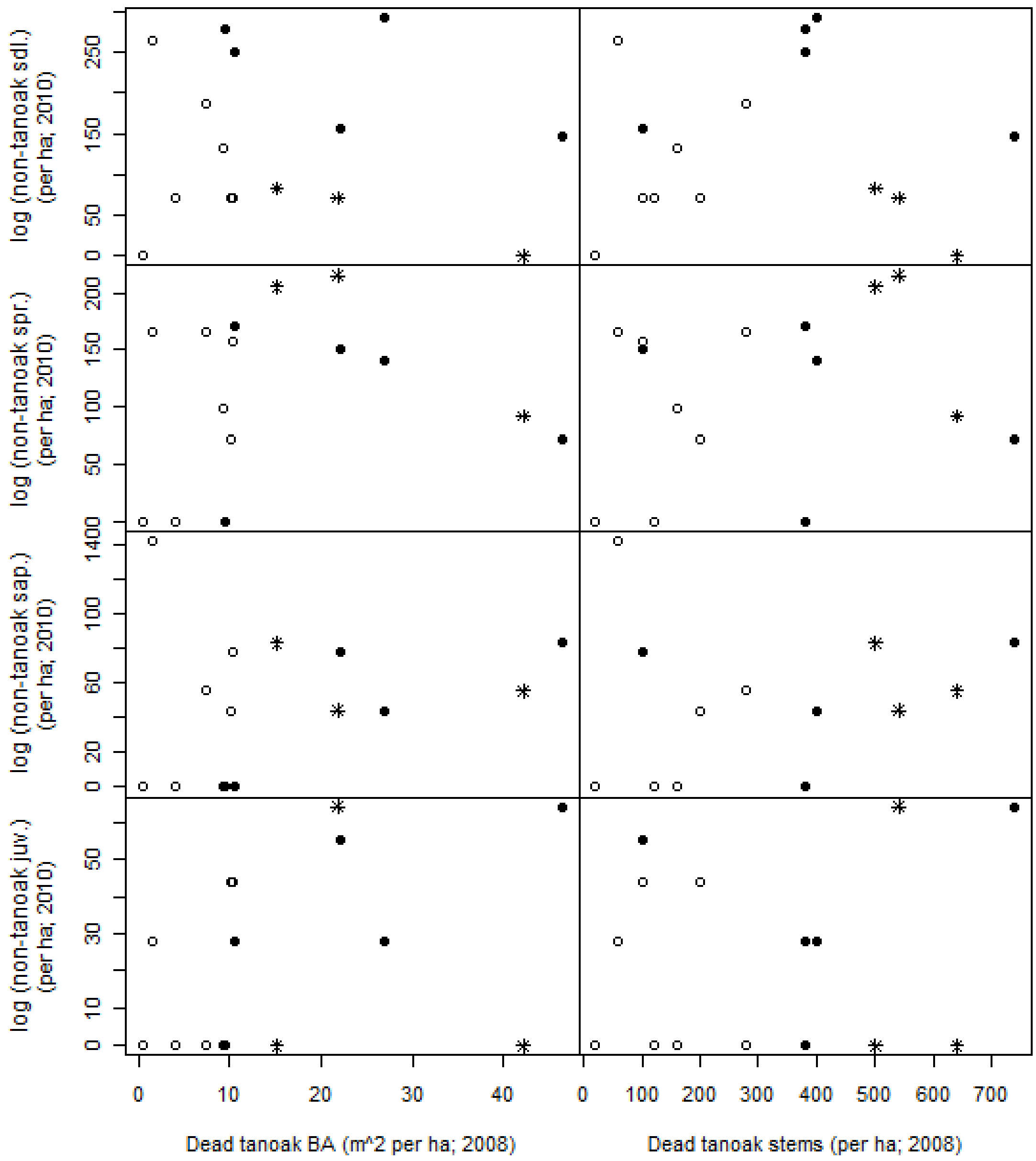

Fig. 1.4. Non-tanoak seedlings, basal sprouts, saplings, and juvenile trees (2010) as a function of tanoak mortality (2008). Solid circles and asterisks were deemed severely impacted ("severe" plots); asterisks indicate "regen-deficient" plots. Note that the y-axis has been log-transformed. Abbreviations are as follows: "sdl" = seedling, "spr" = basal sprout, "sap" = sapling," juv" = juvenile tree.

Severely impacted areas: regeneration and mortality

In the eight "severe" plots (those with $\geq$ 300 dead stems and/or $\geq$ 15 m^2 dead BA, per ha), the regeneration stratum was generally dominated by tanoak and redwood, but seedlings of other species were present at higher levels in certain areas (Table 1.1). The median density of tanoak seedlings, basal sprouts, saplings, and juvenile trees was 1960, 4600, 180, and 0 per ha, respectively. Corresponding values for redwood were 1380, 1500, 100, and 40. Redwood accounted for 100% of non-tanoak basal sprouts, saplings, and juvenile trees, and the majority of non-tanoak seedlings in most plots (median non-tanoak seedlings = 1740; median redwood seedlings = 1380). Douglas-fir seedlings occurred in three of the eight severely impacted plots and exceeded densities of 3500 per ha in two of these plots. Pacific madrone and California bay seedlings were each present in four severely impacted plots, but their densities never exceeded 600 and 160 per ha, respectively. Seedlings of California nutmeg and bigleaf maple each occurred in only one plot, at densities of 240 and 40 per ha, respectively.

In these plots, the median amount of dead tanoak (absolute value and percent of total), in terms of BA and stem counts, was 21.9 (m^2 per ha; 66.4%) and 450 (per ha; 68.0%), respectively (Table 1.1). As quantified by percent dead, the most severely impacted plot (B) exhibited mortality exceeding 90%, in terms of both stem counts and BA. When quantified with absolute mortality, the most severely impacted plot (D) contained 46.4 m^2 dead BA per ha and 740 dead stems per ha. The median amount of dead tanoak that was *broken/fallen* (bole broken at a diameter of $\geq$ 5 cm), in terms of BA and stem counts, was 15.8 (75.2% of dead) and 270 (79.1% of dead), respectively.

Three plots (which I refer to as "regen-deficient"; A, B, and C) exhibited a total density of non-tanoak seedlings that was less than the density of dead tanoak stems (Table 1.1). Regeneration in these plots was consistently dominated by tanoak and redwood, but numbers were highly variable between plots and regeneration categories. With regard to other tree species, no basal sprouts, saplings, or juvenile trees were present in any plot, and seedlings were very uncommon. Seedlings of California bay (B: 160 per ha) and bigleaf maple (C: 40 per ha), the only other species present, occurred in only one plot each, both at densities insufficient to replace the number of tanoak trees that had already died by 2008. Densities of redwood basal sprouts, saplings, and juvenile trees, as well as tanoak regeneration (all categories combined), exceeded densities of dead tanoak stems in most (in the case of redwood) or all (in the case of tanoak) plots, but it is unlikely that these sources of regeneration will be able to fully re-occupy mortality gaps; this statement is justified in the discussion.

In the three "regen-deficient" plots, canopy cover was highly variable (54.2, 82.5, and 90.1%; for A, B, and C, respectively), as was dead tanoak BA (42.2, 21.8, and 15.2 m^2 per ha; Table 1.1). The density of dead tanoak stems was more consistent (640, 540, and 500 per ha), as was the percent of total tanoak that was dead, whether quantified by BA (93.0, 95.6, and 82.6%) or stem counts (86.5, 93.1, and 80.6%). The percent of dead tanoak that had broken/fallen was also consistently high, whether quantified by BA (81.5, 91.7, and 76.3%) or stem counts (78.1, 88.9, and 80.0%), suggesting that much of this mortality occurred well before the 2008 measurements.

Table 1.1. Regeneration, canopy cover, and mature tanoak data (abundance, mortality, and deterioration) in "severe" plots.

Plot ID (or median value)		median	A	B	C	D	E	F	G	H
Tanoak	sdl	1960	360	240	4640	3160	5440	1240	1120	2680
	spr	4600	3840	560	5840	9960	4360	4840	5880	4360
	sap	180	2120	0	80	1720	960	240	120	80
	juv	0	0	0	0	0	360	0	0	0
Redwood	sdl	1380	0	40	240	960	1800	20400	37520	56560
	spr	1500	360	8640	6800	200	1720	2880	0	1280
	sap	100	120	80	280	280	240	0	0	80
	juv	40	0	160	0	160	120	40	0	40
Pacific madrone	sdl	20	0	0	0	600	40	0	40	200
	spr	0	0	0	0	0	0	0	0	0
	sap	0	0	0	0	0	0	0	0	0
	juv	0	0	0	0	0	0	0	0	0
California bay	sdl	20	0	160	0	0	80	40	40	0
	spr	0	0	0	0	0	0	0	0	0
	sap	0	0	0	0	0	0	0	0	0
	juv	0	0	0	0	0	0	0	0	0
Bigleaf maple	sdl	0	0	0	40	0	0	0	0	0
	spr	0	0	0	0	0	0	0	0	0
	sap	0	0	0	0	0	0	0	0	0
	juv	0	0	0	0	0	0	0	0	0
Douglas-fir	sdl	0	0	0	0	0	0	80	3640	3920
	spr	0	0	0	0	0	0	0	0	0
	sap	0	0	0	0	0	0	0	0	0
	juv	0	0	0	0	0	0	0	0	0
California nutmeg	sdl	0	0	0	0	0	0	0	240	0
	spr	0	0	0	0	0	0	0	0	0
	sap	0	0	0	0	0	0	0	0	0
	juv	0	0	0	0	0	0	0	0	0
All non-tanoak species	**sdl**	**1740**	**0**	**200**	**280**	**1560**	**1920**	**20520**	**41480**	**60680**
	spr	1500	360	8640	6800	200	1720	2880	0	1280
	sap	100	120	80	280	280	240	0	0	80
	juv	400	0	160	0	160	120	40	0	40
Canopy Cover	%	83.3	54.2	82.5	90.1	55.5	75.1	88.4	95.1	84.1
Total Tanoak	BA	39.8	45.4	22.8	18.4	52.6	55.8	34.0	34.2	53.8
	stems	760	740	580	620	920	180	800	940	780
Dead Tanoak	BA	21.9	42.2	21.8	15.2	46.4	22.0	10.6	9.6	27.0
	stems	**450**	**640**	**540**	**500**	**740**	**100**	**380**	**380**	**400**
Broken/Fallen Dead Tanoak	BA	15.8	34.4	20.0	11.6	34.4	21.8	2.0	3.2	3.8
	stems	270	500	480	400	600	80	120	140	100
% Dead (of Total)	BA	66.4	93.0	95.6	82.6	88.2	39.4	31.2	28.1	50.2
	stems	68.0	86.5	93.1	80.6	80.4	55.6	47.5	40.4	51.3
% Broken/Fallen (of Dead)	BA	75.2	81.5	91.7	76.3	74.1	99.1	18.9	33.3	14.1
	stems	79.1	78.1	88.9	80.0	81.1	80.0	31.6	36.8	25.0

Note. Plots are identified and ordered (i.e. A through H) by the number of non-tanoak seedlings; plots A, B, and C are "regen-deficient". All values are provided as densities per ha (except proportional metrics). Canopy cover and regeneration values are from 2010; tanoak abundance, mortality, and deterioration values are from 2008. "Broken/fallen" = trees with boles broken at a diameter of $\geq$ 5 cm; "sdl" = seedling; "spr" = basal sprout; "sap" = sapling; "juv" = juvenile tree.

Discussion

Main findings

Despite a significant reduction in canopy cover, my data suggest that a regenerative response to tanoak mortality is *not* occurring in SOD-impacted redwood forests. Tree regeneration was abundant in some mortality gaps, but regeneration levels were generally equivalent in severely impacted areas and relatively unaffected areas. These results were consistent across all mortality metrics, regeneration categories, and species (with the exception of tanoak saplings, which increased with dead tanoak basal area, and tanoak juvenile trees, which exhibited a negative relationship with dead tanoak stem density). Redwood and tanoak dominated the regeneration stratum in heavily diseased areas (and throughout the entire study area), while regeneration of other tree species was present only in isolated patches, and typically in very low densities.

Cobb et al. (2010) suggested that California bay may benefit more than any other tree species from SOD-induced tanoak mortality in redwood forests, because of positive feedbacks between inoculum loads and the abundance of California bay (which supports the most prolific sporulation of any host, but is not killed by *P. ramorum*; Davidson et al. 2008), as well as similarities in growth form and size between tanoak and California bay. However, at my study site, current regeneration patterns do not support this assertion. Although California bay seedlings occurred in 50% of "severe" plots, their densities were uniformly low (never exceeding 160 per ha, with a median of 20), and California bay basal sprouts, saplings, and young trees were entirely absent from all "severe" plots. In contrast, redwood regeneration occurred in all of these plots, and redwood seedlings alone had a median density of 1380 per ha (69 times that of California bay), suggesting that redwood is currently much better poised to claim the space previously held by tanoak.

Deficiencies in regeneration

Although broad patterns indicate that regeneration is sufficient to replace dead tanoaks, I have identified some patches (1/20 ha in size) in which the density of dead tanoak stems exceeded the density of non-tanoak seedlings. Tanoak regeneration and other forms of redwood regeneration (basal sprouts, saplings, and juvenile trees) were abundant in some of these plots, but I have deemed these plots deficient in regeneration for the following reasons: a) *P. ramorum* is established in all SOD-impacted areas and tanoak regeneration is thus unlikely to survive to maturity (Cobb et al. 2010), and b) redwood basal sprouts will not be able to fully re-occupy large mortality gaps because these sprouts necessarily emerge at the base of existing redwood trees, which tend to exist in dense discrete clumps in second-growth redwood-tanoak forest (Ramage and O'Hara 2010; Douhovnikoff et al. 2004), and generally exhibit a strong vertical growth habit. The same rationale applies in large part to redwood saplings and young trees, many of which were associated with established trees and most likely of sprout origin.

While additional regeneration will almost certainly appear in the future, an insufficient passage of time does not appear to fully explain the paucity of regeneration in some mortality gaps (or the corresponding lack of a regenerative response to tanoak mortality throughout the study area). Using data collected in a neighboring redwood forest as part of a separate but related project in which individual tanoaks were evaluated in 2007 and again in 2009 (Ramage et al. 2010), I calculated the following: of the trees that were broken/fallen in 2009, 39% were dead but intact in 2007 and only 7% were alive in 2007. These numbers suggest that the vast majority of broken/fallen trees in the "regen-deficient" plots (and in the other "severe" plots) died at least two years prior to the 2008 measurements. Because regeneration tallies were conducted in 2010, I can infer that the recruitment environment (i.e. the forest floor) was experiencing increased light levels for at least four years. In one "regen-deficient" plot (B), historical data document that SOD-induced tanoak mortality began at least nine years prior to regeneration tallies (Spencer 2004), which is considerably longer than the typical masting intervals for most tree species at my study site (Burns and Honkala 1990, Hobbs et al. 1992).

Mechanisms that may be contributing to the deficiency of seedling recruitment in some areas, and the general absence of a regenerative response to tanoak mortality, include: (a) dispersal limitation (which is suggested the general paucity of mature seed producing trees other than redwood and tanoak within the study area), (b) unidentified abiotic constraints (e.g. fine-scale soil properties that support tanoak but inhibit other species), (c) absence of conditions associated with historical disturbances (e.g. in contrast to fire, flooding, slope failure, and uprooting events [which dominated the pre-settlement disturbance regime of redwood forests; Lorimer et al. 2009], little or no mineral soil is exposed as a result of SOD-induced mortality), (d) direct suppression by *P. ramorum* (which can kill seedlings of some tree species that are relatively unaffected when mature; Davidson et al. 2002), (e) indirect effects of SOD (e.g. high levels of generalist decay fungi can build up on decaying root systems and overcome the defenses of young seedlings; Edmonds et al. 2000, Baumgartner and Rizzo 2001), and/or (f) competition with tanoak sprouts arising from the root systems of top-killed trees (tanoak sprouts often form dense clumps that may inhibit proximate regeneration; Cobb et al. 2010; Burns and Honkala 1990).

Tanoak regeneration patterns / Confirmation of disease presence

The positive relationship between tanoak saplings and tanoak mortality (dead basal area) probably reflects the initial tendency of tanoaks that are top-killed by SOD (as well as tanoaks that are infected but still living), to sprout vigorously (Ramage et al. 2010; Cobb et al. 2010) and/or increased growth rates of advanced regeneration in mortality gaps. The absence of a relationship between tanoak mortality and tanoak seedlings or basal sprouts may: a) indicate a balance between disease-induced recruitment and mortality within these regeneration classes, and/or b) reflect the fact that tanoak seedlings and sprouts (which are extremely shade tolerant; Burns and Honkala 1990) are often abundant in healthy stands. The strong negative relationship between tanoak juvenile stems and tanoak mortality (dead stems) suggests that individuals in this size class (3-10 cm DBH) are suffering high rates of SOD-induced mortality and/or not recruiting in diseased areas.

Laboratory tests confirmed that *P. ramorum* was present in five of the eight "severe" plots, and it was abundantly clear that SOD was also causing mortality in the other three "severe" plots. Negative tests probably resulted because sampling followed two very dry years and false negatives are common in dry conditions (Rizzo et al. 2005); two plots that tested negative were confirmed positive in a previous study that was conducted in a wetter year (Spencer 2004). Furthermore, all "severe" plots exhibited (a) tanoak mortality that was extensive and locally intensive, which is solely associated with SOD (Swiecki and Bernhardt 2006), (b) trees in various stages of decline and deterioration, which is characteristic of SOD disease progression, and (c) typical SOD symptoms (bleeding, bole cankers, *Hypoxylon* fungi, beetle holes and/or frass, and canopy dieback) and deterioration patterns (incremental collapse of standing dead trees; Swiecki and Bernhardt 2006; McPherson et al. 2010).

Conclusions and management considerations

SOD may ultimately create a *niche opportunity* in redwood forests (i.e. an opportunity for an absent or uncommon species to invade or increase in abundance; sensu Shea and Chesson 2002), but I have not discovered evidence that this phenomenon is occurring. Rather, tree species other than redwood and tanoak have made only small and highly variable incursions into mortality gaps, and some areas appear to lack sufficient regeneration for full re-occupancy of growing space, demonstrating that the future composition of SOD-impacted redwood forests is still far from certain. The ultimate ability of potential tanoak replacement species to co-exist with redwood in areas previously dominated by tanoak may only be apparent if and when such species are able to recruit in high numbers; at present, dispersal and recruitment limitation (both of which may be highly stochastic) are likely the dominant community assembly processes, but as these species begin to actively compete in areas previously occupied by tanoak, deterministic niche-related processes may become more important. For instance, tanoak develops a deep taproot (Burns and Honkala 1990), a characteristic that likely helps it to co-exist with redwood (which does not develop a taproot; Burns and Honkala 1990), suggesting that other deeply rooted tree species may be best equipped to compete with redwood in the absence of tanoak.

Land managers who wish to minimize the long-term impacts of tanoak decline (e.g. trophic cascades resulting from the loss of tanoak acorns, reduced *resistance* and/or *resilience* in the face of future threats; sensu Suding et al. 2004) should consider the intentional establishment of other native tree species in heavily impacted areas. Such efforts could optionally focus upon species at or near the northern extent of their range, in anticipation of generally warming climatic conditions (i.e. *managed relocation*, sensu Richardson et al. 2009). By choosing to direct ecological trajectories, managers may successfully alter long-term characteristics such as species composition and stand structure, but such actions will be most efficient in the early stages of community assembly (Thompson et al. 2001). Furthermore, because SOD-induced tanoak mortality gaps are a novel occurrence, and novel ecosystems are likely to present unfamiliar and unforeseen challenges (Hobbs et al. 2006), it is prudent to assume that successful plantings (or other mitigation actions) may require considerable experimentation. As an alternative approach, managers may opt to actively maintain the open nature of these sites, so that if and when SOD-resistant tanoak genotypes are discovered, these genotypes can be readily reintroduced into areas where tanoak previously dominated.

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Chapter 2

Sudden oak death-induced tanoak mortality in coast redwood forests: Current and predicted impacts to stand structure

Benjamin S. Ramage

Tanoak (*Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*) is one of the most widespread and abundant associates of coast redwood (*Sequoia sempervirens*), but little is known about the structural relationships between these two species. Knowledge of such relationships is essential for a thorough understanding of the impacts of sudden oak death (caused by the exotic pathogen *Phytophthora ramorum*), which is currently decimating tanoak populations throughout the redwood range. In this study, I utilized a stratified plot design and a stand reconstruction technique to assess structural impacts, at present and in the future, of this emerging disease. I found that residual trees in diseased plots were more aggregated than trees in unaffected plots, and I predicted that the loss of tanoak will lead to the following short-term changes: (1) greater average diameter, height, height-to-live-crown, and crown length, (2) higher standard deviations of diameter, height, and crown length, and (3) larger average nearest neighbor differences for diameter, height, and crown length. In addition, plots lacking tanoak (living or dead) – as compared to plots with tanoak – exhibited (1) greater average diameter, (2) higher standard deviations of diameter and crown length, and (3) increased nearest neighbor differences with regard to diameter, height, and crown length. I also conducted a preliminary exploration of how sudden oak death-induced structural changes compare with typical old-growth characteristics, and how this disease may affect the structure of old-growth forests.

Introduction

Tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H.Oh syn. *Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) is widespread and abundant in coast redwood (*Sequoia sempervirens* (D.Don) Endl.) forests, and is believed to be an integral component of the structure and function of these unique ecosystems (Burns and Honkala 1990, Hunter et al. 1999, Noss 2000). However, the close association between redwood and tanoak may be relegated to history if sudden oak death (SOD) continues to spread throughout coastal California. This emerging forest disease, which is caused by the exotic pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock, is currently threatening several native tree species, but tanoak is the most severely impacted. Current research indicates drastic declines in tanoak populations and mounting evidence (e.g. field studies, genetic resistance trials, disease progression models) suggests that SOD could eventually drive tanoak toward extinction in redwood forests (Rizzo et al. 2005, Maloney et al. 2005, McPherson et al. 2005, Meentemeyer et al. 2004, Davidson et al. 2008).

Forest stand structure is often a key determinant of physiognomic resistance, compositional resilience, ecosystem function, wildlife habitat, biodiversity, hydrologic processes, micro-climatic conditions, and regeneration patterns (Oliver and Larson 1996, Zenner and Hibbs 2000, Kint et al. 2003, Pommerening 2002, Ishii et al. 2004, McElhinny et al. 2005, Chang 2006). Stands with greater vertical and/or horizontal heterogeneity are generally believed to support a higher number of species and to be more productive than compositionally similar stands with more uniform structures (Pommerening 2002, Ishii et al. 2004, McElhinny et al. 2005), and stands with multiple canopy strata are thought to be *resistant* and/or *resilient* (sensu Millar et al. 2007) to a broader spectrum of disturbances than single-stratum stands (O'Hara 2006). Stand structure influences several hydrological processes (Ford and Vose 2007, Fernandez et al. 2006, Staelens et al. 2006, Andre et al. 2008), and may have a greater effect on wildlife habitat value than tree species composition; throughout the western United States, northern goshawks (*Accipiter gentilis* L.) tend to select stands with large trees and closed canopies, with little apparent concern for the component tree species (Greenwald et al. 2005). In redwood forests, marbled murrelets (*Brachyramphus marmoratus* Gmelin) nest exclusively in tall trees with large limbs, but do not appear to discriminate between redwood and other conifers capable of achieving very large sizes, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Noss 2000). In general, redwood forests with greater structural diversity are believed to support a greater number of vertebrate species (Noss 2000).

While several non-spatial structural attributes (e.g. total basal area, standard deviation of height) have tremendous predictive value, spatially explicit metrics are often necessary to explain ecological processes and functions. Horizontal positioning of trees is particularly predictive of light levels and regeneration patterns (Oliver and Larson 1996, Kint et al. 2003), as well as several hydrological phenomena; at similar stocking levels, canopy interception and throughfall rates are affected by the spatial pattern of stems (Oliver and Larson 1996, Chang 2006, Fernandez et al. 2006). Species diversity may also be affected by spatially explicit factors; for example, following timber harvest in western Oregon and Washington states, Luoma et al. (2004) found that species of ectomycorrhizal fungi differed between dispersed and aggregated retention units. In redwood forests, horizontally heterogeneous stands likely support more species than more homogenous stands, and growth rates of young trees are generally greater in more exposed patches (Noss 2000, O'Hara et al. 2007). However, very few data exist documenting the specific implications of horizontal spatial patterns in redwood ecosystems; such patterns may be particularly complex given the tendency of both redwood and tanoak to produce basal sprouts (especially after disturbance), forming multi-stemmed clumps and contributing to small-scale site persistence (Burns and Honkala 1990, Noss 2000, Waring and O'Hara 2008).

Despite the widely recognized importance of three-dimensional structural characteristics, and the abundance of tanoak in redwood forests (often as a persistent lower canopy layer; Hunter et al. 1999, Waring and O'Hara 2008), no previous initiatives have examined the spatially explicit structural relationships between these two species, and very few have considered any structural attributes of tanoak. Although the ecological value of tanoak is undeniable (tanoak is a prolific producer of large and highly nutritious acorns; Burns and Honkala 1990), its structural worth is not well understood. I hypothesized that: (1) stands with abundant tanoak exhibit greater structural complexity than stands lacking tanoak; (2) SOD-induced tanoak mortality has reduced, or will reduce, the structural complexity of affected stands; and (3) non-spatial metrics cannot fully characterize the structural attributes of tanoak in redwood forests. I tested these hypotheses, while developing a framework for understanding SOD-induced structural changes, by examining the current impacts of tanoak mortality, predicting the immediate impacts of 100% tanoak mortality, and comparing structures in areas with and without tanoak. In addition, I conducted preliminary explorations of SOD impacts in old-growth forests, and considered relationships between SOD-induced second-growth structures and typical old-growth redwood structures (which are characterized by larger trees, greater vertical complexity, and more uniform dispersion patterns; Noss 2000, Sillett and Van Pelt 2007, Waring and O'Hara 2008, Douhovnikoff et al. 2004).

Methods

Field research was conducted in three different coastal California counties, at sites which contain redwood forest and are infected with *P. ramorum*. Specific study locations were as follows: Henry Cowell Redwoods State Park (Santa Cruz County), Marin Municipal Watershed District (Marin County), and Humboldt Redwoods State Park (Humboldt County). Within these three sites, I installed a total of 13 plots (23 meter radius; 1/6 hectare) in areas satisfying the following criteria: (a) sufficient redwood coverage (at least 25% redwood canopy cover in all four quadrants of a ¼ hectare extended plot); (b) between 50 and 200 meters from trails or roads; and (c) slopes less than 60% (31 degrees). Plots were installed within representative areas capturing the extremes of tanoak abundance and disease severity: (a) little or no tanoak ["no-tanoak"; NT]; (b) abundant tanoak with little or no SOD ["healthy"; H]; or (c) abundant tanoak with severe SOD ["diseased"; D]. Areas deemed "representative" were identified as part of previous related research (currently unpublished) by the authors of this paper; suitable areas (which ranged in size from approx. one to three hectares) were subjectively selected (using ocular cover class estimates of tanoak abundance and mortality), but precise plot locations were randomized.

I did not verify the presence of *P. ramorum* in diseased plots, but I am confident that these plots were indeed infected because (a) mortality levels were very high and no other agent is known to cause such severe and widespread mortality of tanoak (Swiecki and Bernhardt 2006), (b) presence of the pathogen has been previously confirmed in the general vicinity of all diseased plots (Waring and O'Hara 2005, Spencer 2004, Maloney et al. 2005), and (c) characteristic symptoms of SOD (see Rizzo et al. 2005) were common. Some "healthy" plots may also have been infected with *P. ramorum* (areas that are entirely unaffected have become very rare at many infected sites), but any resulting tanoak mortality was much lower than in "diseased" plots. Within my study area, redwood forest with high abundance of hardwoods other than tanoak was very uncommon, and thus NT plots were located in areas with a small or non-existent hardwood component. Most plots (11) were installed in second-growth forest, but two were installed in old-growth forest in order to facilitate a preliminary examination of variables related to old-growth status. Exact harvest dates could not be determined for all second-growth plots due to incomplete management histories and the tendency of redwood to produce discontinuous growth rings (Waring and O'Hara 2006), but all available data indicate that all were harvested in the late 1800s or early 1900s. Key characteristics of all plots are provided in Table 2.1.

Table 2.1. Key characteristics of sample plots.

ID [1]	Plot [2]	County	Status & (% Dead)[3]	Second-growth / Old-growth	Slope Position	Slope (deg)
1	HCR-S1	Santa Cruz	Diseased (49)	Second-growth	Mid	16
2	HCR-S5	Santa Cruz	No Tanoak	Second-growth	Lower	15
3	HCR-S6	Santa Cruz	Healthy (10)	Second-growth	Mid	8
4	HRSP-S5	Humboldt	Healthy (10)	Old-growth	Lower	14
5	HRSP-S7	Humboldt	Healthy (12)	Second-growth	Lower	12
6	HRSP-S8	Humboldt	No Tanoak	Second-growth	Alluvial	2
7	HRSP-S9	Humboldt	No Tanoak	Old-growth	Alluvial	1
8	MMWD-43	Marin	Diseased (90)	Second-growth	Ridge	19
9	MMWD-S1	Marin	Healthy (24)	Second-growth	Mid	22
10	MMWD-S2	Marin	No Tanoak	Second-growth	Ridge	15
11	MMWD-S4	Marin	No Tanoak	Second-growth	Upper	17
12	MMWD-S7	Marin	Healthy (21)	Second-growth	Ridge	10
13	MMWD-S9	Marin	Diseased (74)	Second-growth	Ridge	18

[1] ID numbers correspond to labels on Figs. 2.4 through 2.6. [2] Plot names correspond to Figs. 2.1 through 2.3.
[3] Numbers in parentheses indicate the percent of tanoak stems that were dead.

All trees greater than or equal to 10 cm diameter-at-breast-height (DBH) were mapped by recording distance and azimuth from plot center (at breast height), and the following variables were recorded for each tree: species, health status, DBH, height, and height-to-live-crown (HLC). Height and HLC were measured with a Laser Ace hypsometer (Measurement Devices Ltd., York, UK). Multi-stemmed trees that were split below breast height were counted as separate trees. Crown ratio and crown length were subsequently calculated using height and HLC for each tree. In order to capture recent SOD-induced tanoak mortality, tanoak stems that were broken below breast height were recorded, provided that the fallen bole wood was relatively intact (i.e. it did not compact when stepped upon); in such cases, I estimated pre-death DBH, distance, and azimuth. Dead individuals of other tree species were not recorded if broken below breast height. In order to reconstruct height (for tanoak trees that were dead and broken/fallen) and HLC (for all dead tanoak trees), I used all living tanoak trees in the dataset to construct models fitting height and HLC against DBH. Simple linear models were used for both height ($p < 0.0001$, $r^2 = 0.53$) and HLC ($p < 0.0001$, $r^2 = 0.30$) because neither curvature nor heteroscedasticy were apparent in residual plots, and I found little statistical support for nonlinear models. The general allometric equation (height [or HLC] = $a + b*DBH^c$), one of the simplest nonlinear models commonly used for height vs. DBH relationships (Temesgen & Gadow 2004), provided good visual fits, but the inclusion of the exponential parameter only minimally improved r^2 values (to 0.56 and 0.31 for height and HLC, respectively). Height and HLC were not reconstructed for any species other than tanoak because this study focuses specifically on SOD-induced tanoak mortality and, for all other species, the percentage of stems that were dead was very low (e.g. redwood) and/or the total number of occurrences was very low (e.g. pacific madrone, *Arbutus menziesii* Pursh).

Individual tree-based variables were then used to calculate several plot-level metrics, which included basic structural attributes (simple totals and means), non-spatial measures of structural complexity (plot-level standard deviations), and spatially explicit measures of structural complexity: mean nearest neighbor differences (the plot-level mean difference between each tree and its nearest neighbor, with respect to several variables of interest), and the Clark & Evans aggregation index (Bailey & Gatrell 1995; Kint et al. 2003). The Clark & Evans aggregation index, which expresses the ratio of the average distance between each tree and its nearest neighbor to the average distance expected under a random distribution of points, is a metric of horizontal complexity (uniform stands represent simple structures while clumped stands are more complex). Patterns relating to DBH (standard deviations as well as nearest neighbor differences) are also indicative of horizontal complexity, while comparable patterns involving height and HLC are indicative of vertical complexity. In both dimensions (horizontal and vertical), and with both approaches (standard deviations and mean nearest neighbor differences), larger values signify greater structural complexity. For all spatially explicit metrics, I imposed a buffer (i.e. a guard area) of three meters, meaning that all focal points were required to be at least three meters from the plot boundary, while secondary points (i.e. nearest neighbors) could be selected from all points within the plot.

After calculating the plot-level summary statistics described above, I used these data to explore a conceptual model of potential past and future scenarios. I compared healthy, diseased, and no-tanoak plots, as well as reconstructed pre-SOD conditions (0% tanoak mortality) and projected future conditions (100% tanoak mortality); in addition, I examined predicted trends over time within each plot. My inferential framework rests upon existing research indicating that the current patchy distribution of SOD in redwood forests, at scales of tens to hundreds of meters, is primarily a result of historical and stochastic factors (Maloney et al. 2005, Rizzo et al. 2005, Moritz et al. 2008), as opposed to underlying biotic or abiotic conditions. Therefore, it is likely that consistent differences between healthy and diseased areas are caused by SOD, and I was thus able to assess structural changes resulting from SOD-induced tanoak mortality with only one season of field data. In contrast, differences between areas with and without tanoak may be controlled by other factors (e.g. soil properties), and thus I do not definitively assert tanoak presence as the ultimate determinant of structural patterns.

All statistical analyses utilized second-growth plots only; comparisons with old-growth plots were strictly qualitative. I used Tukey's Honestly Significant Difference (HSD) tests to identify differences among two separate sets of sample groups. The first HSD test (which I refer to as *observed*) assessed current differences between sampling strata (healthy, diseased, and no-tanoak), and the second HSD test (which I refer to as *inferred*) assessed differences between the following three groups: reconstructed 0% tanoak mortality plots (healthy and diseased plots combined), projected 100% tanoak mortality plots (healthy and diseased plots combined), and no-tanoak plots. In addition, the difference between 0% and 100% tanoak mortality was calculated for each plot individually, and a one-sample t-test was conducted to determine if these intra-plot differences, collectively, were significantly different from zero (referred to as *predicted*). Although I could have included a random effect (plot ID) in the *inferred* comparison between 0% and 100% mortality plots, such an analysis would have been redundant with the intra-plot *predicted* analyses; results were identical when a random effect was included in the *inferred* analyses. Dead stems of species other than tanoak were excluded from all analyses. The statistical software R, version 2.8.0, by The R Foundation for Statistical Computing, was used to conduct all analyses and create all figures; the supplemental package Spatstat, version 1.14-9, was used for all spatially explicit calculations.

Results

Many structural variables were significantly related to tanoak presence and/or tanoak mortality (Table 2.2). The loss of tanoak should obviously result in an immediate reduction in stem counts and basal area (by a predicted average of 438 stems and 23.8 square meters per hectare), but my results also show that 0% tanoak mortality reconstruction plots tended to have *more* stems and *less* basal area than plots without tanoak. Similarly, I found that mean DBH was predicted to increase with the loss of tanoak, and that 0% mortality reconstructions had lower mean DBH than 100% mortality projections and plots without tanoak. These findings demonstrate tanoak's smaller average DBH relative to redwood, as well as its tendency to form dense stands in redwood forests (see Figs. 2.1 through 2.3 for illustrations of representative second-growth plots in each sampling strata).

Table 2.2. Summary of main results. The "*predicted* intra-plot changes" column expresses the results of one-sample t-tests assessing whether within-plot differences between 0% and 100% tanoak mortality are significantly different from zero, and if so, the predicted direction of change (see methods section). The number of asterisks indicates the significance level: one symbol = 0.01 < p < 0.05; two symbols = p < 0.01; parentheses indicate borderline significance (0.10 < p < 0.05). The "group comparisons" column displays all significant relationships resulting from Tukey's HSD tests (see methods section); *inferred* (*i*) and *observed* (*o*) relationships are distinguished with parenthetical notations. All analyses consider second-growth plots only. "NN Diffs" is an abbreviation for nearest neighbor differences. Numerical results are provided in the chapter appendix.

Variable	***predicted* intra-plot changes (0% → 100% mort.)**	**group comparisons (*inferred* & *observed* relationships)**
Total Stems	decrease **	0% mort. > 100% mort. (*i*); 0% mort. > no-tanoak (*i*)
Total Basal Area	decrease **	0% mort. < no-tanoak (*i*); 100% mort. < no-tanoak (*i*); diseased < no-tanoak (*o*)
Mean DBH	increase **	0% mort. < 100% mort.(*i*); 0% mort. < no-tanoak (*i*)
Mean Height	increase **	no significant relationships
Mean HLC	increase *	no significant relationships
Mean Crown Length	increase *	no significant relationships
Mean Crown Ratio	not significant	no significant relationships
SD of DBH	increase *	0% mort. < no-tanoak (*i*);
SD of Height	increase *	no significant relationships
SD of HLC	(increase)	no significant relationships
SD of Crown Length	increase **	0% mort. < no-tanoak (*i*)
SD of Crown Ratio	not significant	no significant relationships
Mean NN Diffs: DBH	increase *	0% mort. < 100% mort.(*i*); 0% mort. < no-tanoak (*i*); healthy < no-tanoak (*o*); diseased < no-tanoak (*o*)
Mean NN Diffs: Height	increase **	0% mort. < no-tanoak (*i*)
Mean NN Diffs: HLC	not significant	no significant relationships
Mean NN Diffs: Crown Length	increase *	0% mort. < no-tanoak (*i*)
Mean NN Diffs: Crown Ratio	(increase)	no significant relationships
C&E Aggregation Index	decrease **	0% mort. > 100% mort. (*i*); healthy > diseased (*o*)

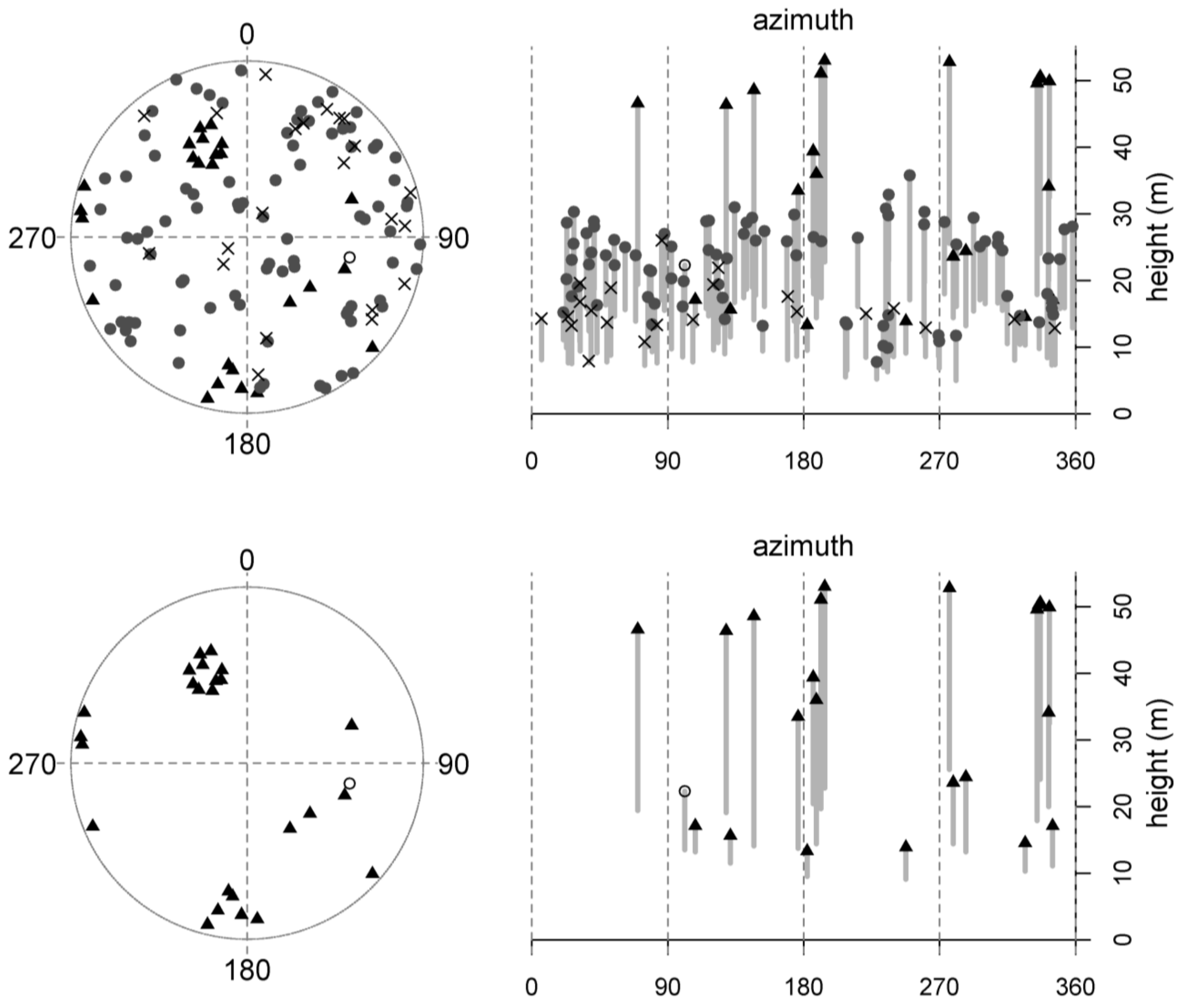

Fig. 2.1. A representative healthy plot (MMWD-S7; see Table 2.1). Trees are mapped (left) and represented vertically (right; top height and height-to-live-crown are plotted against azimuth, thus "unrolling" the 360 degree view from plot center, and achieving a two-dimensional image by flattening all distances from plot center into a single plane). The top set of graphs displays all trees, including reconstructed dead tanoaks, and the bottom set illustrates this plot after the removal of all tanoaks (both living and dead). Symbols represent the following: "X"s = dead tanoak; gray circles = living tanoak; black triangles = redwood; open circles = hardwoods other than tanoak; no conifers other than redwood were present in this plot. Gray bars display the length of the live crown (the symbol at the top of each bar is the total tree height and the lower limit of each bar is the height-to-live-crown).

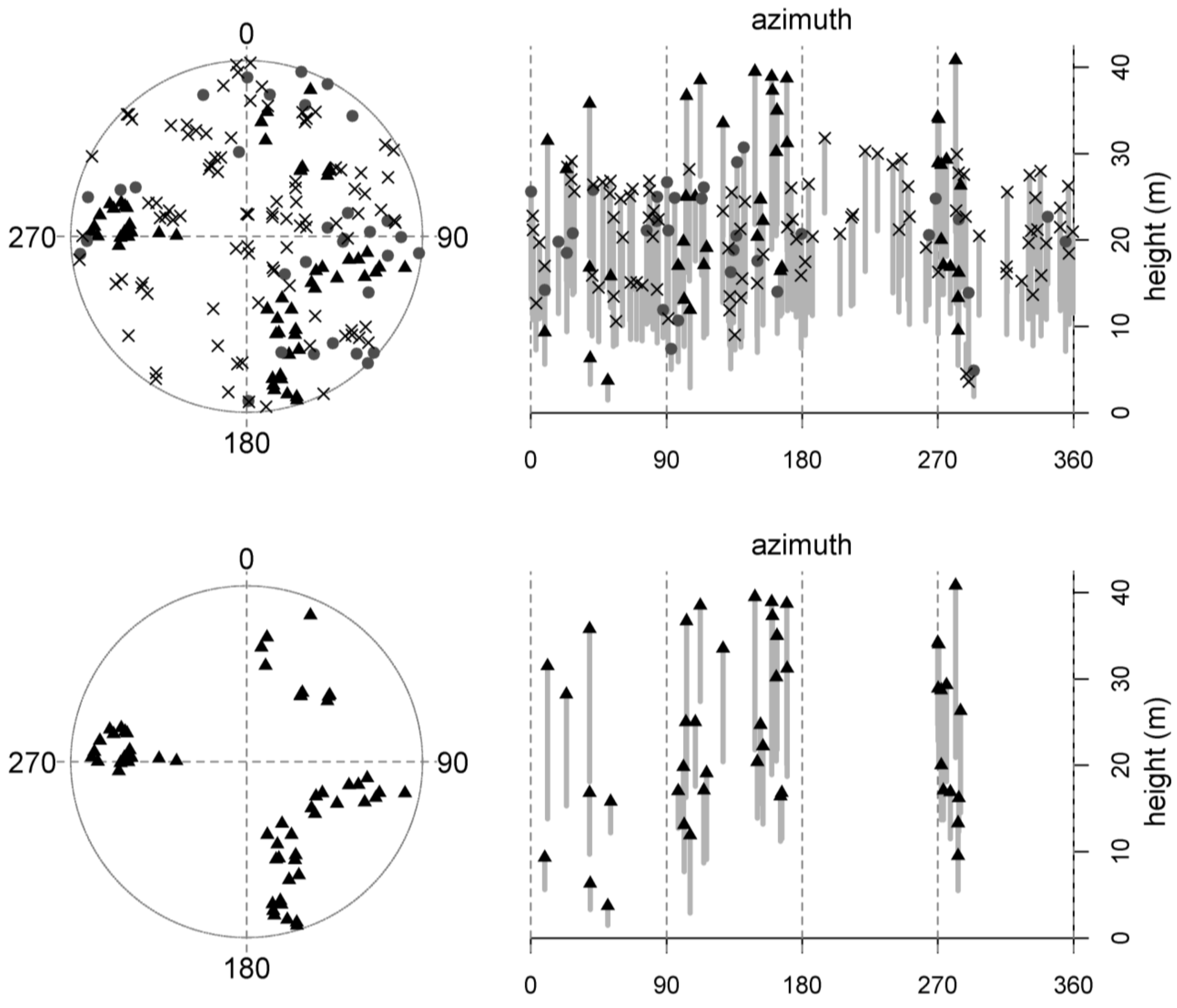

Fig. 2.2. A representative diseased plot (MMWD-S9; see Table 2.1). Symbology follows that of Fig. 2.1.

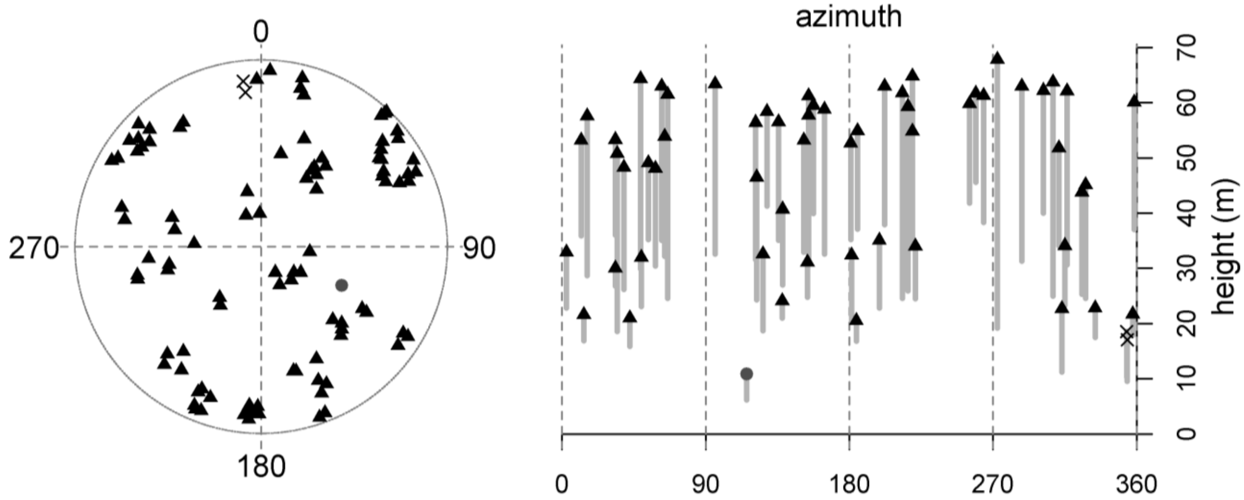

Fig. 2.3. A representative no-tanoak plot (HCR-S5; see Table 2.1). Symbology follows that of Fig. 2.1.

Mean height, mean HLC, and mean crown length increased with the predicted loss of tanoak, but Tukey's HSD tests failed to detect any differences between observed or inferred groups. As an example, I found that mean tree height within each plot was predicted to increase by an average of 5.7 meters, but because of large variations within each sampling stratum, no differences between groups were apparent (Fig. 2.4). Mean crown ratio exhibited no observed, inferred, or predicted relationships with tanoak presence or mortality (Fig. 2.5).

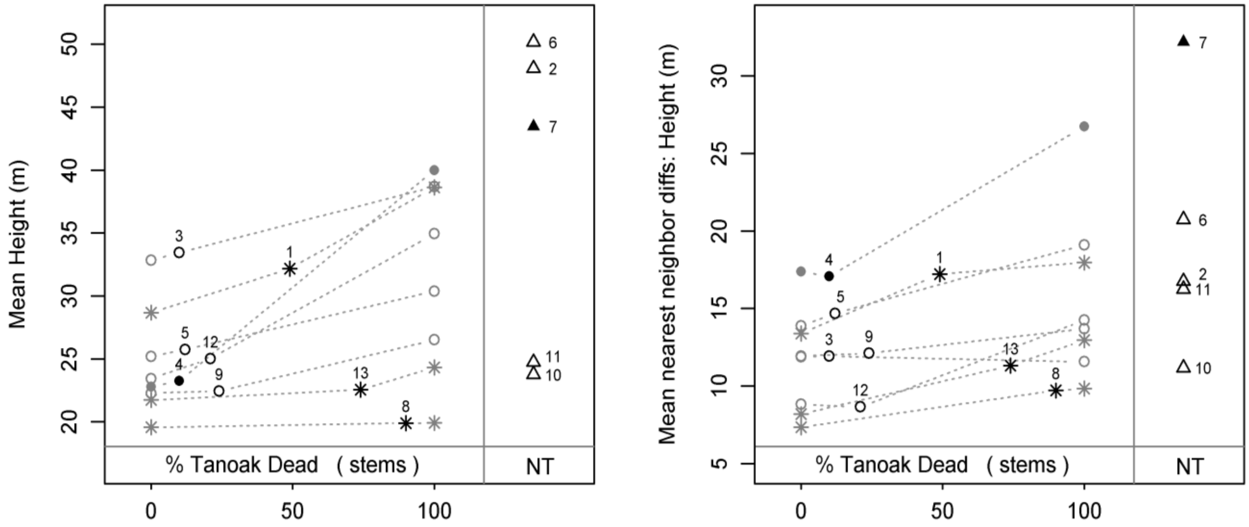

Fig. 2.4. Mean height (left) and mean height difference between nearest neighbors (right) as a function of plot status and disease progression. Black numbered symbols represent present conditions of all 13 sampled plots: circles = healthy plots (H); stars = diseased plots (D), triangles = plots without tanoak (NT); open symbols = second growth plots; closed symbols = old growth plots. Grey symbols represent reconstructed pre-SOD conditions (0% tanoak dead) and projected future conditions (100% tanoak dead) for all plots with tanoak. Grey dotted lines connect each plot's present condition to its respective pre-SOD and future conditions, thereby displaying predicted transitions for each plot. Plot ID numbers correspond to Table 2.1.

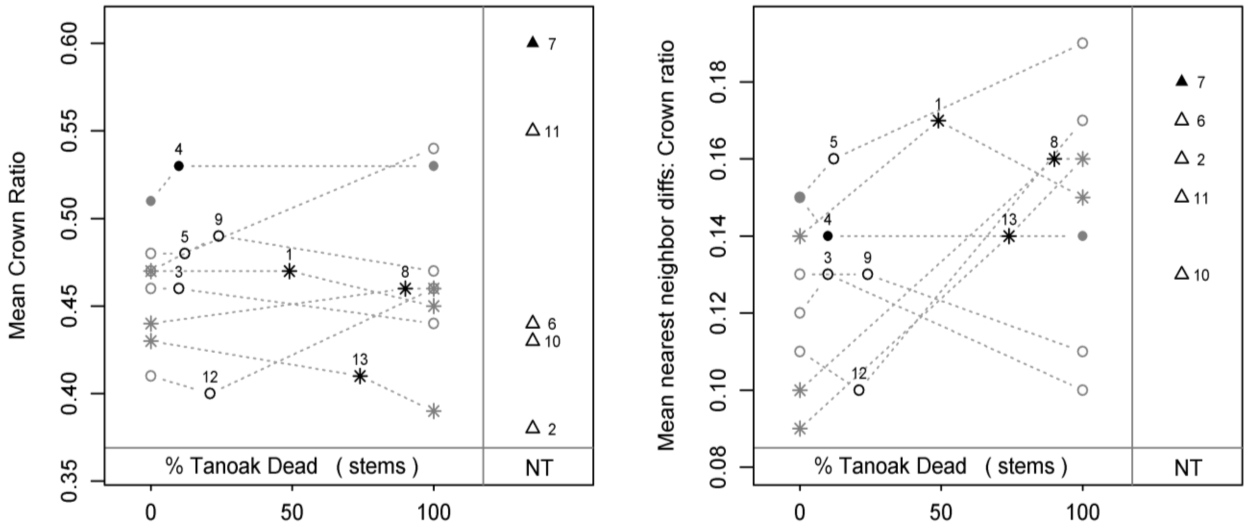

Fig. 2.5. Mean crown ratio (left) and mean crown ratio difference between nearest neighbors (right) as a function of plot status and disease progression. Symbology follows that of Fig. 2.4.

Several measures of structural complexity were related to tanoak presence and/or SOD-induced tanoak mortality. Mean DBH difference between nearest neighbors was predicted to increase with the loss of tanoak, and 0% mortality reconstructions had lower values than 100% mortality projections and plots without tanoak; in addition, mean DBH difference between nearest neighbors was observed to be higher in no-tanoak plots than in either healthy or diseased plots. Mean nearest neighbor height difference increased with the predicted removal of tanoak, and 0% mortality reconstruction plots had lower values than plots without tanoak (Fig. 2.4). Results for mean crown length difference between nearest neighbors were qualitatively identical to those for mean height difference between nearest neighbors. Mean HLC difference between nearest neighbors exhibited no observed, inferred, or predicted relationships with tanoak presence or mortality. Observed and inferred mean crown ratio differences between nearest neighbors were similarly non-significant, but there was a borderline positive trend predicted with the loss of tanoak (Fig. 2.5). Results for non-spatial structural complexity metrics (plot-level standard deviations) were similar to those for nearest neighbor differences, but non-spatial metrics exhibited fewer significant relationships (Table 2.2).

Spatial aggregation of stems was strongly impacted by tanoak mortality. Plots became "clumpier" (lower Clark & Evans aggregation index values) with the predicted loss of tanoak, and 100% mortality projections exhibited more clustering than 0% mortality reconstructions (Fig. 2.6; these patterns are also clearly evident in Figs. 2.1 through 2.3). Additionally, diseased plots were more clustered than healthy plots, indicating that – unlike most of my predicted trends – this impact had already occurred at the time of field measurements. Aggregation of stems within no-tanoak plots was not significantly different from any group with tanoak.

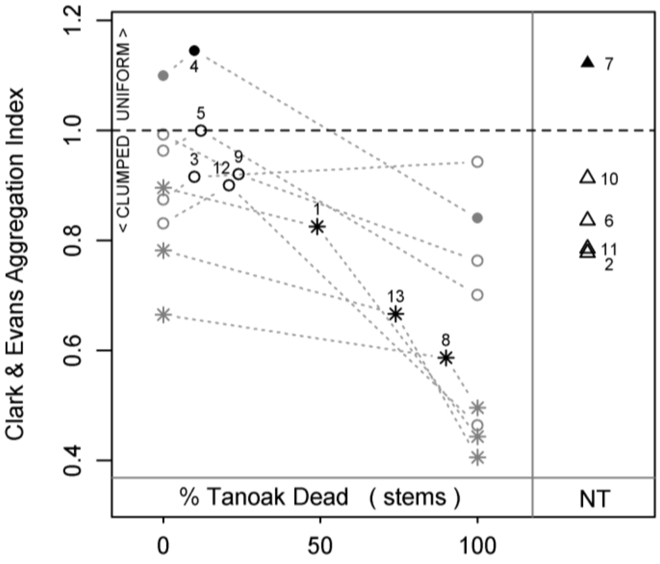

Fig. 2.6. Clark &Evans aggregation index as a function of plot status and disease progression. Lower index values indicate a greater degree of clustering. Symbology follows that of Fig. 2.4.

Most variables displayed characteristic distinctions between old-growth and second-growth redwood forests (Table 2.3), demonstrating that the two old-growth plots were representative; for instance, both old-growth plots were less aggregated (higher Clark & Evans values) than comparable (i.e. H or NT) second-growth plots (Fig. 2.6), and all nearest neighbor differences were higher in old-growth plots than in comparable second-growth plots (see Figs. 2.4 and 2.5 for examples). Following the predicted loss of tanoak from second-growth redwood forests, the values of most structural variables shifted towards old-growth values (H-OG and/or NT-OG), or exhibited inconsistent relationships with old-growth (H-OG and/or NT-OG). Only one variable, Clark & Evans aggregation index, diverged from both H-OG and NT-OG with the predicted loss of tanoak.

Table 2.3. Preliminary relationships between second-growth and old-growth. In the "Healthy" and "No Tanoak" columns, relationships are displayed for metrics in which all second-growth plot values (within the specified sampling strata) were consistently higher or consistently lower than the old-growth plot. In the "SG to *H*-OG?" column, "towards" indicates that the removal of tanoak was predicted to shift values of the given metric (for second-growth plots) towards the value of the healthy old-growth plot, while "away" indicates a predicted shift in the opposite direction of the healthy old-growth value. In the "SG to *NT*-OG?" column, "towards" indicates that the removal of tanoak was predicted to shift values of the given metric (for second-growth plots) towards the value of the no-tanoak old-growth plot, while "away" indicates a predicted shift in the opposite direction of the "no-tanoak" old-growth value. In the "OG vs SG trend" column, "similar" indicates that the removal of tanoak from the healthy old-growth plot was predicted to have qualitatively identical impacts (i.e. same direction of change) as the removal of tanoak from second-growth plots. Zeros indicate no clear pattern between second-growth and old-growth.

Variable	**Healthy**	**No Tanoak**	**SG to *H*-OG?** (0% to 100%)	**SG to *NT*-OG?** (0% to 100%)	**OG vs. SG trend** (0% to 100%)
Total Stems	SG > OG	SG > OG	towards	towards	similar
Total Basal Area	0	SG < OG	0	away	similar
Mean DBH	0	SG < OG	0	towards	similar
Mean Height	0	0	0	0	similar
Mean HLC	SG > OG	0	away	0	similar
Mean Crown Length	0	SG < OG	0	towards	similar
Mean Crown Ratio	SG < OG	SG < OG	0	0	0
SD of DBH	SG < OG	SG < OG	towards	towards	similar
SD of Height	SG < OG	SG < OG	towards	towards	similar
SD of HLC	SG < OG	SG < OG	towards	towards	similar
SD of Crown Length	SG < OG	SG < OG	towards	towards	similar
SD of Crown Ratio	0	0	0	0	0
Mean NN Diffs: DBH	SG < OG	SG < OG	towards	towards	similar
Mean NN Diffs: Height	SG < OG	SG < OG	towards	towards	similar
Mean NN Diffs: HLC	SG < OG	SG < OG	towards	towards	similar
Mean NN Diffs: Crown Length	SG < OG	SG < OG	towards	towards	similar
Mean NN Diffs: Crown Ratio	0	SG < OG	0	0	0
C & E Aggregation Index	SG < OG	SG < OG	away	away	similar

Discussion

My analyses indicate that several important structural characteristics are likely to be affected by the loss of tanoak from redwood forests, and I was able to detect a current difference in “clumpiness” between healthy and diseased plots. Predicted reductions in total stem counts and total basal area are an obvious immediate impact of SOD-induced tanoak mortality, and predicted instantaneous increases in mean DBH, mean height, mean HLC, and mean crown length are consistent with the larger size of redwood relative to tanoak. However, if new cohorts eventually regenerate in areas experiencing high levels of tanoak mortality (a regenerative response was *not* evident at the time of field sampling; unpublished data and chapter 1 of this dissertation), all of these basic structural attributes may rapidly shift towards their pre-SOD values.

I initially hypothesized that tanoak might be increasing the structural complexity of redwood forests, but I have found no evidence to support this hypothesis. On the contrary, the three measures of vertical complexity that were significantly related to tanoak (mean height difference between nearest neighbors, mean crown length difference between nearest neighbors, and standard deviation of crown length) indicated decreased structural diversity when tanoak was present (0% reconstruction as compared to no-tanoak plots), and predicted increases immediately following the loss of tanoak. Similarly, mean DBH difference between nearest neighbors, a form of horizontal structural complexity, was negatively affected by tanoak. Plots without tanoak exhibited higher values than healthy plots, diseased plots, and 0% mortality reconstructions, and the loss of tanoak was predicted to result in an immediate increase in mean DBH difference between nearest neighbors. All of these structural complexity metrics should also be affected by future regeneration, but unlike the basic structural attributes discussed above, a new cohort should cause these variables to diverge even farther from their pre-SOD values. Although few distinctions were apparent between plot-level standard deviations and nearest neighbor differences, several relationships were only detected with nearest neighbor differences, demonstrating that my spatially-explicit analyses provided additional information. For instance, in contrast to the nearest neighbor DBH results outlined above, there were no observed differences in plot-level standard deviation of DBH between plots with tanoak and plots without tanoak.

With respect to several attributes (DBH, height, and crown length), average nearest neighbor differences and/or plot-level standard deviations appear to be reduced by the fairly dense lower canopy layer of similarly sized tanoak trees (e.g. Figs. 2.1 and 2.2). However, these metrics of structural diversity may not capture all ecologically relevant structural characteristics; while patches of similarly sized trees will decrease neighbor nearest differences (and plot-level standard deviations, but to a lesser extent), they may increase other structural quantification metrics (e.g. “patch-types”; sensu Zenner and Hibbs 2000). For instance, the juxtaposition of a plot with a dense sub-canopy layer (e.g. Fig. 2.1) and a plot with a less contiguous lower canopy (e.g. Fig. 2.3) may be more relevant to some wildlife species than the contrasting characteristics of neighboring trees. Relevant metrics would necessarily require a coarser resolution (spatial grain), rendering any such analyses meaningless – or at least unreliable – at the scale of my plots. Several observations suggest that SOD-induced tanoak mortality may be accelerating the emergence of old-growth structural attributes in second-growth redwood stands. For example, tanoak mortality should lead to immediate as well as long-term increases in vertical complexity, an attribute that is generally characteristic of old redwood forests (Noss 2000, Sillett and Van Pelt 2007). My preliminary comparison of second-growth and old-growth plots suggested that, with the removal of tanoak, most structural metrics in second-growth plots should move closer to old-growth values (Table 2.3). In addition, another study concluded that SOD-induced tanoak mortality was increasing growth rates and basal sprout regeneration of neighboring redwood trees (Waring and O'Hara 2008). A notable exception to the potential shift towards old-growth characteristics was the predicted and observed increases in clumpiness. Old-growth redwood stands tend to exhibit much more uniform dispersion patterns than second-growth stands, which are characterized by dense clusters of trees surrounding cut stumps (Waring and O'Hara 2008, Douhovnikoff et al. 2004). However, this short-term increase in horizontal structural complexity could lead to a longer-term acceleration towards old-growth characteristics.

Given that the current distribution of SOD is very patchy at many scales, and that the dispersion of tanoak within redwood forests is similarly non-uniform, the structural impacts of SOD may be analogous to a large-scale form of variable density thinning. This method, which aims to increase structural complexity as well as growth rates of residual trees, has been proposed as a strategy to accelerate the transition from second-growth to old-growth in many forest types (Carey 2003), including coast redwood (O'Hara et al. 2010). While the structural impacts of SOD-induced tanoak mortality may therefore be desirable to natural resource managers and casual observers alike, the compositional impacts should be much more unsettling. Tanoak is currently widespread and abundant in old-growth redwood stands, especially on upland sites, and thus the loss of this species is likely to profoundly change the ecology of these forests. If SOD becomes established in old-growth redwood forests, my results suggest that the structural impacts will be similar to the impacts predicted for second-growth forests; for all variables for which the predicted loss of tanoak yielded statistically significant changes within second-growth plots (from 0% mortality reconstructions to 100% mortality projections), predictions for old-growth plots were qualitatively identical. However, all results regarding old-growth plots should be interpreted with caution because only two old-growth plots were sampled and no statistical tests were conducted.

My inability to observe many significant differences between healthy and diseased plots (in contrast to the large number of significant predictions and inferences) may indicate that many expected changes have yet to occur, but it is also possible that this lack of evidence was due to small sample sizes; for instance, healthy and diseased plots (present condition) consisted of four and three replicates, respectively, while 0% mortality reconstructions and 100% mortality projections consisted of seven replicates each. As such, I have not dismissed the possibility that many expected changes were already occurring at the time of field measurements. Similarly, structural variables that appeared to be entirely unrelated to tanoak presence and SOD-induced tanoak mortality might have exhibited subtle differences had sample sizes been larger.

Although my reconstructions (0% tanoak mortality prior to SOD) and projections (100% tanoak mortality in the future) test the extremes and may be somewhat unrealistic, these assumptions are within the realm of possibility; background mortality levels for tanoak (i.e. on uninfected sites) are very low, and SOD-induced tanoak mortality is already approaching 100% in some localized areas (Moritz et al. 2008; unpublished data from related research). However, it is important to emphasize that my 100% tanoak mortality projections assess the structural conditions that would exist if all remaining tanoak trees were to die immediately; in reality it could take many years for projected mortality levels to occur, allowing other trees to recruit in the interim period. Similarly, but with respect to my 0% tanoak mortality reconstructions, some recruitment may have occurred in the time that has passed between tree death and field measurements. It is also worth noting that my models using DBH for vertical reconstruction of dead tanoak stems do not capture all of the variation in height and HLC (r^2 equals .53 and .30, respectively), and thus reconstructed structural characteristics do not perfectly represent pre-SOD conditions. Depending upon diameter distributions, as well as precise locations of reconstructed tanoaks, estimated height and HLC values could serve to over- or under-estimate the actual structural complexity that existed prior to tanoak mortality. My inferences and predictions should thus be viewed as a preliminary assessment of the structural changes that may occur as a result of SOD. More complicated procedures (e.g. simulations of disease progression, recruitment, and/or growth responses) could be used in conjunction with my results in order to more accurately forecast future stand structures.

Plots that currently lack tanoak may or may not be representative of the structures that will emerge in the wake of SOD. If tanoak's current distribution is mostly due to dispersal limitation or stochastic factors, structures similar to those characterizing plots without tanoak may develop in infested areas. However, it is probable that underlying abiotic factors (e.g. soil conditions) and/or disturbance regimes (e.g. floods and silt deposition) affect the abundance of tanoak and other tree species within redwood forests (Burns and Honkala 1990, Lorimer et al. 2009). As such, I cannot definitely distinguish between the direct effects of tanoak presence and other potentially confounding factors. For instance, if areas where tanoak is currently thriving are inherently supportive of a lower canopy layer of hardwoods or other smaller statured trees, then pre-SOD structures may eventually re-emerge after the loss of tanoak; feasible replacements could include species such as California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.), canyon live oak (*Quercus chrysolepis* Liebm.), pacific yew (*Taxus brevifolia* Nutt.), and pacific madrone. On the other hand, tanoak may be the only tree species with the ability to effectively compete with redwood (i.e. maintain high relative abundance levels) on some sites. Given this scenario, infected areas would be more likely to acquire structural characteristics that resemble areas currently devoid of tanoak.

Although my data have revealed some interesting patterns, several key questions remain: How long will the immediate structural characteristics of SOD-induced tanoak mortality persist? Will infested stands remain open and aggregated far into the future or will a new cohort of trees quickly establish? Will areas vacated by tanoak begin to resemble areas currently devoid of tanoak, or will entirely new structures emerge? Changes to forest structure have been linked to trophic cascades and various ecosystem processes (Oliver & Larson 1996, Zenner & Hibbs 2000, Kint et al. 2003, Pommerening 2002, Ishii et al. 2004, McElhinny et al. 2005, Chang 2006), and thus these questions should be of great interest to a wide swath of society, encompassing land managers, recreational forest users, and anyone dependent upon ecosystem services from redwood forests. The structural impacts of SOD-induced tanoak decline may be considerable, but the compositional impacts of this emerging disease may be even greater. In redwood forests, total species richness is believed to be higher in areas where other tree species, especially those bearing fruits or nuts, are relatively abundant (Noss 2000), and tanoak acorns in particular are known to sustain a wide range of wildlife species (Burns and Honkala 1990). If tanoak is not replaced by one or more functionally similar tree species (e.g. canyon live oak), redwood forests – which are already relatively poor in tree species – may experience severe reductions in biodiversity; however, it is also important to recognize that diversity could possibly increase as a result of SOD (e.g. if tanoak is replaced by several tree species). The potential for trophic cascades and other compositional impacts, in conjunction with the structural impacts I have documented and/or predicted, suggest that redwood forests are currently experiencing profound and lasting ecological change.

Acknowledgements

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Chapter 2: Appendix

Table 2A.1. Means, standard deviations, and significance classes for *observed* groups. Note that means and standard deviations (summary statistics for sample groups) are provided for plot-level means and standard deviations (response metrics listed in the left column). Within each row, groups that do not share a letter were significantly different in Tukey's HSD tests. All analyses included second-growth plots only. "NN Diffs" = nearest neighbor differences.

	Healthy		Diseased		No-Tanoak	
Total Stems (# / ha)	595.5 ± 49.3	a	438.0 ± 72.8	a	442.5 ± 125.2	a
Total BA (m^2 / ha)	103.8 ± 10.7	ab	69.3 ± 14.2	a	145.7 ± 37.8	b
Mean DBH (cm)	38.5 ± 4.0	a	37.0 ± 6.7	a	54.3 ± 16.0	a
Mean Height (m)	26.7 ± 4.7	a	24.9 ± 6.5	a	36.7 ± 14.4	a
Mean HLC (m)	14.1 ± 2.7	a	13.7 ± 3.4	a	19.9 ± 9.3	a
Mean Crown Length (m)	12.6 ± 2.4	a	11.2 ± 3.3	a	16.8 ± 5.4	a
Mean Crown Ratio	0.458 ± 0.040	a	0.447 ± 0.032	a	0.450 ± 0.072	a
SD of DBH (cm)	27.2 ± 2.2	a	26.2 ± 6.1	a	36.7 ± 6.8	a
SD of Height (m)	11.6 ± 1.0	a	11.0 ± 3.7	a	15.4 ± 4.5	a
SD of HLC (m)	5.7 ± 0.9	a	6.5 ± 2.7	a	8.1 ± 3.4	a
SD of Crown Length (m)	7.6 ± 1.3	a	6.4 ± 2.1	a	10.2 ± 2.4	a
SD of Crown Ratio	0.135 ± 0.024	a	0.147 ± 0.023	a	0.140 ± 0.014	a
Mean NN Diffs: DBH (cm)	23.8 ± 3.0	a	25.8 ± 3.0	a	37.5 ± 5.1	b
Mean NN Diffs: Height (m)	11.9 ± 2.5	a	12.8 ± 4.0	a	16.2 ± 3.9	a
Mean NN Diffs: HLC (m)	6.1 ± 1.0	a	7.2 ± 2.9	a	9.0 ± 3.9	a
Mean NN Diffs: Crown Length (m)	7.3 ± 2.0	a	7.4 ± 2.6	a	11.2 ± 2.8	a
Mean NN Diffs: Crown Ratio	0.130 ± 0.025	a	0.157 ± 0.015	a	0.153 ± 0.017	a
C&E Aggregation Index	0.93 ± 0.05	a	0.69 ± 0.12	b	0.83 ± 0.06	ab

Table 2A.2. Means, standard deviations, and significance classes for *inferred* groups. Note that means and standard deviations (summary statistics for sample groups) are provided for plot-level means and standard deviations (response metrics listed in the left column). Within each row, groups that do not share a letter were significantly different in Tukey's HSD tests. All analyses included second-growth plots only. "NN Diffs" = nearest neighbor differences.

	0% mortality	100% mortality	No-Tanoak
Total Stems (# / ha)	724.3 ± 192.6 a	286.3 ± 82.0 b	442.5 ± 125.2 b
Total BA (m^2 / ha)	99.0 ± 13.2 a	75.3 ± 15.7 a	145.7 ± 37.8 b
Mean DBH (cm)	34.8 ± 5.3 a	50.8 ± 11.9 b	54.3 ± 16.0 b
Mean Height (m)	24.8 ± 4.6 a	30.5 ± 7.3 a	36.7 ± 14.4 a
Mean HLC (m)	13.3 ± 2.3 a	15.9 ± 4.0 a	19.9 ± 9.3 a
Mean Crown Length (m)	11.5 ± 2.4 a	14.6 ± 3.9 a	16.8 ± 5.4 a
Mean Crown Ratio	0.451 ± 0.025 a	0.459 ± 0.046 a	0.450 ± 0.072 a
SD of DBH (cm)	24.5 ± 4.8 a	31.6 ± 7.5 ab	36.7 ± 6.8 b
SD of Height (m)	10.7 ± 2.7 a	12.9 ± 2.5 a	15.4 ± 4.5 a
SD of HLC (m)	5.6 ± 1.7 a	6.3 ± 1.5 a	8.1 ± 3.4 a
SD of Crown Length (m)	6.6 ± 1.9 a	8.4 ± 2.1 ab	10.2 ± 2.4 b
SD of Crown Ratio	0.129 ± 0.178 a	0.140 ± 0.023 a	0.140 ± 0.014 a
Mean NN Diffs: DBH (cm)	20.9 ± 3.2 a	33.5 ± 11.2 b	37.5 ± 5.1 b
Mean NN Diffs: Height (m)	10.8 ± 2.6 a	14.2 ± 3.3 ab	16.2 ± 3.9 b
Mean NN Diffs: HLC (m)	5.8 ± 1.5 a	6.5 ± 2.3 a	9.0 ± 3.9 a
Mean NN Diffs: Crown Length (m)	6.4 ± 2.0 a	9.2 ± 2.5 ab	11.2 ± 2.8 b
Mean NN Diffs: Crown Ratio	0.120 ± 0.022 a	0.149 ± 0.032 a	0.153 ± 0.017 a
C&E Aggregation Index	0.86 ± 0.11 a	0.60 ± 0.20 b	0.83 ± 0.06 ab

Table 2A.3. Means, standard deviations, and significance levels for *predicted* intra-plot changes. Note that means and standard deviations (for predicted intra-plot changes) are provided for plot-level means and standard deviations (response metrics listed in the left column). P-values are from one-sample t-tests assessing whether intra-plot differences (between 0% and 100% tanoak mortality), collectively, were significantly different from zero. All analyses included second-growth plots only. "NN Diffs" = nearest neighbor differences.

	Predicted intra-plot difference: (100% - 0% mortality)	p-value
Total Stems (# / ha)	-438.0 ± 192.0	0.001
Total BA (m^2 / ha)	-23.8 ± 12.3	0.002
Mean DBH (cm)	16.0 ± 10.2	0.006
Mean Height (m)	5.7 ± 3.9	0.009
Mean HLC (m)	2.6 ± 2.1	0.016
Mean Crown Length (m)	3.1 ± 2.5	0.019
Mean Crown Ratio	0.007 ± 0.038	0.634
SD of DBH (cm)	7.1 ± 5.1	0.011
SD of Height (m)	2.2 ± 1.6	0.010
SD of HLC (m)	0.7 ± 0.9	0.084
SD of Crown Length (m)	1.8 ± 1.1	0.004
SD of Crown Ratio	0.011 ± 0.022	0.203
Mean NN Diffs: DBH (cm)	12.6 ± 10.2	0.017
Mean NN Diffs: Height (m)	3.4 ± 2.2	0.006
Mean NN Diffs: HLC (m)	0.68 ± 1.82	0.363
Mean NN Diffs: Crown Length (m)	2.9 ± 2.0	0.010
Mean NN Diffs: Crown Ratio	0.03 ± 0.04	0.097
C&E Aggregation Index	-0.26 ± 0.17	0.008

Chapter 3

The role of fire in the competitive dynamics of coast redwood forests

Benjamin S. Ramage

Fire is a major component of the disturbance regime and a critical determinant of competitive outcomes in many ecosystems. In forests dominated by coast redwood (*Sequoia sempervirens*), fire was frequent and ubiquitous prior to European settlement, but fires have been exceedingly small and rare over the last 70-80 years because of aggressive fire prevention and suppression policies. As a result, many aspects of redwood fire ecology remain poorly understood. However, in 2008 a single storm ignited numerous fires throughout the redwood region, providing a rare opportunity to conduct replicated fire effects research. One year post-fire, I investigated competitive dynamics by quantifying bole survival and basal sprouting, for redwood and associated species, at four field sites that spanned much of the latitudinal range of redwood and encompassed a) second-growth and old-growth stands, b) burned and unburned areas, and c) a wide range of fire severities. I employed a mixed effects analytical framework and found that: 1) the probability of bole survival was greater for redwood than for its primary competitor (tanoak; *Notholithocarpus densiflorus*), 2) this divergence was much more pronounced at higher fire severities, and 3) tanoak exhibited a slight advantage in terms of post-fire basal sprouting, but the dominance of tanoak basal sprouts in burned areas was reduced relative to unburned areas. For many disturbance types in many ecosystems, the empirical data necessary for effective management decisions are lacking, and studies incorporating vegetative tree regeneration are especially scarce. My work demonstrates the importance of utilizing unique field research opportunities to test current theories, while unequivocally documenting that fires of all severities increased the abundance of redwood relative to tanoak, and that higher severity fires more strongly favored redwood.

Introduction

Variation in a range of factors can explain the coexistence of multiple tree species in temperate forests, including the ability to endure and/or respond to disturbance (Nakashizuka 2001, Loehle 2000, Petraitis et al. 1989, White and Jentsch 2001). Similarly, disturbances often have profound effects on competitive dynamics; for instance, species that are competitively inferior in undisturbed environments may become competitively equivalent or superior following disturbance (Suding 2001, Frelich and Reich 1999). Shifts in relative abundance can result from differential responses to the post-disturbance environment (e.g. better utilization of increased light levels) as well as direct disturbance effects (e.g. divergent survival rates, disturbance-activated regeneration; Frelich and Reich 1999, White and Jentsch 2001).

In order to persist in any environment, sedentary species must exhibit successful strategies of *resistance* (the ability to avoid or prevent disturbance impacts) and/or *resilience* (the ability to restore pre-disturbance conditions; *sensu* Millar et al. 2007). For trees, bole survival is analogous to resistance, while post-disturbance basal sprouting and seedling recruitment are forms of resilience (i.e. positive neighborhood effects; *sensu* Frelich and Reich 1999). Survival and regeneration in disturbed environments are not necessarily correlated, and both may be highly dependent upon disturbance type and severity, as well as tree species, bole diameter, and other factors (Frelich and Reich 1999, White and Jentsch 2001). Species-specific knowledge of both survival rates and regeneration patterns, across a range of other relevant variables, is thus required for accurate prediction of post-disturbance communities and long-term forest dynamics.

Post-disturbance seedling recruitment has long been studied, but vegetative sprouting from surviving root systems, which dominates the regeneration stratum in some forest types, has received much less research attention (Bond and Midgley 2001, Loehle 2000, Caplat and Anand 2009, Dietze and Clark 2008). Basal and root sprouts typically grow faster and are often more abundant than conspecific seedlings (Bond and Midgley 2001, Dietze and Clark 2008), and thus seedling recruitment may be of negligible importance for population persistence. Root systems of some woody species have survived for thousands of years through numerous episodes of above-ground mortality (Bond and Midgley 2001), and high rates of post-disturbance basal sprouting have been documented in some tropical forest tree species for which seedling recruitment has rarely or never been observed, suggesting that sprouting may be crucial for the persistence of these species (Bellingham et al. 1994). In addition, basal sprouting patterns may be key determinants of forest physiognomy (Van Bloem et al. 2007). The ability to sprout from the root system is primarily a broadleaf trait, but coast redwood (*Sequoia sempervirens*), which possesses the ability to rapidly initiate vigorous sprout growth from lignotubers (i.e. underground burls), is a notable exception. This characteristic has contributed substantially to redwood's resilience to both natural and anthropogenic disturbances (Del Tredici 1998).

Fire is a critical component of the disturbance regime in many ecosystems, including coast redwood forests. Fires were frequent and ubiquitous in redwood forests prior to European settlement (mean return intervals of 6-25 years have been estimated throughout the entire redwood range; Lorimer et al. 2009), but fires have been relatively rare and small over the last 70-80 years because of fire suppression efforts (Oneal et al. 2006, Donovan and Brown 2007). Due to the scarcity of opportunities to study fire in recent decades, many aspects of redwood fire ecology remain poorly understood (including the role of fire in the regeneration dynamics and long-term persistence of redwood and associated species; Lorimer et al. 2009), thereby forcing land managers to make important decisions without sufficient data.

During the late spring and early summer of 2008, following two years of drought, more than 2,000 fires were ignited in central and northern California, the majority of which were caused by a dry lightning storm on June 20. Numerous fires occurred in redwood forest, burning primarily as low-severity surface fires with occasional small pockets of crown torching, and encompassing both young and old stands on protected public lands that spanned much of the redwood range (Lynn Webb, pers. comm., and Jeff Frey, pers. comm.). These fires have presented a valuable opportunity to examine post-fire survival and regeneration, especially considering that a) fire effects studies in all vegetation types are notoriously plagued by pseudoreplicaton (van Mantgem et al. 2001), and b) the fire season of 2008 could prove to be a harbinger of changing climatic conditions; recent models have predicted increases in the annual area burned for much of northern California, including parts of the redwood region (Fried et al. 2004, Lenihan et al. 2007).

If the bole of any tree is killed by fire, the ability to sprout from surviving belowground tissue is clearly beneficial in terms of maintaining site occupancy. Many second-growth redwood stands, some of which were harvested more than 100 years ago, are stocked in large part by stems that originated as basal sprouts from cut stumps, and Daubenmire & Daubenmire (1975) have also argued that many massive old-growth trees originated as basal sprouts around ancient snags. Post-fire basal sprouting may also be advantageous in the absence of bole death. Fire-induced death of neighboring trees may dramatically reduce canopy cover, and fires that do not kill canopy trees, but cause crown scorch and/or death of subcanopy trees or shrubs, may increase understory light levels enough to facilitate regeneration of shade intolerant species (Veirs 1982). Post-fire sprouting at the base of surviving stems will a) increase the amount of understory light that is captured (potentially providing additional photosynthates to the parent root system and/or excluding competitors), and b) position young stems for rapid release if fire-damaged boles subsequently break or die. Post-disturbance basal sprouting of intact stems may also be a more general phenomenon, as it has been documented in other species following other disturbances; for instance, following a hurricane in Puerto Rico, Van Bloem et al. (2003) found that 32% of trees with no visible damage produced basal sprouts. In my study system, Abbott (1987) and Stuart (1987) have documented that basal sprouts originating at the base of living old-growth redwood trees can persist for at least 78 years and attain considerable size (at least 26 meters in height and 58 cm in diameter). Genets and/or species with more vigorous basal sprout growth will achieve greater relative dominance (at least in the short term), and thus post-fire basal sprouting patterns should be key determinants of future stand structure and composition.

Several anecdotal reports (e.g. Fritz 1931) and retrospective studies (Abbott 1987, Stuart 1987, Brown et al. 1999) have provided evidence that wildfire induces basal sprouting by redwood trees, and one publication has documented sprouting following prescribed fire (Finney and Martin 1993). In addition, fire likely stimulates basal sprouting by species co-occurring with redwood. Of particular importance to competitive dynamics in redwood forests is the post-fire sprouting response of tanoak (*Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*). This highly shade tolerant broadleaf evergreen, which produces acorns that serve as a valuable food source to a wide variety of wildlife species (Tappeiner et al. 1990), is the most abundant associate of redwood in the central and southern regions (*sensu* Sawyer et al. 2000b), and the most abundant broadleaf tree species throughout the entire redwood range (Tappeiner et al. 1990, Sawyer et al. 2000b). Tanoak trees can sprout vigorously following fire (Donato et al. 2009), even in the absence of bole death (Kauffman and Martin 1990), but no relevant studies have been conducted within the redwood region, and thus the relative responses of these two species have not been investigated.

I examine the role of fire in the stand-level competitive dynamics of forests dominated by coast redwood. My specific objectives were to: 1) compare post-fire survival of redwood and tanoak; 2) compare basal sprouting responses of redwood and tanoak; and 3) examine the effects of fire severity on species differences. I hypothesized that: 1) post-fire bole survival rates would be higher for redwood than for tanoak; 2) post-fire basal sprouting responses would be similar for redwood and tanoak; and 3) differences across species would be highly dependent upon fire severity. In addition, I integrate the findings with existing literature to examine the role of fire in the long-term competitive dynamics of redwood forests.

Methods

Site, transect, and plot selection

Field sites were selected to span the latitudinal range of redwood forest that was burned in the late spring and early summer of 2008, to cover a wide range of slope positions, aspects, and associated variation, and to represent old-growth and second-growth stands. I intentionally avoided areas that had undergone partial cutting so that all sites could be clearly categorized as second-growth or old-growth. Field sites are outlined in Table 3.1. All second-growth stands were approximately 60-80 years old in 2008: the areas I sampled at Jackson Demonstration State Forest were logged in the 1920s and 1940s; Eureka Canyon Forest was initially harvested around 1930 and has also undergone occasional individual tree selection harvesting since then (most recently in 1997). At both second-growth sites, to the best of my knowledge, none of the areas I sampled burned in the period between the initiation of the second-growth stand and the fires of 2008. At the Monterey County sites, several fires occurred during the past few decades, but perimeters are not precisely known. Depending upon the specific location, the most recent fires to affect the Monterey County plots probably occurred in 1985, 1977, or 1972 (i.e. 23-36 years prior to the fires of 2008), although it is possible that some small pockets had not burned since 1924. At Montgomery Woods State Park, state fire records (which extend back to 1950) document no fire activity prior to 2008.

Sudden oak death (SOD), a recently introduced disease that is currently causing substantial tanoak mortality in redwood stands throughout much of the redwood range (Rizzo et al. 2005, Maloney et al. 2005), was established in some of my sampling areas and thus the potential impact of this disease must be considered. As of 2009, there were was no record of SOD at Jackson Demonstration State Forest or Eureka Canyon Forest, and – although the causative pathogen had been detected at Montgomery Woods State Park – very little mortality had occurred at this field site (Lynn Webb, pers. comm.). In contrast, SOD was well established in several of the Monterey county sites, and tanoak mortality levels were very high in isolated areas (Rizzo et al. 2005, Maloney et al. 2005).

At each field site, I selected several representative stands that spanned a broad range of slopes, slope positions, aspects, and fire severities (at this stage, fire severity was assessed via visual examination of crown scorch and litter/duff consumption, as well as reports from firefighters and land managers). Within each stand, I installed a linear group of plots (i.e. *transect*). The first plot of each transect was located at a random location at the bottom of a drainage or the top of a ridge, and subsequent plots were installed at regular intervals (50 m or 100 m) up or down the slope, following an azimuth that was predetermined with the aid of a topographic map; precise locations of plot centers were randomized (a random distance between 0 and 10 meters in a random direction). If less than 3 redwoods were present within a 20 meter radius, plot center was randomly relocated (and this was repeated if necessary); this criterion, which effectively defines "redwood forest" for the purposes of this study, was adopted to prevent the establishment of plots in adjacent vegetation types. At every site, transects were installed in stands that had burned in 2008 (i.e. *burned*), as well as in areas that had not burned in at least 20 years (i.e. *unburned*); within each site, the majority of plots (57-82%) were installed in burned areas (Table 3.1). SOD was not considered during plot installation because precise locations of SOD-induced mortality patches were not known, and definitive identification of pre-fire SOD-induced tanoak mortality is impossible in the post-fire environment.

Table 3.1. Field Sites. All counties are in the state of California. All Monterey county ownerships are proximate and treated as one site. Stand age status applies to all sampled areas, but not necessarily to the entirety of each site. "Trans." = transects.

Site	County	Approx. Latitude	Stand Age Status	# of Burned:		# of Unburned:	
				Trans.	Plots	Trans.	Plots
Jackson Demonstration State Forest	Mendocino	39.4 N	SG	5	23	1	5
Montgomery Woods State Park	Mendocino	39.2 N	OG	2	8	2	6
Eureka Canyon Forest	Santa Cruz	37.0 N	SG	3	10	1	3
Pfeiffer Big Sur State Park, Julia Pfeiffer Burns State Park, Big Creek Reserve, & Los Padres National Forest	Monterey	36.1 N	OG	4	15	2	7

Data collection

Circular plots of variable sizes were installed to ensure that at least 3 redwoods ≥ 10 cm diameter at breast height (DBH), hereafter referred to as *mature*, were captured within each plot. All individuals of all tree species ≥ 10 cm DBH were sampled in a 1/100 ha area (5.64 m radius); if less than 3 mature redwoods (living or dead) were present within this radius, the radius (for redwood only, not any other tree species) was extended to 7.98 m (1/50 ha), and then again to 11.28 m (1/25 ha) if necessary. If an 11.28 m radius failed to capture 3 redwoods, additional redwoods were sampled (up to 20 m) to achieve the minimum. All other tree species were sampled within a 5.64 m radius only (redwood sampling was emphasized to satisfy the objectives of a concurrent study).

All data were collected in the summer of 2009 (one year after the fires). Data collection consisted of plot-level as well as individual tree-based variables. If a bole was split below breast height, each fork ≥ 10 cm DBH was treated as a separate tree. For all trees, I recorded DBH and assigned a bole health status of living or dead; a bole was considered dead if no green foliage was present in the original canopy or as epicormic sprouts on the bole or branches (basal sprouts were excluded). For dead boles in burned areas, I recorded my best estimate of whether tree death occurred prior to the 2008 fires or during/after the fires. Evidence of recent death included the presence of fine twigs and dead foliage, as well as vigorous basal sprouting (for applicable species); the absence of basal sprouts was never used to confirm pre-fire mortality, but in a few rare cases basal sprout presence was considered an indicator of recent bole death. Recent bole death almost certainly occurred as a result of fire for the vast majority of trees, but SOD may have contributed in the case of some tanoaks in some of the Monterey county plots.

In burned areas, bole char height was measured for each tree. For all species, I recorded the height of the highest point at which any bole char was visible (with a Laser Ace hypsometer, when necessary), and for redwood trees (which tend to have highly flammable outer bark layers), I also recorded the height of the highest point at which all bark and fissures were completely blackened (on at least one side of the tree). The latter bole char height metric (i.e. *contiguous bole char*), is equivalent to the category 2 bole char of Kobziar et al. (2006). Contiguous bole char height was not recorded for hardwoods because preliminary data collection efforts suggested that hardwood fissures were very rarely blackened and that the degree of charring in bark fissures was more closely related to fissure patterns of individual trees than to fire intensity or severity.

Basal sprouts were quantified with two separate metrics: sprout area (two-dimensional projected areal coverage) and sprout height (the greatest height achieved by any sprout). Basal sprout numbers (i.e. counts) were not examined because pilot work revealed redwood's tendency, following fire, to produce hundreds of densely packed sprouts that are often difficult or impossible to distinguish without destructive sampling techniques. Basal sprouts were defined as all vegetative sprouts < 3 cm DBH arising from litter/duff/soil that were within 30 cm of exposed wood (e.g. bole or root flare), as well as all sprouts arising from exposed wood that were within 30 cm from the litter/duff/soil interface. I focus exclusively on basal sprouts, as opposed to seedlings, because seedlings of all species were scarce and small (typically < 10 cm tall) in burned areas, whereas basal sprouts were ubiquitous and vigorous (frequently > 100 cm tall) and clearly dominated the post-fire regeneration stratum. I also recorded tallies of juvenile basal stems ($\geq$ 3 cm and < 10 cm DBH), living and dead, for each tree. However, in burned areas, my dataset contained only seven living juvenile basal stems (one redwood, six tanoak), compared to a total of 526 mature trees. The extremely low number of living juvenile basal stems in burned areas, and the uncertainty about how many were present prior to burning, impeded meaningful analysis, and thus juvenile basal stems were not considered further.

Data analysis

Prior to data analysis, I calculated a plot-level measure of fire severity: the mean contiguous bole char height (m) for all redwood trees within each plot. I required a standardized plot-level measure so that I could more easily examine the effects of wildfire across species, and I chose to focus on redwood because, due to the experimental design, at least three redwoods occurred in every plot (other species were often absent). I focused on *contiguous* bole char because redwood bark retains char for a very long time, and managers at both of old-growth sites confirmed that non-contiguous charring (i.e. char interspersed with newly exposed bark) was visible on redwood boles prior to the 2008 fires.

All tree species other than redwood and tanoak were omitted from all analyses. Redwood and tanoak respectively accounted for 66% and 26% of total sampled stems in burned areas (and percentages were very similar in unburned areas), limiting the potential for inferences about other species. The total number of occurrences of non-redwood conifers and non-tanoak broadleaved trees, in burned areas, was 24 and 16, respectively; in comparison, comparable numbers for redwood and tanoak were 348 and 138, respectively. In burned areas, trees that were deemed to have experienced bole death prior to the fires of 2008 were excluded from all analyses, and in unburned areas, all trees with dead boles were excluded; as such, the vast majority of trees that died via other mechanisms (including SOD) were omitted.

My overall analytical approach, which was targeted at assessing the effects of fire on stand-level competitive relationships, relied upon an ad-hoc model building process. I constructed mixed effects models to predict post-fire bole survival (burned areas only) and basal sprout area and height (burned and unburned areas) across several relevant covariates, and then focused on differences between redwood and tanoak. Because of the relatively small and manageable number of candidate predictors, I was able to avoid automated model development algorithms (which many statisticians have criticized as inconsistent and blind to underlying biological processes; Quinn and Keough 2002), and instead relied upon an iterative process informed by prior ecological knowledge and graphical examination of predicted values and residuals.

For all analyses, I used the function *glmmPQL* from the *MASS* package in the R statistical software (R Development Core Team 2009). This function uses a penalized quasi-likelihood procedure to adjust for any over-dispersion in the response variable (sprout area and sprout height data were highly non-normal and over-dispersed; Figs. 3A.1 & 3A.2 in the chapter appendix), while accounting for nested random effects (my sampling scheme consisted of plots within transects within sites; Zuur et al. 2009). A binomial distribution (with a logit link function) was specified for the bole survival analysis, and gamma distributions (with logarithmic link functions) were specified for both basal sprout variables.

Bole survival was examined in burned areas only, but sprout area and sprout height were analyzed in both burned and unburned areas (in separate models). Throughout the process of model development for the three primary variables of interest (bole survival, sprout area, and sprout height), nested random effects (site / transect / plot) were consistently included while potential fixed effect predictors were evaluated. Species, DBH, and stand age status were considered as fixed effect predictors in all models. In models for burned areas (bole survival as well as basal sprouting), plot-level fire severity was also considered as a fixed effect predictor. In addition, squared terms and interactions between each of these variables were tested; owing to the potential presence of interaction terms, all continuous predictor variables were centered to reduce multi-collinearity (Quinn and Keough 2002). I did not include plot-level SOD presence or severity as model predictors because of my inability to assess these metrics in the post-fire environment; however, if elevated pre-fire mortality levels increased fire intensity (as suggested by Ramage et al. 2010), such effects would have been indirectly incorporated into the fire severity metric. I did not retain any terms with p-values greater than 0.10 (except for single-term predictors that were components of significant interactions). Other researchers using the function *glmmPQL* (which does not provide deviance, AIC, or qAIC values) have also relied upon p-values of model terms to determine whether such terms should be included in the final model (e.g. Chapman et al. 2009, Laucht et al. 2008, Le Cadre et al. 2008). An outline of model structure is provided in Table 3A.1 in the chapter appendix.

Presentation of results

Throughout the results section of this paper, model output tables display slope estimates and standard errors, as well as standardized slope estimates, on the transformed scale (logit for survival analyses, log(y+1) for sprout area and height). Standardized coefficients, which are included to aid comparison across predictors and models, were calculated as per Quinn and Keough (2002): standardized slope estimate for x_i = fitted slope estimate for x_i * standard deviation of x_i / standard deviation of y (on the transformed scale). In all figures, predicted values are displayed on the original scale of the response variable. DBH was significant in all models and thus effective visual representation of my findings is dependent upon appropriate illustration of the effects of this predictor. Given the overall objective of understanding the effects of fire on stand-level competitive relationships between redwood and tanoak, I have opted to display DBH with curves that represent percentiles, *calculated separately for each species and stand age status* (hereafter referred to as "percentile curves"). For instance, I have used an equivalent line thickness (the graphical parameter I have used to indicate DBH) for second-growth redwood trees of 33.8cm DBH and second-growth tanoak trees of 20.7cm DBH, because these values represent the respective medians for each of these species on second-growth sites (Table 3.2). Examining differences in species performance at equivalent DBH values is an interesting tree-level physiological question, but given that I have focused primarily on the relationship between fire and stand-level competitive dynamics, I believe DBH percentiles are more informative. I do not provide any absolute abundance data because a) this study focuses on fire-induced *changes* in *relative* abundance and b) abundance estimates would be biased by the requirement that at least three redwoods per plot be sampled.

Table 3.2. Distribution statistics for DBH (in burned areas) by species and stand age status. Distributions for unburned areas were very similar.

	Second-growth		Old-growth	
DBH (cm)	redwood	tanoak	redwood	tanoak
maximum	133.2	54.7	351.7	65.6
90th percentile	69.9	36.7	139.6	34.3
median (50th)	33.8	20.7	52.1	15.4
10th percentile	13.5	11.9	12.2	10.5
minimum	10.0	10.0	10.0	10.0

Results

Bole survival

Post-fire bole survival was affected by species, DBH, fire severity, and stand age status (Table 3.3); a squared term for DBH was found to be significant, as well as the following interactions: species*fire severity, and stand age status*DBH. Across all DBH values in young and old stands, increasing fire severity reduced bole survival much more steeply for tanoak than for redwood; the ability to endure fire was comparable for these two species at low fire severity, but redwood exhibited a strong survival advantage at higher fire severity. Due to the presence of significant interaction terms, many of the other differences between redwood and tanoak were conditional upon the values of the predictor variables.

At low fire severity (i.e. a mean plot-level contiguous bole char height on redwood of 0.6 m, which is equivalent to the 10th percentile), there was little difference between second-growth redwood and tanoak trees of median DBH or larger; both had predicted bole survival probabilities approximating or equaling 1 (Fig. 3.1). Old-growth redwoods were similarly resistant to low severity fire, but old-growth tanoaks of median DBH had slightly lower survival probabilities (approx. 0.9), reflecting the fact that the median DBH of tanoak was lower in old-growth stands (15.4 cm) than in second-growth stands (20.7 cm; Table 3.2), and that survival probability was greater in second-growth stands (after accounting for all other model predictors). In young and old stands, bole survival probability declined with decreasing DBH (from median to minimum DBH) more steeply for redwood (not because of an interaction between species and DBH, but because of a larger spread in DBH values for redwood). This resulted in higher survival probabilities for small tanoaks than for small redwoods; for instance, in second-growth stands, bole survival was estimated at approximately 0.7 for the smallest tanoaks and approximately 0.35 for the smallest redwoods.

At moderate fire severity (i.e. a mean plot-level contiguous bole char height on redwood of 2.7 m, which is equivalent to the median), bole survival probabilities for redwood and tanoak trees of median DBH diverged in both second-growth and old-growth stands (Fig. 3.1). Redwood trees of median DBH (or larger) had survival probabilities approaching or equaling 1 (in second-growth and old-growth stands), but estimates were lower for tanoaks of median DBH in second-growth (approx. 0.85) and old-growth (approx. 0.55) stands. In young and old stands, survival probabilities for the smallest and largest trees were very similar for redwood and tanoak; species differences were most pronounced for intermediate DBH values. Survival probabilities for trees of equivalent DBH were nearly identical at moderate fire severity (approx. 1.0 for 30 and 50 cm DBH trees, and approx. 0.25 for 10 cm DBH trees).

At high fire severity (i.e. a mean plot-level contiguous bole char height on redwood of 9.0 m, which is equivalent to the 90th percentile), redwood exhibited a superior ability to survive wildfire across all DBH percentiles, but this difference was most apparent for trees of median DBH; in both young and old stands, survival probabilities were nearly 1 for redwood and close to 0 for tanoak. Patterns were similar for trees of equivalent DBH. Redwood consistently exhibited superior survival probabilities, but these differences ranged from minor (e.g. 10 and 50 cm DBH trees) to very pronounced (e.g. 30 cm DBH trees); the approximate probability of bole survival for 30 cm DBH trees was 0.95 for redwood, but only 0.10 for tanoak.

Table 3.3. Predictors of post-fire bole survival. Redwood was the baseline species and old-growth was the baseline stand age status. Note that the signs on interaction term estimates may be difficult to interpret because of the centering of continuous predictors. $r^2 = 0.73$.

Predictor	Est.	SE	p-value	Stndzd. Est.
(Intercept)	3.4351	0.8403	0.0001	
tanoak	-1.6216	0.4753	0.0007	-0.0967
DBH	0.1183	0.0299	0.0001	0.5643
DBH^2	-0.0004	0.0002	0.0194	-0.2427
fire severity	-0.1867	0.0791	0.0231	-0.0874
second-growth	4.3580	1.3808	0.0874	0.2651
tanoak*fire severity	-0.9186	0.1871	0.0000	-0.2265
second-growth*DBH	0.1636	0.0532	0.0023	0.3961

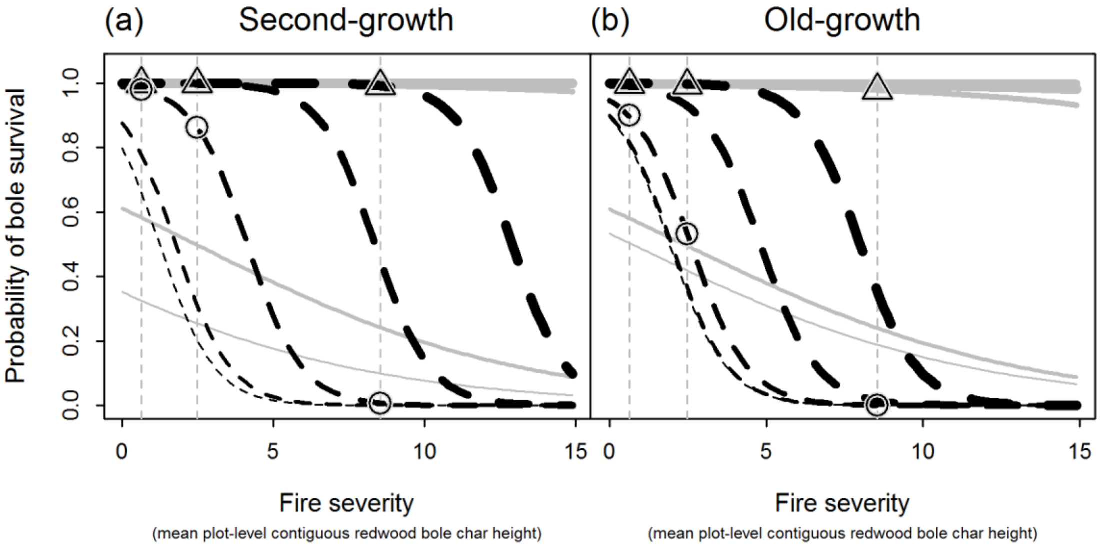

Fig. 3.1. Probability of bole survival as a function of species, DBH, and fire severity. Redwood is displayed with solid gray lines and tanoak is displayed with broken black lines. Fire severity is quantified as the mean contiguous bole char height (m) for all redwood trees within each plot. Limits of the x-axis represent the minimum and maximum fire severities within the dataset, and vertical gray dashed lines mark the 10th percentile (“low”), median (“moderate”), and 90th percentile (“high”) of fire severity. Line thickness indicates tree DBH; lines represent (from the thinnest to the thickest) the minimum, the 10th percentile, the median, the 90th percentile, and the maximum, *calculated separately for each species and stand age status*. For instance, in the second-growth cell, the thickest redwood line represents a DBH of 133.2 cm, while the thickest tanoak line represents a DBH of 54.7 cm (see Table 3.2); note that several redwood curves overlap at the top of the plotting area. Triangles (for redwood) and circles (for tanoak) mark the points at which median DBH curves intersect the 10th percentile, median, and 90th percentile of fire severity.

Basal sprout area

In burned areas, basal sprout area was affected by species, DBH, fire severity, and stand age status (Table 3.4); a squared term for fire severity was found to be significant, as well as the following interactions: species*DBH and stand age status*DBH.   In unburned areas, basal sprout area was affected by species, DBH, and stand age status (Table 3.4); none of these variables were significant as single-term predictors, but two interactions were significant: species*DBH and stand age status*DBH. Patterns for small and large trees were similar to those for median-DBH trees, but predicted sprout area decreased with increasing DBH (although only marginally for old-growth redwoods; Fig. 3.2).

In unburned stands, both young and old, tanoak trees of median DBH exhibited greater sprout area than redwood trees of median DBH. In burned stands, sprout area for median-DBH tanoak trees also exceeded sprout area for median-DBH redwood trees, but differences between species were greatly reduced. In both young and old stands, redwood and tanoak sprout area was nearly identical following fire of low and moderate severity, but tanoak predictions were distinctly higher than redwood predictions in areas that experienced high severity fire. For both species, in second-growth and old-growth stands, my models predicted a slight reduction in sprout area at extreme fire severities (> 90th percentile).

Table 3.4. Predictors of basal sprout area (dm^2). Redwood was the baseline species and old-growth was the baseline stand age status. Note that the signs on interaction term estimates may be difficult to interpret because of the centering of continuous predictors. Burned $r^2 = 0.36$; Unburned $r^2 = 0.18$.

Predictor	Est.	SE	p-value	Stndzd. Est.
Burned model				
(Intercept)	3.5930	0.3103	< 0.0001	
tanoak	-0.2087	0.2179	0.3389	-0.0547
DBH	-0.0003	0.0019	0.8704	-0.0066
fire severity	0.2412	0.0406	< 0.0001	0.4970
fire severity^2	-0.0166	0.0058	0.0069	-0.2153
second-growth	-0.8425	0.3960	0.1672	-0.2258
tanoak*DBH	-0.0304	0.0097	0.0019	-0.1803
second-growth*DBH	-0.0090	0.0037	0.0149	-0.0965
Unburned model				
(Intercept)	2.9845	0.9169	0.0014	
tanoak	0.1022	0.7318	0.8891	0.1022
DBH	-0.0039	0.0035	0.2717	-0.0036
second-growth	-0.2883	1.2696	0.8578	-0.0685
tanoak*DBH	-0.0504	0.0249	0.0448	-0.3203
second-growth*DBH	-0.0222	0.0102	0.0310	-0.1836

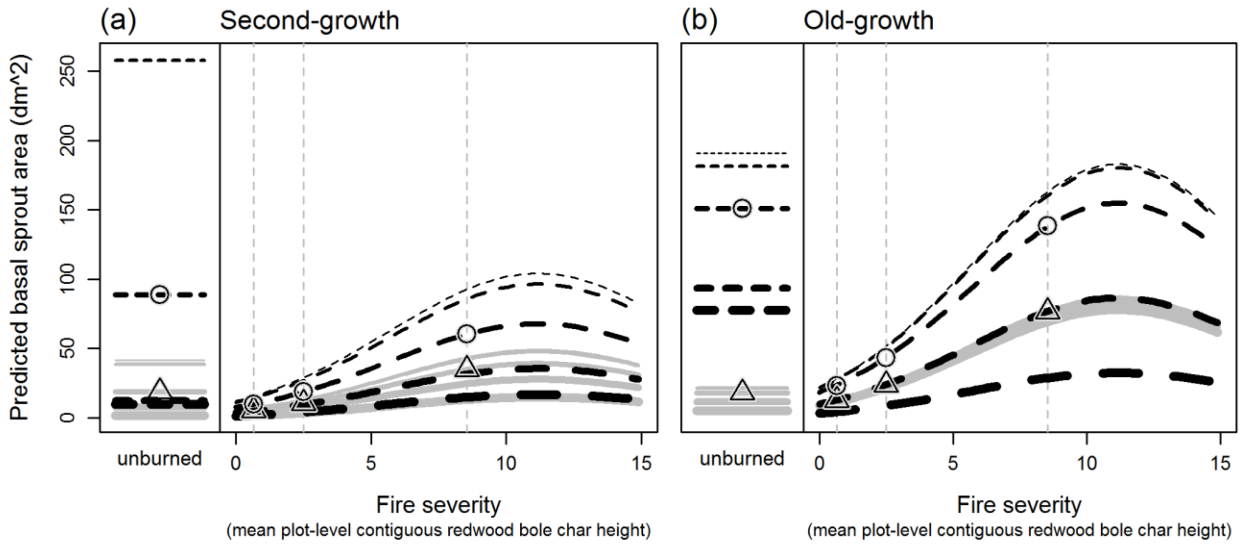

Fig. 3.2. Predicted basal sprout area as a function of species, DBH, burn status, and fire severity. Symbology follows that of Fig. 3.1. In unburned second-growth stands, the predicted value for minimum-DBH tanoak trees was very high (364); the plotting area was constrained below this value in order to maximize visual interpretation of other results. Note that all curves overlap for burned old-growth redwoods.

Basal sprout height

In burned areas, basal sprout height was affected by species, DBH, fire severity, and stand age status (Table 3.5); a squared term for fire severity was found to be significant, as well as the following interactions: species*DBH, species*fire severity, and stand age status*DBH. In unburned areas, DBH was the only significant predictor (Table 3.5), but species was also included so that distinct (albeit statistically indistinguishable) values could be predicted for each species. As in the section above, the following text focuses on trees of median DBH, but predictions for other DBH percentiles can be examined graphically (Fig. 3.3).

Although species was not a significant predictor in unburned areas (after accounting for DBH), DBH was highly significant (and negatively related to sprout height) and tanoak had a much smaller median DBH than redwood on both second-growth and old-growth sites (see Table 3.2). Thus, despite the lack of significance for species as a model term, tanoak generally exhibited taller basal sprouts than redwood on unburned sites. On burned sites, differences between redwood and tanoak trees of median DBH were dependent upon fire severity. In both young and old stands, median-DBH tanoak trees were predicted to exhibit greater sprout height at low and moderate fire severity, while median-DBH redwood trees had slightly higher predicted values at high fire severity. In contrast to sprout area, sprout height differences between species declined with increasing fire severity; this pattern exists because predicted tanoak sprout area peaked at a fire severity less than “high” (the 90th percentile of plot-level contiguous redwood bole char height), while redwood sprout area did not begin to decline until reaching an extreme level of severity.

Table 3.5. Predictors of basal sprout height (dm). Redwood was the baseline species and old-growth was the baseline stand age status. In the unburned model, DBH was the only significant predictor, but species was also included so that distinct (although statistically indistinguishable) values could be predicted and plotted for each species. Note that the signs on interaction term estimates may be difficult to interpret because of the centering of continuous predictors. Burned $r^2 = 0.54$; Unburned $r^2 = 0.19$.

Predictor	Est.	SE	p-value	Stndzd. Est.
Burned model				
(Intercept)	2.2071	0.1178	< 0.0001	
tanoak	-0.2169	0.1119	0.0532	-0.1058
DBH	-0.0003	0.0010	0.7979	-0.0099
fire severity	0.1272	0.0201	< 0.0001	0.4877
fire severity^2	-0.0094	0.0028	0.0021	-0.2258
second-growth	-0.4416	0.1438	0.0917	-0.2201
tanoak*DBH	-0.0167	0.0050	0.0010	-0.1838
tanoak*fire severity	-0.0535	0.0186	0.0042	-0.1076
second-growth*DBH	-0.0054	0.0019	0.0046	-0.1072
Unburned model				
(Intercept)	1.6901	0.3427	< 0.0001	
tanoak	0.3165	0.2387	0.1871	0.1064
DBH	-0.0059	0.0021	0.0059	-0.2318

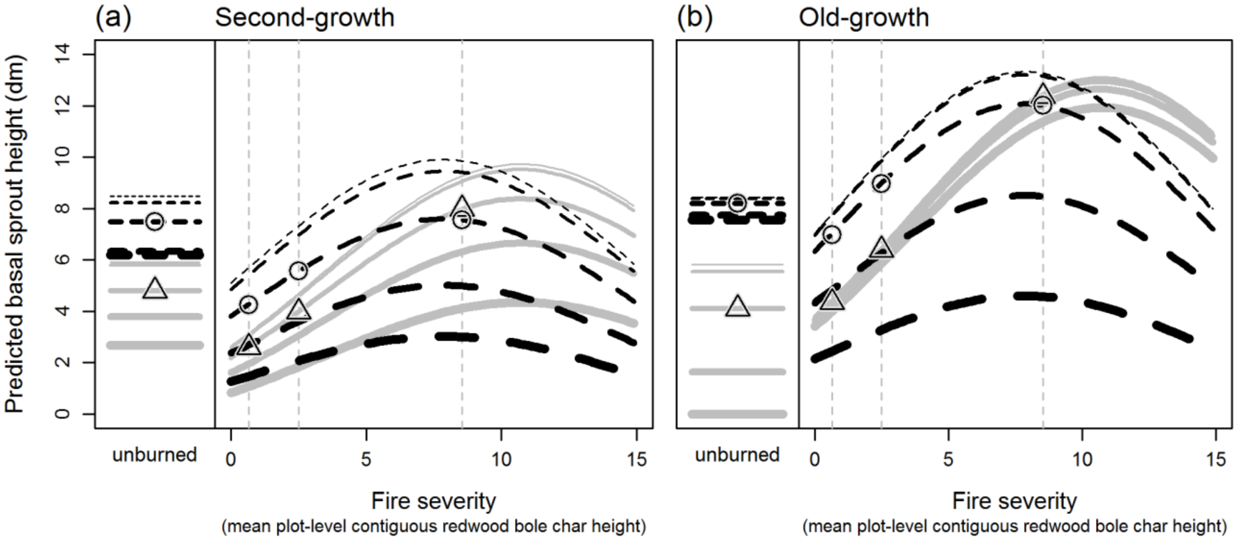

Fig. 3.3. Predicted basal sprout height as a function of species, DBH, burn status, and fire severity. Symbology follows that of Figs. 3.1 and 3.2. Note that several curves overlap for burned old-growth redwoods.

Discussion

Main findings

Redwood and tanoak both demonstrated resistance (bole survival) and resilience (basal sprouting) to fire. Redwood was far superior in terms of bole survival, especially at higher fire severities, while tanoak generally exhibited a slight advantage in terms of post-fire basal sprouting. However, tanoak basal sprouts were also more abundant than redwood basal sprouts in unburned areas, and the dominance of tanoak basal sprouts in the post-fire environment was reduced relative to unburned areas. Considered collectively, my survival and basal sprouting data suggest that fires of any severity will increase the relative abundance of redwood, and that higher severity fires will more strongly favor redwood. These findings should be highly illuminating to managers in the redwood region who are considering the use of prescribed fire and/or debating the degree to which wildfires should be suppressed.

In the discussion of competitive dynamics, it is useful to distinguish between three different vertical strata: the upper canopy layer, the lower canopy layer (i.e. subcanopy), and the regeneration layer (i.e. the understory). The upper canopy of redwood forests is dominated by redwood, and thus mortality of large redwoods would be required for a rapid and pronounced shift in species composition in this stratum. I have shown that large redwood trees (≥ median DBH) are extremely fire-resistant, suggesting that fire is unlikely to cause a rapid shift in upper canopy relative abundance in redwood forests; even in instances of 100% crown scorch, large redwoods typically exhibited vigorous epicormic sprouting from the bole and/or the branches (field observations). In contrast, I have found strong evidence that species composition within the subcanopy layer, which I define as the stratum occupied by mature tanoak trees (and which roughly corresponds to trees between 10 and 50 cm DBH; see Table 3.2), is greatly affected by fire. As fire severity increased, bole survival rates for tanoak dropped much more steeply than for redwood (even for trees of equivalent DBH), suggesting that hotter fires provide a relative advantage to redwood.

The understory layer was entirely consumed by fire in all burned plots, and thus I quantified relative competitive abilities in this stratum with post-fire regeneration, as opposed to differential rates of survival. In areas that had not burned, basal sprout area and height predictions were consistently higher for tanoak than for redwood, indicating that tanoak dominated the regeneration stratum (relative to the abundance of mature trees; my methods do not permit inferences regarding absolute abundance). In burned areas, redwood and tanoak sprouting patterns were differentially affected by DBH and/or fire severity, leading to complex competitive dynamics in post-fire environments. At some combinations of predictor variables, in terms of one or both sprout metrics, fire had the effect of reversing dominance in the understory; for instance, following high severity fire, redwood trees of median DBH were predicted to have slightly taller sprouts than tanoak trees of median DBH, on both second- and old-growth sites. At many other predictor combinations (in terms of both sprout metrics) tanoak maintained understory dominance, demonstrating that post-fire basal sprout growth of tanoak often exceeds that of redwood. However, differences between tanoak and redwood were consistently smaller in burned areas than in unburned areas, suggesting that fires of any severity reduce the dominance of tanoak in the understory.

Mechanistic considerations and connections to previous redwood/tanoak research

No other studies have analytically compared post-fire survival probabilities of redwood and associated tree species, but some survival statistics for redwood alone are available. Finney and Martin (1993) found that redwood survival rates approached or equaled 100% for second-growth trees greater than 50cm DBH (across all intensities of *prescribed* fire), and their models predicted a reduced probability of bole survival for redwoods with smaller DBH and in areas with greater fire intensity. I am unaware of any previous analyses of post-fire tanoak bole survival at the tree or plot scales.

Basal sprout area and height were predicted to increase with decreasing bole diameter and with increasing fire severity, for redwood and tanoak, in young and old stands (although the effect of diameter was minimal for old-growth redwoods). This was likely because of the increased probability of bole death for trees of smaller DBH and in areas of greater burn severity. I experimented with alternative sprout models that included post-fire bole health status as a model predictor (and in these models fire-killed boles were consistently predicted to sprout more vigorously; see Tables 3A.2 & 3A.3 in the chapter appendix), but due to my focus on stand-level sprout patterns as opposed to mechanisms of sprout production, I decided the inclusion of post-fire bole status would only serve to complicate my findings. Although the final sprout models do not explicitly consider bole survival, increases in sprouting resulting from bole death are closely linked to DBH and fire severity and thus implicitly incorporated into all predicted values.

Other mechanisms are also involved in the observed relationships with diameter and fire severity; both of these predictors were significant (as solo predictors and/or in interaction terms) in models that also included post-fire bole status (see Tables 3A.2 & 3A.3 in the chapter appendix). Negative relationships with DBH might result if smaller surviving boles tend to suffer a greater degree of phloem damage than larger boles, interrupting the flow of auxin from the canopy and stimulating basal bud growth, and/or if larger (and generally older) trees retain fewer functional dormant basal buds, which has been proposed for redwood by Powers and Wiant (1970). Positive relationships with sprouting might result if fire triggers a basal sprouting response (e.g. auxin reduction resulting from crown scorch) or if aspects of the post-fire environment in more severely burned areas (e.g. higher light levels) are more conducive to vigorous sprout growth. In the understory of a thinned even-aged stand, O'Hara and Berrill (2010) found that redwood basal sprout leaf area and height increment were positively related to light availability. Negative relationships between sprouting and fire severity, which consistently appeared at very high levels of severity, could occur as a result of dormant bud mortality. For redwood, evidence of fire-induced death of dormant basal buds has been provided by several researchers (Powers and Wiant 1970, Neal 1967, Abbott 1987, Finney 1993).

As is the case with post-fire survival, no previous studies have compared post-fire basal sprouting of redwood and tanoak, but some sprouting data are available for these two species in isolation (see Finney and Martin 1993, Donato et al. 2009, Kauffman and Martin 1990, Tappeiner et al. 1984, Ahrens and Newton 2008, Tappeiner and McDonald 1984). My extremely high sprout area predictions for small tanoak trees in unburned second-growth stands probably resulted from a unique feature of tanoak establishment: even in the absence of disturbance, tanoak seedlings repeatedly die and re-sprout, forming dense multi-stemmed clumps that eventually thin to one or several dominant sprouts (Tappeiner and McDonald 1984). Many of the smallest tanoak trees in the unburned dataset were still surrounded by an expansive clump of smaller sprouts (field observations), while most larger boles had no basal sprouts remaining;

although I did not record sprout numbers, these general patterns are apparent in the relationship between sprout area and DBH in unburned areas (Fig. 3A.3 in the chapter appendix).

The role of fire in the long-term competitive dynamics of redwood and tanoak

Although my data provide only a snapshot of short-term fire effects in redwood forest, I have filled a major gap in the current body of empirical data, thereby necessitating a re-evaluation of existing theories on the longer-term role of fire. Veirs (1982) defined the current paradigm by postulating that redwood and tanoak will continue to co-exist with or without fire, after examining age distributions and fire scar records in redwood forests of the northern redwood region. Several researchers have documented or observed the presence of redwood and tanoak regeneration (ranging from seedlings/basal sprouts to young trees), in quantities sufficient to replace canopy trees, in the understories of redwood forests that have not burned (or been cut) for many decades (e.g. Veirs 1982, Busing and Fujimori 2002). Using a dataset collected over three decades on an alluvial old-growth site, Busing and Fujimori (2002) concluded that small-scale tree fall gaps alone are sufficient for the establishment of redwood regeneration (seedlings as well as sprouts), and documented that tanoak seedlings were also abundant in such gaps. However, all relevant demographic studies have been conducted at lower slope positions (e.g. alluvial flats), prompting Lorimer et al. (2009) to note that it is still unclear whether fire is necessary for redwood regeneration and persistence at upper slope positions.

My results provide evidence that both redwood and tanoak will persist *with* wildfire, at least in the short-term, but also suggest that fire will increase the relative abundance of redwood, supporting the belief held by some foresters and ecologists that fire suppression has led to increased tanoak abundance in redwood forests over the last century. Although no quantitative historical data have been used to test this assumption, it has endured (at least in part) because of the differential regeneration requirements of these two species. Redwood sprouts will die if light levels are not adequate (O'Hara and Berrill 2010), and redwood seedlings exhibit physiological responses that are not consistent with establishment in deep shade (Peer et al. 1999). In contrast, tanoak regeneration often establishes successfully in deep shade beneath multiple canopy layers (Veirs 1982, Tappeiner et al. 1990) and young tanoak trees increase in diameter more rapidly than any co-occurring species when growing beneath a closed canopy (Veirs 1982). In addition, while tanoak readily establishes in thick litter and duff layers (Veirs 1982, Tappeiner et al. 1990), redwood seedling establishment is more successful on mineral soil (Olson et al. 1990), a substrate which is more common following fire.

All data were collected only one year after fire, and thus my projections cannot fully incorporate longer-term phenomena that may result from fire. Delayed fire-induced mortality will probably be minimal because neither redwood nor tanoak are known to suffer significant post-fire attack by beetles or other insects, although the long-term risk of structural failure may increase as a result of fire scars, which can serve as entry points for wood decaying fungi (Olson et al. 1990, Tappeiner et al. 1990). Vigor of surviving trees may be affected; following fire, Abbott (1987) found that growth rates of surviving redwoods increased while growth rates of surviving Douglas-fir trees decreased (I am unaware of any such data for tanoak). Finally, understory light levels will not remain constant (as a result of, e.g., canopy expansion by surviving trees), which could lead to species-specific changes in basal sprout growth and mortality rates.

Competitive relationships may also shift after a series of fires (e.g. following a return to a higher frequency fire regime), and thus even long-term monitoring after a single fire event may fail to fully illuminate the effects of frequent fire on relative species abundances. Available data are inadequate to predict the effects of repeated fires in redwood forests, but it is possible that frequent burning may gradually reduce the abundance of tanoak. Tappeiner and McDonald (1984) noted that stumps of tanoak less than 2 cm DBH sprouted "much less vigorously" than stumps of larger tanoak, and Kauffman and Martin (1990) found that the probability of whole plant mortality decreased significantly with increasing pre-fire aboveground biomass of shrubby tanoaks, suggesting that if adequate recovery has not occurred between fire events, root systems may not survive. Donato et al. (2009) found a similar pattern for all hardwoods pooled (tanoak was not analyzed separately), and documented that the percent cover of tanoak, two years post-fire, was lower in a "short interval" burn area than in the "long interval" burn area; however, they also noted that this difference was slight and concluded that a "short interval" (15 years) should allow for indefinite site persistence. Similarly, Ahrens and Newton (2008) inferred that tanoaks in a cut and burned Douglas-fir forest replaced 72% of pre-disturbance leaf area within 8 years.

All available evidence suggests that fire favors redwood, and thus fire-mediated co-existence of redwood and tanoak would require competitive exclusion by tanoak in the absence of fire. Such an outcome seems highly unlikely considering that redwood can regenerate successfully in tree fall gaps (at least on lower slope positions; Busing and Fujimori 2002); although redwood regeneration may be dependent upon disturbance, it does not appear to require fire or other large-scale disturbances. Even if tanoak could theoretically exclude redwood in the absence of disturbance, the extreme longevity of redwood (> 2000 years on at least some sites; Sawyer et al. 2000a) suggests that disturbances would be required very infrequently to ensure the persistence of this species. As such, fire does not appear to be essential for redwood's persistence, and I must reject the hypothesis that fire facilitates the co-existence of redwood and tanoak (although I cannot assert this statement as definitively with regard to upper slope positions, for which relevant demographic data are lacking).

Fire undoubtedly plays a critical role in the competitive dynamics of redwood forests, but the recently introduced disease sudden oak death (SOD), which is currently causing substantial tanoak mortality in redwood stands throughout much of the redwood range (Rizzo et al. 2005, Maloney et al. 2005), may ultimately prove more consequential. In some redwood stands, tanoak mortality has exceeded 75% (by basal area), with localized areas surpassing 95% (Ramage et al. 2010), and spread risk models have predicted that the disease will ultimately affect the entire redwood region (Meentemeyer et al. 2004). With or without fire, SOD-induced tanoak decline is directly affecting competitive relationships in redwood forests, but the compounded effects (*sensu* Paine et al. 1998) of SOD and fire may lead to the greatest long-term impacts. SOD has increased forest floor fuel loading (Ramage et al. 2010), and areas with recently killed standing dead trees are at a greater risk of crown fire (Kuljian and Varner 2010). Although I was unable to assess pre-fire SOD-induced tanoak mortality in my study plots, any SOD-induced increases in fire intensity were indirectly incorporated into the analyses via my fire severity metric. In addition, because I excluded trees that I assumed dead prior to burning, and pre-fire SOD mortality was very patchy in the one seriously impacted sampling region (Monterey county; Rizzo et al. 2005, Maloney et al. 2005), it is unlikely that SOD had any notable effect on the results. If fires in diseased areas burn with greater intensity, such fires could act as an indirect mechanism through which SOD further reduces the abundance of tanoak relative to redwood. In addition, fires of even low severity pose a lethal threat to tanoak seedlings, any one of which could conceivably contain a gene or set of genes conferring resistance to SOD. In the past, tanoak likely persisted in frequently burned redwood forests, but the re-introduction of fire to SOD-infected redwood stands may increase the likelihood of its complete extirpation.

Scope of inference

Two important factors may limit the scope of inference for my results. First, all study sites were in the central and southern redwood regions, and thus I do not know the extent to which my findings apply to the northern region (within which western hemlock, *Tsuga heterophylla*, co-occurs with redwood and influences competitive dynamics; Sawyer et al. 2000b). Second, it is unclear whether the 2008 fires were characteristic (in terms of intensity, season, and scale) of wildfires and/or prescribed fires that occurred in the past or of those that are likely to occur in the future.

Broader implications

Post-fire basal sprouting has traditionally been viewed dichotomously (i.e. sprouters vs. non-sprouters), but a meta-analysis by Vesk and Westoby (2004) concluded that this simplistic classification does not adequately capture the full range of species responses to fire. They argue that species-level sprouting responses should be quantified by the percentage of individuals that sprout following disturbance. However, my dataset demonstrates that even this approach may be inadequate (for both redwood and tanoak, > 90% of trees that experienced fire-induced bole death produced basal sprouts), and so I have more thoroughly captured the continuous nature of competition in the regeneration stratum by analyzing basal sprout area and height. Similarly quantitative investigations of post-disturbance sprouting have been completed by other researchers, but I know of no other study that has comprehensively assessed post-wildfire competition by simultaneously considering bole survival and continuous tree-level basal sprouting responses.

Sprouting may be particularly important for understanding competitive dynamics in areas disturbed by fire, in ecosystems with species that are not easily classified along a seral gradient, and in other specific contexts. In experimental canopy gaps in the southeastern United States, Dietze and Clarke (2008) found that sprout height growth rates differed substantially with species, and that growth rates were higher for vegetative sprouts than for seedlings, suggesting that long-term canopy composition may be highly dependent upon early sprouting patterns. They also concluded that post-disturbance sprouts are especially important if advanced regeneration is scarce, indicating that vegetative sprouts deserve particular attention in recently burned areas. Caplat and Anand (2009) used a different approach to evaluate the importance of vegetative sprouting; they discovered that the inclusion of sprouting ability in their simulation dramatically altered predictions by allowing tree species typically considered late-successional to rapidly dominate post-disturbance environments, and concluded that a vigorous sprouting ability could enable these species to persist in areas frequently experiencing high severity disturbances. Thus, long-lived shade-tolerant trees that are capable of post-disturbance sprouting blur the traditional distinction between early- and late-successional species. Basal sprouting may also provide critical advantages in specific contexts; for instance, in wetland forests of Borneo, Yamada and Suzuki (2004) found a high incidence of sprouting in the juveniles of a dominant tree species (a phenomenon that is uncommon in tropical forests), and suggested that sprouting may be a strategy to overcome the tendency for decumbency in soft wet soils.

In many ecosystems, future disturbance regimes will depart from those that have been studied through the lens of modern ecological theory. Such shifts may occur for a wide range of reasons, including a) abandonment of suppression efforts targeted at historical disturbances, b) climate change, c) introduction of novel disturbance agents, and d) anthropogenic changes in landscape continuity and geomorphology. Modeling efforts, historical analyses, and controlled experiments all provide valuable information, but sound management decisions must ultimately rely on data collected in the aftermath of naturally occurring disturbances. By promptly recognizing and investigating emerging disturbances, researchers will be able to evaluate current paradigms, improve predictive ability, and facilitate more effective land management strategies.

Acknowledgements

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Chapter 3: Appendix

Table 3A.1. Model structure.

Burn status	burned	burned	unburned
Y	bole survival [0,1]	basal sprout area OR height	basal sprout area OR height
Error distribution	binomial	gamma	gamma
Link function	logit	log(Y+1)	log(Y+1)
Potential fixed effects (evaluated for each model separately)	species, DBH, stand age status, and fire severity (and squared terms and interactions)	species, DBH, stand age status, and fire severity (and squared terms and interactions)	species, DBH, and stand age status (and squared terms and interactions)
Random effects (in all models)	plot nested within transect nested within site	plot nested within transect nested within site	plot nested within transect nested within site

Table 3A.2. Basal sprout area (dm^2) as a function of the predictors in the main text (Table 3.4), as well as post-fire bole status. An interaction between this additional predictor and DBH was significant, but no other interactions with post-fire bole status had p-values < 0.10. Redwood was the baseline species, old-growth was the baseline stand age status, and bole death was the baseline post-fire bole status.

Predictor	Est.	SE	p-value
(Intercept)	4.6351	0.5418	< 0.0001
tanoak	-0.3599	0.2194	0.1017
DBH	0.0399	0.0174	0.0221
fire severity	0.2042	0.0410	< 0.0001
fire severity^2	-0.0130	0.0058	0.0301
second-growth	-0.7652	0.4323	0.2187
tanoak*DBH	-0.0345	0.0099	0.0006
tanoak*second-growth	-0.0097	0.0036	0.0084
bole survival	**-1.1689**	**0.4449**	**0.0089**
bole survival*DBH	**-0.0392**	**0.0173**	**0.0239**

Table 3A.3. Basal sprout height (dm) as a function of the predictors in the main text (Table 3.5), as well as post-fire bole status. No interactions with post-fire bole status had p-values < 0.10. Redwood was the baseline species, old-growth was the baseline stand age status, and bole death was the baseline post-fire bole status.

Predictor	Est.	SE	p-value
(Intercept)	2.3939	0.1257	< 0.0001
tanoak	-0.2369	0.1115	0.0343
DBH	0.0006	0.0010	0.5438
fire severity	0.1257	0.0201	0.0000
fire severity^2	-0.0088	0.0029	0.0037
second-growth	-0.3985	0.1309	0.0931
tanoak*DBH	-0.0152	0.0050	0.0026
tanoak*fire severity	-0.0746	0.0199	0.0002
second-growth*DBH	-0.0049	0.0019	0.0099
bole survival	**-0.2628**	**0.0888**	**0.0033**

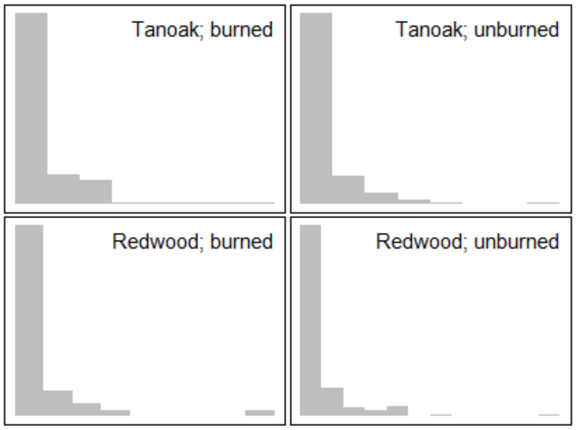

Fig 3A.1. Histograms of basal sprout area.

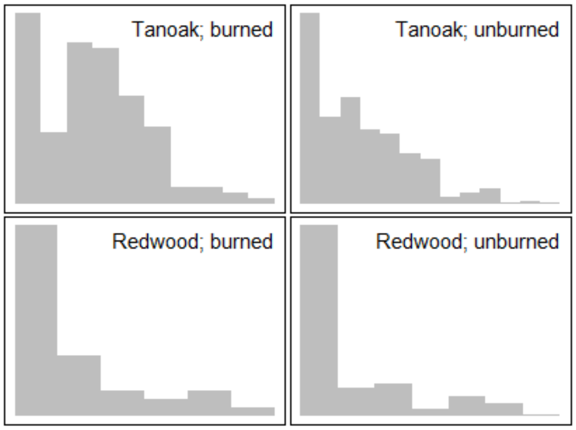

Fig 3A.2. Histograms of basal sprout height.

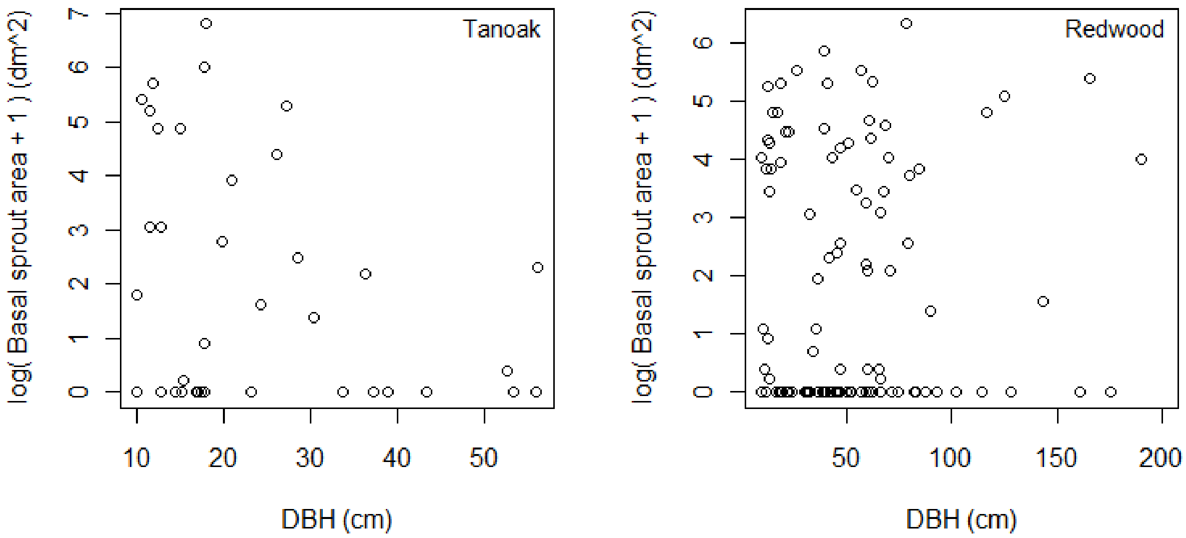

Fig. 3A.3. Basal sprout area vs. DBH in unburned areas (second-growth and old-growth combined). In the scatterplot for redwood, the plot region excludes four very large trees (≥ 200 cm DBH).

Chapter 4: Synthesis and Conclusions

Benjamin Ramage

I have examined two very different disturbances of coast redwood forests: sudden oak death (SOD), which is novel and biotic, and fire, which is historical and abiotic. The effects of these two disturbances differ in many ways, and yet there are also important similarities; for instance, both favor redwood. The remainder of this dissertation integrates the findings of the preceding chapters via a detailed comparison of SOD and fire, as well as a discussion of several other key aspects of the ecology and management of redwood forests.

The structural impacts of SOD are similar to those of fire in that both remove many of the smaller trees from redwood forests. SOD-induced mortality may also be leading to stand structures that are analogous to those produced with variable-density thinning, a method that has been proposed as a strategy to accelerate the transition from second-growth to old-growth in many forest types (Carey 2003), including coast redwood (O'Hara et al. 2010). By removing different amounts of volume at different locations within a stand, variable-density thinning aims to increase horizontal structural complexity as well as growth rates of residual trees, potentially approximating the patchy mortality that is characteristic of SOD. Fire can also lead to patches of high density interspersed with patches of low density if burn severity is highly heterogeneous throughout the stand (Pickett and White 1985), and thus there exists some degree of structural convergence between sudden oak death, fire, and variable-density thinning.

However, the effects of SOD differ from those of fire and variable-density thinning in critical ways. Although SOD and fire both favor redwood (as do many thinning regimes), it is important to recognize that SOD targets tanoak almost exclusively (other susceptible species are rare in redwood forest) and often causes root system mortality in addition to bole death (Cobb et al. 2010). While the structural impacts of SOD-induced tanoak mortality may be desirable to natural resource managers and casual observers alike, and the compositional impacts may initially appear comparable to fire, SOD has the potential to completely eliminate tanoak from redwood forests. In redwood forests, total species richness is believed to be higher in areas where other tree species, especially those bearing fruits or nuts, are relatively abundant (Noss 2000), and tanoak acorns in particular are known to sustain a wide range of wildlife species (Burns and Honkala 1990). Thus, if tanoak is extirpated by SOD, redwood forests – which are already relatively poor in tree species – may experience severe reductions in biodiversity.

Some of the cascading impacts of SOD-induced tanoak decline may be ameliorated if one or more functionally similar tree species is able to replace tanoak in diseased forests; unfortunately, this scenario is not supported by current regeneration patterns, which suggest that redwood may claim the majority of growing space vacated by tanoak. However, robust predictions of which tree species will replace tanoak are hindered by a deficiency of regeneration in many heavily impacted stands. The current deficiency of seedling recruitment in some areas, as well as the general absence of a regenerative response to tanoak mortality, may be due – at least in part – to the novel nature of SOD and the corresponding lack of adaptation in redwood and associated species. All common historical disturbances of redwood forests (fire, flooding, slope failure, and uprooting events; Lorimer et al. 2009) result in the exposure or deposition of mineral soil, and many tree species that occur in redwood forest (including redwood) establish most successfully on this substrate (Burns and Honkala 1990). In contrast, SOD-killed trees tend to deteriorate incrementally, breaking at progressively lower points along the bole and rarely uprooting, thus exposing little or no mineral soil. Other SOD-related mechanisms that may be inhibiting recruitment include: (a) direct suppression by *P. ramorum* (which can kill seedlings of some tree species that are relatively unaffected when mature; Davidson et al. 2002), (b) accumulation of high levels of generalist decay fungi, which can build up on decaying root systems and overcome the defenses of young seedlings (Edmonds et al. 2000, Baumgartner and Rizzo 2001), and (c) competition with tanoak sprouts that initially arise from the root systems of top-killed trees (tanoak sprouts often form dense clumps that may inhibit proximate regeneration; Cobb et al. 2010; Burns and Honkala 1990).

Although the precise mechanisms remain unresolved, there is some evidence suggesting that the novelty of SOD may explain, at least partially, why a vigorous regenerative response by redwood or co-occurring tree species has not occurred in tanoak mortality gaps. A comparison of redwood basal sprouting in SOD-impacted and burned areas provides a concrete illustration of redwood's failure to take full advantage of the growing space being made available by SOD-induced tanoak mortality (Figs. 4.1 and 4.2). Using the datasets described in chapters 1 and 3 (as well as data collected during these efforts that was not explicitly described in these chapters), we are able to compare redwood basal sprouting metrics (areal extent and maximum height) across a gradient of disturbance severity for two different disturbance types (SOD and fire); this comparison is presented here (in the concluding section), as opposed to in a data chapter, because it combines data from two chapters to yield interesting insights and is not substantive enough to comprise a stand-alone chapter. Redwood's basal sprout response (in terms of area and height) increased with fire severity (mean plot-level contiguous redwood bole char height), but redwood basal sprouting did not increase with SOD severity (total plot-level dead tanoak BA); in contrast, my data show a hint of a decline with SOD severity (Fig. 4.1). Basal sprout area and height values were generally greater at higher fire severities than they were across the full range of SOD severity. Note also that because all basal sprouts were consumed by the fires (which occurred one year prior to sampling), even the sprout area and height values that were comparable to the SOD-impacted plots (e.g. at low fire severities) indicate rapid post-fire sprout growth.

Another way to illustrate this discrepancy is to examine relationships between basal sprouting and canopy cover, which allows for identical comparisons across burned and SOD-impacted plots (Fig. 4.2). For both disturbance types, plot-level canopy cover and plot-level disturbance severity (mean contiguous redwood bole char height or total dead tanoak BA) were highly correlated (-0.70 in burned plots; -0.94 in SOD-impacted plots). In burned plots, redwood basal sprout area and height increased markedly with decreasing canopy cover; in contrast, in SOD-impacted plots, basal sprouting patterns were essentially constant across a similar range of canopy cover values (Fig. 4.2).

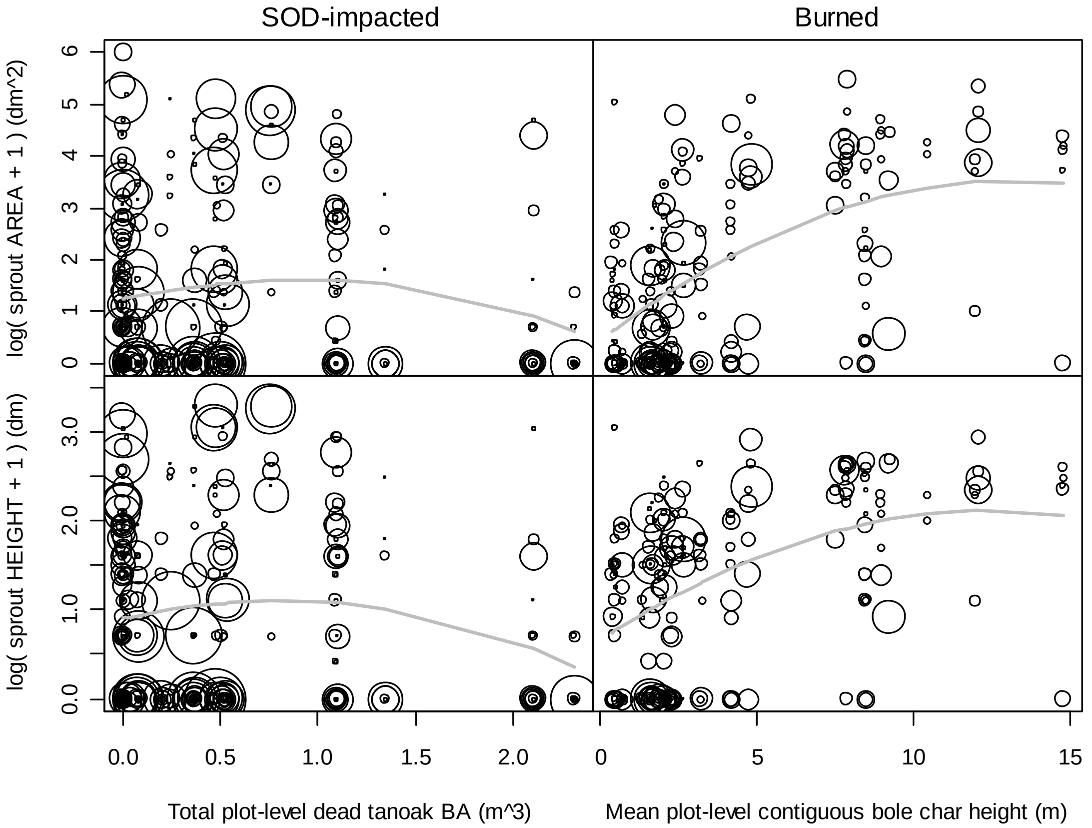

Fig. 4.1. Redwood basal sprout areal extent and maximum height as a function of disturbance severity in plots impacted by SOD or fire. Symbol size corresponds to DBH. Curves were fitted via locally weighted polynomial regression (LOESS). The SOD-impacted dataset is described in chapter 1 and the burned dataset (along with an explanation of the contiguous bole char height metric) is described in chapter 3; for consistency across SOD-impacted and burned plots, old-growth burned plots were not included. Although redwood basal sprout area and height were not analyzed in chapter 1, these data were collected in all SOD-impacted plots during field sampling in 2010; dead tanoak BA values represent 2008 totals. In burned plots, all data were collected in 2009.

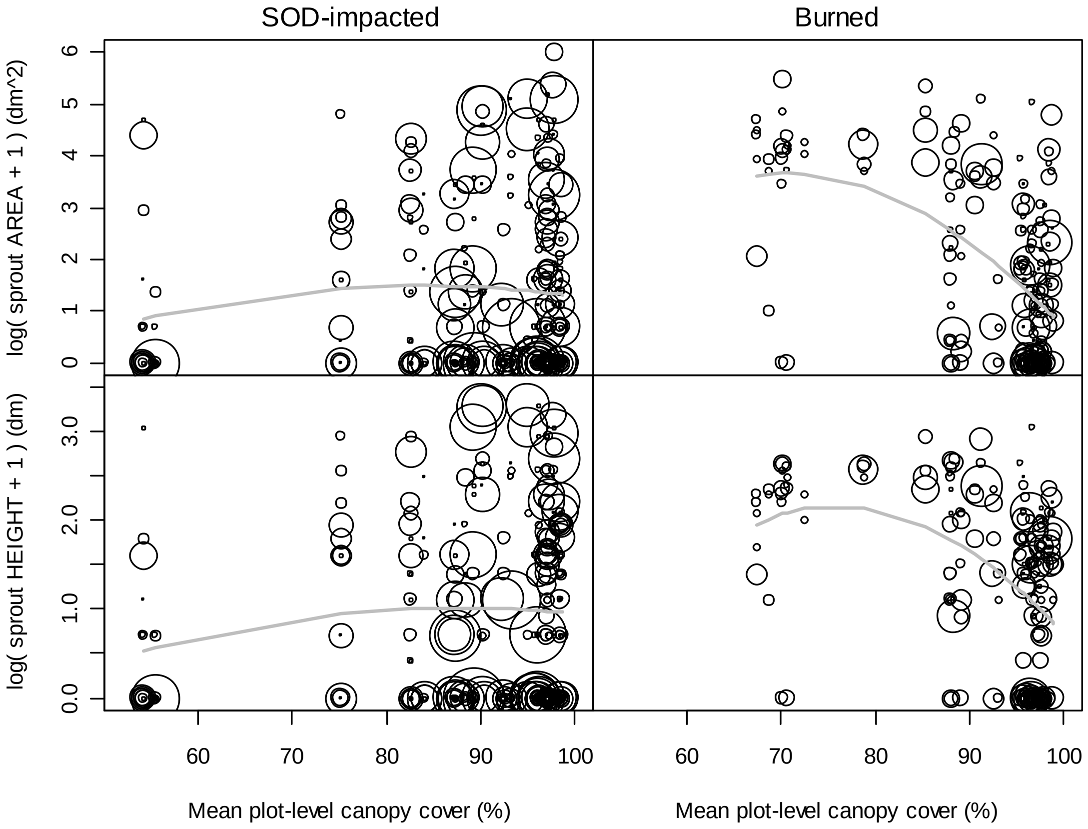

Fig. 4.2. Redwood basal sprout areal extent and maximum height as a function of canopy cover in plots impacted by SOD or fire. Symbol size corresponds to DBH. Curves were fitted via locally weighted polynomial regression (LOESS). The SOD-impacted dataset is described in chapter 1 and the burned dataset is described in chapter 3; for consistency across SOD-impacted and burned plots, old-growth burned plots were not included. Although redwood basal sprout area and height were not analyzed in chapter 1, and canopy cover was not analyzed in chapter 3, these data were collected during field sampling. In SOD-impacted plots, all data were collected in 2010; in burned plots, all data were collected in 2009.

Redwood's prolific post-fire sprouting response, coupled with its lack of response following SOD-induced tanoak mortality of similar magnitude (i.e. comparable reductions in canopy cover), suggests that redwood has not evolved to take advantage of increased light environments in the absence of other triggers. These findings lend support to the theory that fire has been an important factor in the evolutionary history of redwood, and provide evidence that redwood is not particularly well adapted to the novel disturbance that is SOD. Might other tree species that are currently sympatric with redwood (but that have experienced very different disturbance regimes and/or evolved different regeneration strategies) be better equipped to utilize the resources in SOD-induced mortality gaps? If so, such a *niche opportunity* (i.e. an opportunity for an absent or uncommon species to invade or increase in abundance; *sensu* Shea and Chesson 2002) would provide some hope that current levels of tree species diversity will be maintained in SOD-infested redwood forests. However, as discussed above, there is currently no evidence that any tree species are exhibiting regenerative responses to SOD-induced tanoak morality. Rather, tree species other than redwood and tanoak have made only small and highly variable incursions into mortality gaps, demonstrating that the future composition of SOD-impacted redwood forests is still far from certain.

The ultimate ability of potential tanoak replacement species to co-exist with redwood in areas previously dominated by tanoak may only be apparent if and when such species are able to recruit in high numbers; at present, dispersal and recruitment limitation (both of which may be highly stochastic) are likely the dominant community assembly processes, but as these species begin to actively compete in areas previously occupied by tanoak, deterministic niche-related processes may become more important. For instance, tanoak develops a deep taproot (Burns and Honkala 1990), a characteristic that likely helps it to co-exist with redwood (which does not develop a taproot; Burns and Honkala 1990), suggesting that other deeply rooted tree species may be best equipped to compete with redwood in the absence of tanoak. Consideration of stand structure may also be important for accurate predictions of deterministic species replacement; Cobb et al. (2010) suggested that California bay (*Umbellularia californica*) may benefit more than any other tree species from SOD-induced tanoak mortality in redwood forests because of similarities in growth form and size between tanoak and California bay, as well as positive feedbacks between inoculum loads and the abundance of California bay (which supports the most prolific sporulation of any host, but is not killed by *P. ramorum*; Davidson et al. 2008). The latter part of the preceding rationale also highlights the fact that the long-term success of newly establishing species will depend upon their ability to endure the disturbances – both historical and novel – that characterize redwood forest.

P. ramorum has almost certainly become a permanent resident of diseased redwood forests and thus any attempts by tanoak to re-colonize infested areas (e.g. from uninfested patches) are likely to eventually result in small scale disturbances (i.e. SOD-induced mortality). However, if tanoak populations become sufficiently low throughout the redwood landscape matrix (or if most remaining tanoaks exhibit disease resistance), SOD-induced mortality events will become so rare that SOD will no longer represent a major disturbance, and *P. ramorum* will have effectively become a fully integrated "native" pathogen. This scenario represents another dimension of the distinctions between SOD and fire; although fire frequency and severity may fluctuate with climate and other factors, it is hard to imagine that fire could ever lose its capacity to cause significant mortality, even if such mortality is concentrated in smaller size classes.

Fire and sudden oak death are both affecting the stand structure and species composition of coast redwood forests, but the compounded effects (*sensu* Paine et al. 1998) of SOD and fire may lead to the greatest long-term impacts. SOD has increased forest floor fuel loading (Ramage et al. 2010), and areas with recently killed standing dead trees are at a greater risk of crown fire (Kuljian and Varner 2010). If fires in diseased areas burn with greater intensity, such fires could act as an indirect mechanism through which SOD further reduces the abundance of tanoak relative to redwood. In addition, fires of even low severity might pose a lethal threat to tanoak seedlings, any one of which could conceivably contain a gene or set of genes conferring resistance to SOD. In the past, tanoak likely persisted in frequently burned redwood forests, but the re-introduction of fire to SOD-infected redwood stands may increase the likelihood of its complete extirpation. Furthermore, if tanoak does disappear entirely from redwood forests, either via the combined effects of SOD and fire or the isolated effects of SOD, this loss of diversity may reduce "resistance" and/or "resilience" to future threats (*sensu* Suding et al. 2004).

Redwood forests are currently undergoing profound changes, many of which represent challenges to forest health and ecological integrity. Some of these problems are effectively insurmountable; for instance, there is little hope of halting the spread of SOD within patchily infested landscapes. However, other concerns may be amenable to management interventions; for example, the deficiency of regeneration in some SOD-impacted areas may facilitate the planting of tree species selected to maintain wildlife value and other ecosystem services. Such options should be explored immediately because any attempts to direct ecological trajectories will be most efficient in the early stages of community assembly (Thompson et al. 2001). The manipulation of fire (prescription as well as suppression) could also be a component of a strategy designed to minimize the detrimental effects of SOD; there is still a great deal of uncertainty about the interaction between SOD and fire, and future research should explore the possibility of whether particular fire regimes could benefit tanoak in forests that are infested with or threatened by SOD. Redwood forests have changed dramatically throughout the twentieth century, and the SOD-induced shifts that have occurred in the last decade represent another major perturbation, resulting in an ecosystem that is novel in several regards. Novel ecosystems are likely to present unfamiliar and unforeseen challenges (Hobbs et al. 2006), and thus researchers and land managers should expect that successful stewardship of redwood forests will require sustained inquiry and considerable experimentation.

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