Title
Regeneration Dynamics of coast redwood, a sprouting conifer species: A review with implications for management and restoration

Journal
Forests, 8(5)

ISSN
1999-4907

Authors
O'Hara, KL
Cox, LE
Nikolaeva, S
et al.

Publication Date
2017-04-27

DOI
10.3390/f8050144

Peer reviewed

forests

MDPI

Review

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

Kevin L. O'Hara *, Lauren E. Cox, Sasha Nikolaeva, Julian J. Bauer and Rachelle Hedges

Department of Environmental Science, Policy and Management, University of California, 130 Mulford Hall #3114, Berkeley, CA 94720, USA; lecox@berkeley.edu (L.E.C); sashanikolaeva@berkeley.edu (S.N.); julian.bauer1@gmail.com (J.J.B.); rachellenhedges@gmail.com (R.H.)

* Correspondence: kohara@berkeley.edu; Tel.: +1-510-642-2127

Academic Editor: Emanuele Lingua

Received: 15 March 2017; Accepted: 21 April 2017; Published: 27 April 2017

Abstract: Coast redwood (*Sequoia sempervirens* (Lamb. ex. D. Don) Endl.) is unique among conifer species because of its longevity, the great sizes of individual trees, and its propensity to reproduce through sprouts. Timber harvesting in the native redwood range along the coast of the western United States has necessitated restoration aimed to promote old forest structures to increase the total amount of old forest, the connectivity between old forests, and to enhance the resiliency of these ecosystems. After disturbance or harvest, healthy redwood 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}. 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. However, management, including restoration activities, is a contentious issue throughout the native range of redwood because of the history of overexploitation of this resource and perceptions that overexploitation is continuing. This paper reviews the science of early stand dynamics in coast redwood and their implications for restoration and other silvicultural strategies.

Keywords: *Sequoia sempervirens*; coast redwood; restoration; silviculture; old-growth; thinning; multiaged; fire; variable-density thinning; regeneration

1. 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 [1]. Much of this is already preserved in national, state, or local park systems. Other areas that have been harvested exist in a 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, connectivity between old forests, and the overall resiliency of these redwood ecosystems [2,3].

Coast redwood (also known as "redwood") is renowned for its magnificent groves of large trees. Redwood trees reach greater heights (>110 m; [4]) than any other species and redwood forests can store more biomass than any other ecosystem [5,6]. Redwood stand production rates are also exceptional: Jones and O'Hara [7] reported values for mean annual increment and periodic annual increment of 33.2 and 75.6 m^3 ha^{-1} $year^{-1}$ in a young redwood plantation. Similarly, periodic carbon increment can exceed 16 tonnes ha^{-1} year^{-1} [7]. 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 35.68 to 42.15 N, from sea level to 750 m. Coast redwood grows in a strip that is 12–32 km wide and characterized by frequent fog. Old forest groves are found interspersed 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 dating to the Mesozoic era [8]. It is also a hexaploid species; this means that the same gene can be represented by up to three different alleles. This allows for an enormous number of combinations of those alleles in each generation of trees. The greatest genetic diversity is observed within redwood families [9]. Redwood is also an unusual conifer species because of its ability to sprout prolifically after disturbances, including harvest treatments. Trees live in excess of 2000 years and, in old stands, they may host arboreal plant and animal communities in the upper canopy [10]. The heartwood of redwood is decay-resistant and large logs may last centuries on the forest floor. Common associated species include tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh), California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.), red alder (*Alnus rubra* Bong.), coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), knobcone pine (*Pinus attenuata* Lemmon), and others [8]. Conifer species such as western hemlock and coast Douglas-fir have lifespans of up to 500 years or longer, whereas associated broadleaf species have much shorter longevity [8].

A common misconception is that redwood has few stand-level management challenges because of the ease of regeneration and its rapid growth rates [11]. 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 stand-level management and restoration. We also address the contention that management treatments pursuing restoration objectives are ineffective or unnecessary because of redwood's 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. 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 [12]. Ignition sources were primarily lightning and Native American burning [13–16]. Redwood is very resistant to fire primarily because of its thick, insulating bark. It also has the ability to sprout prolifically at the base after disturbance. Fires ranged from low to high intensity but were commonly surface fires that meandered on the forest floor and occasionally into the crowns [12]. This provides a competitive advantage for existing redwood stems against species that are less resistant to fire, sprout less prolifically, or grow more slowly [16]. On alluvial flats where redwood ecosystems are typically most productive [17], flooding and sediment deposition represent another disturbance type [12]. Redwood withstands severe flooding, waterlogged soils, and heavy sediment deposition [12,18,19], 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 [12]. Redwood's adaptations to disturbance make it competitive throughout its range. Typical disturbance regimes can result in a variety of multiaged stand structures ranging from pure stands to complex mixtures with many different conifer and broadleaved trees. Even-aged structures are also possible but not common. Combined with redwood's longevity and great stature, disturbance regimes also contribute to the dominance of redwood on suitable sites across its range.

2.2. Site Productivity

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 a fog-dependent species found in the coastal fog belt [8,20]. In addition to being limited to the coastal fog belt, redwood achieves greater productivity on wetter sites including alluvial flats and riparian zones [8,20]. Site index, as the traditional measure of site quality in forestry has limitations in redwood because of inconsistencies in annual ring formation [21] and annual height growth patterns [22]. Berrill and O'Hara [17,22] 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 fewer broadleaved trees.

Floristic-based vegetation classifications have also been used to describe coast redwood forest associations throughout its range [23]. Differences in associated vegetation species are closely related to site moisture availability [19]. Mahony and Stuart [23] noted that floristic composition and stand structure are highly variable among coast redwood forests. In northern California, Lenihan et al. [24] classified recently harvested coast redwood stands based on understory species and found that associations varied by both level of soil disturbance and site moisture. Sites that were less disturbed were more similar to old-growth redwood stands than highly disturbed sites [25]. Similar vegetation associations that vary with topography have been documented in the central portion of the redwood range [8]. Indicator species may also be used to help identify old forest status, although designated indicator species may occur in multiple developmental stages or be assigned indicator status in stands outside of their native range [26]. Because of this variability, it may be necessary to consider floristic associations in conjunction with site characteristics and disturbance history to evaluate the site productivity and potential for restoration of any redwood stand.

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 stand structure and development must be vigilant to assure that site variation is not an unintended variable.

2.3. Regeneration—Redwood and Other Species

2.3.1. Sprouts

Unlike most conifers, coast redwood primarily relies on vegetative reproduction. New stems sprout from a lignotuber or burl at the base of the original leader [27]. These burls eventually form swelling at the base of the tree. Basal burls serve as storage for many suppressed buds that may sprout after damage to the primary leader, contain carbohydrates and nutrients to facilitate growth of sprouts, generate roots for the tree, and may provide increased stability on steep slopes [8]. The lignotubers are therefore the source of the sprouting ability that distinguishes redwood from most other conifers.

Redwood trees may produce sprouts within weeks after cutting regardless of age, although older trees have reduced sprouting [28]. For example, Barrette [29] reported 95% of young growth stumps produce sprouts and 85% of older stumps produce sprouts. Similarly, others have reported slight declines in redwood sprouting with increasing size and age [30–32] and no decline from prescribed burning [28]. Redwoods can produce in excess of 100 sprouts per clump [33] that grow exceptionally fast in full sunlight, but also self-thin over time. O'Hara et al. [34] reported sprout growth over 1 m $year^{-1}$ through five years in light environments where percent above canopy light was about 40% or greater. 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 [31,35,36]. 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 associated species in the redwood ecosystem resprout after disturbance. In addition to redwood, tanoak, California bay, red alder, among others, are prolific sprouters.

2.3.2. Seedlings

Although redwood trees produce seed each year, seed production varies throughout the range and some areas may experience prolonged periods without significant seed production, though only a proportion of this seed may be sound [20]. Compared to other species, redwood seed requires more moisture than most for germination. High levels of leaf litter accumulation in redwood stands, compared to other forest types, result in relatively few sites suitable for seedling establishment [8]. Seedlings tend to grow less vigorously than redwood sprouts. This is also true for planted seedlings: Jameson and Robards [37] found that planted seedlings only grew to half the size of naturally regenerated sprouts of the same age.

2.4. Spatial and Clonal Patterns

Restoring redwood requires an understanding of spatial 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 [38] found random patterns of large trees in old forest stands on alluvial sites, but smaller trees formed clumped distributions. Van Mantgem and Stuart [39] 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 [40]. However, given the propensity for sprouting following disturbance, young stands typically form much more aggregated patterns than the older stands or forests they replace (Figure 1). These results suggest that, following stand replacement disturbance, redwood stands 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 are to avoid uniform distributions after the thinning [38,39].

Figure 1. Young even-aged redwood forest demonstrating strongly aggregated spatial pattern due to origin of these trees from stump sprout clumps. Photograph taken in Alameda County, CA, USA.

The sprouting ability in redwood creates a spatial distribution pattern where members of one clone, or a distinguishable genotype, are more likely to be clumped together. Narayan [41] found intraclonal distances were usually small and did not exceed 10 m, which was consistent with earlier studies in which clones were identified using allozyme markers [42]. In some cases, however, Narayan [41] found the distance between clones was as great as 60 m. Rogers [42] found even greater distances of up to 340 m and suggested that these disjunct patterns may be the result of redwood's ability to sprout from branches driven into the ground after a tree fall. The individuals found in close proximity or in clonal clumps often belong to more than one genotype [41–43]. This may be a result of several factors, including various patterns of sprout/seedling recruitment. For example, when seedlings and/or sprouts of different genotypes growing in close proximity, fuse together as the stand develops. The genetic difference could also be a result of somatic mutation in the resprouting clones.

Within-stand genetic diversity of redwood is high due to the hexaploid nature of redwood. Mutations have likely accumulated over time and persisted in individuals that are now the only remaining representatives of much greater lineages. The clonal reproduction, while impeding the development of new genotypes, helps to preserve the historically high allelic richness. Occasionally, large numbers of individuals within a clone can be found. Narayan [41] reported the largest number of stems in one clone was 27 stems in old forest stands. Often, however, numbers of ramets or stems per clone tended to be confined to single individuals [41]. Spatial patterns of clones, and variations in clone numbers, are highly variable and will be difficult to emulate with restoration treatments.

3. Stand Dynamics

3.1. Even-Aged Stands

Even-aged stands are not common natural structures in redwood forests. Disturbance regimes that are dominated by fire or flooding and sedimentation [12] 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 heavy-handed extraction practices of early timber harvests, did result in substantial areas of even-aged stands across the redwood range.

Stand development in even-aged redwood forests is, in many ways, typical of development in other even-aged ecosystems. Stem exclusion [44] 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 [45]. A notable difference from other conifer species is the aggregated distribution of young redwood forests due to the sprouting from cut stumps (Figure 1). 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 [16,46]. 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. This includes planted conifer seedlings [37]. However, seedling-origin Douglas-fir will often outgrow the sprout-origin redwood by about age 100 [17,47]. 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 [48]. Alternatively, Douglas-fir, and probably redwood, can grow through a broadleaved canopy to achieve dominant status [49].

3.2. Multiaged Stands

Old redwood stands have complex age structures [12,50]. However, aging large trees is difficult, and most knowledge of age structures is through analysis of cut stumps in harvested stands [51,52].

Given the longevity of coast redwood and low densities of large trees (Table 1), size frequency distributions are highly variable [12,52]. 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 reiterations, that dwarf many other tree species and form complex aerial assemblages of plants and animals many meters off the ground [6,10,53]. 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 [12,51,52].

Table 1. Stand density of old redwood forests showing upper canopy redwood trees and total density (adapted from [54]). Studies varied in minimum diameters reported and in definitions of upper canopy trees.

Location	Latitude° N	Upper Canopy Redwood	Total Density	Source
		Trees ha^{-1}		
Mendocino County—slopes Mendocino County—alluvial flats	39.33 39.33	n/a n/a	913 337	[55] [1]
Humboldt Redwoods St. Pk—(Bull Creek)	40.35	66	167	[5,56,57]
Humboldt Redwoods St. Pk—(Bull Creek)	40.35	88	225	[58] [2]
Humboldt Redwoods St. Pk—(Bull Creek)	40.35	48	163	[59]
Redwood N. Pk. (Prairie Creek) flat Redwood N. Pk. (Prairie Creek) slope Humboldt Redwood St. Pk. flat Humboldt Redwoods St. Pk. Slope	41.38 41.38 40.35 40.35	163 177 160 59	180 276 239 1046	[60] [3]
Redwood N. Pk.	n/a	46	70	[52] [4]
Redwood N. Pk. (xeric) Redwood N. Pk. (mesic)	41.33 41.33	128 180	311 272	[61] [5]
Muir Woods	37.89	n/a	462	[62]
Prairie Creek St. Pk. Humboldt Redwoods St. Pk. (Bull Creek)		107 143	137 146	[50]
Armstrong St. Pk. Humboldt Redwoods St. Pk.	38.88 40.31	74 59	192 122	[38] [6]
Various—Mendocino County	Approx. 38	n/a	763	[63] [7]
Various—Santa Cruz and San Mateo Co.	Approx. 37	n/a	1308	[11]
Big Basin St. Pk. Humboldt Redwoods St. Pk. Redwood N. Pk.	37.18 40.34 41.34	n/a n/a n/a	272 183 170	[41] [8]
Jedediah Smith St. Pk. upper Jedediah Smith St. Pk. lower Prairie Creek St. Pk. upper Prairie Creek Sk. Pk. lower Redwood N. Pk. upper Redwood N. Pk. lower Humboldt Redwoods St. Pk. Montgomery Woods St. Res. Samuel P. Taylor St. Pk. Big Basin St. Pk. Landeis-Hill Big Creek Res.	41.78 41.77 41.37 41.36 41.26 41.20 40.34 39.23 38.02 37.19 36.09	39 48 58 41 49 64 64 68 53 48 76	266 246 247 145 471 426 375 336 475 552 550	[6] [9]

[1] Included trees and shrubs greater than 2 cm dbh; both slope and alluvial values are averages of three plots, alluvial site included one plot from Humboldt Redwoods St. Pk. [2] Upper canopy trees were >100 cm dbh. [3] No minimum diameter set for total trees/ha. [4] Includes all trees >61 cm dbh. [5] Includes all trees >2.54 cm dbh. [6] Values are from one plot at Armstrong and two plots from Humboldt Redwoods St. Pk. For upper canopy trees, minimum diameter was 150 cm and for all trees it was 15 cm. [7] Old forest sites were spread over distance greater than 30 km. [8] Average for two one-ha plots for trees >10 cm dbh. [9] Upper canopy redwoods were >100 cm dbh.

In these complex multiaged stands, a disturbance which makes growing space available can result in similar processes as in even-aged stands but at a smaller scale. Open growing space is filled by seedlings or sprouting species and the site 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 [34,35]. In poor light environments, numbers of stems in individual sprout clumps declined as the light regime declined due to crown closure (Figure 2). In the poorest light environments, entire sprout clumps can die. However, Figure 1 also demonstrates how self-thinning of sprout clumps in better light regimes may be very slow. Because redwood has a high shade tolerance, attains high levels of leaf area index [6,34,35], and has a very plastic crown form capable of quickly reclosing canopy gaps, multiaged stands risk losing regeneration from excessive shade [35]. With sufficient light, understory trees can survive and develop into and through upper canopy layers [35].

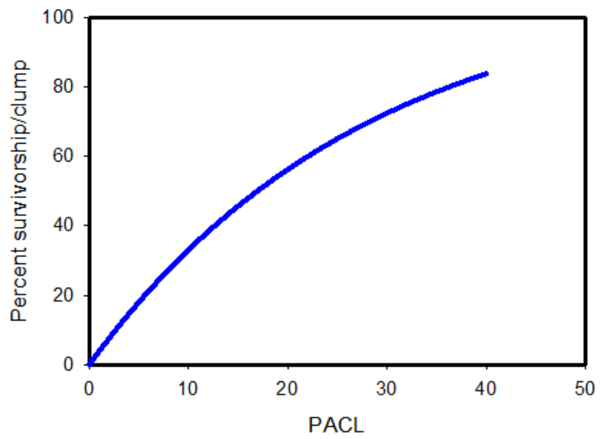

Figure 2. Percent survivorship per redwood clump over a five-year period and the percent above canopy light (PACL). Sprout mortality increases with declining light regime (adapted from [35]).

4. 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. This is also true for restoration. However, throughout the natural range of coast redwood, management, including restoration, is a contentious issue due to the history of overexploitation of this resource, perceptions that overexploitation is continuing, and the iconic nature of these forests. Management of redwood forests has been an explosive issue for decades [64–66] and will likely continue to be contentious.

4.1. Young Redwood 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 variables in existing stand structures is the amount of tanoak present, and this is largely related to site characteristics and management history [67]. After clearcutting, tanoak is an effective competitor to redwood or Douglas-fir because it sprouts prolifically and there are often more tanoak than redwood clumps. Hence, herbicides are commonly used 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 overstory trees in old forest stands (Table 1), cutting these stands results in a relatively small number of redwood sprout clumps with large spaces between these clumps (Figure 3). Interplanting, or enrichment planting, can be used 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 of superior genotypes. Subsequent rotations of stands with enrichment planting 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 [68].

Figure 3. Two-year-old clearcut showing redwood sprout clumps (some of which are indicated with arrows) and spaces between them. Photograph taken in Humboldt County, CA, USA.

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 two or three sprouts per clump, but repeated generations of stumps can form complex patterns of stumps that may extend over several meters. In these cases, more sprouts may be left. Thinning redwood sprout clumps reduces aggregated spatial patterns, promoting a more random arrangement of stems found in even-aged or complex, multiaged stands [29,69–71] and may not always increase sprout growth [71]. Age of sprouts affects sprout size, which affects equipment options for thinning clumps [72]. Precommercial thinning is used between ages 10 and 20 to reduce density and improve average spacing. It has been effective at increasing individual tree sizes. Lindquist [73,74] thinned 19-year-old stands and found increased tree growth, but no effects on stand increment. Thinning in 10- to 12-year-old stands produced similar results [75]. The greatest increment over the 12-year study was at a spacing of approximately 1.2 m. However, thinning heavily at age 9–11 resulted in large amounts of ingrowth, particularly at wider spacings, because of the large amounts of growing space that were left unoccupied (Figure 4; [75]). Hence, it is possible to thin too early in stands of sprouting species like redwood.

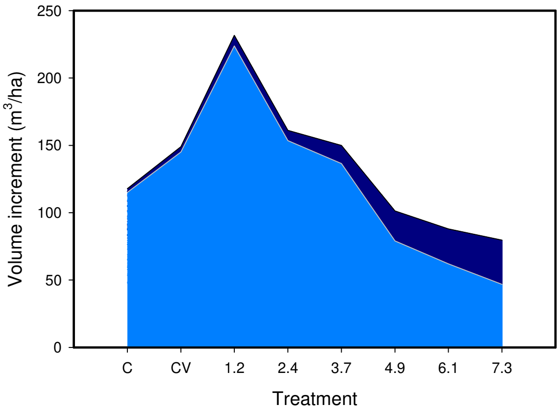

Figure 4. Volume increment from 2001–2012 by treatment (average spacing in meters) showing the added increment from ingrowth (dark blue). The treatments included two types of controls (C = no thinning; CV = no thinning and herbicide treatment of shrubs), and the target spacings from 1.2 to 7.3 m (4 to 24 feet) (adapted from [75]).

Modeling early redwood stand growth confirms results from empirical thinning studies: thinning can substantially increase growth of remaining trees and accelerate process of stand development [76]. Berrill et al. [77] modeled young plantations with and without thinning and found thinning put stands on a more rapid trajectory towards the desired old forest reference condition. One justification of restoration of old redwood forests is to reduce the vulnerability of younger stands to fire. Although thinning creates activity fuels, these hazards are short-lived after thinning. For example, O'Hara et al. [78] measured slash depth after restoration thinning in young stands at the northern end of the redwood range and found they were negligible ten 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 [79]. A potential drawback is the production of epicormics sprouts with severe pruning [80]. 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 [81]. Pruning could be used to remove branches in restoration treatments to accelerate the formation of clear boles and their aesthetic values, although it may be cost prohibitive activity for the agencies typically conducting restoration.

The American black bear (*Ursus americanus* Pallas) can also be an obstacle to restoration in parts of the redwood range [82,83]. The bears scrape off the bark and eat the cambium, thereby injuring or even girdling stems. Coast redwood stems will usually resprout below the girdle. Other conifer species can be killed by this activity. The bears have a preference for more vigorous trees [83,84] and may also prefer redwood to Douglas-fir [83,85]. Thinning to achieve restoration objectives of faster tree growth and lower densities may increase bear damage by encouraging the development of more vigorous trees. The resprouting of girdled redwood stems is contrary to restoration objectives, as it results in an increase in tree density and smaller tree sizes. Repeated bear damage can potentially prevent a stand from achieving restoration objectives.

4.2. Older Redwood Stand Management

Redwood trees respond to the increased growing space provided by thinning in older stands [86]. In Lindquist's Whiskey Springs thinning study at Jackson Demonstration State Forest, even-aged stands exhibited a consistent, strong growth response between the ages of 40 to 75 years to thinning [73,87]. Periodic diameter growth increased with severity of basal area reduction (Figure 5). The lowest retention of basal area resulted in the greatest periodic diameter growth and resulted in the biggest trees. The most severe thinning also exhibited a statistically significant loss in volume production primarily caused by the leave trees not fully occupying the site [86]. Thinning operations accelerate the development of larger diameter redwood trees [73,86,87], promoting old forest structural features beneficial for creation of wildlife habitat [8].

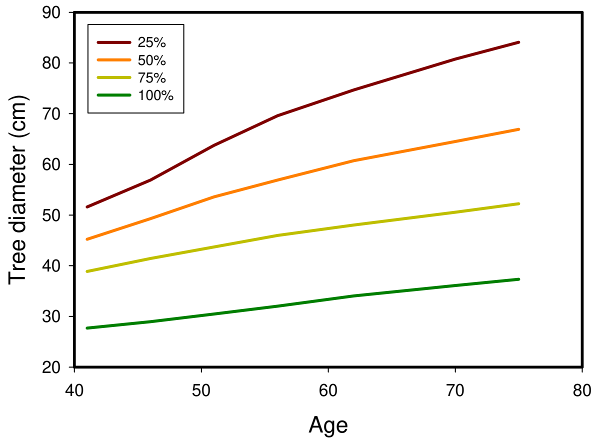

Figure 5. Quadratic mean diameter development with stand age from the Whiskey Springs thinning trial at Jackson Demonstration State Forest. Percent values refer to the residual basal area as compared to the value before thinning at age 40. Initial basal area was approximately 92 m^2 ha^{-1} [87].

Variable retention silviculture is an alternative to clearcutting in redwood stands that also imparts some features of old forest stands. Berrill and O'Hara [88] used the Multiaged Stocking Assessment Model (MASAM) [89] to model a range of growing space occupancy by understory and overstory cohorts across dispersed retention management regimes. Manipulating overstory density had little effect on final stand volume but did have a major effect on the volume increment for both overstory and understory components. Greater overstory density increased the volume increment of the overstory component while decreasing the volume increment of the understory, reflecting a reduction in growing space available to the understory. These modeling results indicated that variable retention systems can provide old forest features while providing timber production. Variable retention therefore offers a restoration option for linking old forests in managed landscapes.

Most restoration strategies will attempt to develop or accentuate multiaged structures in redwood forests since natural even-aged stands are rare [12]. Regeneration is often more of a consideration in multiaged redwood silviculture than in even-aged stands [35]. Aggressive redwood crown development will rapidly occupy new growing space and suppress regeneration if the allotted growing space is not sufficient for regeneration to reach the canopy. To account for the aggressive crown development, it is recommended to substantially reduce density at the end of the multiaged cutting cycle. This maximizes understory vigor and productivity, as redwood stands can quickly return to pre-harvest crown closure after a light harvest. Heavier harvests on longer cutting cycles create stands with lower densities and larger trees, while allowing regeneration to develop [35,36].

4.3. Restoration

Restoration objectives in redwood forests are primarily focused on restoring old forest structures. Within this old forest umbrella, other objectives include increasing tree and stand growth to develop large trees and structural complexity, developing complex spatial patterns, maintaining genetic diversity and complex clonal patterns, controlling invasive plants, and others. Prescriptions are therefore 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 form of restoration is directing young stands towards old forest structures with early stand management treatments such as thinning. Thinning has a demonstrated effectiveness for increasing tree growth rates (Figure 5; [73–75,86,87]), which is a primary objective of many restoration treatments. For example, the Del Norte Coast Redwood State Park at the northern edge of the redwood range, is a former industrial timberland converted to park status. Young stands were established after clearcutting as high density plantations with little spatial diversity. Some of these were replanted with Douglas-fir. Forms of variable-density thinning (VDT; [90]) are being tested as a means to improve diversity and increase the proportion of redwood to historic level [81,87]. VDT attempts to diversify stand structures by thinning stands to have greater horizontal, vertical, or species diversity. Methodologies for VDT are developing and many alternative methods have been tested (e.g., [91–95]). Generally, the more successful methods for creating stand complexity, the more difficult they are to implement [93].

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 catastrophic 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 [85].

Another restoration objective is to reduce the amount of tanoak where previous harvesting practices focused on the removal of redwood and other conifers. These former treatments often resulted in tanoak-dominated stands or stands with increased proportions of tanoak. Restoration treatments may vary depending on the extent of the tanoak. In some cases, stands may be clearcut and replanted to redwood or other conifer species, with herbicides used to control sprouting tanoak [96–98]. In other cases, herbicides may be injected into tanoak stems that are left to die in place.

Many restoration activities are focused on managing invasive organisms. The presence of sudden oak death (SOD; Phytopthora ramorum S. Werres, A.W.A.M. de Cock), an invasive forest pathogen, has resulted in widespread mortality of tanoak in redwood forests since 2000 [99]. In the southern portion of the redwood range, Beh et al. [100] found that higher occurrences of California bay laurel, a non-susceptible host, were associated with higher rates of SOD in areas that had experienced high severity wildfire. SOD affects tanoak in redwood stands and infected stems typically exhibit rapid mortality. Tanoak decline, as a result of SOD, results in aggregated stem spatial patterns [101] and disproportionately affects larger tanoak trees [102]. After SOD-induced tanoak mortality, redwood stems are unlikely to establish new stems in these recently formed gaps because of the poor sexual reproduction. Small gaps may be captured by overstory redwood stems through crown expansion, rather than through regeneration of tanoak [48]. Larger gaps may be colonized by redwood sprouts or seedlings or regeneration of other species. Residual redwoods and other SOD-resistant species may benefit in increased growth [48]. Tanoak mortality also results in higher fuel loads compared to stands unaffected by SOD. This increased fuel level alters wildfire behavior and results in increased redwood mortality—at least at the southern extent of the redwood range—overwhelming the characteristic fire resistance of the species [103].

One of the more prominent groups of invasive plants are various species of eucalyptus (*Eucalyptus* spp.) that have either spread into redwood forests or were purposely introduced. Although these eucalyptus trees 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. Disturbances may allow exotic plant species to become established in coast redwood stands. Larger canopy openings and more intense understory light conditions facilitate the establishment of exotic, invasive species [104]. Pampas grass (*Cortaderia selloana* (Schult. & Schult. f.) Asch. & Graebn.), jubata grass (*Cortaderia jubata* (lem.) Stapf), and Scotch (*Cytisus scoparius* (L.) Link) and French broom (*Genista monspessulana* (L.) L.A.S. Johnson) are exotic species that are typically controlled with mechanical removal and herbicide. Such species typically persist along roadways and near stand boundaries, in high light environments. DiTomaso et al. [105] suggested that herbicide alone may be as effective as mechanical removal with herbicide at controlling jubata grass. Given wind blown seed spread of several km, control of pampas and jubata grass will be ongoing. Likewise, roadside and in-stand control of broom species will also be a long-term process as seeds remain viable on the ground for more than a decade. Invasive species, such as pampas grass, jubata grass, and Scotch and French broom, may impede the regeneration and growth of native tree and shrub species, and their removal is a common restoration objective.

An alternative to active redwood restoration is to allow stand development to proceed without silvicultural intervention. For example, Russell et al. [11] advocated a "natural recovery", whereby self-thinning and other related processes are left to occur at their own rates. This "natural recovery" assumes a rate of self-thinning that restores clearcut stands to old forest stands in several centuries, but the old forest stands used for reference conditions [11,63] had unusually high densities (Table 1). Self-thinning is likely to take many centuries to achieve the densities of typical old forest stands. 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 [5,12,51,52]. By neglecting to understand old forest age structure and density, Russell et al. [11] and Russell and Michels [63] have essentially created a comparison where the occurrence of a declining density trajectory is used to suggest natural development will achieve the correct target structure. However, they fail to demonstrate how structural complexity will be achieved in the old forest communities that are targeted. This error is further compounded by the exceptionally high densities assumed for old redwood forests.

Results from chronosequence studies (i.e., [11,63]) are most valid when each site in the sequence is identical except for age, and when sample sites have the same history "in both its biotic and abiotic components [106]". Redwood forest sites are highly variable (because of topography, moisture, latitude, soils), and floristic associations are also numerous across site type and disturbance history [19,23]. Floristic associations should be compared among similar site types close in proximity if effects of disturbance are being evaluated [24]. Potential differences in site-specific history may additionally compound any comparison between redwood stands on dissimilar sites. Hence, the chronosequence approach used by Russell et al. [11] and Russell and Michels [63] may have produced erroneous results because of the wide environmental gradients between distant sample locations.

5. Climate Change and Genetic Diversity

Two redwood traits may make the species more vulnerable to climate change. One is the uncommonness of sexual reproduction and the other is the long-lived nature of the species: both contribute to slow adaptation to change. The reliance of redwood on fog moisture is high. The species benefits from fog condensation [107], and is also capable of the direct foliage absorption of water and nitrogen [108,109]. A 33% reduction in fog frequency in the last century [110] may have already increased the environmental stresses on redwood populations. The necessity of adapting to the limitation in moisture might be especially pronounced in the southern populations that are already experiencing stronger selective pressures. Douhovnikoff and Dodd [111] reported that fragmentation in the redwood populations south of the Sonoma–Mendocino border (south of 36.8° N) may indicate that these populations will have difficulty adapting to the new climatic conditions and thus are a greater conservation priority.

Restoration strategies in a changing climate should include a broad set of tools, as it is not clear yet how species will adapt to the increase in the temperature [112]. Multiple scenarios need to be considered. The already difficult process of migration of trees to new habitats, restricted to maximum distances of seed dispersal, is further complicated in redwood because the species is reliant on a sprouting reproduction strategy. The data from common garden trials might be used to evaluate the potential for the assisted migration in redwood. It may be possible to shift the range of the species further north, along the coastline of Oregon, where moisture conditions will be suitable for species survival and reproduction. Another strategy may be enrichment planting of drier and warmer provenances to diversify the gene pool of existing redwood stands and increase their resilience to climate change. However, with either assisted dispersal or blending of provenances, active management of redwood forests will be necessary.

6. Conclusions

Redwood is an unusual conifer species, primarily because of its prolific sprouting ability, but also because of its longevity and resilience to disturbance. This sprouting ability provides rapid regeneration after harvest, but is spatially aggregated in cutover 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 to management include the social scrutiny that accompanies managing of such an iconic species, and the difficulties in obtaining full stocking of desirable species. For this latter 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. Restoration treatments in existing stands have recognized the value of reducing density and its effect on increasing tree growth rates and developing structural complexity. Although the process of restoration of old forest redwood structures may take centuries, the value of accelerating this process to achieve regional goals of greater amounts and improved connections between old forests have 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.

The complexity of redwood forests creates many challenges for management and restoration and there is much to be learned. Given the longevity of the species, our present understanding of the species is only a snapshot in time. Longer term study with fluctuations in climate will yield new understandings. Additional knowledge of other reactions to a changing climate, particularly on the limits of the redwood range, will be especially helpful. Disturbance dynamics and effects on long-term stand structure are also topics for future exploration. The potential of prescribed fire as a restoration tool is also unexplored. Finally, landscape-level concerns related to connectivity of isolated patches of old redwood forest have been the impetus for much of the restoration activity to date. More research is needed to examine these landscape patterns and the different types of stand structures that can meet these needs.

Acknowledgments: This review was supported, in part, by the Save the Redwoods League and the by the USDA National Institute of Food and Agriculture. Lynn Webb provided helpful review comments.

Author Contributions: This review was conceived, researched, and written by all five coauthors.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Fox, L. Current status and distribution of coast redwood. In *Coast Redwood Forest Ecology and Management*; LeBlanc, J., Ed.; University of California: Berkeley, CA, USA, 1996; pp. 18–19.

2. Hartley, R.K. Redwood forest conservation: Where do we go from here? In *Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers*; Standiford, R.B., Weller, T.J., Piirto, D.D., Stuart, J.D., Eds.; PSW-GTR-238; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2012; pp. 3–10.
3. California State Park and Recreation Commission; National Park Service. *Redwood State and National Parks General Management Plan*; Redwood National and State Parks: Humboldt/Del Norte Counties, CA, USA, 2000.
4. Koch, G.W.; Sillett, S.C.; Jennings, G.M.; Davis, S.D. The limits to tree height. *Nature* **2004**, *428*, 851–854. [CrossRef] [PubMed]
5. Busing, R.T.; Fujimori, T. Dynamics of composition and structure in an old *Sequoia sempervirens* forest. *J. Veg. Sci.* **2002**, *13*, 785–792. [CrossRef]
6. Van Pelt, R.; Sillett, S.C.; Kruse, W.A.; Freund, J.A.; Kramer, R.D. Emergent crowns and light-use complementarity lead to global maximum biomass and leaf area in *Sequoia sempervirens* forests. *For. Ecol. Manag.* **2016**, *375*, 279–308. [CrossRef]
7. Jones, D.A.; O'Hara, K.L. Carbon density in managed coast redwood stands: Implications for forest carbon estimation. *Forestry* **2012**, *85*, 99–110. [CrossRef]
8. Noss, R.F. *The Redwood Forest: History, Ecology and Conservation of the Coast Redwoods*; Island Press: Washington, DC, USA, 2000.
9. Anekonda, T.S. *A Genetic Architecture Study of Coast Redwood*; University of California: Berkeley, CA, USA, 1992.
10. Sillett, S.C.; Van Pelt, R. Trunk reiteration promotes epiphytes and water storage in an old-growth redwood forest canopy. *Ecol. Monogr.* **2007**, *77*, 335–359. [CrossRef]
11. Russell, W.; Sinclair, J.; Michels, K.H. Restoration of coast redwood (*Sequoia sempervirens*) forests through natural recovery. *Open J. For.* **2014**, *4*, 106–111.
12. Lorimer, C.G.; Porter, D.J.; Madej, M.A.; Stuart, J.D.; Veirs, S.D., Jr.; Norman, S.P.; O'Hara, K.L.; Libby, W.J. Presettlement and modern disturbance regimes in coast redwood forests: Implications for the conservation of old-growth stands. *For. Ecol. Manag.* **2009**, *258*, 1038–1054. [CrossRef]
13. Lewis, H.T. *Patterns of Indian Burning in California: Ecology and Ethnohistory*; Ballena Press: Ramona, CA, USA, 1973.
14. Brown, P.M.; Baxter, W.T. Fire history in coast redwood forests of the Mendocino Coast, California. *Northwest Sci.* **2003**, *77*, 147–158.
15. Stuart, J.D.; Stephens, S.L. North Coast Region. In *Fire in California's Ecosystems*; Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E., Eds.; University of California: Berkeley, CA, USA, 2006; pp. 147–169.
16. Ramage, B.S.; O'Hara, K.L.; Caldwell, B.T. The role of fire in the competitive dynamics of coast redwood forests. *Ecosphere* **2010**, *1*, 1–18. [CrossRef]
17. Berrill, J.-P.; O'Hara, K.L. How do biophysical factors contribute to height and basal area development in a mixed multiaged coast redwood stand? *Forestry* **2016**, *89*, 170–181. [CrossRef]
18. Stone, E.C.; Vasey, R.B. Preservation of Coast Redwood on Alluvial Flats. *Science* **1968**, *159*, 157–161. [CrossRef] [PubMed]
19. Zinke, P.J. The redwood forest and associated north coast forests. In *Terrestrial Vegetation of California*, New Expanded, ed.; Barbour, M.G., Major, J., Eds.; California Native Plant Society: New York, NY, USA, 1977; pp. 679–698.
20. Olson, D.F.J.; Roy, D.F.; Walters, G.A. *Sequoia sempervirens* (D. Don) Endl. Redwood (Agriculture Handbook 654). In *Silvics of North America, Volume 1. Conifers*; USDA Forest Service: Washington, DC, USA, 1990; pp. 541–551.
21. Waring, K.M.; O'Hara, K.L. Estimating relative error in growth ring analyses of second-growth coast redwood (*Sequoia sempervirens*). *Can. J. For. Res.* **2006**, *36*, 2216–2222. [CrossRef]
22. Berrill, J.P.; O'Hara, K.L. Estimating site productivity in irregular stand structures by indexing basal area or volume increment of the dominant species. *Can. J. For. Res.* **2014**, *44*, 92–100. [CrossRef]
23. Mahony, T.M.; Stuart, J.D. Status of vegetation classification in redwood ecosystems. In *Proceedings of the Redwood Science Symposium: What Does the Future Hold?* PSW-GTR-194; USDA Forest Service: Albany, CA, USA, 2007; pp. 207–214.

24. Lenihan, J.M.; Lennox, W.S.; Muldavin, E.H.; Veirs, S.D. *A Handbook for Classifying Early Post-Logging Vegetation in the Lower Redwood Creek Basin*; Technical Report Number 7; Redwood National Park, National Park Service: Arcata, CA, USA, 1982.
25. Lenihan, J.M. *The Forest Associations of the Little Lost Man Creek Research Natural Area, Redwood National Park, CA*; Humboldt State University: Arcata, CA, USA, 1986.
26. Loya, D.T.; Jules, E.S. Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecol.* **2008**, *194*, 179–194. [CrossRef]
27. Del Tredici, P. Lignotubers in *Sequoia sempervirens*: Development and ecological significance. *Madrono* **1998**, *45*, 255–260.
28. Powers, R.F.; Wiant, H.V. Sprouting of old-growth coastal redwood stumps on slopes. *For. Sci.* **1970**, *16*, 339–341.
29. Barrette, B.R. *Redwood Sprouts on the Jackson State Forest*; State Forestry Note No. 29; California Division of Forestry: Sacramento, CA, USA, 1966.
30. Boe, K.N. *Natural Regeneration in Old-Growth Cuttings*; Research Note PSW-94; USDA Forest Service: Berkeley, CA, USA, 1965.
31. Wiant, H.V., Jr.; Powers, R.F. Sprouting of old-growth redwood. In *Proceedings Society of American Foresters Convention 1966*; Society of American Foresters: Washington, DC, USA, 1967; pp. 88–90.
32. Lindquist, J.L. *Sprout Regeneration of Young-Growth Redwood: Sampling Methods Compared*; Research Note PSW-337; USDA Forest Service: Berkeley, CA, USA, 1979.
33. Neal, R.L., Jr. *Sprouting of Old-Growth Redwood Stumps—First Year after Logging*; Research Note PSW-137; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 1967.
34. O'Hara, K.L.; Stancioiu, P.T.; Spencer, M.A. Understory stump sprout development under variable canopy density and leaf area in coast redwood. *For. Ecol. Manag.* **2007**, *244*, 76–85. [CrossRef]
35. O'Hara, K.L.; Berrill, J.-P. Dynamics of coast redwood sprout clump development in variable light environments. *J. For. Res.* **2010**, *15*, 131–139. [CrossRef]
36. O'Hara, K.L. *Multiaged Silviculture: Managing for Complex Forest Stand Structures*; Oxford University Press: Oxford, UK, 2014.
37. Jameson, M.J.; Robards, T.A. Coast redwood regeneration survival and growth in Mendocino county, California. *West. J. Appl. For.* **2007**, *22*, 171–175.
38. Dagley, C.M. Spatial pattern of coast redwood in three alluvial flat old-growth forests in northern California. *For. Sci.* **2008**, *54*, 294–302.
39. Van Mantgem, P.J.; Stuart, J.D. Structure and dynamics of an upland old-growth forest at Redwood National Park, California. In *Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers*; Standiford, R.B., Weller, T.J., Piirto, D.D., Stuart, J.D., Eds.; PSW-GTR-238; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2012; pp. 333–343.
40. Berrill, J.-P.; O'Hara, K.L. Influence of tree spatial pattern and sample plot type and size on inventory estimates for leaf area index, stocking, and tree size parameters. In *Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers*; Standiford, R.B., Weller, T.J., Piirto, D.D., Stuart, J.D., Eds.; PSW-GTR-238; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2012; pp. 485–497.
41. Narayan, L. *Clonal Diversity, Patterns, and Structure in Old Coast Redwood Forests*; University of California: Berkeley, CA, USA, 2015.
42. Rogers, D.L. Genotypic diversity and clone size in old-growth populations of coast redwood (*Sequoia sempervirens*). *Can. J. Bot.* **2000**, *78*, 1408–1419.
43. Douhovnikoff, V.; Cheng, A.M.; Dodd, R.S. Incidences size and spatial structure of clones in second-growth stands of coast redwood *Sequoia sempervirens* (*Cupressaceae*). *Am. J. Bot.* **2004**, *91*, 1140–1146. [CrossRef] [PubMed]
44. Oliver, C.D.; Larson, B.C. *Forest Stand Dynamics*; McGraw-Hill, Inc.: New York, NY, USA, 1990.
45. Reineke, L.H. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* **1933**, *46*, 627–638.
46. Stein, W.I. *Umbellularia californica* (Hook and Arn.) Nutt. In *Silvics of North America, Volume 2 Hardwoods. Agriculture Handbook 654*; Barnes, R.H., Honkala, B.H., Eds.; USDA Forest Service: Washington, DC, USA, 1990; pp. 826–834.

47. Wensel, L.C.; Krumland, B.E. A site index system for redwood and Douglas-fir in California's north coast forest. *Hilgardia* **1986**, *54*, 1–14. [CrossRef]
48. Waring, K.M.; O'Hara, K.L. Redwood/tanoak stand development and response to tanoak mortality caused by Phytophthora ramorum. *For. Ecol. Manag.* **2008**, *255*, 2650–2658. [CrossRef]
49. Hunter, J.C.; Barbour, M.G. Through-growth by *Pseudotsuga menziesii*: A mechanism for change in forest composition without canopy gaps. *J. Veg. Sci.* **2001**, *12*, 445–452. [CrossRef]
50. Sawyer, J.O.; Sillett, S.C.; Libby, W.J.; Dawson, T.E.; Popenoe, J.H.; Largent, D.L.; Van Pelt, R.; Viers, S.D.J.; Noss, R.F.; Thornburgh, D.A.; et al. Redwood trees, communities and ecosystems: A closer look. In *The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods*; Noss, R.F., Ed.; Island Press: Washington, DC, USA, 2000; pp. 81–118.
51. Fritz, E. Some popular fallacies concerning California redwood. *Madrono* **1929**, *1*, 221–224.
52. Viers, S.D.J. Coast redwood forest: Stand dynamics, successional status, and the role of fire. In *Proceedings of the Symposium on Forest Succession and Stand Development in the Pacific Northwest*; Means, J.E., Ed.; Oregon State University: Corvallis, OR, USA, 1982; pp. 119–141.
53. Pelt, R.V.; Sillett, S.C. Crown development of coastal *Pseudotsuga menziesii*, including a conceptual model for tall conifers. *Ecol. Monogr.* **2008**, *78*, 283–311. [CrossRef]
54. Dagley, C.M.; O'Hara, K.L. *Potential for Old Forest Restoration and Development of Restoration Tools in Coast Redwood: A Literature Review and Synthesis*; Save-the-Redwoods League: San Francisco, CA, USA, 2003.
55. Westman, W.E.; Whittaker, R.H. Pygmy forest region of northern California—Studies on biomass and primary productivity. *J. Ecol.* **1975**, *63*, 493–520. [CrossRef]
56. Fujimori, T. Stem biomass and structure of a mature *Sequoia sempervirens* stand on the Pacific Coast of northern California. *J. Jpn. For. Soc.* **1977**, *59*, 435–441.
57. Busing, R.T.; Fujimori, T. Biomass, production and woody detritus in an old coast redwood (*Sequoia sempervirens*) forest. *Plant Ecol.* **2005**, *177*, 177–188. [CrossRef]
58. Sugihara, N.G. *The Role of Treefall Gaps and Fallen Trees in the Dynamics of Old Growth Coast Redwood (Sequoia sempervirens (D. Don) Endl.) Forests*; University of California: Berkeley, CA, USA, 1992.
59. Van Pelt, R.; Franklin, J.F. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Can. J. For. Res.* **2000**, *30*, 1231–1245. [CrossRef]
60. Pillers, M.D.; Stuart, J.D. Leaf-litter accretion and decomposition in interior and coastal old-growth redwood stands. *Can. J. For. Res.* **1993**, *23*, 552–557. [CrossRef]
61. Combs, W.E. *Stand Structure and Composition on the Little Lost Man Creek Research Natural Area*; Redwood National Park; Humboldt State University: Arcata, CA, USA, 1984.
62. McBride, J.; Jacobs, D. *Ecology of Redwood and the Impact of Man's Use of the Redwood Forest as a Site for Recreational Activities: A Literature Review*; Muir Woods Research Project Techinical Report No. 1; University of California for the Muir Wood National Monument, National Park Service: Mill Valley, CA, USA, 1977.
63. Russell, W.; Michels, K.H. Stand development on a 127-yr chronosequence of naturally regenerating *Sequoia sempervirens* (*Taxodiaceae*) forests. *Madrono* **2010**, *57*, 229–241. [CrossRef]
64. Schrepfer, S.R. *The Fight to Save the Redwoods; A History of Environmental Reform, 1917–1978*; University of Wisconsin Press: Madison, WI, USA, 1983.
65. Harris, D. *The Last Stand: The War Between Wall Street and Main Stree over California's Ancient Redwoods*; Times Books/Random House: New York, NY, USA, 1995.
66. Rodrigues, K. The history of conflict over managing coast redwoods. In *Coast Redwood Forest Ecology and Management, Proceedings of the Conference on Coast Redwood Ecology and Management, Humboldt State University, Arcata, CA, USA, 18–20 June 1996*; LeBlanc, J., Ed.; University of California: Berkeley, CA, USA, 1996; pp. 52–54.
67. Thornburgh, D.A. Managing redwoods. In *The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods*; Noss, R.F., Ed.; Island Press: Washington, DC, USA, 2000; pp. 229–262.
68. California Department of Forestry and Fire Protection. *California Forest Practice Rules*; California Department of Forestry and Fire Protection: Sacramento, CA, USA, 2015.
69. Boe, K.N. *Thinning Promotes Growth of Sprouts on Old-Growth Redwood Stumps*; Research Note PSW-290; USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: Berkeley, CA, USA, 1974.
70. Cole, D.W. *Effects of Thinning on Redwood Sprout Growth*; California Forestry Note No. 84; California Dept. Forestry: Sacramento, CA, USA, 1982.

71. Cole, D.W. Redwood sprout growth 3 decades after thinning. *J. For.* **1983**, *81*, 148–150.
72. Keyes, C.R.; Matzka, P.J.; Wright, K.C.; Glebocki, R.; Han, H.S. Early precommercial thinning of redwood sprout clumps: Evaluation of four techniques. *Int. J. For. Eng.* **2008**, *19*, 28–36.
73. Lindquist, J.L. *Precommercial Stocking Control of Coast Redwood: A Seventeen-Year Status Report (1981–1998)*; Report No. 2; California Department Forestry and Fire Protection: Sacramento, CA, USA, 2004.
74. Lindquist, J. Precommercial stocking control of coast redwood at Caspar Creek, Jackson Demonstration State Forest. In *Proceedings of the Redwood Region Forest Science Symposium: What Does the Future Hold?* Standiford, R.B., Giusti, G.A., Valachovic, Y., Zielinski, W.J., Furniss, M.J., Eds.; PSW-GTR-194; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2007; pp. 295–304.
75. O'Hara, K.L.; Narayan, L.; Cahill, K.G. Twelve-year response of coast redwood to precommercial thinning treatments. *For. Sci.* **2015**, *61*, 780–789. [CrossRef]
76. Van Mantgem, P.; Das, A. An individual-based growth and competition model for coastal redwood forest restoration. *Can. J. For. Res.* **2014**, *44*, 1051–1057. [CrossRef]
77. Berrill, J.-P.; Beal, C.B.; LaFever, D.H.; Dagley, C.M. Modeling young stand development towards the old-growth reference condition in evergreen mixed-conifer stands at Headwaters Forest Reserve, California. *Forests* **2013**, *4*, 455–470. [CrossRef]
78. O'Hara, K.L.; Narayan, L.; Leonard, L.P. Ten-year results from a variable-density thinning trial in coast redwood. 2017; In prep.
79. O'Hara, K.L. Coast redwood responses to pruning. In *Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers*; Standiford, R.B., Weller, T.J., Piirto, D.D., Stuart, J.D., Eds.; PSW-GTR-238; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2012; pp. 529–538.
80. O'Hara, K.L.; Berrill, J.-P. Epicormic sprout development in pruned coast redwood: Pruning severity, genotype, and sprouting characteristics. *Ann. For. Sci.* **2009**, *66*, 409. [CrossRef]
81. Cown, D.; Marshall, H.; Silcock, P.; Meason, D. Sawn timber grade recovery from a planted coast redwood stand growing in New Zealand. *N. Z. J. For. Sci.* **2013**, *43*, 8. [CrossRef]
82. Giusti, G.A. Black bear feeding on second growth redwoods: A critical asessment. In Proceedings of the 14th Vertebrate Pest Conference, Sacramento, CA, USA, 6–8 March 1990; Davis, L.R., Marsh, R.E., Eds.; University of California: Davis, CA, USA, 1990; pp. 214–217.
83. Perry, D.W.; Breshears, L.W.; Gradillas, G.E.; Berrill, J.P. Thinning Intensity and Ease-of-Access Increase Probability of Bear Damage in a Young Coast Redwood Forest. *J. Biodivers. Manag. For.* **2016**, *5*, 3–9. [CrossRef]
84. Kimball, B.A.; Nolte, D.L.; Engeman, R.M.; Johnston, J.J.; Frank, R. Chemically mediated foraging preference of black bears (*Ursus americanus*). *J. Mammal.* **2008**, *79*, 448–456. [CrossRef]
85. O'Hara, K.L.; Nesmith, J.C.B.; Leonard, L.; Porter, D.J. Restoration of old forest features in coast redwood forests using early-stage variable-density thinning. *Restor. Ecol.* **2010**, *18*, 125–135. [CrossRef]
86. Oliver, W.W.; Lindquist, J.L.; Strothmann, R.O. Young-growth redwood stands respond well to various thinning intensities. *West. J. Appl. For.* **1994**, *9*, 106–112.
87. Webb, L.A.; Lindquist, J.L.; Wahl, E.; Hubbs, A. Whiskey Springs long-term coast redwood density management; Final grown, sprout, and yield results. In *Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers*; Standiford, R.B., Weller, T.J., Piirto, D.D., Stuart, J.D., Eds.; PSW-GTR-238; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2012; pp. 571–581.
88. Berrill, J.P.; O'Hara, K. Modeling coast redwood variable retention management regimes. In *Proceedings of the Redwood Region Forest Science Symposium: What Does the Future Hold?* Standiford, R.B., Giusti, G.A., Valachovic, Y., Zielinski, W.J., Furniss, M.J., Eds.; PSW-GTR-194; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2007; pp. 261–269.
89. Berrill, J.-P.; O'Hara, K.L. Simulating multiaged coast redwood stand development: Interactions between regeneration, structure, and productivity. *West. J. Appl. For.* **2009**, *24*, 24–32.
90. Carey, A.B. Biocomplexity and restoration of biodiversity in temperate coniferous forest: Inducing spatial heterogeneity with variable-density thinning. *Forestry* **2003**, *76*, 127–136. [CrossRef]

91. Comfort, E.J.; Roberts, S.D.; Harrington, C.A. Midcanopy growth following thinning in young-growth conifer forests on the Olympic Peninsula western Washington. *For. Ecol. Manag.* **2010**, *259*, 1606–1614. [CrossRef]
92. Pukkala, T.; Lähde, E.; Laiho, O. Variable-density thinning in uneven-aged forest management—A case for Norway spruce in Finland. *Forestry* **2011**, *84*, 557–565. [CrossRef]
93. O'Hara, K.L.; Leonard, L.P.; Keyes, C.R. Variable-density thinning and a marking paradox: Comparing prescription protocols to attain stand variability in coast redwood. *West. J. Appl. For.* **2012**, *27*, 143–149. [CrossRef]
94. Dodson, E.K.; Ares, A.; Puettmann, K.J. Early responses to thinning treatments designed to accelerate late successional forest structure in young coniferous stands of western Oregon, USA. *Can. J. For. Res.* **2012**, *355*, 345–355. [CrossRef]
95. Kuehne, C.; Weiskittel, A.R.; Fraver, S.; Puettmann, K.J. Effects of thinning induced changes in structural heterogeneity on growth, ingrowth, and mortality in secondary coastal Douglas-fir forests. *Can. J. For. Res.* **2015**, *45*, 1448–1461. [CrossRef]
96. Burns, R.M. Silvicultural systems for the major forest types of the United States. In *Agricultural Handbook No. 445*; U.S. Department of Agriculture: Quilcene, WA, USA, 1983.
97. Tappeiner, J.C.; McDonald, P.M.; Hughes, T.F. Survival of tanoak (*Lithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) seedlings in forests of southwestern Oregon. *New For.* **1986**, *1*, 43–55. [CrossRef]
98. Piirto, D.D.; Smith, B.; Huff, E.K.; Robinson, S.T. Efficacy of herbicide application methods used to control tanoak (*Lithocarpus densiflorus*) in an uneven-aged coast redwood management context. In *Coast Redwood Forest Ecology and Management*; LeBlanc, J., Ed.; University of California: Berkeley, CA, USA, 1996.
99. Ireland, K.B.; Hardy, G.E.S.J.; Kriticos, D.J. Combining inferential and deductive approaches to estimate the potential geographical range of the invasive plant pathogen, *Phytophthora ramorum*. *PLoS ONE* **2013**, *8*, e63508. [CrossRef] [PubMed]
100. Beh, M.M.; Metz, M.R.; Frangioso, K.M.; Rizzo, D.M. The key host for an invasive forest pathogen also facilitates the pathogen's survival of wildfire in California forests. *New Phytol.* **2012**, *196*, 1145–1154. [CrossRef] [PubMed]
101. Ramage, B.S.; O'Hara, K.L. Sudden oak death-induced tanoak mortality in coast redwood forests: Current and predicted impacts to stand structure. *Forests* **2010**, *1*, 114–130. [CrossRef]
102. Cobb, R.C.; Filipe, J.A.N.; Meentemeyer, R.K.; Gilligan, C.A.; Rizzo, D.M. Ecosystem transformation by emerging infectious disease: Loss of large tanoak from California forests. *J. Ecol.* **2012**, *100*, 712–722. [CrossRef]
103. Metz, M.R.; Varner, J.M.; Frangioso, K.M.; Meentemeyer, R.K.; Rizzo, D.M. Unexpected redwood mortality from synergies between wildfire and an emerging infectious disease. *Ecology* **2013**, *94*, 2152–2159. [CrossRef] [PubMed]
104. Blair, B.C.; Letourneau, D.K.; Bothwell, S.G. Disturbance, resources, and exotic plant invasion: Gap size effects in a redwood forest. *Madrono* **2010**, *57*, 11–19. [CrossRef]
105. DiTomaso, J.M.; Drewitz, J.J.; Kyser, G.B. Jubatagrass (*Cortaderia jubata*) control using chemical and mechanical methods. *Invasive Plant Sci. Manag.* **2008**, *1*, 82–90. [CrossRef]
106. Johnson, E.A.; Miyanishi, K. Testing the assumptions of chronosequences in succession. *Ecol. Lett.* **2008**, *11*, 419–431. [CrossRef] [PubMed]
107. Dawson, T.E. Fog in the Calfornia redwood forest: Ecosystem inputs and use by plants. *Oecologia* **1998**, *117*, 476–485. [CrossRef] [PubMed]
108. Limm, E.B.; Simonin, K.A.; Bothman, A.G.; Dawson, T.E. Foliar water uptake: A common water acquisition strategy for plants of the redwood forest. *Oecologia* **2009**, *161*, 449–459. [CrossRef] [PubMed]
109. Templer, P.H.; Weathers, K.C.; Ewing, H.A.; Dawson, T.E.; Mambelli, S.; Lindsey, A.M.; Webb, J.; Boukili, V.K.; Firestone, M.K. Fog as a source of nitrogen for redwood trees: Evidence from fluxes and stable isotopes. *J. Ecol.* **2015**, *103*, 1397–1407. [CrossRef]
110. Johnstone, J.A.; Dawson, T.E. Climatic context and ecological implications of summer fog decline in the coast redwood region. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 4533–4538. [CrossRef] [PubMed]

111. Douhovnikoff, V.; Dodd, R.S. Lineage divergence in coast redwood (*Sequoia sempervirens*), detected by a new set of nuclear microsatellite loci. *Am. Midl. Nat.* **2011**, *165*, 22–37. [CrossRef]
112. Chin, A.R.O.; Sillett, S.C. Phenotypic plasticity of leaves enhances water-stress tolerance and promotes hydraulic conductivity in a tall conifer. *Am. J. Bot.* **2016**, *103*, 796–807. [CrossRef] [PubMed]