**Regeneration Dynamics of Coast Redwood, a Sprouting Conifer Species: A Review with Implications for Restoration**

**Abstract**

Coast redwood (*Sequoia sempervirens*)is unique among conifer species because of its longevity, great sizes of individual trees, and its propensity to reproduce through sprouts. This sprouting capability includes sprouting from burned trees, cut stumps, down logs, and even severed branches or tree tops. Conversely, redwood is not effective at reproducing sexually. Resulting old forests have complex spatial patterns of clones intermixed with other unique individuals. After disturbance or harvest, healthy stumps sprout vigorously, often producing dozens of sprouts within two years of disturbance. These sprouts form highly aggregated spatial patterns because they are clustered around stumps that may number less than 50 ha-1. Growth and self-thinning of sprouts is rapid in full-sunlight. In partial shade, self-thinning may be rapid but growth may be slow. Entire sprout clumps may die in low quality light environments. Thinning of sprouts can accelerate individual tree growth, providing an effective restoration strategy to accelerate formation of large trees and old forest structures or increase stand growth for timber production. This paper reviews the science of early stand dynamics in coast redwood and their implications for restoration and other silvicultural strategies.

**1.0. Introduction**

Restoration is an increasingly common management objective in coast redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) forests.  Decades of over-harvesting in the redwood range have left a small percentage of old presettlement forests (Fox 1996). Much of this is already preserved in national, state, or local park systems. Other areas that have been harvested exist on public and private land and exist in wide range of stand structures resulting from variation in time since harvest, harvest methods, site qualities, and subsequent management activities. Many public agencies and conservation organizations have concluded that restoration is needed to direct the developmental trajectory of some previously harvested stands towards old forest structures to increase the total amount of old forest and increase the overall resiliency of these redwood ecosystems.

Coast redwood is renowned worldwide for its magnificent groves of large trees. Redwood trees reach greater heights (>110 m; Koch et al. 2004) than any other species and redwood forests can store more biomass than any other ecosystem (Fujimori 1977, Van Pelt et al. 2016). Redwood stand production rates are also exceptional: Jones and O’Hara (2012) reported values for mean annual increment and periodic annual increment of 33.2 and 75.6 m3 ha-1yr-1 in a young redwood plantation. Similarly, periodic carbon increment can exceed 16 tonnes ha-1 yr-1 (Jones and O’Hara 2012). The natural range of the species is limited to the Pacific coast of central and northern California, and the southwest corner of Oregon over a latitudinal range from 35.683 to 42.150N. Old forest groves are found throughout much of this range. Redwood is also an increasingly popular plantation species in New Zealand and China.

Redwood is an ancient conifer species in the *Taxodiaceae* family and dating to the Mesozoic era. It is also a hexaploid species with great genetic diversity within individual trees or within-families (Sawyer et al. 2000). Redwood is also an uncommon conifer species due to its ability to sprout prolifically after disturbances including harvest treatments. Trees live in excess of 2,000 yrs and, in old stands, they may host arboreal plant and animal communities in the upper canopy (Sillett and Van Pelt 2007). The heartwood of redwood is decay-resistant and large down logs may last centuries.

A common misconception is that redwood has few management challenges because of the ease of regeneration and its rapid growth rates (Russell et al. 2014). However, management challenges do exist and are often unique for this species, particularly with regard to density management and restoration. In this review, we address the regeneration dynamics of this unusual species and their implications for restoration.  We also address the contention that management treatments pursuing restoration objectives are ineffective or unnecessary because of redwoods unique silvical characteristics. Our specific objectives were to:

1)      Review the regeneration dynamics of coast redwood after a variety of disturbance events;

2)      Review the dynamics of stand development and density management in even-aged and multiaged stands;

3)      Discuss the implications for management of stands of different structures and managing for different objectives including restoration; and

4)      Discuss the implications for management with climate change and the presence of invasive organisms.

**2.0. Environment and species characteristics**

*2.1. Disturbance History*

Disturbance regimes in coast redwood forests are dominated by fire which historically occurred throughout the entire redwood range (Lorimer et al. 2009). Ignition sources were primarily lightning and Native American burning. Redwood is very resistant to fire due primarily to its thick, insulating bark, and its sprouting ability. Fires range from low to high intensity, but were commonly surface fires that meandered on the forest floor and occasionally into the crowns. This provides a competitive advantage for existing redwood stems against competitors that are less resistant to fire, sprout less prolifically, or grow more slowly (Ramage et al. 2010). On alluvial flats where redwood ecosystems are typically most productive (Berrill and O’Hara 2016), flooding and sediment deposition represent another disturbance type (Lorimer). Redwood withstands severe flooding, waterlogged soils, and heavy sediment deposition (Stone and Vasey, Zinke , Lorimer), thereby providing another competitive advantage to redwood on sites where flooding occurs. Mass movement, wind damage, insects, and pathogens are generally not major threats to redwood (Lorimer). Redwood’s adaptations to disturbance give it a competitive advantage throughout its range. These disturbance regimes can result in a variety of stand structures complex multiaged and ranging from pure stands to complex mixtures with many different conifer and broadleaved trees. Even-aged structures are also possible. Combined with redwood’s longevity and great stature, disturbance regimes also contribute to the dominance or redwood on suitable sites across its range.

*2.2. Site Productivity (needs more general refs)*

Redwood’s limited range is evidence of its sensitivity to site conditions. Isolated to a relatively narrow strip on the Pacific coast, the range of coast redwood is indicative of the site-sensitivity of the species. It is known as a fog-dependent species because it found in the coastal fog belt ( ). Redwood, and other plants in redwood forests, will absorb moisture from fog through foliar uptake (Dawson 1998, Limm et al. 2009). In addition to be limited to the coastal fog belt, redwood reaches its best development on wetter sites including alluvial flats and riparian zones ( ). Site index, as the traditional measure of site quality in forestry has limitations in redwood because of inconsistencies in annual ring formation Waring and O’Hara 2006), and annual height growth patterns (Berrill and O’Hara 2014). Berrill and O’Hara (2014, 2016) explored the complex biophysical factors that affect redwood height and basal area increment revealing different factors affecting each. Redwood volume increment was greater on lower slopes, soils with higher pH, and sites with more Douglas-fir and less broadleaved trees.

Floristic-based vegetation classifications have also been used to describe coast redwood forest associations throughout its range (Mahoney and Stuart 2007). Such classifications are closely related to site moisture availability. In a review of redwood vegetation classifications, Mahoney and Stuart (2007) noted that floristic composition and stand structure is highly variable among coast redwood forests. Because of this variability, it may be necessary to consider floristic associations in conjunction with site characteristics to evaluate the (potential old-growth?) status of a redwood stand. Add a few more sentences about floristic classification – Noss, Barbour, etc.

All measures support the view that redwood is highly site-sensitive. This sensitivity is evident across scales from the limits on the redwood range to importance of microsite factors in influencing productivity. This site sensitivity also indicates that comparisons of redwood growth and development must be vigilant to assure that site variation is not an unintended variable.

*2.3 Regeneration - redwood and other species (Lauren)*

*2.3.1. Sprouts*

Unlike most conifers, coast redwood primarily relies on vegetative reproduction. Redwood trees produce sprouts within weeks after cutting regardless of age, although older trees have reduced sprouting (Powers and Wiant). For example, Barrette (1966) reported 95% sprouting in young growth stumps and 85% in older stumps. Similarly, others have reported slight declines in redwood sprouting with increasing size and age (Boe 1965, Wiant and Powers 1967, Lindquist 1979) and no declines from prescribed burning (Powers and Wiant). Redwoods can produce in excess of 100 sprouts per clump (Neal 1967) that grow exceptionally fast in full sunlight. Sprouts tend to grow more vigorously than stems of seed origin, whether naturally regenerated or planted (Jameson and Robards 2007). O’Hara et al. (2007) reported sprout growth over 1 m yr-1 through five years in light environments where percent above canopy light was about 40% or greater. Redwood sprout clumps also decline in density as they develop. This process has been described in a sprout clump production model where the development of new photosynthetic capacity in the clump occurs until a physiological equilibrium is reached (Wiant and Powers 1966, O’Hara and Berrill 2010, O’Hara 2014). After this point, the clump is primarily self-sufficient and no longer relying on stump reserves. Whether the dynamics of clump self-thinning change at this point is not known.

Many species in the redwood ecosystem resprout after disturbance. In addition to redwood, tanoak (*Notholithocarpus* *densiflorus*), California bay (*Umbellularia* *californica*), red alder (*Alnus* *rubra*), and other species are prolific sprouters. Common conifer associates include coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), grand fir (*Abies grandis*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), knobcone pine (*Pinus attenuata*), and others.

*2.3.2. seedlings*

Redwood trees begin to produce seed around 20 years old. As trees age, seed viability increases, with maximum viability occurring around 250 years of age (Roy 1966). Pollination and subsequent seed production is dependent on weather, as pollen movement is facilitated with drier weather. Generally, seed is dispersed during the winter. Although redwood trees produce seed each year, seed production varies throughout the range and some areas may experience prolonged periods without seed production. Between 1 and 31% of seed produced is sound seed and the germination of this sound seed is usually greater than 80% (Roy 1966). Although redwood seeds are relatively small and light, dispersal is limited because of the lack of wings for wind dispersal (Boe 1974). Compared to other species, redwood seed requires more moisture than most other species for germination. Seedlings are susceptible to damping off within the first year (Hepting 1971). Seedlings tend to grow less vigorously than redwood sprouts. Jameson and Robards (2007) found that planted seedlings only grew to half the size of naturally regenerated sprouts of the same age.

*2.4. Spatial and Clonal Patterns*

Spatial patterns in redwood stands are highly variable depending on site factors, disturbance history, and time since disturbance. Additionally, the scale of analysis and the sizes of trees included in a spatial analysis may influence the results. For example, Dagley (2008) found random patterns of large trees in old forest stands on alluvial sites, but smaller trees might form clumped distributions. Van Mantgem and Stuart (2012) also found random patterns of old forest trees on upland sites which were clumped at smaller spatial scales. In young growth forests, spatial patterns may be highly variable depending on site (Berrill and O’Hara 2012). However, given the propensity for sprouting following disturbance, young stands typically form much more aggregated patterns than the older trees or forests they replace (Figure x). These results, suggest redwood stands following stand replacement disturbance such as clearcutting probably develop from highly aggregated patterns to more random patterns in older stands. This is largely due to the process of self-thinning within clumps from many to few stems over many centuries of development. More complex multiaged stands may express both patterns: clumpiness in younger patches and randomness in older. The implications for restoration treatments that respace trees are to avoid uniform distributions of post-thinning trees (Dagley, Van Mantgem and Stuart).

The sprouting ability in redwood creates a distribution pattern, in which members of one clone, or a distinguishable genotype, are more likely to be clumped together.  Narayan (2015), indicated that the intraclonal distances are usually small and do not exceed 10 meters. That was consistent with earlier studies, in which clones were identified using allozyme markers (Rogers, 2000).  In some cases, however, Narayan (2015) found the distance between clones may be as great as 60 meters. Rogers (2000) indicated even greater distances of up to 340 meters and suggested that the disjunct patterns that she had observed might be a result of the redwood’s ability to sprout from the branches driven into the ground after a tree fall.

The individuals found in close proximity or in clonal clumps often might belong to more than one genotype (Narayan, 2015; Rogers, 2000; Douhovnikoff, 2004). This may be a result of several factors, including various patterns of sprout/seedling recruitment and somatic mutations in the resprouting clones.

Within-stand genetic diversity of redwood is high due to the hexaploid nature of the species and its large historical range. The mutations occurring in the species might have accumulated over time, and persisted in the individuals that are now the only remaining representatives of much greater lineages.  The clonal reproduction, while not allowing for the development of new genotypes, helps to preserve the historically high allelic richness. Occasionally, greater numbers of individuals within a clone can be found. Narayan reported the largest stems in one clone was 27 stems. Most often, however, numbers of ramets or stems with a clone tend to be confined to single individuals (Narayan, 2015). It is possible that selection harvesting results in less genetic diversity as trees of certain size and features are targeted. While not always the case, it is plausible that the larger-sized trees belong to the same genotype, and selection harvesting is acting as a force against this genotype, resulting in the decrease in the overall genetic diversity.

**3.0. Stand Dynamics**

*3.1. Even-aged Stands*

Even-aged stands are not common as natural structures in redwood forests. Disturbance regimes that are dominated by fire or flooding and sedimentation (Lorimer et al.) do not typically result in redwood-dominated even-aged stands. Instead, relatively uncommon disturbances such as landslides, or more severe fires that might occur on the drier sites at the edge of the redwood range, may result in even-aged stands. However, management activities such as clearcutting or seed tree systems, or the extraction practices of the early timber harvests, also resulted in substantial areas of even-aged stands across the redwood range.

Even-aged redwood stands originating after disturbances typically include a mixture of seedling and sprout regeneration. Many species in the redwood ecosystem resprout after disturbance. In addition to redwood, tanoak (*Notholithocarpus* *densiflorus*), California bay (*Umbellularia* *californica*), red alder (*Alnus* *rubra*), and other species are prolific sprouters. Common conifer associates include coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), grand fir (*Abies grandis*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), knobcone pine (*Pinus attenuata*), and others.

Redwood trees produce sprouts after cutting regardless of age, although older trees have reduced sprouting (Powers and Wiant). For example, Barrette (1966) reported 95% sprouting in young growth stumps and 85% in older stumps. Similarly, others have reported slight declines in redwood sprouting with increasing size and age (Boe 1965, Wiant and Powers 1967, Lindquist 1979) and no declines from prescribed burning (Powers and Wiant). Redwoods can produce in excess of 100 sprouts per clump (Neal 1967) that grow exceptionally fast in full sunlight. O’Hara et al. (2007) reported sprout growth over 1 m yr-1 through five years in light environments where percent above canopy light was about 40% or greater. Redwood sprout clumps also decline in density as they develop. This process has been described in a sprout clump production model where the development of new photosynthetic capacity in the clump occurs until a physiological equilibrium is reached (Wiant and Powers 1966, O’Hara and Berrill 2010, O’Hara 2014). After this point, the clump is primarily self-sufficient and no longer relying on stump reserves. Whether the dynamics of clump self-thinning change at this point is not known.

Stand development in even-aged redwood forests is, in many ways, typical of development in other even-aged ecosystems. Stem exclusion (Oliver and Larson) is quickly reached as trees compete for dominance and growing space. Redwood approaches a stand-level maximum-density line with a similar slope as other species although with a higher intercept (Reineke). A notable difference from other conifer species is the aggregated distribution of young redwood forests due to the sprouting from cut stumps. There are few studies of self-thinning of individual sprout-clumps and none of sprout clump dynamics in full sunlight.

Other species, particularly tanoak, are prolific sprouters that quickly reoccupy growing space following a disturbance (Stein 1990, Ramage et al. 2010). However, faster growing conifers and some broadleaved trees soon emerge as dominants. The rapid initial height growth of redwood sprouts generally allows them to outgrow their competitors initially. This includes planted conifer seedlings (Robards and Jameson). However, seedling-origin Douglas-fir will often outgrow the sprout-origin redwood by about age 100 (Wensel and Krumland 1986, Berrill and O’Hara 2016). Hence young forests often include a large Douglas-fir component that may persist through the first century or longer of even-aged development. Redwood and Douglas-fir will eventually outgrow tanoak and other broadleaved species (Waring and O’Hara 2008). Alternatively, Douglas-fir, and probably redwood, can grow through a broadleaved canopy to achieve dominant status (Hunter and Barbour).

*3.2. Multiaged Stands*

Old redwood stands complex age structures which are typically multiaged (Sawyer, Lorimer ). Aging large trees if difficult and most knowledge of age structures is through analysis of cut stumps in harvested stands (Fritz, Viers). Given the longevity of coast redwood and low densities of large trees (Table 1), size frequency distributions are highly variable (Viers, Lorimer ). The replacement regime in these old forests is predominantly driven by individual or group tree falls, or trees dying in place. Larger gaps may be successfully colonized by new seedlings or sprouts of redwood or other species. In other cases, but not commonly, disturbances may create patches of even-aged trees. Most notable of old forest dynamics is the complexity in the shapes and arrangement of tree stems and crowns. These trees form multiple stems, or reinterations, that dwarf many other tree species and form complex aerial assemblages of plants and animals many meters off the ground. (Sillett and Van Pelt 2007, Van Pelt and Sillett, Van Pelt et al.). The relatively small number of old forest trees in these stands, their longevity, and their immense size combine to form a “super structure” that is both immense in size, and slow to change. Indeed, our limited understanding of these old forest ecosystems is in part due to the relatively short period of time humans have been studying them. (Fritz 1929; Viers 1982; Lorimer),

In addition to their structural complexity and attributes of size and longevity, redwood forests are also highly productive. Total standing biomass in old redwood forests can exceed 5,000 Mg ha-1 and carbon can exceed 2500 Mg ha-1 (Westman and Whittaker, Fujimori, Busing and Fujimori 2002, Van Pelt et al. 2016). These complex stand structures have leaf area indices over 19, a uniquely high value attributed to their extremely diverse canopies (Van Pelt et al. 2016).

In these complex multiaged stands, where standing trees are present, a disturbance which makes growing space available can result in similar processes as in even-aged stands. This growing space is filled by seedlings or sprouting species and that microsite begins a process of stem exclusion. However, the poorer quality light environment may encourage a different suite of species. For example, redwood clumps require sufficient light to persist and develop (O’Hara et al. 2007, O’Hara and Berrill 2010). In poor light environments, numbers of stems in individual sprout clumps declined as the light regime declined due to crown closure (Figure y). In the poorest light environments, entire sprout clumps can die. However, Figure y also demonstrates how self-thinning of sprout clumps at better light regimes may be very slow. Because redwood has a high shade tolerance, attains high levels of LAI, and has a very plastic crown form capable of quickly reclosing canopy gaps, multiaged stand risk losing regeneration from excessive shade. With sufficient light, understory trees can survive and develop into and through upper canopy layers.

**4.0. Invasives**

*4.1 SOD (Lauren and Kevin)*

*4.2 Plants (Lauren)*

**5.0. Management**

Forest management may be used to pursue many alternative objectives ranging from managing for timber production to restoration. For managed stands, the combination of different previous harvest methods, site quality variation, time since harvest, and post-harvest management activities creates a vast, multidimensional array of existing or potential stand structures. This array of existing and potential stand structures therefore requires a wide array of silviculture: there is not one approach, one silvicultural system, or one form of management that can work for all situations. However, throughout the natural range of redwood, management is a contentious issue due to the history of overexploitation of this resource, perceptions that overexploitation is continuing, and the iconic nature these forests. Management of redwood forests has been an explosive issue for decades (Schrepfer; Harris), and will likely continue be contentious.

*5.1. Young stand management.*

Given redwood’s shade tolerance and prolific sprouting ability, it is amenable to many different silvicultural systems and stand structures. Hence in the redwood region, industrial owners will commonly use even-aged systems such as clearcutting, or multiaged systems like single tree and group selection. One of the variations in existing stand structures is the amount of tanoak present and this is largely related to the site characteristics and management history. After clearcutting, tanoak is an effective competitor to redwood or Douglas-fir because it sprouts prolifically and there are usually more tanoak clumps than redwood clumps. Hence, it is common to use herbicides to control tanoak and other shrub species. These treatments are most commonly hand applications of chemicals directly to target plant species.

Given the low numbers of trees in redwood stems in old forest stands (Table x), cutting these stands results in a relatively small number of redwood sprout clumps with large spaces in between these clumps (Figure z). It is common to use interplanting, or enrichment planting, to increase the redwood stocking in these stands whether they are being managed with even-aged or multiaged systems. Planting stock is either from seedlings, or, more commonly in recent years, from tissue culture from superior genotypes. Subsequent rotations of stands with enrichment planting of improved clonal material will not likely need additional planting because of better spatial arrangements of existing redwood trees. Rotations are approximately 50 years, the lowest rotation length permitted in California.

Early thinning or precommercial thinning is common to reduce overall stand density and to reduce the number of sprouts in redwood sprout clumps. Sprout clumps are typically thinned to 2 or 3 sprouts per clump, but repeated generations of stumps can former complex patterns of stumps that may extend over several meters. In these case, more sprouts may be left. Thinning redwood sprout clumps increases residual tree growth rates and reduces aggregated spatial patterns (Barrette 1966, Boe 1974, Cole 1982, 1983). Age of sprouts affects sprout size which affects equipment options for thinning clumps (Keyes et al. 2008). Broadscale precommercial thinning is used between ages 15 and 20 to reduce density and improve average spacing. It has been effective at increasing individual tree sizes. Lindquist (2004, 2007) thinned 19-year-old stands and found increased tree growth, but no effects on stand increment. Similarly, thinning in 10- to 12-year-old stands produced similar results (O’Hara et al 2015). The greatest increment over the 12-year study was at a spacing of approximately 1.2 m. However, thinning heavily at age 10-12 resulted in large amounts of ingrowth, particularly at wider spacings, because of the large amounts of growing space that were left unoccupied (Figure w). Hence it is possible to thin too early in stands of sprouting species like redwood.

Modeling early redwood stand growth confirms results from empirical thinning studies: thinning can substantially increase growth of remaining trees (Van Mantgem and Das). More specifically to redwood forest restoration, Berrill et al. (2013) modeled young plantations with and without thinning and found thinning put stands on a more rapid trajectory towards the desired old forest reference condition.

As one justification of restoration of old redwood forests is to reduce their vulnerability to fire, thinning creates activity fuels which are short-term hazards after thinning. For example, O’Hara et al. (2017), measured slash depth after restoration thinning in young stands at the northern end of the redwood range and found they were negligible 10 years after thinning. In other parts of the range, these fuels might be more persistent, but thinning appears to have beneficial long-term effects as a fuel reduction strategy.

Another silvicultural treatment in young redwood stands is pruning. Artificial pruning can increase clearwood production and possibly increase the proportion of more valuable heartwood (O’Hara 2012). A potential drawback is the production of epicormics sprouts with severe pruning (O’Hara and Berrill 2009). However, there is no significant interest in pruning from industrial owners in the redwood region due to cost and uncertainties over future markets. However, there is international interest from countries where redwood plantations are being established (Cown et al. 2013).

Competition and bears

5.2 older stands (Julian) cite Oliver et al., Whiskey springs (Lindquist), and multiaged

*5.3. Restoration*(Rachelle and Kevin)

Restoration prescriptions are necessarily highly variable depending on the site and stand conditions, and the specific objectives of the stand. Hence it is difficult to generalize about restoration strategies across the region. Nevertheless, forest restoration in the redwood region is active with hundreds of hectares undergoing treatment. The primary type of restoration is the directing of young stands towards old forest structures with early stand management treatments. For example, the Del Norte Coast Redwood State Park is former industrial timberland recently converted to park status. Young stands that were established after clearcutting as high density plantations with little spatial diversity. Some of these were replanted with Douglas-fir. Various forms of variable density thinning (VDT; Carey ) are being tested as a means to improve diversity and increased the proportion of redwood to historic levels (O’Hara et al. 2010, 2017). VDT attempts to diversify stand structures by thinning stands to have greater horizontal, vertical, or species diversity. The technology of VDT is emerging and many alternative methods have been tested (refs). Generally, the more successful methods for creating stand complexity, the more difficult they are to implement (O’Hara et al. 2012).

Although redwood stands are highly resilient to fire, disturbances such as fire are generally considered undesirable in redwood forests that are in parks or adjacent to vulnerable natural resources or communities. Reducing fuels and making stands more resistant to fire is another restoration objective in redwood. These treatments also involve thinning to increase spacing between trees, decrease continuities of crown fuels, and eliminate overly dense, stagnated areas within stands (need references here).

Restoration may also focus on reducing invasive pests. There are a number of invasive plant species that are found in redwood forests. One of the more prominent are various species of eucalyptus (Eucalyptus spp.) that have either spread into redwood forests or were purposely introduced. Although these eucalyptus are not competitive with redwood on better sites, on the margins of the redwood range they can be more difficult. Effective treatments may involve cutting and herbicide use to kill the tree and subsequent sprouts. (maybe another a few more sentences about other plants.)

An alternative to active restoration is allow stand development to proceed without silvicultural intervention. For example, Russell et al. (2014) have advocated a “natural recovery” whereby self-thinning and other related processes are left to occur at their own rates. Russell’s “natural recovery” strategy for restoration fails on two critical issues: 1) it assumes a rate of self-thinning that restores clearcut stands to old forest stands in several centuries but the old forest stands have unusually high densities. Old redwood forest stands are highly variable but their densities are typically considerably lower than the old forest stands described by Russell (both references)(Table x). Self-thinning is likely to take many centuries to achieve the densities of typical old forest stands; and 2) the reliance on simple chronosequences of even-aged stand development following clearcutting presumes an even-aged target old forest structure. However, the overwhelming preponderance of stand reconstruction data for old forest stands indicates these have complex multiaged structures (Fritz 1929; Viers 1982; Busing and Fujimori 2002; Lorimer). By neglecting to understand old forest age structure and density, Russell has essentially created a “straw dog” comparison where merely having a declining density trajectory is used to suggest natural development will achieve the correct target structure but ignores the complex age structures of the old forest communities that are targeted. This error is further compounded by the exceptionally high densities assumed for old redwood forests. Add a couple of sentences about chronosequence assumptions and floristic classification/indicator species.

**6.0. Climate change and genetic diversity** (Sasha)

The long-lived nature of the species suggests potential difficulty in adaptation to the climate change. The range of coast redwood is restricted to a strip along the Pacific coast of California, the area subject to the intensive summer fogs. The reliance of redwood on the fog moisture is high. The species utilizes fog water intercepted by the foliage and dripped onto the ground (Dawson, 1998) and is also capable of the direct foliage water absorption (Limm et al, 2009). The 33% reduction in fog frequency in the last century (Johnstone and Dawson , 2011) might increase the environmental pressures experienced by the redwood populations. The ability to adapt to the limitation in moisture might be especially pronounced in the southern populations that are already experiencing stronger selective pressures. Douhovnikoff and Dodd (2011) indicated the fragmentation in the redwood populations south of the Sonoma-Mendocino border and suggested that these populations might have difficulty adapting to the new climatic conditions and thus are of greater conservation priority.

The restoration strategies in the time of changing climate should include a broader set of tools, as it is not clear yet how the species will adapt to the increase in the temperature (cite some of the recent Dawson/Sillett work). Multiple scenarios need to be considered. The already difficult process of migration to new habitats in trees, restricted to maximum distances of seed dispersal is further complicated in redwood because the species employ a sprouting reproduction strategy.  The data from common garden trials, when seedlings from various regions are tested for survival and productivity under specific environmental conditions, might be used to evaluate the potential for the assisted migration in redwood. Perhaps, it will be possible to shift the range of the species further north, into central and north Oregon, along the coastal line, where moisture conditions will be suitable for species survival and propagation. Another strategy may be enrichment planting of genotypes from drier and warmer provenances to diversity the gene pool of existing redwood stands and increase their resilience to climate change.

**7.0. Conclusions**

Redwood is an unusual conifer species primarily due to its prolific sprouting ability. This sprouting provides rapid regeneration after harvest, but is spatially aggregated in cutover old forest stands. Redwood may also be the most productive conifer species given rapid individual tree growth rates and its capacity to tolerate high stocking levels. Challenges include the social scrutiny that accompanies managing of such an iconic species, and the difficulties obtaining full stocking of desirable species. For this later challenge, interplanting of redwoods and aggressive control of shrubs and competing plants are standard operating procedures. Redwood sprouts can also be persistent in their aggregated spatial patterns, thereby necessitating thinning to increase growth and form more random spatial patterns.

Restoration of old forest stand structures is an increasingly common objective in the redwood region as public agencies and other entities attempt to increase the total amount of these structures and to consolidate blocks of old forest structures to provide connections or linkages. Most redwood restoration approaches recognize the complex age structures and the unique clonal patterns of old redwood forests and are using silvicultural treatments that will accentuate stand complexity. Many of these efforts have used variable-density thinning to promote more variable stand structures, decrease highly aggregated spatial patterns in young stands, and encourage more diversity in age class structure. All restoration treatments in existing stands have recognized the value in reducing density and its effect on increasing tree growth rates. Although the process of restoration of old forest redwood structures may always take centuries, the value of accelerating this process and assuring it achieves the regional goals of greater amounts and improved connections between old forests has become well-recognized. Simply stated, an active management approach is generally viewed as the best way to restore old redwood forests and the ecological values they provide.





Figure Y. Percent survivorship per redwood clump over a five-year perod and the percent above canopy light (PACL). Sprout mortality increases with declining light regime (adapted from O’Hara and Berrill 2010)



Figure z. Two-year-old clearcut showing redwood sprout clumps and spaces between them.



Figure w. Volume increment from 2001-2012 by treatment showing the added increment from ingrowth (dark blue). The treatments included two types of controls (C = no thinning; CV = no thinning and herbicide treatment of shrubs), and the target spacings from 1.2 to 7.3 m (4 to 24 feet) (adapted from O’Hara et al. 2015). Fix caption

Table 1**.** Stand density of old redwood forests showing upper canopy redwood trees and total density. (Adapted from Dagley and O’Hara 2003). Studies varied in minimum diameters reported and in definitions of upper canopy trees.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Location** | **Latitude**  **O N** | **Upper canopy redwood** | **Total density** | **Source** |
| trees ha-1 | |
| Mendocino County - slopes | 39.33 | -- | 913 | Westman and Whittaker 1975[[1]](#footnote-1) |
| Mendocino County- alluvial flats | 39.33 | -- | 337 |
| Humboldt Redwoods St. Pk – (Bull Creek) | 40.35 | 66 | 167 | Fujimori 1977, Busing and Fujimori |
| Humboldt Redwoods St. Pk – (Bull Creek) |  | 88 | 225 | Sugihara 1992[[2]](#footnote-2) |
| Humboldt Redwoods St. Pk – (Bull Creek) |  | 48 | 163 | Van Pelt and Franklin 2000 |
| Redwood NP (Prairie Creek) flat | 41.38 | 163 | 180 | Pillers and Stuart 1993[[3]](#footnote-3) |
| Redwood NP (Prairie Creek) slope | 41.38 | 177 | 276 |
| Humboldt Redwood St. Pk. flat | 40.35 | 160 | 239 |
| Humboldt Redwoods St. Pk. Slope | 40.35 | 59 | 1046 |
| Redwood NP |  | 46 | 70 | Veirs 19813 |
| Redwood NP (xeric) | 41.33 | 128 | 311 | Combs 1984[[4]](#footnote-4) |
| Redwood NP (mesic) | 41.33 | 180 | 272 |
| Muir Woods | 37.89 |  | 462 | McBride and Jacobs 19776 |
| Prairie Creek St. Pk. |  | 107 | 137 | Sillett7 |
| Bull Creek |  | 143 | 146 |
| Armstrong St. Pk. | 38.88 | 74 | 192 | Dagley 2008[[5]](#footnote-5) |
| Humboldt Redwoods St. Pk. | 40.31 | 59 | 122 |
| Various – Mendocino County | Approx.. 38 |  | 763 | Russell and Michels 2010[[6]](#footnote-6) |
| Various – Santa Cruz and San Mateo Counties | Approx. 37 |  | 1308 | Russell et al. 2014 |
| Big Basin St. Pk. | 37.18 |  | 272 | Narayan 2015[[7]](#footnote-7) |
| Humboldt Redwoods St. Pk. | 40.34 |  | 183 |
| Redwood N.Pk. | 41.34 |  | 170 |
| Jedediah Smith St.Pk. upper | 41.78 | 39 | 266 | Van Pelt et al. 2016[[8]](#footnote-8) |
| Jedediah Smith St.Pk. lower | 41.77 | 48 | 246 |
| Prairie Creek St.Pk. upper | 41.37 | 58 | 247 |
| Prairie Creek Sk.Pk. lower | 41.36 | 41 | 145> |
| Redwood N.Pk. upper | 41.26 | 49 | 471 |
| Redwood N.Pk. lower | 41.20 | 64 | 426 |
| Humboldt Redwoods St.Pk. | 40.34 | 64 | 375 |
| Montgomery Woods St.Res. | 39.23 | 68 | 336 |
| Samuel P. Taylor St.Pk. | 38.02 | 53 | 475 |
| Big Basin St.Pk. | 37.19 | 48 | 552 |
| Landeis-Hill Big Creek Res. | 36.09 | 76 | 550 |

2 Numbers reported for upper canopy redwood and other conifer classes represent the total number/area

(i.e., author does not distinguish between upper and lower canopy for redwood and other conifers). In

addition, no minimum diameter limit was set.

3 Summary of Table. 5. Includes all trees > 61 cm (24 inches) dbh.

7 Results are reported in Sawyer et al. 2000. Number reported for redwood is the

total number/area.

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1. Included trees and shrubs greater than 2 cm dbh; both slope and alluvial values are averages of 3 plots, alluvial site included one plot from Humboldt Redwoods St. Pk. [↑](#footnote-ref-1)
2. Upper canopy trees were > 100 cm dbh [↑](#footnote-ref-2)
3. No minimum diameter set for total trees/ha. [↑](#footnote-ref-3)
4. Includes all trees > 2/54 cm dbh [↑](#footnote-ref-4)
5. Values are from one plot at Armstrong and two plots from Humboldt Redwoods St. Pk. For upper canopy trees, minimum diameter was 150cm and for all trees it was 15 cm. [↑](#footnote-ref-5)
6. Old forest sites were spread over distance greater than 30 km [↑](#footnote-ref-6)
7. Average for two one-ha plots for trees > 10 cm dbh [↑](#footnote-ref-7)
8. Upper canopy redwoods were > 100 cm dbh; [↑](#footnote-ref-8)