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Natural Recovery of Second-Growth Coast Redwood Stands in the Santa Cruz Mountains

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NATURAL RECOVERY OF SECOND-GROWTH COAST REDWOOD STANDS IN THE
SANTA CRUZ MOUNTAINS

A Thesis

Presented to

The Faculty of the Department of Environmental Studies

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Jeffrey M. Sinclair

May 2013

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The Designated Thesis Committee Approves the Proposal Titled
NATURAL RECOVERY OF SECOND-GROWTH COAST REDWOOD STANDS

IN THE SANTA CRUZ MOUNTAINS

by

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May 2013

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ABSTRACT

NATURAL RECOVERY OF SECOND-GROWTH COAST REDWOOD STANDS IN THE SANTA CRUZ MOUNTAINS

by Jeffrey M. Sinclair

The natural recovery of coast redwood forests following a logging event is not fully understood. Recent studies, in the redwood central range, have found that un-restored and unmanaged second-growth forest stands can begin to recover and exhibit characteristics of old-growth stands within 100 years or less. The goal of this study was to determine if redwood stands in their southern range are recovering naturally. A total of 160 sample plots were selected randomly within old-growth and second-growth study sites. The data collected included stand density, tree size structure, canopy cover, species diversity, and species composition. Special habitat features were analyzed and included measurements of snags, large woody debris (LWD), fire hollows, and observations of reiterated trunks in second-growth stands. Mean comparisons and trends among the second-growth stands and old-growth stands were analyzed to determine the stage of development of second-growth stands. The second-growth stands were also examined to see if they exhibited old-growth characteristics. Results demonstrated that several stand characteristics were recovering naturally and that second-growth forests appear to be progressing through the stand development stage of understory reinitiation. These findings suggest that unmanaged second-growth redwood stands have the potential for natural recovery in their southern range.

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Introduction

Forests throughout the world have suffered great loss of land and biodiversity due to anthropogenic disturbances. Coast redwood (*Sequoia sempervirens* D. Don Endl.) (Henceforth the terms redwood and *Sequoia sempervirens* will be used interchangeably) forests have not been immune, as these unique ecosystems too, have lost a vast majority of their natural landscape. In approximately 150 years, 95% of the primary redwood forest has been lost to logging (Noss, 2000). The redwood forests naturally occur in a small portion of the Pacific mountain ranges of Northern California and Southern Oregon (Sawyer et al., 2000a). These forests provide important habitat for endangered wildlife such as the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*) (Cooperrider et al., 2000). The forests are home to shade-tolerant and fog-dependent plants that coexist symbiotically with *Sequoia sempervirens* (Burgess & Dawson, 2004; Dawson, 1998; Loya & Jules 2008; Sawyer et al., 2000a). Recently, the forests have also been looked to as carbon sinks to offset the effects of global climate change (Gonzalez et al., 2010; Madej, 2010; Noss, 2000). However, many *Sequoia sempervirens* forests are still threatened by logging.

The entire forest community is impacted by logging. Areas are left void of trees or with greatly reduced numbers. Forage habitat is removed and soils are compacted or eroded away. Moreover, richness and diversity of native shrubs and herbs are reduced (Cambell et al., 2011; Corns, 1988). Non-native plants invade and out-compete native plants, as they often do in areas where canopy gaps have been created (Rivas-Ederer & Kjeldsen, 1998; Russell & Jones, 2001). In addition, canopy removal introduces greater

solar radiation and reduces fog moisture retention. These logging impacts cause lasting damage to forest ecosystems, such as the *S. sempervirens* forests.

Despite over a century of logging, the natural recovery process of *S. sempervirens* is not fully understood. Currently, much of the research focuses on possibilities of redwood forest restoration through management, such as thinning, which may have potential impacts similar to those with logging (Harrod et al., 2009; Miesel, Boerner, & Skinner, 2009; O'Hara et al., 2010). Several studies have addressed the impacts of logging on *S. sempervirens* forests (He et al., 2010; Banner & LePage, 2008; D'Amato, Orwig, & Foster, 2009). However, comprehensive research on the process of natural recovery has been limited to a study conducted in the central range of *S. sempervirens* forest communities (Russell & Michels, 2010). The purpose of this thesis was to expand upon the current literature by providing insight into the natural recovery from logging of *Sequoia sempervirens* in their southern range.

Literature Review

Characteristics of *Sequoia Sempervirens*

Sequoia sempervirens is one of the largest plant species on the planet, and many of the trees are among the tallest (McBride, 1977). Fifteen individuals have been found to be greater than 110 m in height. Currently, the tallest individual has been measured at 112 m in height. (Sawyer et al., 2000b). There are also many *S. sempervirens* trees reaching heights close to or above 100 m in height (Dagley, 2008; Sawyer et al., 2000b).

Sequoia sempervirens has thick, dark brownish-red bark that is soft and fibrous. The bark has wide, deep grooves that run vertically up the length of the tree and can

weather to a gray color in older trees (McBride, 1977). *Sequoia sempervirens* is an evergreen species with leaves that grow in a linear form off terminal shoots and exposed branches (McBride, 1977). The leaves are flat narrow needles that fan out. Cones are small, reddish-brown, and globed-shaped. They range in size from 15 – 30 mm in diameter and mature in one year (Hickman, 1993; McBride, 1977). *Sequoia sempervirens* seed dispersal and seedling growth typically occurs on mineral soils, fallen logs, root-wad mounds, and slopes that have disturbed soil from gravity-induced movement (Lorimer et al., 2009; Russell & Michels, 2010). Although regeneration can occur from seedlings, most of the recruitment takes place as a result of vegetative sprouting (Dagley, 2008; Russell & Michels, 2010).

Vegetative sprouting. *Sequoia sempervirens* is capable of vegetative sprouting, which is common among angiosperms but rare in conifers (Bond & Midgley, 2001; Douhovnikoff, Cheng, & Dodd, 2004; McBride, 1977; Russell & Michels, 2010). Sprouting can result in new roots and limbs, but it can also produce asexual regeneration from vegetative material or dormant buds (Douhovnikoff et al., 2004; McBride, 1977). Dormant buds are often located in the root collar but can also occur on the roots, stem, and branches (Dagley, 2008; Russell & Michels, 2010). Sprouting on the original tree takes place when dormant buds produce growth as a result of damage to the primary stem (McBride, 1977; Sawyer et al., 2000b). In order for sprouts to form, there has to be a nutrient bank from which they can draw from the original stem (Bellingham & Sparrow, 2000; Sawyer et al., 2000b). The adequacy of a species nutrient bank has been thought to

determine the success of sprouts; however, further research is needed for confirmation (Bellingham & Sparrow, 2000).

Basal sprouts can result in clonal trees, called ramets, which can remain persistent beyond the life of the main stem tree (Douhovnikoff et al., 2004). Ramets typically grow faster than seedlings (Bond & Midgley, 2001). As these clonal sprouts mature, they are able to reproduce sexually through seed germination and asexually through further vegetative sprouting. The number of clonal generations that can be produced over time is limitless (Douhovnikoff et al., 2004).

Sequoia sempervirens' ability to sprout has benefits for survival. Sprouting ability in plants can reduce population turnover and reduce reliance on seed germination for reproduction. In addition, sprouting in stands of *S. sempervirens* allows the species to withstand disturbances as sprouts grow to fill open gaps left in the canopy (Bond & Midgley, 2001; Busing & Fujimori, 2002). However, there are reproductive tradeoffs (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). Generally, sexual reproduction is less effective in sprouting plants because their seedlings have lower survival rates compared to nonsprouting plants (Bond & Midgley, 2001).

Foliar uptake of fog. The range of *S. sempervirens* is limited to regions that are regularly subjected to coastal fog (Ewing et al., 2009; Sawyer et al., 2000b). Fog is an important contributor to climatic conditions along coastal ecosystems, such as the mountain regions of the cloud forests of Costa Rica, the Chilean and Peruvian Andes, and low elevation regions of Newfoundland and California (Burgess & Dawson, 2004). Fog

occurs when wind-initiated coastal upwelling mixes with a warm layer of air (Sawyer et al., 2000b). The air is then filled with small water droplets that make up fog. These droplets generally do not precipitate unless they encounter solid surfaces because the vertical settling rate is too slow. Fog is referred to as occult precipitation because it does not typically register on rain gauges (Burgess & Dawson, 2004). However, the canopy of *S. sempervirens* stands have space for the air to pass through and large surface areas that are able to collect fog from the air (Burgess & Dawson, 2004; Dawson, 1998).

Sequoia sempervirens collects fog through foliar uptake which occurs when fog moves through a water potential gradient within a branch, leaf, or stem. Once the water is absorbed, the water content of the tree is increased, and in some cases the water demand can be met (Limm, Simonin, Bothman, & Dawson, 2009). When fog is not directly absorbed by the canopy the water can drip to the understory and supply water to the understory plants with shallow roots. Several plant species in the *S. sempervirens* forest can absorb water through foliar uptake, including western sword fern (*Polystichum munitum*), Douglas-fir (*Pseudotsuga menziesii*), madrone (*Arbutus menziesii*), California huckleberry (*Vaccinium ovatum*), California polypody (*Polypodium californicum*), and redwood sorrel (*Oxalis oregana*) (Dawson, 1998; Limm, Simonin, Bothman, & Dawson, 2009). Limm, Simonin, Bothman, and Dawson (2009) determined that 80% of the species selected from a coast redwood forest were able to absorb water through foliar uptake.

The dry summer months of the redwood region coincide with the highest demand for water in *S. sempervirens* and other plant species within the ecosystem. Dawson (1998) found that during the summer months, 19% of the water demand in *S. sempervirens* was met by foliar uptake. Percentages were even higher for understory species that received fog water once it had fallen from the canopy to the soil. Fog from canopy condensation supplied 70% of the water demand of redwood sorrel during the dry summer months and 100% of the water demand of western sword fern during the same period (Dawson, 1998). The research that has been done on fog and its relation to *S. sempervirens* stands shows that both fog and the canopies that disperse water to the understory are very important to plants within these stands.

Stand Characteristics

There is no universal definition of old-growth forests; however, it is generally accepted that they are made up of stands that have never been harvested (Sawyer et al., 2000b). Stands are generally considered second growth when they are made up of trees that have grown back after experiencing some harvesting that removed the original trees. There are general characteristics known to ecologists that are used to identify old-growth and second-growth *S. sempervirens* stands (Sawyer et al., 2000b). Stand density within *S. sempervirens* forests varies between age classes. Stand density tends to be higher in young second-growth stands, but as age increases the density of redwood stands decreases as a result of natural thinning (Russell & Michels, 2010). Old-growth stands tend to be less uniform and have densities ranging from 50 – 100 trees per hectare (ha) (Lorimer et al., 2009; O'Hara, Nesmith, Leonard, & Porter, 2010; Sawyer et al., 2000b).

Sequoia sempervirens can often be the dominant species in their range based on specific basal area compared to total basal area. This dominance grows with the age of the stand and is more apparent in old-growth stands. Along with dominance, tree size is a characteristic often used in identifying old-growth and second-growth stands. Analysis of diameter distributions has shown that tree size typically increases with age (Gellman & Zielinski, 1996; Russell & Michels, 2010). It has also been shown that *S. sempervirens* is larger than associated tree species throughout the majority of age classes in recovering second-growth stands (Russell & Michels, 2010).

The level of canopy cover is an important characteristic in comparing old-growth and second-growth stands because it can affect the amount of water from fog drip that reaches understory plants and seedlings (Dawson, 1998; Limm et al., 2009). Canopy cover also impacts the amount of light that reaches the understory. An opening in the canopy accelerates the growth of plants growing in shade as a result of more light (Fritz, 1930; Roy, 1966). Canopy cover is a characteristic that is variable throughout the lifespan of a stand.

Shrub and herb cover are two other elements to consider when looking at old-growth and second-growth *S. sempervirens* stands. Shrub cover has been found to be variable throughout different age classes. This variability of shrub cover can be attributed to disturbances that create canopy gaps allowing the penetration of more light and thus growth in the understory. Herb cover has been found to be much lower in second-growth stands than old-growth stands (Russell & Michels, 2010).

There are many species that grow within a redwood forest, but certain plants, more than others, are more commonly found within *S. sempervirens* stands. The composition of plant species in a stand is related to harvest history. Species such as trillium (*Trillium ovatum*), Calypso orchid (*Calypso bulbosa*), and redwood violet (*Viola sempervirens*) have all been found in greater numbers in old-growth stands and second-growth stands older than 100 years. Mountain iris (*Iris douglasiana*), sugar scoop (*Tiarella trifoliata* L.), and vanilla leaf (*Achlys triphylla*) have also been found throughout the age classes of *S. sempervirens* stands but in much lower numbers throughout second-growth stands as compared to old-growth stands (Russell & Michels, 2010).

Special Habitat Features

Old-growth stands contain special habitat features that are not typically present in younger stands because the features develop over long periods of time (Harrod et al., 2009; Miesel et al., 2009; Sawyer et al., 2000b; Willet, 2001). Snags and large woody debris (LWD) are two important old-growth stand features. Snags are standing trees that are dead as a result of events such as thinning or fire (Harrod et al., 2009; Willet, 2001). LWD typically consists of downed logs of varying age and levels of decay. Wildlife such as birds, small mammals, and salamanders greatly depend on both snags and LWD for habitat (Harrod et al., 2009; Miesel et al., 2009; Sawyer et al., 2000b). Availability of snags is considered one explanation for why studies have reported higher cavity-nesting bird populations in old-growth stands (Hazard & George, 1999).

Another special habitat feature found in old-growth *Sequoia sempervirens* stands is the hollows that develop over time at the base of trees as a result of repeated fire exposure and pathogenic agents that cause decay within the core of the tree (Gellman & Zielinski, 1996). Many of these basal hollows are larger than five meters in diameter and provide unique habitat opportunities for wildlife such as bats, which use the hollows as shelter, a place for hibernation, and roosting (Gellman & Zielinski, 1996).

Old-growth *Sequoia sempervirens* trees often have multilayered canopies with reiterated trunks and large lateral branches (Sawyer et al., 2000b; Sillet & Van Pelt, 2007). It is unknown what triggers the growth of reiterations and lateral branches, but the formations are often attributed to fire, wind, or fungi disturbance which can create wounds that release dormant buds in the tree (Williams & Sillet, 2007). These disturbances are thought to assist in creating unique canopy structures (Sawyer et al., 2000b; Sillet & Van Pelt, 2007).

Another important feature of old-growth *S. sempervirens* is that it can support epiphytes, which grow in the canopy of a mature *S. sempervirens*, including mosses and vascular plants such as ferns, shrubs, and sometimes other trees. Many epiphytes are shrub, herb, or tree species that are also common to the understory, such as huckleberry (*Vaccinium ovatum*), leather fern (*Polypodium scolieri*), California bay laurel (*Umbellularia californica*), and tanoak (*Lithocarpus densiflorus*). Epiphytes are typically found in older trees with reiterated trunks and branches. Organic material can

accumulate in the crotch of a well-developed reiterated trunk creating an arboreal soil that is able to retain water and support epiphytic plants (Williams & Sillet, 2007).

Forest Disturbances

Natural and human-caused disturbances in forests affect tree size, crown structure and cover, stand density, and understory vegetation. Forest recovery is initiated following disturbances. Although *S. sempervirens* stands are tolerant of many different types of disturbances, they can still be altered and develop new growth and stand complexity, such as special habitat features, through the process of natural recovery (Lorimer et al., 2009; Sawyer et al., 2000b). Frequency and size of forestland disturbances vary and can be dependent on geography and climate. The main disturbances impacting redwood forests include wind, insect and animal damage, fire, and logging (Lorimer et al., 2009; O'Hara et al., 2010; Rentch et al., 2010; Sawyer et al., 2000b).

Wind disturbance. Strong wind is common throughout the *S. sempervirens* forest ranges (Lorimer et al., 2009; Sawyer et al., 2000b). Winds are particularly high during October through March and have been recorded up to 100 km/h. Disturbances such as wind blow-down are particularly apparent in older stands in which trees are taller and have larger canopies. The trees in older stands typically have a larger above-ground to below-ground biomass ratio, which creates more drag in the wind and tension on the shallow root systems of *S. sempervirens* (Rentch et al., 2010). Uprooted trees from wind blow-down have been found to be four times more common than snapped trees in *S.*

sempervirens stands (Lorimer et al., 2009). However, wind can snap tops of trees, reiterated trunks, and branches, which ultimately contribute to the *S. sempervirens* canopy complexities (Lorimer et al., 2009).

Animal damage. *Sequoia sempervirens* are exposed to animals and insects in similar ways as other tree species. However, the *S. sempervirens* is not nearly as susceptible to these disturbances as most species. Insects, including certain types of beetles, mites, and moths, can attack redwood trees but are rarely capable of causing the level of damage that would result in mortality (Sawyer et al., 2000b).

Mammals such as black-tailed deer (*Odocoileus hemionus columbianus*) and black bears (*Ursus americanus*) can inflict life threatening damage to the *S. sempervirens*. Typically, it is the younger and smaller trees that are subjected to mammal disturbances. Black-tailed deer will browse the *S. sempervirens* samplings and sprouts, whereas black bears strip the bark from young redwoods to eat the sugary sap and terpenes found in the cambium layer of the tree (O'Hara et al., 2010; Russell, Carnell, & McBride, 2001; Sawyer et al., 2000b). Stripping the bark from a redwood can cause mortal damage if the tree is completely girdled. Typically, trees that are most susceptible to black bears are approximately 13 – 64 cm in diameter. It is uncommon for old-growth stands to encounter this type of disturbance (O'Hara et al., 2010; Russell et al., 2001).

Fire Disturbance. Fire is a significant part of the disturbance regime and has been a major part of the ecological history of *S. sempervirens* forests (Binkley et al., 2007; Dagley, 2008; Finney, 1993). Although it can damage and kill trees, seedlings, and

understory plants, fire can also promote growth and stand complexity (Binkley et al., 2007). Understory diversity and development can be encouraged when canopy and duff layers are burned off, creating access to soil and light. Competition among species that can thrive after this type of disturbance, such as redwood and western hemlock, also promotes diversity (Lorimer et al., 2009). Stand complexity can be enhanced as a result of special habitat features such as snags, LWD, and fire hollows forming from dead or damaged trees subjected to fire (Gellman & Zielinski, 1996; Harrod et al., 2009; Willet, 2001). Fire can also encourage stand complexity by releasing dormant buds in the form of basal sprouts and trunk reiterations (Finney, 1993; Sawyer et al., 2000b; Sillet & Van Pelt, 2000).

Human disturbance: impacts of logging. *Sequoia sempervirens* is highly valued for its timber, which has excellent quality wood fiber (Douhovnikoff et al., 2004; Jameson & Robards, 2007). Native Americans were the first to harvest *S. sempervirens*. Several tribes including the Yurok, the Pomo, Sinkyone, Coast Yuki, and Mattole built homes, sweat lodges, assembly halls, and canoes using redwood trees. Native Americans typically did not fell the trees themselves but rather utilized redwoods found lying on the forest floor or as drift wood (Barbour et al., 2001). European settlers began logging as early as the beginning of the 1800s with the Spanish harvesting wood for their missions. Throughout the early period of logging the process was slow and difficult with many limitations. As technology changed and demand grew, so did the harvesting of redwoods. Techniques for logging have ranged from selective harvesting to clear-cutting entire stands (Barbour et al., 2001).

There are many ecological impacts associated with logging that affect both flora and fauna of the *S. sempervirens* forests (Jameson & Robards, 2007; Russell, 2009; Russell & Jones, 2001). Soil can be compacted as a result of logging, which lowers nitrogen levels for remaining plants (Corns, 1988; Jussy, Ranger, Bienaime, & Dambrine, 2004; Stone & Wallace, 1998). Soil erosion also occurs when root systems are removed and soil stability is decreased (Cambell et al., 2011). Impacts to the soil affect the native herbs and shrubs located in the understory. Diversity and richness of native species can be diminished (Loya & Jules, 2008). Some vascular plants are able to recover relatively quickly after logging while others remain permanently absent. Impacts to specialized fungi also are attributed to decreased vascular plant populations following a harvest (Loya & Jules, 2008).

When a *S. sempervirens* forest is logged there are areas where the canopy is open in places it had not been before. This introduces more light to the understory, which can encourage invasive species to enter the area and out-compete shade-tolerant native species (Rivas-Ederer & Kjeldsen, 1998; Russell & Jones, 2001). In addition, extracting the canopy from a *S. sempervirens* forest restricts water supply to understory species that rely on fog captured by the canopy (Burgess & Dawson, 2004; Dawson, 1998). Removing the trees also removes the important canopy habitat.

Fauna is significantly impacted by logging through the loss of canopy habitat, understory habitat, and special habitat features. Forage and nest habits are often completely removed once a forest is harvested. Special habitat features such as large

woody debris, snags, reiterated trunks, and fire hollows, which provide diverse forage and nest habitats, are also removed. These features are not replenished immediately following a timber harvest. They take time to form and become useful habitat elements of the forest.

Timber harvesting can also negatively impact adjacent un-harvested land. (Russell & Jones, 2001). Russell and Jones (2001) studied the effects on a *S. sempervirens* forest stand edge, (the area between managed and preserved stands). Their results exhibited negative impacts to stand characteristics such as canopy height, crown dieback, seedling density, and richness of trees. Furthermore, species diversity along the edge was decreased, which can ultimately lead to a decrease in solar radiation.

Successional Models for *Sequoia sempervirens*

Succession is the process of naturally replacing plant or animal communities in stages over time (Prach & Walker, 2011). Plant succession is an ecological process important to forest recovery because it impacts many different aspects of an ecosystem, including the water and nutrient cycles, gas exchange, productivity, and biodiversity (Falkowski et al., 2009). Models have been developed to visualize the process of succession and several of them have been applied to *S. sempervirens* forests.

Seral and climax stage theories. Frederick Clements proposed a model for plant succession that identified the process as having stages that ultimately lead to a climax or final stage. The stages prior to the climax stage were referred to as seral stages. Clements believed that succession can initiate with a pioneer species or at a later seral

stage (Clements, 1928). Since Clements' initial model for plant succession was proposed, many other models regarding the topic have arisen.

There are two main models regarding Clementsian succession and *S. sempervirens*. One is that *S. sempervirens* is a seral species that requires disturbance, such as fire or flooding, to thrive and be productive (Busing & Fujimori, 2002; Lorimer et al., 2009). This seral stage theory is supported by studies such as Stone and Vasey (1968) that found nutrient and mineral cycling in *S. sempervirens* forests relied heavily on fire or other disturbances, such as flood and landslides. Nutrient and mineral cycling is crucial to *S. sempervirens*. Stone and Vasey discuss the observation that nutrients, such as nitrogen, can be obstructed within soils of undisturbed areas. Without the necessary amount of nitrogen *S. semperivens* cannot retain their vitality (Stone & Vasey, 1968). According to the seral stage theory, since *S. semperivens* dominance is a subclimax stage in succession they would be replaced by other species such as western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), western redcedar (*Thuja plicata*), and tanoak if they were not maintained by consistent disturbances (Busing & Fujimori, 2002; Lorimer et al., 2009; Stone & Vasey, 1968).

Another model suggests *S. sempervirens* is a dominant species in the climax stage of succession (Roy, 1966). This climax theory suggests *Sequoia sempervirens* is able to thrive following a disturbance, such as fire, but does not depend on it (Lorimer et al., 2009). Busing and Fujimori (2002) found in their study that *S. sempervirens* is capable of regeneration without fire. They found that the *S. sempervirens* mortality rates were

very similar to in-growth rates as it appeared they were able to regenerate as a result of gap disturbances, such as overstory blow-down leading to canopy openings.

According to the climax theory, *S. sempervirens*' adaptation to disturbances allows it to maintain long-term dominance over other species (Binkley et al., 2007). It has also adapted to thrive in areas with poor and silted soil where other conifers could not (Busing & Fujimori, 2002). Although other trees can have higher regeneration rates, they do not have strong enough resilience or life-spans to overcome the *S. sempervirens* as the dominant species. The climax theory asserts that in order for other species to gain dominance, the *S. sempervirens* would have to experience a great decline in regeneration over many centuries (Busing & Fujimori, 2002).

Initial floristics model. While Clements (1928) laid out a uniform structure for succession, it is uncommon to see such uniformity in nature. The idea of applying any type of successional model to an ecosystem was challenged by Gleason (1926). He believed that it was impossible to do so because there was no true structural uniformity in nature, and interpretation of species' associations was variable.

According to Gleason (1926), vegetation change is more related to proximity than temporal change. Following a disturbance, adjacent vegetation has the most likelihood of reestablishing itself in the disturbed area and acting as the next stage in succession. Since vegetation association is variable, succession following disturbance is difficult to predict.

Gleason (1926) considered transition zones to be problematic as well when attempting to identify seral stages. He questioned if they should be labeled as mixtures of

ecosystems or successional transitions from one type of ecosystem to another, such as an oak woodland advancing into a recently disturbed *S. sempervirens* dominated forest or vice versa. Gleason concluded that the vegetation is the result of altering migrations from adjacent areas and varying environmental conditions rather than clear seral stages of succession.

Multiple pathways model. It is understandable that disagreement regarding the appropriate succession model for *S. sempervirens* forests has arisen. The species has characteristics that seem to place it in different successional stages. It has characteristics of a seral stage species such as shade tolerance and variable aged-stands. It also has the ability to recover and resprout after disturbances. However, the *S. semperivens* seedlings are not typical to the understory in old-growth stands. Also, the thick bark that allows it to withstand fire disturbances could be considered a characteristic of a climax stage species (Binkley et al., 2007; Lorimer et al., 2009).

Part of the reason that *S. sempervirens* has been difficult to place within a successional stage is because the models based on Clementsian theory focus mainly on the sequence of replacement after disturbances. The traditional succession models do not take into consideration a species like *S. sempervirens* with adaptive traits that allow it to survive many different disturbances. These models also do not take into account the frequency and size of disturbances. Small frequent disturbances are going to have a different effect on an ecosystem than one large, infrequent event. Similar successional

paths may follow the same types of disturbance events, but if there are a variety of random disturbances, this may not be the case (Cattellino et al., 1979).

The Multiple Pathways Model accounts for the unique characteristics of *S. sempervirens*. This model considers the reproduction and survival of a species, the method of persistence, conditions needed for establishment, and the life history of a species when placing it in a succession sequence. An understanding of these different attributes allows for a description and prediction of the successional sequence following varied and temporally inconsistent disturbance events in gap phase succession (Cattellino et al., 1979).

Gap phase succession. Gap phase succession occurs when natural canopy gaps form as a result of a tree mortality or blow-down, increasing the availability of light to lower vertical strata (Busing & Fujimori, 2002). Trees can die naturally from being knocked over by such disturbances as wind, fire, landslides, and floods (Beaty & Taylor, 2001; Lorimer et al., 2009). Older forest stands often have larger canopy gaps created as a result of the trees possessing larger canopies and knocking down other trees as they fall (Rentch et al., 2010). Although rare for *S. sempervirens*, trees can also be mortally impacted by bears, disease, and insects and become snags leaving gaps in the canopy (Lorimer et al., 2009; O'Hara et al., 2010). Small scale disturbances such as wind blow-downs have become the focus of redwood dynamic and succession studies because large scale disturbances are rare (Mailly, Kimmins, & Busing, 2000; Russell & Michels, 2010). When gaps in the canopy are created as a result of disturbance, successional processes

take place as understory trees utilize the space and light to grow and fill the gaps (Russell & Michels, 2010).

Stand development model. The Multiple Pathways Model accounts for variables not addressed by Clements (1928) and it can be used when describing Gap Phase Succession. However, the model relies heavily on disturbance events and does not describe in detail the development of a stand following a disturbance.

Oliver (1981) presents four stages of stand development following a disturbance. The stages in order are stand initiation, stem exclusion, understory reinitiation, and old-growth. Four similar stages were also described by Peet and Christensen (1980): establishment, thinning, transition, and steady-state. The stand initiation, or establishment stage of forest succession, is the first stage to follow a disturbance. During this time plants are reestablishing themselves through new seed dispersal, buried seeds, and vegetative sprouting. The stem exclusion or thinning stage takes place as the canopy becomes interconnected, reducing light to the understory and growing space. Understory species remain but seedlings will die, tree regeneration is reduced, and natural thinning occurs. The process of natural tree thinning opens up gaps in the canopy for light to reach the understory and room for individual trees to grow larger. Following this stage is understory reinitiation, or the transition stage, at which point understory plants such as herbs and shrubs reestablish and begin to represent an old-growth understory. The final stage is the old-growth or steady-state stage, which could also be considered equivalent to the climax stage in the Clementsian model. At this stage the stand consists of mature

trees that have increased in age, height, and diameter. Understory plants have been established and are compatible with the conditions of the ecosystem. Die-back and thinning still occur during this stage as a result of disturbances, which allow for variation in the stand and special habitat features to appear (Barnes et al., 1998).

Natural Recovery Following Logging

Studies that look at natural recovery of forests after logging help researchers understand the succession that takes place as a result of human disturbance. A study by He et al. (2010) focused on the *Picea crassifolia* in the Qilian Mountains of northwestern China. This region had been heavily logged for half a century and in recent decades there were attempts to reforest the area. Researchers compared primary *Picea crassifolia* forest stand characteristics to those in second-growth stands of 30 and 70 years. In doing this research, they hoped to get a better understanding of the current succession and future successional trend for these second-growth forests. Results showed that logging increased stand density but declined from self-thinning over many years. The spatial distribution of the trees was determined based on the residual trees in the stand and the amount of canopy cover, soil nutrients, and water competition. The study also found that heterogeneity of age decreased and tree ring growth was highest after initial cutting (He et al., 2010).

Studies have also compared understory vegetation in different unmanaged second-growth stands to old-growth stands to observe natural recovery after logging and successional processes taking place. The results of these studies vary among the different

forest types. For example, Banner and LePage (2008) compared second-growth stands ranging from 28 to 98 years to old-growth stands in a temperate rainforest of British Columbia. They found high similarities in species composition and cover with understory vegetation. However, the researchers were uncertain about the amount of time needed to reach the old-growth or steady-state stage of succession because of the long life span of the forests and variability of disturbances (Banner & LePage, 2008).

D'Amato, Orwig, and Foster (2009) compared vegetation in eastern hemlock (*Tsuga canadensis*) second-growth stands over a hundred years old to old-growth stands and found more differences in composition and cover than the previous study mentioned. The composition of the canopy trees was similar in both the second-growth and old-growth stands. However, the old-growth stands had higher species richness and diversity of understory species. Although the second-growth stands were older than those in the previous study, they were still in a stage of stem exclusion, or self-thinning. Over time, the understory of the second-growth may become increasingly similar to that of the old-growth as the stands progress further through succession (D'Amato, Orwig, & Foster, 2009).

Natural recovery of *Sequoia sempervirens*. Natural recovery from logging was studied by Russell and Michels (2010) in *S. sempervirens* forests in the central part of their range. The study looked at characteristics of second-growth stands within a 127-year chronosequence and compared them to old-growth stands. This study was done to see if the second-growth redwood stands were following a similar stand development

pattern, as presented by Oliver (1981), of stand reinitiation, stem exclusion, understory reinitiation, and old-growth. The results were analyzed to see if characteristics found in second-growth stands progressed towards or reached statistical equivalence with characteristics of old-growth stands.

Many second-growth stand characteristics were able to reach statistical equivalence with old-growth stands within the 127-year chronosequence. Herbaceous and shrub species richness was found to be greater in second-growth stands but reduced in older stands. Shrub cover eventually reached statistical equivalence with old-growth reference sites in stands 81 years and older (Russell & Michels, 2010). Stand density was found to decrease with age as a result of natural thinning and reached statistical equivalence with old-growth stands. Canopy cover was very low in the youngest age classes of the study and reached statistical equivalence to old-growth in second-growth stands older than 81-years (Russell & Michels, 2010).

Although not all common redwood plant associates reached statistical equivalence to old-growth stands; some did, such as the calypso orchid, trillium, and redwood violet. Non-native species occurrence in second-growth stands reached statistical equivalence to old-growth stands by the 60-year age class in which no non-natives were recorded. Also, species diversity reached statistical equivalence to old-growth stands in second-growth stands 81-years and older (Russell & Michels, 2010).

Russell and Michels (2010) found that diversity of plant species within *S. sempervirens* stands is typically high in younger post-harvest age classes due to the

proliferation of non-native and invasive species. As stand age increases, diversity decreases and eventually second-growth stands can reach equivalence to old-growth stands. However, diversity, like shrub and herb cover, is responsive to openings in the canopy caused by natural thinning. More light to the understory can increase diversity in later stand ages (Russell & Michels, 2010).

Several characteristics did not reach statistical equivalence but trended towards old-growth equivalence within the 127-year chronosequence. The study found that average tree height, diameter, and basal area were typically smaller in second-growth stands but increased with age. *Sequoia sempervirens* dominance was not as high in second-growth stands as old-growth stands, but it too increased with age. Herbaceous cover and some commonly associated plant species populations also did not meet statistical equivalence with old-growth stands but were trending towards it as age increased (Russell & Michels, 2010).

After comparing the characteristics of the second and old-growth stands, the study found that the *S. sempervirens* forests of the central range appeared to be following the stand development model presented by Oliver (1981). Stands reinitiated and thinned as they progressed through age and the stem exclusion stage. Understory was beginning to reinitiate and in the older stands of the chronosequence were trending toward old-growth characteristics (Oliver, 1981; Russell & Michels, 2010). These results showed that the *S. sempervirens* forests were able to recover naturally after logging but that it was a slow process.

Problem Statement

Recent studies in Mendocino, California found un-restored and unmanaged second-growth redwood stands beginning to exhibit characteristics of old-growth stands within 100 years or less (Russell, 2009; Russell & Michels, 2010). These studies were conducted in the Central Range of California which has different soils, precipitation levels, and temperatures than the southern redwood range, including the Santa Cruz Mountains (Sawyer, et al., 2000a). Because of the different climate and soil conditions of these two regions, it was necessary to conduct further research in the southern redwood range to fully understand the potential for natural recovery of second-growth stands. The goal of this study was to address the question: Do second-growth redwood stands develop characteristics of structure and composition similar to old-growth stands in the absence of post-harvest management in the southern part of their range?

Study Questions

1. How does the stand density, size structure, canopy cover, diversity, and species composition in second-growth stands (80 – 160 years) compare to those within old-growth redwood stands?
2. How do special habitat features, such as snags, large woody debris (LWD), fire hollows, and reiterated trunks in second-growth stands compare to those within old-growth redwood stands?

Hypotheses

H1: Unmanaged second-growth redwood stands (80 – 160 years) will trend toward, or reach statistical equivalence with, old-growth reference conditions for each of the following variables: stand density, size structure, canopy cover, diversity, and species composition.

H2: Special habitat features in second-growth stands will trend toward, or reach statistical equivalence with, old-growth reference conditions. Special habitat features include snags, large woody debris (LWD), fire hollows, and reiterated trunks.

Method

Study System

The natural range of *S. sempervirens* stretches from the southern border of Oregon to Monterey County, California, along a 900 km portion of the Coast Range. The width of the *S. sempervirens* region varies from 12 - 32 km (Lorimer et al., 2009). This study focused on the southern range in the Santa Cruz Mountains of Central California (Figure 1). The Santa Cruz Mountains span 119 km from San Francisco to the Pajaro River, with elevations ranging from sea-level to 1,154 m (Baker et al., 2006).

Figure 1. Pictorial representation of study region and state parks (SP) (not to scale).

Climate in the Santa Cruz Mountains is characterized as Mediterranean because of the predominantly mild, rainy winters and cool, dry summers (Lorimer et al., 2009). The southern range differs from the central and northern redwood region in precipitation levels, which tend to be lower in the south, resulting in a longer dry season (Sawyer, et al., 2000a). Average annual precipitation in the Santa Cruz Mountains varies from the coast to inland. The coast averages 70 cm a year, while the higher elevations receive up to 147 cm of precipitation (Baker et al., 2006).

Sequoia sempervirens forests of the Santa Cruz region are typically considered riparian because of the close proximity with which the trees grow to creeks and ravines (Sawyer, et al., 2000a). *Sequoia sempervirens* can grow in soil types with different moisture levels, but most stands within the natural range grow in soils that are wet for the majority of the year, with only approximately 30 days of aridity. Due to the dryer climate

in the Santa Cruz Mountains, soils that are most suitable for redwood growth are less available than those found in the central and northern redwood ranges (Sawyer, et al., 2000a).

The soils in the southern range also contribute to the divergence of vegetation types from the central and northern redwood regions. Vegetation in the Santa Cruz Mountains consists of forests, chaparral, coastal scrubs, and grasslands (Sawyer, et al., 2000a). In these forests, Douglas-fir and *S. sempervirens* typically make up the canopy trees and the understory is comprised typically of tanoak, coast live oak (*Quercus agrifolia*), interior live oak (*Quercus wislizeni*), Shreve oak (*Quercus parvula* var. *shrevei*) and California bay laurel (Baker et al., 2006).

Fire has played a part in shaping the Santa Cruz Mountain's redwood ecosystem. Tree scars and stumps in Big Basin Redwood State Park show a 50 year fire interval (Greenlee & Langenheim, 1990). The largest fire recorded in the Santa Cruz Mountains occurred in 1948 and burned 20,000 acres. Following that forest fire, laws were put into place to attempt to suppress major forest fires (Greenlee & Langenheim, 1990). More recently, the region has been subjected to smaller fires. Several occurred in the summers of 2008 and 2009, the largest being the Lockheed Fire that burned 7,817 acres in the Bonny Doon and Swanton areas of Santa Cruz County (Cal Fire, 2009).

Logging in the Santa Cruz Mountains began within a decade of the arrival of Spanish settlers (Barbour et al., 2001; Carranco & Labbe, 1975). The Santa Cruz Mountains were the epicenter of the redwood logging industry, which became prominent in the region during the 1800s and 1900s. Sawmills were opening up throughout Santa

Cruz in the mid 1800s and by 1880 there were 50 logging mills located in the Santa Cruz area (Greenlee & Langenheim, 1990). Early on, the work was done by individual loggers using hand tools like saws and axes which made the process slow and difficult, limiting the amount of wood harvested (Andrews, 1958; Barbour et al., 2001; Hyde & Leydet, 1964). As technology improved, loggers were able to harvest as much wood as they desired, which resulted in clear-cut forests. The Santa Cruz Mountains were harvested heavily during the economic boom times, such as the Gold Rush when there was an increase in population and high demand for home building (Barbour et al., 2001).

Logging practices began to shift with California's Forest Practice Act (FPA) of 1945 which encouraged selective harvesting, allowed more government involvement with private logging, and increased awareness of unsustainable forestry practices. However, the act was unable to curb all of the extensive clear-cutting of redwoods and was ruled unconstitutional in 1971. A new FPA was passed in 1973 and required Timber Harvest Plans, which were put into place to reduce the amount of environmental impacts associated with logging (Barbour et al., 2001). Currently, there are logging companies in the Santa Cruz Mountains that continue to cut but some have moved to selective harvesting (L. McQuery, personal communication, August 4, 2011).

Study sites. The five state parks in the Santa Cruz Mountain range that were chosen as the research areas for this project were, Henry Cowell Redwood State Park, Butano State Park, Castle Rock State Park, Big Basin Redwood State Park, and Portola Redwood State Park. These parks support land use associated with eco-tourism such as camping, hiking, and fishing. Surrounding land uses, outside of the parks, include

agriculture, small town residential, commercial development, and logging. Most of the *S. sempervirens* forests in the Santa Cruz Mountains consist primarily of second-growth stands.

Henry Cowell Redwood State Park is unique in that it supports both ridge-top redwood old-growth and a small portion of alluvial flat redwood old-growth. The park also has large areas of second-growth redwood stands. Logging in Henry Cowell started as early as the 1850s and continued into the early 1900s before the land was purchased by the State of California and turned into a state park. Logging took place near Henry Cowell and the Fall Creek Unit within the Zayante Creek and Newell Creek Basins. Records show that, from 1880 to 1886, 8,000 acres were harvested, and by 1886 the majority of the acreage had been cut (Hamman, 1980).

Butano State Park is located approximately two miles east of the ocean and has a diverse ecosystem. Redwood stands are oriented near the Butano Creek which flows west through the park and out to the ocean. As elevation increases the ecotone shifts quickly to chaparral or Douglas-fir and oak woodland. There is a mix of old-growth redwood stands and second-growth stands that are predominantly close together. The area was logged in the late 1800s to early 1900s. Butano was established as a state park in 1957 (California State Parks, 2008).

Castle Rock State Park is located at the headwaters of the San Lorenzo River. The park consists primarily of higher elevation flora like Douglas-fir and oak woodland dominated stands. It also has upland redwood dominated forests that are abundant in canyon bottoms and near stream courses at low to mid-elevations of the park (California

Department of Parks & Recreation, 2000). There are a small number of old-growth redwoods, but the stands are primarily second-growth. The park was heavily logged in the 1890s. From 1887 to 1902, two loggers, the Dougherty Brothers, logged 7,000 acres along the upper portion of the San Lorenzo River (Hamman, 1980). Castle Rock was opened as a state park in 1968 (California Department of Parks & Recreation, 2000).

Big Basin Redwood State Park is located west of Castle Rock and just south of Butano. Waddell creek flows through Big Basin creating vast riparian habitat, by which the redwood stands grow. This park primarily consists of old-growth redwood but also includes chaparral, oak woodland, Douglas-fir, closed-cone pine, and second-growth redwood stands. Areas that were logged consisted primarily of chaparral and hardwoods (California State Parks, 2012). Logging was conducted by William Waddell from 1860 to 1870 before he was killed by a grizzly bear. The area that was primarily logged is located five miles up from the coastline along Waddell Creek and extending to Berry Creek (L. McQuery, personal communication, August 4, 2011; California State Parks, 2012). This same area was logged by Big Creek lumber from 1946 to the early 1950s before it was purchased by the state and added to the existing park property (L. McQuery, August 4, 2011). Big Basin was converted to a state park in 1902 (California State Parks, 2012).

Portola Redwood State Park is located approximately ten miles from the coast and is the northern most park incorporated in this study. The parks in this study closest to Portola are Castle Rock and Butano which both have second-growth redwood stands. Portola has similar vegetation groups as the other parks in this study, including chaparral, oak and Douglas-fir woodland. However, Portola State Park is mainly made up of

redwood dominated stands which consist almost entirely of old-growth redwoods. The redwood stands are ridge top old-growth with a mixture of tanoak and Douglas-fir trees. Portola became a state park in 1945 (California Department of Parks and Recreation, 1984b).

Study Design

The research questions and hypotheses were addressed with a replicated sample design. Ten sites were selected, including five old-growth redwood reference sites and five second-growth redwood sites (Figure 2). Each old-growth site had at least two associated second-growth sites that were similar in geographical location, elevation, terrain, and ecosystem type.

Figure 2. Old-growth compared to second-growth. Study sites not to scale and were not necessarily arranged as shown above.

Study sites were chosen within the parks through a combination of methods. Reference maps of the parks showing areas of old-growth were used to assist in site selection (California State Parks, 2008, 2012; California Department of Parks & Recreation, 2000). Land purchase records were also researched and referenced for potential study site locations (California Department of Parks & Recreation, 1983, 1984a,

1984b). An increment bore was used to determine second-growth stand age. Core sampling of redwood stands was done prior to site selection and throughout the sampling process. Seven to twenty trees per site were cored as a proportion of randomly selected plots from each second-growth site to estimate approximate ages. Library research, accompanied with land purchase records and tree coring, gave a confident estimate of stand age for each site.

Eighty, 0.032 hectare (20 m diameter), nested, circular sample plots were selected randomly within both old-growth and second-growth study sites (Figure 3). All 160 plots were randomly selected in the field using a GPS device along with a compass. Starting points were selected at the beginning of a trail in a redwood area. If sampling of a site was carried on for more than one day, then sampling was continued from a point along the trail near the last plot sampled. The compass was spun from the trail starting point at random once to determine direction and then again to determine distance to walk. Buffers of 200 m were set between adjacent age-class boundaries and main roads. Sample plots were located a minimum of 20 m from adjacent sample plots and 10 m from habitat features such as riparian areas and rock outcroppings. Each 20-meter diameter plot had three subplots in which cover of all herbaceous species was estimated. The circular subplots were 2 m in diameter and located at the center, northern edge, and southern edge of the main sample plot. Similar study designs have been used in the same forest type by other researchers (Loya & Jules, 2008; Russell & Jones, 2001; Russell & Michels, 2010).

Figure 3. Study site and 20 m diameter nested circular sample plot.

Data Collection

The data collected within 20 m diameter circular sample plots to address H1 included stand density, tree size, canopy cover, species diversity, and species composition. Stand density was measured by taking a visual count of the total number of trees within the plot taller than one meter. Measurements of stand density also included percent cover of herbaceous plants, which was measured through ocular estimate on 2 m diameter nested circular plots, and the percent cover of all shrub species within the entire plot. Tree size was measured by determining the diameter with a DBH (diameter at breast height) meter tape, approximately 1.4 m above ground level. Canopy cover was measured at waist height using a spherical densiometer. Species diversity and species composition was determined by identifying all plants within the sample plots using the Jepson Manual (Hickman, 1993).

Addressing H2, occurrence of special habitat features, included measurements of snags, large woody debris (LWD), fire hollows, and reiterated trunks. Visual observation of snag height was recorded along with the DBH. The occurrence and size of all LWD greater than 10 cm in diameter and two meters in length were recorded. DBH was verified from the middle of the LWD. Length of LWD was put into categories of short (2 – 8 m), medium (9 – 15 m), and long (> 15 m). Fire hollows were counted. The depth from the outer bark to the deepest point of depression, width at middle, and height at outer bark of each fire hollow was measured. Binoculars were employed to find any location of second-growth trees exhibiting reiterated trunks. Observations and locations of these structures were noted, photographed with a digital camera, and recorded with a handheld GPS unit. The approximate height and size of trunk reiterations was also recorded.

Analytical Methods

SPSS statistical software was used to run linear regression analyses on all second-growth data to see if there was a significant correlation with age. When a second-growth characteristic was significantly correlated to age the linear regression was graphed and compared to the old-growth average. This was done to determine at what age the second-growth characteristic began trending towards or reached statistical equivalence with the old-growth average. Non-linear quadratic regressions were used with species richness and diversity. This test was chosen in place of a linear regression because the data were better represented by the quadratic form. Species diversity was determined using the

Shannon-Weaver Diversity Index. If there was no correlation with age, second-growth data were compared to old-growth data using means comparison tests.

The means comparison tests consisted of a combination of parametric One-Way ANOVAs, Multifactorial ANOVAs, *t*-tests, and the non-parametric test equivalents. The parametric tests were run first, simultaneously with tests that determined if the data met parametric assumptions. The Levene's test was used to check the homogeneity of variances and the K-S test was done to check for normality of the data. The majority of the data did not meet parametric assumptions. Primarily, non-parametric tests such as Mann-Whitney U and Kruskal-Wallis tests were used in place of the parametric tests. However, in some cases the parametric test p-values had to be used instead of the non-parametric test p-values because the parametric values were more consistent with what could be seen with the descriptive statistics and graphs.

Results

Stand Density

A total of nine tree species were recorded within the study sites: redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), tanoak (*Lithocarpus densiflorus*), California bay laurel (*Umbellularia californica*), *Quercus* spp. likely to be Shreve oak (*Quercus parvula* var. *shrevei*), madrone (*Arbutus menziesii*), California buckeye (*Aesculus californica*), big leaf maple (*Acer macrophyllum*), and California hazelnut (*Corylus cornuta* var. *californica*), which was included as a small tree as oppose to a shrub (Hickman, 1993). Regression analysis indicated that stand-age had a

significant negative correlation in total tree density per hectare in second-growth stands, $F(1, 78) = 4.451, p = .038$. However, further analysis using a Mann-Whitney U test indicated that on average second-growth stand density of trees per hectare ($M = 971.89, SE = 47.94$) was significantly lower than old-growth even in the youngest second-growth stands ($M = 1307.78, SE = 104.24$), $U = -2.93, p = .027$ (Figure 4). Generally, old-growth sites had higher tree density, with only one site, Henry Cowell, falling significantly lower than all second-growth stands. Portola had the highest number of trees per hectare in old-growth stands whereas Castle Rock-2 had the highest number in second-growth stands (Figure 5).

Figure 4. Mann-Whitney U test between mean tree per hectare in second-growth stands and old-growth stands with 95% confidence intervals.

Figure 5. Mean tree per hectare in all ten study sites of second-growth and old-growth stands.

A separate analysis of the density of *S. sempervirens*, using ANOVA, indicated no significant difference between the density of redwoods per hectare in second-growth and old-growth stands, $F(1, 158) = 2.728, p = .101$. A post hoc ANOVA test was run with the old-growth study site Henry Cowell-2 removed as an outlier. Second-growth redwood density per hectare ($M = 674.55, SE = 44.50$) was significantly greater than old-growth redwood density ($M = 364.51, SE = 25.50$), $F(1, 145) = 33, p < .001$. The California buckeye, hazelnut, and big leaf maple trees all had densities per hectare in second-growth stands that were statistically equivalent to densities per hectare in old-growth stands, $F(1, 158) = 1.818, p = .179$, $F(1, 158) = 1.866, p = .174$, and $F(1, 158) = 1.391, p = .240$, respectively. Douglas-fir, tanoak, and California bay trees all had significantly higher densities per hectare in old-growth stands than in second-growth stands, $F(1, 158) = 9.24, p = .003$, $F(1, 158) = 35.182, p < .001$, and $F(1, 158) = 4.752, p = .031$, respectively. Second-growth stands had significantly higher densities per hectare

of the *Quercus* spp. and madrone trees than old-growth stands, $F(1, 158) = 13.148$, $p < .001$ and $F(1, 158) = 14.491$, $p < .001$, respectively (Table 1). There was a great deal of stand density variation between study sites (Figure 6). The Old-Growth Henry Cowell-2 had the greatest density of redwood, Portola had the greatest density of tanoak, and the old-growth Butano site had the highest density of Douglas-fir.

Table 1.

Second-growth and old-growth means and standard errors per hectare for the nine tree species.

Tree species	Second-growth		Old-growth	
	Mean	Standard error	Mean	Standard error
<i>Sequoia sempervirens</i>	674.56	44.51	515.16	85.63
<i>Pseudotsuga menziesii</i>	13.52	4.03	69.96	18.12
<i>Lithocarpus densiflorus</i>	197.16	33.67	674.56	73.10
<i>Umbellularia californica</i>	12.72	5.14	37.37	10.07
<i>Quercus</i> spp.	52.07	12.45	6.36	1.99
<i>Arbutus menziesii</i>	14.71	3.48	1.19	0.68
<i>Aesculus californica</i>	3.58	2.65	0.00	0.00
<i>Corylus cornuta</i> var. <i>californica</i>	3.58	1.96	0.80	0.56
<i>Acer macrophyllum</i>	0.00	0.00	2.39	2.02

Figure 6. Mean tree per hectare in all ten study sites for the three main tree species: *S. sempervirens*, *P. menziesii*, and *L. densiflorus*.

Diameter Distribution

Diameter distribution of size classes, based on Guisti (2007) and Russell and Michels (2010), was compared between second-growth and old-growth stands (Figure 7). Stems per hectare that were in the diameter size class of 100 – 149 cm were statistically equivalent across second-growth ($M = 4$, $SE = 0.60$) and old-growth stands ($M = 5.40$, $SE = 0.70$), $F(1, 1,438) = 2.36$, $p = .125$. The majority of old-growth diameter distribution of stems per hectare was significantly greater than the second-growth stands. Surprisingly, the size class of less than 5 cm in old-growth stands ($M = 70$, $SE = 11.56$) had significantly greater amount of stems per hectare than the less than 5 cm size class in second-growth stands ($M = 30.30$, $SE = 4.10$), $F(1, 1,438) = 10.50$, $p = .001$. The size class of 5 – 24 cm in old-growth stands ($M = 39.75$, $SE = 4$) had significantly greater

amount of stems per hectare than the 5 – 24 cm size class in second-growth stands ($M = 21$, $SE = 2.60$), $F(1, 1,438) = 15.53$, $p < .001$.

The two largest size classes in old-growth stands also had significantly more stems per hectare than in second-growth stands. The size class of 150 – 199 cm in old-growth stands ($M = 3.44$, $SE = 0.53$) had significantly greater amount of stems per hectare than the 150 – 199 cm size class in second-growth stands ($M = 0.40$, $SE = 0.15$), $F(1, 1,438) = 31.19$, $p < .001$. The size class of greater than 200 cm in old-growth stands ($M = 2.12$, $SE = 0.42$) had significantly greater amount of stems per hectare than the greater than 200 cm size class in second-growth stands ($M = 0.18$, $SE = 0.09$), $F(1, 1,438) = 20.40$, $p < .001$.

Stems per hectare of the diameter size class 25 – 49 cm in second-growth stands ($M = 23.85$, $SE = 2.67$) were statistically more abundant than the 25 – 49 cm size class in old-growth stands ($M = 12.90$, $SE = 1.28$), $F(1, 1,438) = 13.65$, $p < .001$. Also, stems per hectare of the diameter size class 50 – 99 cm in second-growth stands ($M = 28.17$, $SE = 3.25$) were statistically more abundant than the 50 – 99 cm size class in old-growth stands ($M = 8.90$, $SE = 0.94$), $F(1, 1,438) = 32.60$, $p < .001$.

Figure 7. Diameter distribution between second-growth and old-growth stands for all tree species combined.

The distribution of size classes was also compared separately for the three major tree species: redwood, Douglas-fir, and tanoak. Redwood tree diameter distribution in second-growth stands was statistically equivalent in old-growth stands for three different size classes. The two smallest size classes, less than 5 cm and 5 – 24 cm, were statistically equivalent across second-growth stands ($M = 3.45$, $SE = 0.49$, and $M = 4.49$, $SE = 0.54$, respectively) and old-growth stands ($M = 7.41$, $SE = 2.49$, and $M = 3.09$, $SE = 0.31$, respectively), $H = 2.44$, $p = .467$, and $H = 4.97$, $p = .129$, respectively. The size class 100 – 149 cm in second-growth stands ($M = 1.08$, $SE = 0.12$) was also statistically equivalent to the same size class in old-growth stands ($M = 1.24$, $SE = 0.13$), $H = 0.79$, $p = .394$.

Redwoods had two size classes that were more abundant in second-growth stands than in old-growth stands. The amount of trees in the size class of 25 – 49 cm in second-growth stands ($M = 4.65$, $SE = 0.48$) was significantly greater than amount of trees in the

same size class in old-growth stands ($M = 1.34$, $SE = 0.17$), $H = 42.91$, $p < .001$. The size class 50 – 99 cm in diameter also had significantly greater amounts of trees in second-growth stands ($M = 7.38$, $SE = 0.49$) than in old-growth stands ($M = 1.71$, $SE = 0.16$), $H = 119.12$, $p < .001$.

There were two size classes of redwoods that were more abundant in old-growth stands than in second-growth stands. These size classes were the two largest. The size class of 150 – 199 cm had a significantly larger number of trees in old-growth stands ($M = 0.84$, $SE = 0.11$) than in second-growth stands ($M = 0.10$, $SE = 0.04$), $H = 39.024$, $p < .001$. The size class of greater than 200 cm also had a significantly larger number of trees in old-growth stands ($M = 0.56$, $SE = 0.102$) than in second-growth stands ($M = 0.05$, $SE = 0.03$), $H = 23.89$, $p < .001$.

Douglas-fir trees had three size classes that were statistically equivalent between second-growth and old-growth. The size class of trees less than 5 cm in diameter in second-growth stands ($M = 0.14$, $SE = 0.07$) was statistically equivalent to the same size class in old-growth stands ($M = 0.09$, $SE = 0.04$), $H = 0.344$, $p = .732$. Trees that were 5 – 24 cm in diameter within second-growth stands ($M = 0.10$, $SE = 0.06$) were also statistically equivalent to the 5 – 24 cm diameter category within old-growth stands ($M = 0.45$, $SE = 0.22$), $H = 2.458$, $p = .056$. The number of trees with diameters greater than 200 cm in second-growth stands ($M < 0.01$, $SE < 0.01$) were statistically no different than the number of greater than 200 cm diameter trees in old-growth stands ($M = 0.04$, $SE = 0.02$), $H = 3.078$, $p = .081$.

The average number of Douglas-fir trees in the remaining size classes in second-growth stands was statistically less than old-growth stands. Trees in the 25 – 49 cm diameter size class within second-growth stands ($M = 0.06$, $SE = 0.03$) were significantly less abundant in old-growth stands ($M = 0.26$, $SE = 0.06$), $H = 8.38$, $p = .002$. The same was found for the 50 – 99 cm diameter size class within second-growth stands ($M = 0.06$, $SE = 0.03$) which were significantly less in old-growth stands ($M = 0.26$, $SE = 0.06$), $H = 8.38$, $p = .005$. The average number of trees in the 100 – 149 cm diameter size class within second-growth stands ($M = 0.05$, $SE = 0.03$) was determined to be significantly less than in old-growth stands ($M = 0.25$, $SE = 0.07$), $H = 7.71$, $p = .011$. Finally, the average trees in the 150 – 199 cm diameter size class within second-growth stands ($M = 0.01$, $SE = 0.01$) was significantly less than the old-growth stand average ($M = 0.14$, $SE = 0.05$), $H = 6.82$, $p = .009$.

There was only one statistically equivalent tanoak diameter size class between second-growth and old-growth stands. Diameters greater than 100 – 149 cm in second-growth stands ($M < 0.01$, $SE < 0.01$) were statistically no different in quantity than in old-growth stands ($M = 0.04$, $SE = 0.02$), $H = 3.08$, $p = .081$.

The average number of tanoak trees in the four smallest size classes in second-growth stands was statistically smaller than the average number of trees in those size classes within old-growth stands. The average number of trees less than 5 cm in diameter within second-growth stands ($M = 4.24$, $SE = 0.88$) was significantly less than the average number in old-growth stands ($M = 11.94$, $SE = 1.64$), $H = 17.12$, $p < .001$.

Similarly, trees in the 5 – 24 cm diameter size class within second-growth stands ($M = 0.90$, $SE = 0.15$) were significantly less abundant in old-growth stands ($M = 6.88$, $SE = 0.76$), $H = 60.04$, $p < .001$. Average number of trees in the 25 – 49 cm diameter size class within second-growth stands ($M = 0.94$, $SE = 0.24$) were significantly fewer in old-growth stands ($M = 1.83$, $SE = 0.23$), $H = 7.25$, $p < .001$. Lowest averages were recorded in the 50 – 99 cm diameter size class and second-growth stands ($M = 0.11$, $SE = 0.04$) were significantly lower than old-growth stands ($M = 0.51$, $SE = 0.10$), $H = 12.97$, $p = .001$. There were no tanoaks found in the last two size classes of 150 – 199 cm and greater than 200 cm in second-growth or old-growth stands.

Total Basal Area and Dominance

Total basal area (dbh/ha) in old-growth stands ($M = 90,835$, $SE = 6,611$) was significantly greater than total basal area in second-growth stands ($M = 57,004$, $SE = 2,762$), $T(158) = 18.63$, $p < .001$ (Figure 8). Redwood basal area, separately, in old-growth stands ($M = 76,762$, $SE = 6,920$) was also significantly greater than redwood basal area in second-growth stands ($M = 51,964$, $SE = 2964$), $F(1, 158) = 10.85$, $p = .001$. Total Douglas-fir basal area in old-growth stands ($M = 9,058$, $SE = 1,580$) was significantly greater than Douglas-fir basal area in second-growth stands ($M = 1,188$, $SE = 463$), $F(1, 158) = 22.82$, $p < .001$. Like Douglas-fir and redwood, old-growth tanoak total basal area ($M = 4,595$, $SE = 600$) was significantly greater than second-growth tanoak basal area ($M = 1,358$, $SE = 292$), $F(1, 158) = 23.50$, $p < .001$. Variation between sites was apparent (Figure 9).

Figure 8. Mean total basal area per hectare between second-growth and old-growth stands for all tree species combined with 95% confidence intervals.

Figure 9. Mean tree basal area per hectare in all ten study sites for the three most common tree species: *S. sempervirens*, *P. menziesii*, and *L. densiflorus*.

Two tree species had significantly greater total basal area in second-growth stands than old-growth stands. The first was the *Quercus* spp., which had total basal area in second-growth stands ($M = 1,341$, $SE = 354$) significantly greater than the *Quercus* spp. basal area in old-growth stands ($M = 86.80$, $SE = 46.22$), $F(1, 158) = 12.36$, $p = .001$. The second was madrone, which had significantly greater total basal area in second-growth stands ($M = 1,037$, $SE = 249$) than in old-growth stands ($M = 28.30$, $SE = 17.85$), $F(1, 158) = 16.33$, $p < .001$.

Four tree species were statistically equivalent between second-growth and old-growth stands. Out of the four, bay trees had the greatest total basal area. Second-growth bay tree total basal area ($M = 112$, $SE = 62.10$) was statistically equivalent to bay basal area in old-growth stands ($M = 288$, $SE = 110$), $F(1, 158) = 1.90$, $p = .17$. Second-growth total basal area of California buckeye ($M = 0.32$, $SE = 0.30$), hazelnut ($M < 0.01$, $SE < 0.01$), and big leaf maple ($M = 0.001$, $SE = 0.001$) were all statistically equivalent to old-growth total basal area of California buckeye ($M < 0.01$, $SE < 0.01$), hazelnut ($M = 0.18$, $SE = 0.12$), and big leaf maple ($M = 16.30$, $SE = 15$), $F(1, 158) = 1.20$, $p = .27$, $F(1, 158) = 2.03$, $p = .16$, and $F(1, 158) = 1.20$, $p = .30$, respectively.

Redwood was the most dominant tree species per hectare in both second-growth and old-growth stands. However, relative dominance of redwood in second-growth stands ($M = 27.70$, $SE = 0.65$) was significantly higher than redwood dominance in old-growth stands ($M = 25.30$, $SE = 0.78$), $H = 5.491$, $p = .002$. There were also significantly higher relative dominances of the *Quercus* spp. ($M = 1.07$, $SE = 0.30$) and madrone trees

($M = 0.91$, $SE = 0.30$) in second-growth stands compared to the relative dominances of the *Quercus* spp. ($M = 0.05$, $SE = 0.03$) and madrone trees ($M = 0.02$, $SE = 0.02$) in old-growth stands, $H = 13.180$, $p < .001$, and $H = 12.148$, $p < .001$, respectively.

Second-growth stands and old-growth stands shared some statistically equivalent tree dominances. Bay trees in second-growth stands ($M = 0.20$, $SE = 0.15$) were statistically equivalent to old-growth stands ($M = 0.42$, $SE = 0.40$) with regards to relative dominance, $H = 0.325$, $p = .709$. California buckeye ($M < 0.01$, $SE < 0.01$) hazelnut ($M < 0.01$, $SE < 0.01$), and big leaf maple trees ($M < 0.01$, $SE < 0.01$) in second-growth stands were all statistically equivalent to old-growth stands (All $M < 0.01$, all SE 's < 0.01) with regards to relative dominance $H = 1.61$, $p = 0.156$, $H = 1.62$, $p = 0.156$, and $H = 1.10$, $p = 0.156$, respectively.

Only two of the tree species had greater dominance in old-growth stands than in second-growth stands. Douglas-fir relative dominance in old-growth stands ($M = 3.72$, $SE = 0.67$) was significantly greater than Douglas-fir relative dominance in second-growth stands ($M = 0.70$, $SE = 0.30$), $H = 16.55$, $p < .001$. Tanoak relative dominance was also significantly greater in old-growth stands ($M = 2.30$, $SE = 0.33$) than in second-growth stands ($M = 1.21$, $SE = 0.30$), $H = 5.91$, $p < .001$ (Figure 10).

Figure 10. Relative dominance (specific basal area/total basal area) of *Sequoia sempervirens*, *Pseudotsuga menziesii*, and *Lithocarpus densiflorus* for all ten second-growth and old-growth study sites.

Percent Cover

The canopy cover in second-growth stands ($M = 69.89$, $SE = 0.97$) had a significant positive trend with stand age, $F = 9.90$, $p = .002$ ($R^2 = 0.113$) and reached statistical equivalence with old-growth stands ($M = 73.88$, $SE = 0.94$) at approximately 140 years (Figure 11). Canopy cover was strongly correlated to stand age but not any other variable. There was a lot of variation in canopy cover throughout second-growth and old-growth sample plots (Figure 12). Second-growth canopy cover ranged from 52% to 91%. Old-growth canopy cover ranged from 50% to 89%. Second-growth and old-growth canopy cover had equal ranges of 39%. There was not a lot of variation amongst sites with range of canopy cover percentages. Portola plots had the least amount of

variation with a range of 20% for canopy cover. Henry Cowell ridge top old-growth had the most variation with a range of 35% for canopy cover.

Figure 11. Linear Regression of second-growth percent canopy cover's correlation with age and old-growth percent canopy cover mean reference line with standard error lines.

Figure 12. Percent canopy cover of all ten second-growth and old-growth study sites.

A Mann-Whitney U test was conducted to determine if the mean shrub cover of second-growth redwood stands had already reached statistical equivalence with the mean shrub cover of old-growth redwood stands. The results showed average second-growth shrub cover ($M = 13.79$, $SE = 1.35$) was statistically equivalent to average old-growth shrub cover ($M = 15.93$, $SE = 1.98$), $U = -0.890$, $p = .893$ (Figure 13). Percent shrub cover was not uniform throughout second-growth and old-growth study sites. There was variation amongst old-growth and second-growth sites with Butano having the highest percent shrub cover of old-growth sites and Castle Rock-2 of the second-growth sites (Figure 14).

Figure 13. Mean percent shrub cover between second-growth and old-growth stands with 95% confidence intervals.

Figure 14. Percent shrub cover for all ten second-growth and old-growth study sites.

A Mann-Whitney U test indicated that average overall herb cover for second-growth stands ($M = 5.15$, $SE = 1.06$) was statistically equivalent to that of old-growth stands ($M = 7.88$, $SE = 1.45$), $U = -1.52$, $p = .963$ (Figure 15). Regression of average herbaceous cover with stand age yielded no significant trend. There was much more extreme variation in herbaceous cover than shrub cover and canopy cover between study sites (Figure 16).

Figure 15. Mean averaged herb cover between second-growth and old-growth stands with 95% confidence intervals.

Figure 16. Averaged percent herb cover for all ten second-growth and old-growth study sites.

There were a total of 47 native plants and six non-native plants found in all of the sites combined. The native plants consisted of 29 herbs and 18 shrubs. The non-native plants included four herbs and two shrubs. Native understory cover was statistically equivalent between second-growth ($M = 20.87$, $SE = 2.07$) and old-growth stands ($M = 23.03$, $SE = 2.60$), $U = 0.08$, $p = .981$. Non-native understory cover was significantly lower in old-growth stands ($M = 0.30$, $SE = 0.08$) than in second-growth stands ($M = 0.82$, $SE = 0.18$), $U = 2.72$, $p < .001$. More types of non-native species were found in old-growth sites than in second-growth sites. However, old-growth sites had a smaller frequency of plots with non-natives than second-growth sites.

Twelve redwood associates were identified and analyzed against stand age (Table 2). There was a positive linear correlation with stand age for trillium cover in second-growth redwood stands, $F = 2.94$, $p = .008$ ($R^2 = 0.345$). Second-growth trillium cover

($M = 0.27$, $SE = 0.05$) reached statistical equivalence with old-growth trillium cover ($M = 0.56$, $SE = 0.35$) at approximately 120 years (Figure 17).

Figure 17. Linear Regression of second-growth averaged percent *Trillium ovatum* cover's correlation with age and old-growth percent *Trillium ovatum* cover mean reference line with standard error lines.

Second-growth percent cover for redwood sorrel, Pacific starflower (*Trientalis latifolia*), hooker's fairy bells (*Disporum hookeri*), *Galium* spp., California hedge nettle (*Stachys bullata*), slim solomon's seal (*Smilacina stellata* var. *sessifolia*), wetern sword fern, and bracken fern (*Pteridium aquilinum* var. *pubescens*) were all statistically equivalent to old-growth percent cover. Second-growth percent cover of redwood violet and hairy honeysuckle (*Lonicera hispidula*) was significantly greater than old-growth

percent cover of those species. Old-growth percent cover of huckleberry was significantly greater than percent cover of the same species in second-growth stands.

Table 2.

Redwood associates' means, standard errors, and p-values for second and old-growth stands.

Old-growth redwood associates	Second-growth		Old-growth		p-value
	Mean	Std. error	Mean	Std. error	
<i>Trillium ovatum</i>	0.27	0.05	0.56	0.35	.008
<i>Oxalis oregana</i>	4.91	1.42	5.86	1.30	.622
<i>Trientalis latifolia</i>	0.20	0.07	0.09	0.03	.207
<i>Disporum hookeri</i>	0.14	0.06	0.06	0.02	.217
<i>Viola sempervirens</i>	0.35	0.14	0.02	0.01	.021
<i>Galium</i> ssp.	0.40	0.08	0.30	0.09	.327
<i>Stachys bullata</i>	0.13	0.05	0.10	0.08	.773
<i>Smilacina stellata</i> var. <i>sessifolia</i>	0.04	0.02	0.01	0.01	.145
<i>Vaccinium ovatum</i>	1.22	0.36	9.50	2.00	< .001
<i>Polystichum munitum</i>	2.80	0.50	2.25	0.50	.416
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	1.80	0.30	1.64	0.41	.757
<i>Lonicera hispidula</i>	2.08	0.31	0.50	0.10	<.001

Species Richness and Diversity

Fifty four plant species were recorded in the sample plots. There was greater variation of total species richness per plot in second-growth stands ($M = 15.36$, $SE = 0.64$) than in old-growth stands ($M = 10.33$, $SE = 0.46$). Second-growth total species richness had a range of 26 per plot while old-growth stands had a range of 18. Second-growth stands had a minimum richness of three per plot and old-growth stands had a minimum of two. Total species richness per plot in second-growth stands was significantly correlated with age, $F = 29.10$, $p < .001$ ($R^2 = 0.43$).

Total understory species richness per plot was also significantly correlated with age $F = 29.60, p < .001$ ($R^2 = 0.43$). Understory species richness was lowest in the early ages of 80 – 100 years. There was an increase in understory richness from 110 – 130 years passed the old-growth average. Understory richness began to decline at around 140 years. It continued to decline and trended toward old-growth equivalence as age increased but did not return to old-growth equivalence (Figure 18). Second-growth understory species richness ($M = 11.78, SE = 0.57$) had a range of 24 while old-growth richness ($M = 7.36, SE = 0.45$) had a range of 16. Second-growth stands had a minimum richness of one and old-growth stands had a minimum of zero (Figure 19).

Figure 18. Quadratic regression of second-growth total understory plant richness correlation with age and old-growth total understory plant richness mean reference line with standard error dashed lines.

Figure 19. Mean understory plant richness per plot for all ten second-growth and old-growth study sites.

Second-growth shrub species richness per plot was significantly correlated with age and had a similar temporal progression as total understory species richness, $F = 23.20$, $p < .001$ ($R^2 = 0.38$). Richness was lowest in the early ages of 80 – 100 years. There was an increase in shrub species richness from 110 – 130 years. Shrub richness began to decline later than total understory richness at around 150 years. Shrub species richness per plot reached statistical equivalence with old-growth shrub species richness between 160 – 170 years (Figure 20). Second-growth stands ($M = 5.53$, $SE = 0.27$) had a greater variation of shrub richness with a range of 11 than old-growth stands ($M = 2.76$, $SE = 0.17$) that had a range of seven (Figure 21). Both second-growth and old-growth stands had minimum richness of zero.

Figure 20. Quadratic regression of second-growth total shrub richness correlation with age and old-growth total shrub richness mean reference line with standard error dashed lines.

Figure 21. Mean shrub richness for all ten second-growth and old-growth study sites.

Second-growth herb species richness ($M = 6.25$, $SE = 0.38$) was significantly correlated with stand age, $F = 20.60$, $p < .001$ ($R^2 = 0.35$). Similar to shrub and total understory richness, herb richness was lowest in the early ages of 80 – 100 years. There was an increase in understory species richness from 110 – 140 years that surpassed old-growth equivalence. Herb richness began to decline later than both shrub and total understory richness around 160 years. Herb richness did not return to statistical equivalence with old-growth herb richness ($M = 4.60$, $SE = 0.33$) (Figure 22). Second-growth stands also had a greater variation of herb richness with a range of 14 than old-growth stands that had a range of 12. Both second-growth and old-growth stands had minimum richness of zero (Figure 23).

Figure 22. Quadratic regression of second-growth mean herb richness correlation with age and old-growth total plant richness mean reference line with standard error dashed lines.

Figure 23. Mean herb richness for all ten second-growth and old-growth study sites.

Species diversity per plot was determined using the Shannon-Weaver Diversity Index. Second-growth understory species diversity was significantly correlated with age, $F = 38.66, p < .001$ ($R^2 = 0.50$). Understory species diversity was lowest in the early ages of 80 – 100 years. There was an increase in understory story diversity from 110 – 130 years that surpassed old-growth equivalence. Understory species diversity began to decline at approximately 140 years. It continued to decline and trend toward old-growth equivalence as age increased but did not return to old-growth equivalence (Figure 24). Second-growth understory species diversity ($M = 1.63, SE = 0.61$) had a range of 2.58 while old-growth richness ($M = 0.97, SE = 0.57$) had a range of two. Second-growth and old-growth stands both had a minimum diversity of zero (Figure 25).

Figure 24. Quadratic regression of second-growth mean species diversity correlation with age and old-growth species diversity mean reference line with standard error dashed lines.

Figure 25. Mean species diversity for all ten second-growth and old-growth study sites.

Special Habitat Features

Reiterated trunks. A total of six trunk reiterations were recorded in second-growth sites. Three of the reiterations were located within one sample plot of Henry Cowell second-growth (Figure 26, 27, and 28). These reiterations ranged from approximately 8 – 15 cm in diameter. Another reiteration was discovered within a second-growth plot of Castle Rock and had a DBH of approximately 40 cm (Figure 29). Two were discovered in the Henry Cowell Fall Creek Unit during reconnaissance for site selection. They were both approximately 20 cm in diameter. The Castle Rock reiteration was the largest discovered and had the most potential for habitat use followed by the two reiterations in the Fall Creek Unit. All reiterations occurred approximately 9 – 15 m up the main trunk of the tree.

Figure 26. Reiterated trunk found on redwood tree within the second-growth Henry Cowell 1 study site.

Figure 27. Reiterated trunk found on redwood tree within the second-growth Henry Cowell 1 study site.

Figure 28. Reiterated trunk found on redwood tree within the second-growth Henry Cowell 1 study site.

Figure 29. Reiterated trunk on a second-growth redwood tree in the Castle Rock 1 study site.

Figure 30. Two second-growth trees with trunk reiterations in the Henry Cowell Fall Creek Unit.

Snags. A Mann-Whitney U test indicated that density of snags per hectare in second-growth stands ($M = 145.88$, $SE = 12.56$) was significantly greater than snag density in old-growth stands ($M = 79.92$, $SE = 8.34$), $U = 4.64$, $p < .001$. Snag density varied within second-growth and old-growth study sites. However, snag density within second-growth study sites was consistently higher than snag density of old-growth study sites (Figure 31).

Figure 31. Mean snag per hectare for all ten second-growth and old-growth study sites.

Average DBH of snags was also compared between second-growth and old-growth stands. An Independent Samples t-test was used to compare the means for snag DBH of second-growth and old-growth stands. The Independent Samples t-test results showed that average snag DBH in second-growth stands ($M = 14.94$, $SE = 0.63$) was statistically equivalent to the average snag DBH in old-growth stands ($M = 13.91$, $SE = 1.83$), $t = 0.53$, $p < .593$ (Figure 32).

Snags were broken into three categories of DBH that were determined by the California Wildlife Habitat Relationship Program (Ohmann, 1992). The majority of both second-growth and old-growth snags were found to be in the lowest category of 0 – 23 cm. Second-growth stands had more snags in both the 0 – 23 cm and 23 – 76 cm categories than old-growth stands. There were only two snags in second-growth stands and four in old-growth stands that were greater than 76 cm (Table 3).

Figure 32. Mean snag DBH between second-growth and old-growth stands with 95% confidence intervals.

Table 3.

Total number of second-growth and old-growth snags in three DBH size categories set by the California Wildlife Habitat Relationship Program.

Snag DBH density by size class				
Site	0-23	23-76	76>	Total
Second-growth	311	54	2	367
Old-growth	159	22	4	185
Total	470	76	6	552

Surprisingly, the average snag height in second-growth stands ($M = 7.36$, $SE = 0.28$) was also significantly higher than average snag height in old-growth stands ($M = 5.48$, $SE = 0.43$), $U = 14.17$, $p < .001$. There were a greater number of snags in second-growth stands as compared to old-growth stands and there were a greater number of snags in each height category of 0 – 12 m, 12 – 24 m, and greater than 24 m. The majority of snags for both second-growth ($n = 302$) and old-growth stands ($n = 172$) were 0 – 12 m in height. Only nine snags were found to be greater than 24 m tall (Table 4).

Table 4.

Total number of second-growth and old-growth snags in three height categories.

Snag height(m) density by size class				
Site	0-12m	12-24m	>24m	Total
Second-growth	302	52	5	359
Old-growth	172	13	4	189
Total	474	65	9	548

The relationship between snag DBH and snag height was determined using a Pearson Correlation. In second-growth stands there was a significant and strong correlation between snag DBH and snag height, $r = .560$, $p < .001$. Old-growth stands also had a significant and strong correlation between snag DBH and snag height, $r = .837$, $p < .001$. The combined second-growth and old-growth snag data show that overall there is a significant and strong correlation between snag DBH and snag height, $r = .668$, $p < .001$.

Large woody debris. A Mann-Whitney U test indicated that there was no significant difference between total second-growth LWD density ($M = 2330.38$, $SE = 297.06$) and total old-growth LWD density ($M = 2039.11$, $SE = 227.98$), $U = 0.367$, $p = .582$. However, there was significant variation of LWD density within second-growth and old-growth study sites (Figure 33).

Figure 33. Mean large woody debris per hectare for all ten second-growth and old-growth study sites.

LWD length was separated into three size classes: short (2 – 8 m), medium (9 – 15 m), and long (> 15 m). All three density means in the second-growth stands' length categories short, medium, and long ($M = 45.71$, $SE = 7.08$, $M = 24.64$, $SE = 3.79$, and $M = 22.66$, $SE = 3.76$, respectively) were statistically equivalent to the old-growth length category density means ($M = 38.95$, $SE = 4.73$, $M = 27.03$, $SE = 4.04$, and $M = 28.62$, $SE = 3.90$, respectively) $H = 0.629$, $p = .979$, $H = 0.185$, $p = .588$, and $H = 1.210$, $p = .147$, respectively. A multiple regression test showed no significant correlation with age in second-growth stands for all three size classes. A post hoc test was run to compare the means of second-growth LWD densities by length category and old-growth LWD densities by length category.

Mann-Whitney U indicated that average LWD DBH in old-growth stands ($M = 38.73$, $SE = 2.14$) was significantly higher than average LWD DBH in second-growth stands ($M = 23.60$, $SE = 1.32$), $U = -6.07$, $p < .001$.

Figure 34. Mean large woody debris DBH between second-growth and old-growth stands with 95% confidence intervals.

Second-growth average DBH in the short length category for LWD ($M = 25.59$, $SE = 2.50$) was statistically equivalent to the old-growth average DBH of LWD in the short category ($M = 24.33$, $SE = 1.45$), $U = 0.440$, $p = .094$. Average LWD DBH in the medium category of old-growth stands ($M = 34.90$, $SE = 3.09$) was significantly greater than average LWD DBH in the medium category of second-growth stands ($M = 21.37$, $SE = 1.40$), $U = -3.99$, $p = .001$. Average LWD DBH in the long length category of old-growth stands ($M = 60.49$, $SE = 5.16$) was also significantly greater than average LWD

DBH in the long length category of second-growth stands ($M = 25.82$, $SE = 2.01$), $U = -6.27$, $p < .001$.

Fire hollows. A total of 10 fire hollows were found in second-growth stands and 119 in old-growth stands. Fire hollows were found on one madrone, 13 tanoak, and 113 redwood trees (Table 5). Several trees had more than one fire hollow and these were counted as separate fire hollows on the same tree. The average fire hollow density for second-growth stands was 3.98 per hectare and the average fire hollow density for old-growth stands was 52.87 per hectare.

Table 5.

Total number of snags per species in both second-growth and old-growth stands.

Fire hollows per trees species		
Tree species	Second-growth	Old-growth
Madrone	1	0
Tanoak	0	13
Redwood	9	104
Snag	0	2
Total	10	119

The four variables measured with each tree/fire hollow were tree DBH, fire hollow height at opening, width from middle, and depth from middle. Each of these variables was compared between second-growth and old-growth. Fire hollow depth average within old-growth stands ($M = 73.74$, $SE = 5.07$) was significantly greater than the average depth of fire hollows in second-growth stands ($M = 32.50$, $SE = 5.49$), $U = 4.91$, $p = .005$. Fire hollow depth was also significantly and positively correlated to tree

DBH, $F = 10.98$, $p < .001$. The average fire hollow height, width, and tree DBH for second-growth stands ($M = 120$, $SE = 29.44$, $M = 40$, $SE = 9.19$, and $M = 122.63$, $SE = 15.87$, respectively) were all statistically equivalent to the average fire hollow height, width, and tree DBH within old-growth stands ($M = 129.56$, $SE = 9.31$, $M = 63.46$, $SE = 4.22$, and $M = 170.92$, $SE = 7.50$, respectively), $H = 0.08$, $p = .672$, $H = 2.26$, $p = .064$, and $H = 2.79$, $p = .079$, respectively.

Discussion

This in-depth analysis of stand structure, composition, and special habitat features in both second and old-growth stands in the Santa Cruz Mountains provides evidence of how second-growth redwood forests in their southern range are recovering naturally. Many stand characteristics were analyzed in order to attain a full representation of the forest as a whole. The hypotheses of this study were that second-growth stands would trend towards or reach old-growth equivalence with regards to stand characteristics and special habitat features. Several of the stand characteristics and special habitat features in second-growth stands were statistically equivalent to the old-growth reference stands such as canopy, shrub, and herbaceous cover, native plant and redwood associate cover, understory richness, snag DBH, and LWD density. However, there were also several stand characteristics that did not reach statistical equivalence such as basal area, non-native species cover, LWD diameters, huckleberry cover, and fire hollow density.

Though not all variables measured reached statistical equivalence with old-growth reference sites, second-growth stands appeared to be proceeding through the stand

development stages outlined by Oliver (1981). The four stages include stand initiation, stem exclusion, understory reinitiation, and old-growth (Oliver, 1981). This study indicated that second-growth stands in the Santa Cruz Mountain parks are progressing through the understory reinitiation stage of stand development. Stand density was significantly lower in second-growth stands than in old-growth stands, which indicates that the natural stem exclusion stage has finished. The understory reinitiation stage appears to be taking place as most of the understory characteristics were trending towards or reached old-growth equivalence.

Stand Characteristics

Total tree density per hectare in second-growth stands decreased with age, likely due to natural thinning (Busing & Fujimori, 2002). Studies such as those by Fritz (1945) and Russell and Michels (2010) also found evidence of natural thinning and a decrease in total tree density with age. Russell and Michels determined that stands began to exhibit old-growth density at 41 – 60 years but did not reach statistical equivalence within the timeframe of the chronosequence. Contrary to the findings of Russell and Michels, this study found second-growth stands had already reached statistical equivalence with old-growth stands in total tree density per hectare at a minimum of approximately 80 years. This finding contradicts much of the current research that has found second-growth stands to be denser than old-growth stands (Russell & Michels, 2010). It also contradicts studies that assert that, in order for tree density to reach old-growth equivalence, active management is necessary (Harrod et al., 2009; Miesel, Boerner, & Skinner 2009; O'Hara et al., 2010).

There are several potential explanations for this unexpected finding. One explanation could be that the “stem exclusion phase,” of the four phases of succession had already taken place (Oliver, 1981). Another explanation could be that in the southern redwood range there is naturally a greater abundance of tanoak and Douglas-fir trees within old-growth forests which make the stands denser. This study found that old-growth stands had significantly greater averages of tanoak and Douglas-fir trees than second-growth stands. Along with greater abundance of tanoak and Douglas-fir in old-growth stands, there was also an outlier with redwood density in the second Henry Cowell old-growth site. This site was in the alluvial flat portion of the park and received some active thinning management in the form of cutting and controlled burns. As a result these areas had a much greater abundance of sprouts. The result of greater tree densities in these managed stands contradicts studies that argue for active silvicultural management to decrease tree densities (Harrod et al., 2009; Miesel et al., 2009; O’Hara et al., 2010). However, even with this outlier removed, old-growth stands still had greater total tree density per hectare than second-growth stands but a significantly lower redwood density compared to second-growth stands.

Diameter distribution in the second-growth sites were characteristic of what would be found in stands from 80 – 160 years. Similar to old-growth, the stands were made up of mixed size-class diameter distributions rather than all trees of one size (Russell & Michels, 2010). Second-growth stands were dominated by medium sized diameter redwood trees ranging from 25 – 99 cm and they were statistically equivalent to old-growth stands in the redwood 100 – 149 cm range. Overall, old-growth stands had

many more of the smallest diameter trees (<5 – 24 cm) and largest diameter trees (>150 cm). Old-growth stands having a significantly greater amount of the smaller diameter trees was an unexpected result. Second-growth redwood stands were found to have more of the smaller diameter trees in the study done by Russell and Michels (2010) within the redwood central range. In this study of the southern range, second-growth stands contained the majority of mid-size trees (25 – 149 cm). Although second-growth redwoods did not reach equivalence to old-growth stands with the largest diameters of greater than 150 cm, the second-growth stands had the healthy mixed diameter distribution that are exhibited in old-growth stands.

Total basal area was significantly greater in old-growth stands than in second-growth stands. This is consistent with other studies' findings (Busing & Fujimori, 2002, 2005; Russell & Michels, 2010). Redwood total basal area was also significantly greater in old-growth stands than in second-growth stands. Redwood was the most dominant tree species in both second-growth and old-growth stands. Redwood dominance is supported by literature such as Busing & Fujimori (2002), Lorimer (2009), Roy (1966), and Binkley et al. (2007) that found the species to be resistant to disturbances and able to thrive as a climax species. Second-growth redwood dominance was slightly greater than old-growth redwood dominance, in this study. This can likely be explained by the fact that the second and third most dominant trees, Douglas-fir and tanoak respectively, were significantly greater than, and almost twice as dominant in old-growth stands compared to second-growth stands.

Management practices such as thinning have been prescribed to increase basal area and decrease stand density in redwoods (Harrod et al., 2009; Miesel et al., 2009; O'Hara et al., 2010). However, in this study, both total tree density and redwood tree density were statistically equivalent between second and old-growth stands. The next two dominant trees that could potentially be thinned are already significantly less dense in second-growth stands than in old-growth stands. Russell and Michels (2010) found that by 81 – 100 years second-growth stands were similar to old-growth stands in total basal area. Old-growth equivalence was not reached by the 130 year cut off in that study's chronosequence (Russell & Michels, 2010). Similarly, old-growth basal area equivalence was not met by 130 years in this study, nor in 160 years. Although tree density may reach old-growth equivalence through natural thinning, it appears to take longer for basal areas to recover.

Canopy cover in second-growth stands increased with age. Although there was a great deal of variation in cover, that variation was equally found in the old-growth stands. Stands did not reach statistical equivalence as early as stands older than 81 years which was the case in Russell & Michels (2010) study. However, canopy cover trended towards old-growth equivalence at that age and reached old-growth equivalence in stands greater than 135 years. Tree density decreased with stand age in a pattern that somewhat mirrored the rise in canopy cover. This suggests that, as the canopy opened up from natural thinning, the canopy cover was filled in by remaining trees at a similar rate. This is consistent with older redwood stands which are characterized by dense but insular canopies (Loya & Jules, 2008).

Understory plant cover in second-growth stands was statistically equivalent to old-growth stand understory cover. This suggests that the “understory reinitiation” phase, of the four phases of succession, took place prior to 80 years of age (Oliver, 1981). This is consistent with findings from Russell and Michels (2010) study in which shrub cover reached old-growth equivalence by 81 years. However, in that study the herbaceous layer did not reach old-growth equivalence within the timeframe of the chronosequence while in this study, the herbaceous layer was already statistically equivalent by 80 years. Unlike other studies, this study did not find that herb and shrub cover were strongly correlated with variables such as total basal area or canopy cover (Gilliam & Turrill, 1993; Gilliam, Turrill, & Adams, 1995).

Second-growth native understory species cover reached old-growth equivalence within 80 years. The study done by Russell and Michels (2010) found different results in the central redwood range. In their study native herb cover was significantly lower in second-growth stands than in old-growth stands and only native shrub cover was able to reach old-growth equivalence. This suggests that redwood stands in the southern range may have been able to naturally recover native understory species more quickly than redwood stands in the central range.

In this study, non-native understory species cover was significantly greater in second-growth stands than in old-growth stands. This is consistent with Russell and Michels (2010). In their study, 10 non-natives were recorded in second-growth stands, but cover declined with stand age until year 60 of the chronosequence, at which point

non-natives disappeared. Every age beyond 60, including old-growth, was void of non-natives. Unlike Russell and Michels (2010), non-natives were present in both second-growth and old-growth stands and did not appear to decline with stand age. This may be a result of more human accessibility to the sites sampled in this study compared to those sampled in Russell and Michels (2010). It may also be that, since the climate and soils are dryer in the southern range, non-native species are able to out-compete natives.

Percent cover for individual redwood associates was consistent with total understory cover. Eight of the twelve redwood associates identified in second-growth stands were equivalent in cover to old-growth and two were greater. Trillium cover took longer to recover than the other redwood associates. Percent cover remained low until approximately 115 years when it started to trend toward old-growth equivalence. Trillium cover eventually reached old-growth equivalence at approximately 140 years. This is consistent with the Russell and Michels (2010) study that also found that trillium eventually reached old-growth equivalence. The 140 year timeframe for recovery is also consistent with the Kahmen and Jules (2005) study that found trillium populations seemed to continue to grow centuries after the initial disturbance.

The slow recovery is supported by several studies that have found trillium to be exceptionally sensitive to timber harvesting (Jules & Rathcke, 1999; Kahmen & Jules, 2005; Russell & Michels, 2010). There are several explanations for why trillium is sensitive to timber harvesting and slow to recover. Some of the reasons include slow seed set recovery, seed predation, extreme elements directly following a harvest, and low

individual persistence during timber harvests (Jules & Rathcke, 1999; Kahmen & Jules, 2005).

Huckleberry was the only redwood associate that had significantly greater cover in old-growth stands. The proliferation of huckleberry in several old-growth stands was extremely apparent in the field. Loya and Jules (2008) made a similar observation of stands entirely populated by woody shrubs. In this study, huckleberry was strongly correlated with overall shrub cover, and more so than any other understory species. Huckleberry was also negatively correlated with almost every herbaceous species. This suggests that larger woody species may have an easier time recovering following a disturbance. It also suggests that larger woody species may prevent access to light or nutrients and inhibit growth for herbaceous species.

Total second-growth understory species richness did not have the same results as understory cover. Total species richness in second-growth stands was lowest in the younger ages of 80 – 100 years. Understory species richness sharply increased beyond old-growth average from 100 – 140 years. Average species richness in old-growth stands was lower which is consistent with other research (Loya & Jules, 2008). Second-growth understory richness started decreasing after 140 years but did not return to old-growth equivalence. Herb and shrub species richness both had similar curves as compared to total species richness. They both rose sharply after 100 years, surpassing old-growth equivalence, and started trending downwards after 140 years, but only shrub species richness returned to old-growth equivalence after 160 years. The increase in species

richness could have been a result of an increase in non-native species that declined as aged increased. This suggests that, although understory reinitiation has taken place, the understory has not entirely reached the “old-growth stage” (Oliver, 1981). However, data showed a trend toward it.

Species diversity in second-growth stands followed a similar trend as second-growth species richness. The lowest diversity was found in the 80 – 100 year stands. Diversity rose significantly after 100 years, passing the old-growth average and not declining until 140 years. Second-growth diversity did not return to old-growth equivalence but trended toward it. These results are not consistent with the study done by Russell and Michels (2010) in which second-growth species diversity had a negative trend that reached statistical equivalence to old-growth stands in 81 years. A high point in diversity was observed in both this study and Russell and Michels’ study. However, Russell and Michels were able to attribute the dramatic increase in diversity to a natural thinning event that took place around the same time. Contrary to Russell and Michels, this study found that second-growth tree density was at a high approximately the same time as the dramatic increase in species diversity. This increase in tree density occurring at approximately 120 years may have been the catalyst for a decline in species diversity in the later stand ages.

Special Habitat Features

Reiterated trunks commonly occur in old-growth redwood stands and mature stands rather than younger stands (Sillett & Van Pelt, 2007). According to much of the

research these canopy structures grow as a result of non-fatal disturbances that stimulate new growth from dormant buds within the main trunk (Sawyer et al., 2000b; Sillet & Van Pelt, 2007; Williams & Sillet, 2007). It is unclear whether there is a direct correlation with the formation of reiterated trunks to age. In this study, six reiterations were discovered in second-growth stands, which may mean that these stands could be considered mature. Based on anecdotal observation, there appeared to be more reiterations in old-growth stands.

During the course of this study it was observed that certain areas of the Santa Cruz Mountains produced trees with reiterations whereas others did not. Henry Cowell, Butano, and Big Basin all had a significant amount of reiterations in their old-growth stands. However, no reiterations were observed in Portola. All of these areas exhibited clear signs of disturbances with fallen trees, snags, and fire hollows, which would suggest that they all had similar opportunities to sprout reiterations. The reiterations that were observed in the old-growth stands appeared to show up in groups. This was also the case within second-growth stands. Based on the observations of clear groupings of potentially genetically similar or same trees, there is a possibility that certain trees may be more genetically susceptible to growing reiterations than others; in which case, the formation of reiterated trunks may not only be a direct result of disturbances.

Snags are extremely important to forests because they diversify the habitat and nesting opportunities for birds and other wildlife. Forests with few snags are less likely to be able to support breeding populations of native wildlife (Ohmann, 1992). Studies

have found that nesting wildlife utilize snags with larger DBH and greater height (Ohmann, 1992; Ohmann, McComb, & Zumrawi, 1994; Poulin, Villard, Edman, Goulet, & Eriksson, 2008; Spiering & Knight, 2005). This makes these snag characteristics valuable to a forest.

Several studies have suggested that second-growth stands have smaller snags, and in order for DBH and height to increase, the stand density needs to decrease (Miesel, Boerner, & Skinner, 2008). Those studies suggest that management in the form of mechanical thinning is the way to reach this goal (Miesel, Boerner, & Skinner, 2008). However, this study found that average second-growth snag DBH was statistically equivalent to old-growth average snag DBH. Second-growth snag height was found to be statistically higher than old-growth snag height. This implies that no management is necessary for redwood stands to naturally recover and produce similar size snags to old-growth stands within 80 years.

According to the California Wildlife Habitat Relationship Program, in conifer vegetation types like the redwood dominated forests of the Santa Cruz Mountains, the ideal large snag size is greater than 76 cm DBH (Ohmann, 1992). In this study, only two snags in second-growth stands and four in the old-growth stands were found greater than 76 cm DBH. This may mean that neither the old-growth stands nor the second-growth stands of the Santa Cruz Mountains have enough healthy snag sizes. It may also be that the wildlife in the Santa Cruz Mountains are capable of utilizing habitat found in the abundance of medium to smaller snag sizes.

Snag density per hectare was significantly higher in second-growth stands than old-growth stands. This contradicts a study by Willet (2001) in which the number of snags in old-growth plots was greater than the number in second-growth plots. However, Willet's study looked at snags on a much smaller scale. The sites that this study looked at may have a higher density because the snags have not gone through a natural thinning process.

Woody debris, during the different stages of decay, contributes to soil development and is an important wildlife habitat feature for many vertebrate and invertebrate species (Dunn & Bailey, 2012; Hanson, Lorimer, Halpin, & Palik, 2012; White, McGill, & Lechowicz, 2012). Second-growth average woody debris density per hectare and densities by size classes were all statistically equivalent to old-growth stands. This implies that second-growth redwood stands are able to naturally recover understory dynamics and habitat such as woody debris.

Small woody debris is important because it restores nutrients to the soil more quickly than larger woody debris (Dunn & Bailey, 2012; Vanderwel, Thorpe, Shuter, Caspersen, & Thomas, 2008; White, McGill, & Lechowicz, 2012). However, the larger diameter woody debris is often more ideal for wildlife and herbs or seedlings that have difficulty establishing on the forest floor (White, McGill, & Lechowicz, 2012). These two factors of small and large woody debris imply that it is best for a forest to have a diverse understory with a mixture of small and large woody debris. In this study, second-growth had statistically equivalent amounts of woody debris in all of the length size

classes. However, average diameter of woody debris was significantly greater in old-growth stands than in second-growth stands. When broken up into length categories the second-growth short woody debris was statistically equivalent to old-growth. The medium and long length categories did not reach old-growth equivalence. The data show that, although second-growth stands have reached old-growth equivalent density with woody debris, they have not yet been able to recover the size diversity of woody debris.

Fire hollows were found in both second-growth and old-growth stands but there were significantly more found in old-growth stands. This is consistent with current research that has found old-growth stands to have more fire hollows than younger stands (Mazurek & Zielinski, 2004; Zielinski & Gellman, 1999). Research also shows fire hollows tend to occur on larger trees and that the larger hollow volumes are used the most for roosting by such animals as bats (Mazurek & Zielinski, 2004; Zielinski & Gellman, 1999). This study found that second-growth trees with fire hollows were statistically equivalent in average diameter to old-growth trees with fire hollows. This study also found that second-growth fire hollow height and width at opening were statistically equivalent to old-growth stands but the average depths were not. This suggests that the second-growth trees in the Santa Cruz Mountains have reached the average DBH for fire hollow development but have not had the time and disturbance regime to develop as many as old-growth stands.

Recommendations

The results of this study demonstrate the ability of second-growth coast redwoods in the Santa Cruz Mountains to naturally recover from the most significant disturbance, logging, in the absence of additional management. This study describes second-growth and old-growth stands including, understory species diversity, density, and size structure for all species, not just the dominant species, coast redwood. There are many other opportunities and needs for research throughout the entire redwood range.

It is important to study all aspects of a redwood forest because, much like any other community, one part of a forest can affect another, such as canopy cover and understory cover. This study incorporated many characteristics of redwood stands in the southern portion of the redwood range, which has a different climate and soil regime than the rest of the redwood range. However, every aspect of the ecosystem was not included. Additional research should be done on the soils and other abiotic parts of the ecosystem that were not detailed in this study.

Many studies that test or analyze the results of silvicultural management consider primarily only the redwood trees as the focus. Height, DBH, and stand density are analyzed closely and prescriptions are given based on these studies' results. Often times the prescriptions of silvicultural management are for restoration projects. However, restoration projects need to look at an entire ecosystem when planned. Otherwise, the ecosystem is not truly being restored, but rather one part of it is being changed, which may or may not benefit the entire system. There is more need for study of the redwood

ecosystem as a whole and how all characteristics of previously harvested redwood stands are recovering naturally, from restoration, or thinning.

The spatial distribution of redwoods was not recorded during this study but has an effect on stand characteristics such as stand density and canopy cover. Redwoods are a species that reproduce primarily through sprouting. This can lead to a much different layout than species that reproduce only by seed. Redwoods are known for their “fairy rings” which are circular distributions of redwood trees commonly formed after a larger tree was removed naturally or anthropogenically from the center of the ring. The outer redwoods of the circle are often associated with the same root system as the original tree. Studies should be done to look at how second-growth stands compare to old-growth stands with regards to spatial distribution, in an attempt to explain how second-growth stands are naturally recovering spatially. Field data should include genetic information so an understanding of how redwoods sprout after a disturbance, such as logging, can truly be achieved. This could also elucidate how old-growth stands are made up of shared genetics and clones as compared to naturally recovered second-growth stands. Genetic information of fairy rings and redwood groupings could also provide a great educational opportunity for state parks that could provide signage to show which trees are separate individuals and which are clones connected through the same root system.

Reiterated trunks are another feature of redwoods that are not fully understood. The common belief is that reiterations only occur in old-growth stands. This belief is based on the idea that these structures are formed over hundreds of years from

disturbances. This study located six reiterated trunks from different trees across three different parks and within second-growth stands. This shows that these features can occur in approximately one hundred years. As such, this study was not able to determine how these were able to form in a shorter time than commonly thought possible. However, field observations prompted the thought of genetic influence on the formation of reiterated trunks. Additional studies should be done using genetics to determine if some redwoods are more genetically susceptible to growth of reiterations than others after disturbance and without disturbance.

The redwood forest is unique partially because the redwood tree is a very unique species. It has the capability to sprout, survive disturbances, take in water and supply it to the rest of the understory, and be the overall dominant species while maintaining features that some consider would make it a seral species. The redwood forest is ripe for research opportunities and should continue to be analyzed in new ways. Second-growth stands provide great opportunity to see how redwood forests recover from major disturbances. The results of this study show many features of second-growth redwoods in the Santa Cruz Mountains have recovered naturally or appear to be recovering to old-growth standards after being heavily logged. As a result of these findings it is not recommended that any silvicultural management take place within second-growth stands of the Santa Cruz Mountains. Anthropogenic influence of this nature could potentially interfere with the recovery of second-growth stands. This study provides evidence that these stands are recovering naturally overtime.

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Appendix A. Native Species List

Native species recorded in second-growth and old-growth (OG) study sites: Henry Cowell (HC), Butano (BT), Big Basin (BB), Castle Rock (CR), and Portola (POR).

Native Species	Second-growth	Old-growth
<i>Trillium ovatum</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Oxalis oregana</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Trientalis latifolia</i>	HC1, HC2, BT, CR1, CR2	HCOG1, BBOG, BTOG, POR
<i>Asarum caudatum</i>	HC1	HCOG2, BTOG
<i>Disporum hookeri</i>	HC1, HC2, BT, CR1, CR2	HCOG1, BBOG, BTOG, POR
<i>Trillium chlorpetalum</i>	BT, CR2	HCOG1, BTOG, POR
<i>Viola sempervirens</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Galium</i> spp.	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Stachys bullata</i>	HC1, BT, CR1, CR4	HCOG1, HCOG2, BBOG, BTOG
<i>Smilacina racemosa</i> var. <i>amplexicaulis</i>	HC1, HC2, CR2	HCOG1
<i>Smilacina stellata</i> var. <i>sessifolia</i>	CR1, CR2	HCOG1, BTOG, POR
<i>Viola ocellata</i>	HC1, HC2, CR1, CR2	HCOG1
<i>Viola glabella</i>	HC1	HCOG2
<i>Adenocaulon bicolor</i>	HC1, CR2	HCOG2
<i>Vancouveria</i> <i>planipetala</i>	HC1	
<i>Cardamine californica</i> var. <i>californica</i>	HC1	HCOG1
<i>Asyneuma</i> <i>prenanthoides</i>	HC1	
<i>Clintonia andrewsiana</i>	BT	BTOG
<i>Whipplea modesta</i>	HC1	
<i>Corallorhiza striata</i>	HC1	
<i>Iris douglasiana</i>	HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Polygala californica</i>	HC1	
<i>Nemophila parviflora</i>	HC1	

Native Species	Second-growth	Old-growth
<i>Cynoglossum grande</i>		HCOG1
<i>Scoliopus bigelovii</i>	HC1, HC2	
<i>Calypso bulbosa</i>	HC1, HC2, BT, CR1, CR2	HCOG1, BTOG, POR
<i>Vicia</i> spp.	HC1, HC2, BT, CR1, CR2	HCOG1, BBOG
<i>Satureja douglasii</i>	HC2, CR1, CR2	
<i>Anemone deltoidea</i>	HC1, HC2	
<i>Grossularia Sanguineum</i>		HCOG2
<i>Mahonia aquifolium</i>	HC1	
<i>Toxicodendron diversilobum</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG
<i>Rhododendron occidentale</i>	HC2	HCOG1, BBOG
<i>Symphoricarpos albus</i>	HC1, HC2, CR1, CR2	POR
<i>Vaccinium ovatum</i>	HC1, HC2, BT, CR1, CR2	HCOG1, BBOG, BTOG, POR
<i>Rhamnus californica</i>	HC1, HC2, BT, CR1	HCOG2, BBOG, POR
<i>Rosa gymnocarpo</i>	HC1, HC2, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Polystichum munitum</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Pteridium aquilinum var. pubescens</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG
<i>Polypodium californicum</i>	HC1, BT, CR2	BTOG
<i>Pityrogramma triangularis</i>	HC1, HC2, CR1	HCOG1
<i>Woodwardia fimbriata</i>	HC1	
<i>Rubus ursinus</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BTOG
<i>Ceanothus</i> spp.	HC1	
<i>Fragaria californica</i>		HCOG2
<i>Rush</i>	HC1	
<i>Dryopteris arguta</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Lonicera hispidula</i>	HC1, HC2, BT, CR1, CR2	HCOG1, BBOG, BTOG, POR
<i>Sequoia sempervirens</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Pseudotsuga menziesii</i>	HC1, BT, CR1, CR2	HCOG1, BBOG, BTOG, POR

Native Species	Second-growth	Old-growth
<i>Lithocarpus densiflorus</i>	HC1, HC2, BT, CR1, CR2	HCOG1, HCOG2, BBOG, BTOG, POR
<i>Umbellularia californica</i>	HC1, CR1, CR2	HCOG2, POR
<i>Quercus</i> spp.	HC1, HC2, CR1, CR2	HCOG1, BBOG, BTOG, POR
<i>Arbutus menziesii</i>	HC1, HC2, CR1, CR2	BBOG, POR
<i>Aesculus californica</i>	HC1	
<i>Corylus cornuta</i> var. <i>californica</i>	CR2	HCOG2
<i>Acer macrophyllum</i>		HCOG2