EFFICACY OF FOREST RESTORATION TREATMENTS ACROSS A 40-YEAR CHRONOSEQUENCE AT REDWOOD NATIONAL PARK

By

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ABSTRACT

EFFICACY OF FOREST RESTORATION TREATMENTS ACROSS A 40-YEAR CHRONOSEQUENCE AT REDWOOD NATIONAL PARK

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Following 20th century logging, much of the natural coast redwood (*Sequoia sempervirens*) range consists of dense second-growth stands with slow tree growth and low biodiversity. There is a landscape-scale effort in much of coastal northern California to increase tree growth rates and ecosystem biodiversity via thinning treatments, thereby hopefully accelerating the development of old-growth forest characteristics. Redwood National Park (RNP) has been experimenting with thinning in these forest types since the 1970s. Given the interesting history of logging and restoration in RNP and the future plans for widespread thinning in this region, my thesis examined the effects of land management on forest productivity, biodiversity, and ecocultural resources. The first chapter provides a basic history of land management within the North Coast region. The second chapter investigates how redwood physiology, redwood growth, and forest biodiversity respond to restoration treatments. My Chapter 2 investigations found that thinning second-growth redwood forests 1) does not meaningfully influence tree water status, 2) increases tree gas exchange in the short-term, 3) increases tree growth in the long-term, 4) increases understory plant diversity, and 5) does not affect bird or mammal diversity. Collectively, these findings demonstrate that thinning second-growth redwood

forests has the potential to accelerate the development of old-growth characteristics. This verification of the efficacy of restoration treatments is important information for land managers, as plans are currently underway to apply these treatments at the landscape-scale. Ideally, this thesis can provide useful baseline data to aid future assessments of long-term forest responses to contemporary restoration efforts.

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INTRODUCTION AND METHODS

The first chapter of this thesis examines land and forest management practices in the redwood region over time. Because the second chapter of this thesis is based in Redwood National Park (RNP) on land that was managed and inhabited by the Yurok people for millennia prior to RNP establishment, it seemed appropriate to first provide an overview of past land use at this richly-historied site before scientifically exploring the interactions between contemporary forest management and forest responses. Through an analysis of primary and secondary literature, I provide a basic overview of land use and ownership changes for the land that is currently RNP.

The following presentation and interpretation of archival material tells the story of land management, land acquisition, and sociocultural ties across time. A significant amount of the literature presented was researched through primary and secondary sources in the Special Collections and Archives room of the Humboldt State University Library. Other sources of information include official government and Tribal webpages. The temporal window (1895-1968) on which RNP was created spanned 13 U.S. presidencies and the addition of six states to the Union (Table 1). The events leading up to the establishment of the RNP are controversial, from the removal of indigenous peoples almost completely off their ancestral homelands by the end of the nineteenth century, to the first federal 'legislative taking'[1] of private land in U.S. history in 1968.

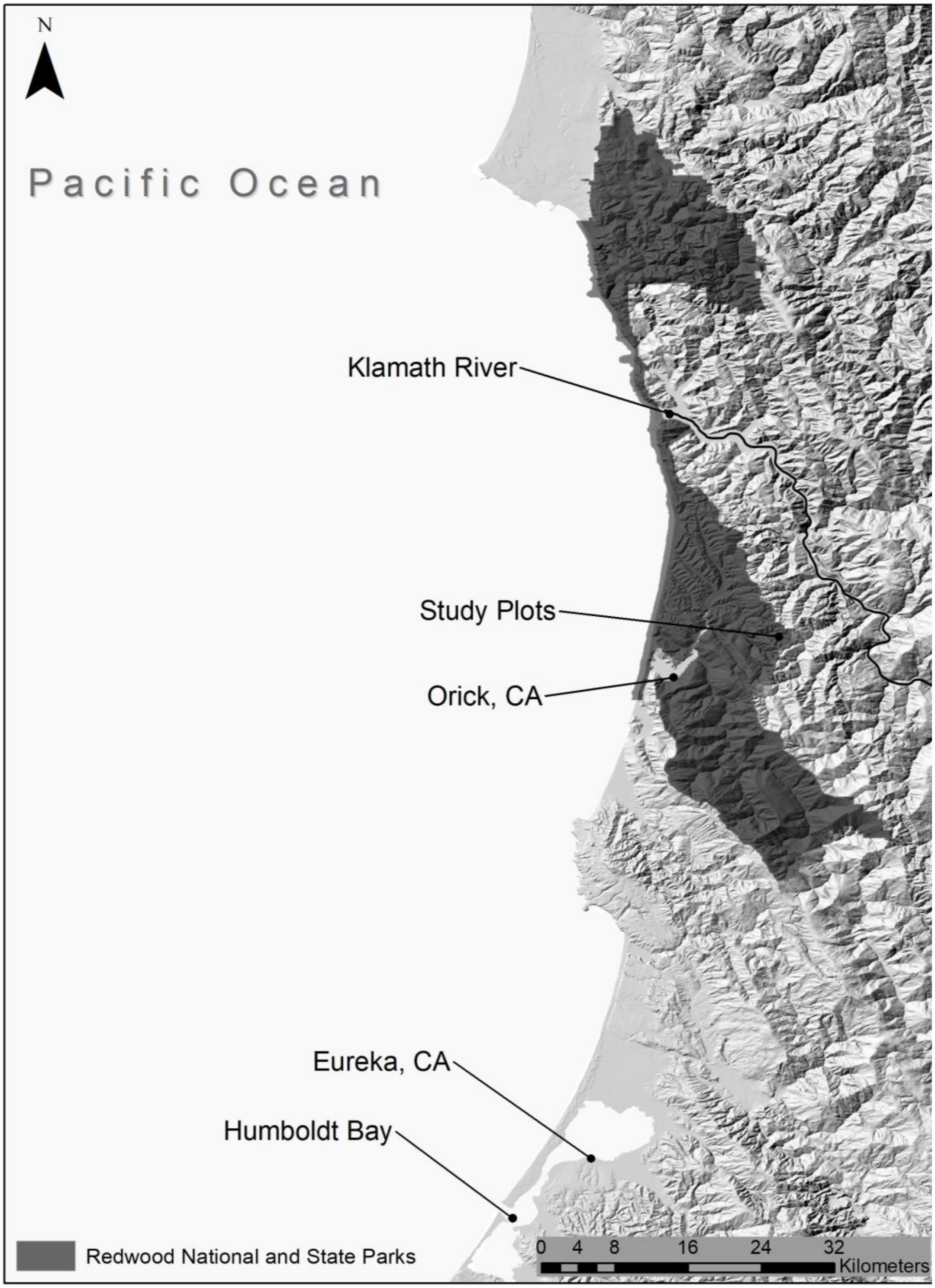

Figure 1. Map of Redwood National and State Parks and surrounding areas located in northern California.

Table 1. Timeline of historical events in the redwood region. Abbreviation of terms include: Redwood State Park (RSP), Redwood National Park (RNP), Lyndon B. Johnson (LBJ), and California Environmental Quality Act (CEQA).

Year	Historical Event	Year	Historical Event
1841	Pre-emption Act	1949	Warren T. Hannum's call for sustainable logging
1850	First operational sawmill on Humboldt Bay	1958	Annual redwood harvest peaks
1852	Henry A. Crabb proposes RSP	1963	National Geographic funds a study, *The Redwoods*
1855	Yurok Reservation established	1964	Findings from *The Redwoods* publicly released
1856	First commercially felled redwood	1964	Responses to *The Redwoods*
1862	Homestead Act	1965-1968	President LBJ delivers conservative messages calling for RNP
1878	Timber & Stone Act	1966	LBJ issues moratorium on logging within proposed RNP
1879	Carl Schurz proposes RSP	1968	LBJ voices support for RNP in State of the Union address
1882	Steam Donkey invented	1968	RNP established
1889	First written records of lumber production	1971	*Bayside Timber v. San Mateo County Board of Supervisors*
1895	First concept of RNP introduced	1972-1973	Findings from Redwood Creek watershed study released
1899	All redwood forest land privately owned	1973	Z'berg-Nejedly Act passed
1900	Steam Donkey upgraded with high-line cable	1975	CA Supreme Court rules Forest Practice Rules subject to CEQA
1902	First RSP established at Big Basin	1977	Jimmy Carter becomes president
1906	San Francisco earthquake	1977	RNP Expansion Act introduced
1918	Save the Redwoods League established	1977	Carter's Environmental Message delivered
1923	Prairie Creek RSP established	1978	RNP expanded to include Redwood Creek watershed
1925	Del Norte Coast RSP established	1978	First restoration treatments in RNP undertaken on Holter Ridge
1929	Jedediah Smith RSP established	2002	RNP expanded to include Mill Creek watershed
1929	Onset of Great Depression	2019	Yurok Lands Act introduced
1945	Forest Practice Act passed		

SUBSISTENCE AND ECOCULTURAL RESOURCES

The first people to see the coast redwoods (*Sequoia sempervirens* [D.Don.] Endl.) were most likely the ancestors of indigenous peoples who migrated throughout North America and lived on these lands since time immemorial.[2] Through archaeology and historiography, the land comprising and surrounding RNP (Figure 1) can be traced in ownership at the time of European arrival to four indigenous tribes: the Chilula, Hupa, Tolowa, and Yurok (Figure 2). In the pre-European era, this land and its many ecosystems stood at the center of the aforementioned tribes' ecocultural resources and subsistence practices. Each aspect of the forest, prairies, and oak woodlands was, and remains to this day, paramount to indigenous life. In addition to depending on the land spiritually and socio-culturally, tribes were historically physically dependent on the landscape for tools, shelter, and migration routes. Prior to presenting my scientific study of RNP sites on lands historically occupied by the Yurok people, I will first describe the deep connection between these lands and their indigenous peoples.

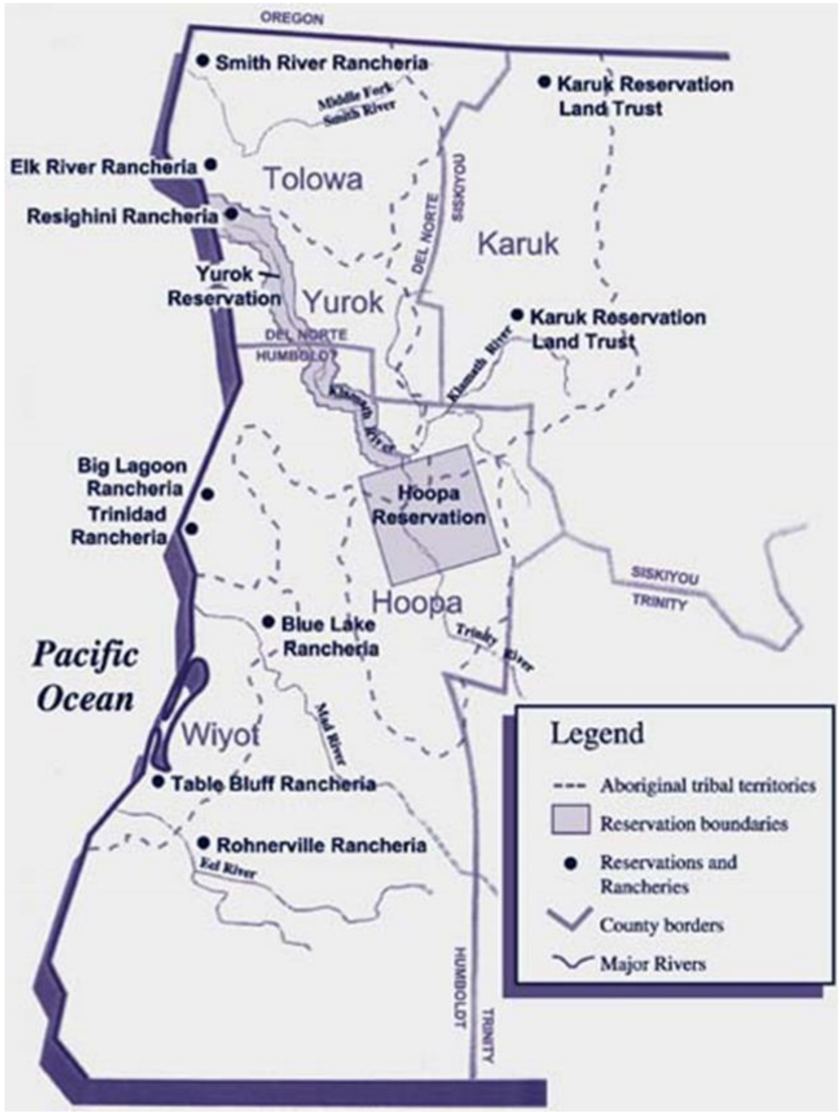

Figure 2. "Local Northwest California Tribes." Credit: Northern California Indian Development Council.[3]

A continuous thread connects the soil that provides water and nutrients essential for plant growth, the animals that depend on these plants, and the peoples who spiritually, culturally, and physically depend on these lands, plants, and animals. Due to their deep cultural connection to the environment, the Yurok focused on land, subsistence, and resource management practices that were sustainable for their population's continued use[4]. This management balance between spiritual and material needs can be described as follows:

> The relationship was a dynamic one: the Yurok used various tools to maintain and develop their forest, and at the same time they let the environment guide them in determining where to live and in other aspects of life. Much of this information is embodied in Yurok spiritual tradition.[5]

According to Yurok legend, when their ancestors first arrived in the lower Klamath River region, they were given land by their creator, Wah-Peck-oo-May-ow. On that land, the tallest trees on earth grew and the Yurok were given instruction on how to utilize them:

> In the beginning, when Wah-Peck-oo-May-ow permitted the spirits to decide what they wanted to be on earth, two of them chose to be Redwood Trees. After they had grown to adulthood and were five or six feet in diameter, a great war between human beings raged around Cappel, a village on the Klamath River, and once the trees were wounded…Wah-Peck-oo-May-ow decreed that in the future the Redwood must not be used for fire wood but could be used by human beings to build their homes and canoes. To prevent burning, he gathered the bark of the Cascarea, the dogwood bark, the fern bark and other bitter barks and dried them in them into a flour. To this he added swamp water and poured this medicine on the tops of the Redwood Trees. This made the wood so bitter that fire would not eat it.[6]

The Yurok believe that items made from redwood contain spirits and that these items therefore embody the Yurok's sacred connection to the land.[7] This spiritual bond between peoples and land was honored by the Yurok, as evidenced by their persistent dedication to sustainably manage the natural resources on which they depended.[8] With an expansive territory including prairies, oak woodlands, and redwood forests, the Yurok used the Klamath River as a main waterway to efficiently access both food and ecocultural resources. Redwood canoes enabled this efficient transportation and secured spiritual connections between tribes. Transportation between tribes' villages and subsistence sites was also achieved through a series of trail systems; Holter Ridge, the study location for the second chapter of this thesis, was an important intertribal trail.[9] Accessibility to these different sites ensured that the Yurok were able to sustainably forage for both food and ecocultural resources, as the widespread collection of resources ensured that no areas were completely depleted.

In addition to functioning as a transportation system, the Klamath River also provided salmon, a major staple of the traditional Yurok diet. The Yurok utilized underbrush and trimmings to make temporary dams, catching and often smoking the fish on the banks. [10] Within forests and prairies, foraging practices fostered grass seed, mushrooms, chinquapin nuts, and other plants. Oak groves were also especially important to traditional subsistence methods, as they provided acorns which was the main starch.[11] Coastal areas of the Yurok territory yielded shellfish, seaweed, and salt. In addition to food resources, this varied terrain provided multiple ecocultural resources for useful products such as baskets and shelters[12]. Plant fibers gathered from multiple landscapes supported a rich culture of basketry, a sacred tradition alive and well today.

To complement their low-impact reliance on multiple foraging, hunting, and gathering zones for subsistence and ecocultural resources, the Yurok also used fire to manage manage the landscape. These indigenous peoples effectively used controlled burning to prevent Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) encroachment in prairies, woodlands, and forests.[13] Controlled burning also cleared understory vegetation and stimulated sprouting in many plant species, thereby creating a steady supply of materials needed for daily life. For example, autumn burning of hazelnut (*Corylus cornuta* Marshall) would produce young one- to two-foot shoots the following spring that could be gathered to make large baskets.[14] Today, although European settlers have encroached and appropriated their land, the Yurok continue to maintain spiritual, cultural, and ancestral connections with the land through traditional activities such as basketry, hunting, fishing, and harvesting acorns.

The complex ties between people and the landscape for the Yurok and other indigenous tribes of this area such as the Karuk, Hoopa, Tolowa, and Wiyot are too numerous to fully examine in this study. Nevertheless, the perspectives provided here exemplify how indigenous subsistence and ecocultural resource management shaped the landscape prior to pre-European settlement. These tribes' sustained stewardship of natural resources are admirable and a standard towards which contemporary societies should aspire.

WESTWARD EXPANSION

When Euro-American settlers arrived in the redwood region, they brought with them the belief that white Americans were destined to conquer all of North America. This rallying cry was known as Manifest Destiny and according to its principals, “American Anglo-Saxons were an innately superior people who were destined to bring good government, commercial prosperity, and Christianity to the American continent and the world.”[15] Early settlers deemed the indigenous people unsuited to care for the land in the way their God intended. These settlers cleared brush and trees, including redwood, to farm and ranch on the land.[16] Eradication methods such as repeated burning and grass seeding were commonly used to extripate native vegetation.[17] Today, the local landscape and views on forest management are largely legacies of these settler-colonial land use practices.[18] In 1855, the federal government established the Yurok Reservation and the Tribe was forced to relocate away from their ancestral homeland.[19] Within a short time, most of the Yuroks’ land was claimed by the settlers.

The early land ownership laws were simple and readily used by the timber companies and ranchers to acquire large tracts of land. The federal government wanted the land ‘settled up’ as fast as possible and offered cheap land to Americans willing to stake a claim in newly acquired states. The Pre-emption Act of 1841 permitted nearly anyone to purchase public land for $1.25 ($31.40 adjusted for inflation in 2019)[20] per 0.4 hectares (1 acre) and under the Homestead Act of 1862 they could claim up to 64.7 hectares (160 acres) of surveyed public land.[21, 22] In 1878, the Timber and Stone Act was passed, allowing for the purchase of 64.7 hectares (160 acres) of timberland for $2.50 ($62.12 adjusted for inflation in 2019)[23], so long as the land was improved through logging and mining.[24] By the end of the 19th century, all of the redwood forested land in Humboldt County, CA was owned by lumbermen and ranchers.[25]

One example of how these early land ownership laws were exploited can be found in Eureka, CA. Local bagmen, individuals who profit from clandestine activities, would find groups of stand-by sailors and take them to the government land office where each would file a claim on 64.7 hectares (160 acres) of timberland. The sailor would then redeed the claim for around $50 ($1,025 adjusted for inflation in 2019)[26] to the bagman who would then redeed that same claim to a timber company eager to acquire more land.[27] Numerous individuals went to jail for breaking the Homestead Act, which was recounted in a book by convicted Oregon timberland fraud kingpin Stephen Puter. He and his business partner, Horace G. McKinley, illegally acquired 776 hectares (1,920 acres) in Oregon City, OR[28] and 6,993 hectares (17,280 acres) in Deschutes County, OR[29] by using false names, bribing Deputy Clerks, and providing false affidavits and proofs of homesteading. It is very likely that other timberland owners used similar tactics to amass an untold number of land deeds and substantially increase their land holdings.

A HISTORY OF LOGGING IN THE REDWOOD REGION

In 1850, the first operational sawmill on Humboldt Bay was constructed and commercial logging in Humboldt County began. Spruce (*Picea sitchensis* [Bong.] Carrière) and fir (*Abies grandis* [Douglas ex D. Don] Lindl.) were the genera most familiar to the early lumber pioneers, predominantly from the eastern U.S., and were the first to be felled. Logging occurred very close to Humboldt Bay because water provided a reliable transportation system. Several logs would be tied together to make a raft and then floated across the water to a sawmill. Due to the immense size of redwood and lack of appropriate sawmill machinery, it wouldn't be until 1856 that lumbermen were able to successfully fell and saw these massive trees.[30]

Redwood sparked a craze in San Francisco because of its unique red color, ease to work with, non-warping qualities, and resistance to rot.[31] Once the uses and benefits of redwood were fully realized, demand around the country began to grow, albeit cyclically. When demand was high, production would often over compensate and in-turn, cause a sharp decline in price. Sawmill owners large and small understood that they needed to expand current markets and create new ones to stay in business. A number of them banded together, pooling financial resources to form a 'joint Stock Company,' but less than a year later it failed.[32] This example demonstrates how due to the cyclical price of redwood, it was difficult for small mills to make ends meet when the market was low; consequently, only large timber companies survived the early years of logging.[33]

Harvesting redwood has never been an easy process, as it is often dangerous and difficult.[34] A tree was usually cut about two to three meters above the ground to ensure that none of the non-merchantable lumber associated with the large, buttressed bases made it to the mill.[35] After a chopper felled a tree, the branches were removed and the bark was peeled off. When this material dried out, it was set on fire to clear away debris that would otherwise hinder processing. After the trunk was sawed into several small logs, they were dragged out of the forest by a team of oxen to a skid road (Figure 3).[36] For the largest redwood logs, measuring five to six meters in diameter, the lumbermen would drill a hole into the center, deploy an explosives cartridge, and blast the log into quarter sections easier for oxen to move.[37] This practice of dragging logs across the forest floor commonly damaged the soil and lower trunks of residual trees.[38]

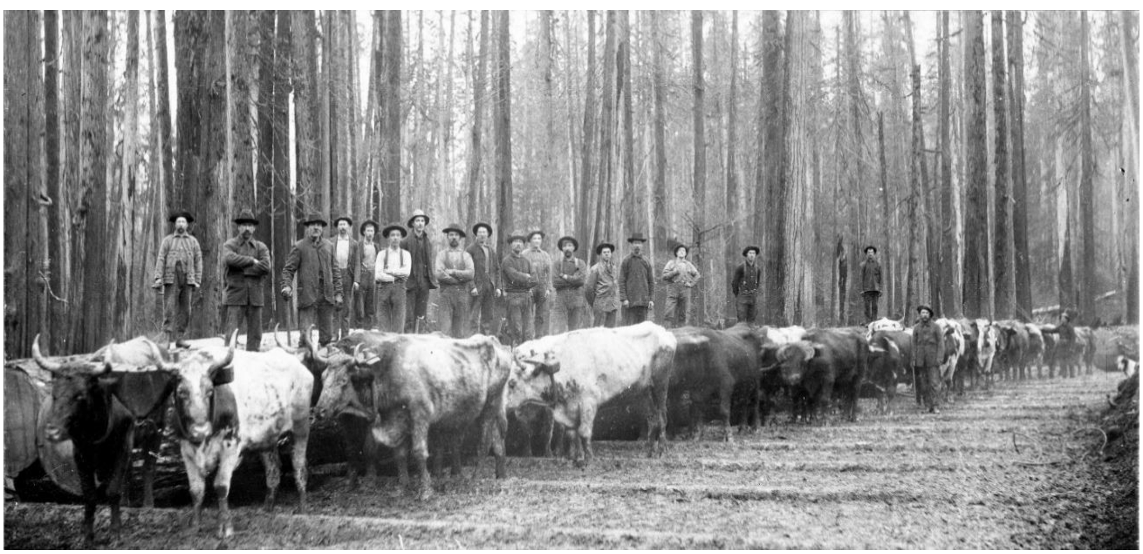

Figure 3. "Lumbermen pose with a team of oxen ready to yard logs out of the forest." Credit: Palmquist collection.[39]

Eventually, logging sites moved too far into the forest for oxen to be used and railroads had to be built. The first railroads (aka tramways or pole roads) were made of wood and built along ravines. They helped to extend the reach of timber harvesting farther into the forest.[40] Temporary dams were built on streams to collect the spring flood water where logs would be stored in the reservoirs created by the dam until it was time to transport them to the mill. When that time came, the dam was blown up with explosives, allowing the force of water to transport the logs down to Humboldt Bay.[41] Although logging technology was still in its infancy, in 1881 a Eureka, CA lumberman and inventor, John Dolbeer, revolutionized the timber industry with his new logging machine.

Figure 4. "Donkey steam engine logging a steep slope in Humboldt County." Credit: Ray Jerome Baker.[42]

The steam donkey, termed for its size and lack of horsepower, consisted of a boiler, a steam engine, and a winch that together could drag logs out of the woods faster than oxen (Figure 4). The winch also allowed for self-transportation up steep grades, making previously inaccessible timberlands harvestable.[43] Although there were no written records of lumber production until 1889, estimates based on the harvested hectarage indicate that 5,895,126 m^3 (2,498,213,317 board feet [one board foot measures 12 in x 12 in x 1 in]) of merchantable lumber were cut in Humboldt County between 1855 and 1888.[44] In the early 1900s, the steam donkey was upgraded with a high-line cable, launching a new method of timber extraction, termed high-lead yarding: logs would be dragged on one end while the other end was suspended in the air by a system of cables. With the advancement of railroads and technologies, logging of all trees on nearly all terrain became possible and eventually oxen teams went obsolete.

The earthquake that devastated San Francisco on April 18, 1906 and the resulting fires that engulfed approximately 24,000 structures pushed both the demand for and price of lumber to all-time highs.[45] Two days following the earthquake, with fires still burning, lumber was already being hauled in to rebuild the city. About 189 m^3 (80,000 board feet) of lumber was brought in to Golden Gate Park every day for the construction of outhouses and barracks. In the two weeks following the earthquake, 2,676 m^3 (1,134,000 board feet) of lumber was used to construct housing for 7,500 people.[46] To meet the demand for lumber, with redwood being preferred due to its fire-resistant qualities, logging companies increased the number of employees' daily work hours and operated mills on double time. In October 1906, the volume of redwood shipped to San Francisco was twice what it was in October 1905, a record-setting month in itself.[47]

The cut rate of redwood increased by an average of 1,179,869 m^3 (500 million board feet) per year from 1905 to 1929.[48] During that time, logging entered into a new era with the advent of the bulldozer and the Caterpillar tractor. Together, they built skid roads and could yard trees faster than any previous technologies and without any geographic limitations.[49] Waterways that were once impediments to logging could now be simply built over. For example, tractors could build a road across a stream by dropping logs across it and compacting dirt over the top, allowing for logging equipment to cross over (Figure 5).[50] Faster and more powerful lumber trucks were hauling logs to the mill in less time than ever before.[51]

Figure 5. “Pre-WWII tractor in the woods.” Credit: Boyle Collection.[52]

In August 1929, the U.S. entered the Great Depression. During those years, the annual cut rate of redwood fell to 318,565 m^3 (135 million board feet).[53] Mills were shut down and many people who relied on the forest, both directly and indirectly, lost their livelihoods. Many timber companies and land owners were unable to meet their financial obligations and as a result had to forfeit whatever holdings they had back to their respective creditors. Governments that had to take back land were eager to sell it off as fast as possible. One such example occurred during the early 1940s in Del Norte County when the Board of Supervisors was selling 4,407 hectares (10,000 acres) of forfeited land for $1.00 ($14.41 adjusted for inflation in 2019)[54] per 0.4 hectare (1 acre). Due to a typographical error, the land was actually advertised for $0.10 ($1.44 adjusted for inflation in 2019)[55] per 0.4 hectare (1 acre). The County did nothing to fix the mistake and sold the land off to local residents at this remarkably low cost. Some of these buyers turned around and sold their deeds to the timber companies for a nice profit.[56]

In 1945, the State Board of Forestry passed the California Forest Practice Act, requiring timber harvests to leave 10 seed trees per hectare (four per acre). Although this self-regulating Board of Forestry consisted of industry executives who theoretically had good intentions to create sustainable yield standards, ‘high-grading’ was a common practice and the residual seed trees were generally low-quality. Lumbermen didn’t want to take these low-quality trees to the sawmill anyway, as their meager profit would not justify the efforts and costs associated with felling and transportation, so it was not a considerable loss to leave behind a few seed trees.

Thus, when the thriving post-WWII housing industry created a boom for the timber industry, sustainable land management practices were a low priority.[57] In this era, demand for homes skyrocketed with the onset of the 'baby boomer' generation and advances in logging technology made fulfillment of those demands possible. Although in 1947 many tracts of old-growth redwood forest still existed, redwoods were felled throughout the 1950s three times faster than any year prior to 1950, with a peak annual cut of over 2,359,737 m^3 (1 billion board feet)[58] occurring in 1958.[59] As forests were being rapidly harvested with minimal consideration for regeneration, the repercussions for not developing sustainable land management practices became clear (Figure 6). At a 1949 redwood logging conference, California's Director of Natural Resources Warren T. Hannum stated:

> We have approximately 3,000,000 acres of cutover land that is practically idle and not producing any new forest. It was once our best timberland and could have been producing 1.5 billion board feet annually had foresight been exercised and suitable measures taken to maintain adequate production. We are still too apathetic toward fire; many good seed trees that could have been logged in another 20 years is destroyed by slash fires. We create too much waste in the redwood belt and we need to find economical uses for residual waste.[60]

Figure 6. “Clear cut hillside, train on trestle loaded with logs.” Credit: Palmquist collection.[61]

The expansion of the logging industry and increasing population greatly contributed to the emergence of the conservation movement. Americans were once again seeking to expand their horizons and they found this in the form of outdoor recreation. A surge in automobile ownership during the 1950s and the expansion of the National Highway System in 1955 allowed families to travel to never-been-before places[62] such as the redwood forest. They expected to see wild landscapes and hear the sounds of the natural world but instead they saw logging trucks and heard chainsaws.[63] These experiences greatly contributed to the emergence of the conservation movement and increased opposition to logging.

EARLY REDWOOD CONSERVATION EFFORTS

Two of the earliest attempts to create a redwood state park were made by Henry A. Crabb of the California Legislature in 1852 and Secretary of the Interior Carl Schurz in 1879. Due to a lack of public support their efforts were unsuccessful. Finally, through efforts made by the Sempervirens Club and a passionate environmentalist named Phoebe Hearst, Big Basin Redwoods State Park was established in 1902 in Santa Cruz County.

In 1918, Save the Redwoods League (hereafter, the League) was formed by a trio of individuals who wanted to purchase old-growth redwood forests and create redwood parks for recreation and preservation. They advocated for the State of California to use taxpayer dollars to match funds the League acquired through private donations to purchase redwood forests for public enjoyment. Throughout the 1920s, three Redwoods State Parks were founded thanks to efforts made by the League: Prairie Creek (1923), Del Norte Coast (1925), and Jedediah Smith (1929).[64] Land owners played a key role in the development of the Parks by selling tracts of their land to the League.

One of the first concepts of a national park for redwoods was made by an early member of the Sierra Club in 1895. When the idea was pitched six years later in 1901 to the ‘Conservation President’ Theodore Roosevelt, he took no action to create a park but stated he was concerned over the redwoods’ eventual fate. In 1908, the first federal park dedicated to preserving redwoods was established at Muir Woods in Marin County.[65] Two other recommendations for a redwood national park were made to Congress, one in 1920 and the other in 1946, but these efforts were unsuccessful.[66] Then, in April 1963, the National Geographic Society funded a study, *The Redwoods: A National Opportunity for Conservation and Alternatives for Action*. The study was led by the National Park Service and the goal was to find the most effective way to preserve redwood forests for public recreation and enjoyment.[67]

On September 15, 1964, findings from *The Redwoods* were released. It approximated that of the original 809,371 hectares (2,000,000 acres) of old-growth redwood forest, only 303,514 hectares (750,000 acres) remained, and that of this remaining hectarage, only 121,405 hectares (300,000 acres) were untouched by commercial timber operations with only 19,580 hectares (48,383 acres, roughly 2.5% of the original forest) preserved in state parks.[68] The report estimated that if a federal park were created, revenues generated by rougly 1.2 million annual visitors would mitigate economic losses potentially realized by local timber communities. There was also mention of a prospective land trade between affected timber companies and the federal government.[69] The report concluded it was of national interest to immediately preserve old-growth redwood forests in the form of a national park for enjoyment by future generations.[70] While the 'national enthusiasm' for a redwood national park was overwhelming, there nevertheless were opponents, largely members of the timber industry and would-be affected communities. As such, a heated controversy developed between supporters and adeversaries as options to preserve the remaining old-growth redwoods were explored.

THE FIGHT FOR A REDWOOD NATIONAL PARK

Upon release of *The Redwoods* report, conflict arose among neighboring communities in northern California about the headquarters location for the proposed park. McKinleyville lobbied to be the headquarters location due to its close proximity to both Humboldt State University and commercial aviation. Orick competed for the headquarters location as the small timber-based town hoped this attraction would bolster their economy. Klamath argued to host the location as it would complement the new town being built along the Klamath River. Crescent City wanted the location because their town would be the terminal point of the ‘Yellowstone-to-the-Redwoods’ project, if it were to be realized; this idea was for a national scenic highway connecting Yellowstone National Park to a redwood national park.[71] The one thing all communities unanimously agreed upon was the economic downturn that would surely hit their communities following park establishment.

Five timber companies were slated to have land fedearlly annexed for the creation of the park: 1) Arcata Redwood Company, 7,284 hectares (18,000 acres); 2) Georgia-Pacific, 5,463 hectares (13,500 acres); 3) Pacific Lumber Company, 1,619 hectares (4,000 acres); 4) Rellim (Miller) Redwood Company, 1,821 hectares (4,500 acres); and 5) Simpson Timber Company, 4,047 hectares (10,000 acres). The plan was for approximately 25,269 hectares (62,440 acres) of timberland, including 13,549 hectares (33,480) of old-growth, to be withdrawn from these five companies, a few other landowners, and Prairie Creek Redwood State Park; these lands would then be preserved in a national park for redwoods.[72]

At the center of the controversy between government-backed conservationists wanting to establish a park and the timber industry wanting to keep harvesting trees was Orick, a small community centered around logging. Many local residents argued that Orick would be in financial ruins if the federal government annexed the surrounding private timberlands. In response to *The Redwoods*, K.F. Laudenschlager, Comptroller of the Arcata Redwood Company, gave a presentation on October 1, 1964 and stated:

> It [*The Redwoods*] is a masterful presentation illustrated in color; a genuine work of art climaxed by the discovery of some unusually tall trees on our property. This piece of colossal bad luck is the appealing peg on which the whole proposal is hung. We have old-growth timber which will last our company 44 years at the present rate of cutting, plus an indefinite period of life on young growth. I hope to convince you that this move is totally unnecessary and to urge each of you to take action in order to prevent this land grab.[73]

The Arcata Redwood Company was the main employer and driver of the local economy, paying $350,000 ($2,926,849 adjusted for inflation in 2019)[74] in taxes annually. Laudenschlager rebutted the idea of a possible land trade with the government saying that it “would amount to robbing Peter to pay Paul.” He argued some mill operators would lose their log supply and that the U.S. Forest Service was unlikely to willingly give land holdings to the Department of the Interior for a redwood national park. Six Rivers National Forest owned 5,666 hectares (14,000 acres) of old-growth redwood forest along the Klamath River, and *The Redwoods* report was unclear about what specific federal land would be traded for inclusion in the national park. In response to the idea that 1.2 million tourists would fill the tax gap, Laudenschlager countered that tourist dollars would not drive economic development to the same degree as local communities, as "tourists don't make major purchases or spend close to 100% of their paychecks locally."[75] The next day during a presentation to the Orick Chamber of Commerce, Arcata Redwood Company comptroller L.J. Chapman stated that 52.6% of the Orick Elementary School budget came from their company. He argued that national parks don't pay taxes and therefore a substantial hole would open up in the community's budget.[76] Local governments echoed the concern of tax revenue losses and felt they should be compensated for it.

The Humboldt County Board of Supervisors stated in their response to *The Redwoods* that "serious consideration should be given by the Federal Government to some sort of in lieu tax…we are not only talking about the tax base of county government but of schools." The Board had a vision of what the long-term economic and social repercussions would entail. Their statement went on to say:

> As the interim report points out, the economic picture in Humboldt County is not bright (pp. 37 & 50). Any Federal land acquisition could compound this situation as to jobs, industry, and tax structure. The result could be a new pocket of poverty, precisely the type of thing that the Federal Government is now trying to combat…and it could result in new Federal expenses and responsibilities in combating future conditions in Humboldt County.[77]

The Del Norte County Board of Supervisors sent a letter to President Lyndon B. Johnson on October 5, 1964 informing him of the economic downturn that was sure to hit the regional timber communities if a national park were created. They also wrote that the Secretary of the Department of the Interior, Stewart Udall, "is not exercising the leadership necessary for the responsibility he holds. He is exercising socialistic tactics to gain a Government land grab of private property with no regard for private enterprise or for private industry." The Board went on to say that the "methods of data collection were biased and unfair."[78] Their concerns were soon supported by industry analysts who agreed the methods and facts stated in the report were not well-founded. The Northern California Section of the Society of American Foresters reviewed *The Redwoods* with its members and National Park Service officials. When comments were issued in November 1964, the Society stated:

> The report does not provide even the minimum factual basis essential for serious study as to whether or not the long-time public interest would be best served by the establishment of the proposed park. Redwood is not a vanishing species as the report implies on pages 17, 33 and elsewhere. Generalized statements on the ecology and growth of redwood are incomplete and misleading. The economic analysis portion of the report is erroneous, admittedly incomplete, and failed to consider many of the important aspects which are involved.[79]

Some argued that friction among the public, government, conservationists, and industry could be eased if an alternative park were created. The oldest conservation group in the U.S., the American Forestry Association, called for an alternate park that would provide both a sustainable yield operation and places for people to recreate. The redwood timber industry financed their own report, the *Redwood Park and Recreation Plan*, which proposed an alternate park that balanced land use for both recreation and industry (Figure 7).[80] Sonoma State College professor, botanist, and ecologist Dr. Kenneth Stocking stated that the timber companies should try to "control the park's intelligent development rather than fight it."[81] He further argued that the costs to acquire the proposed park lands could be used to reforest agriculture lands that were once productive redwood forests.

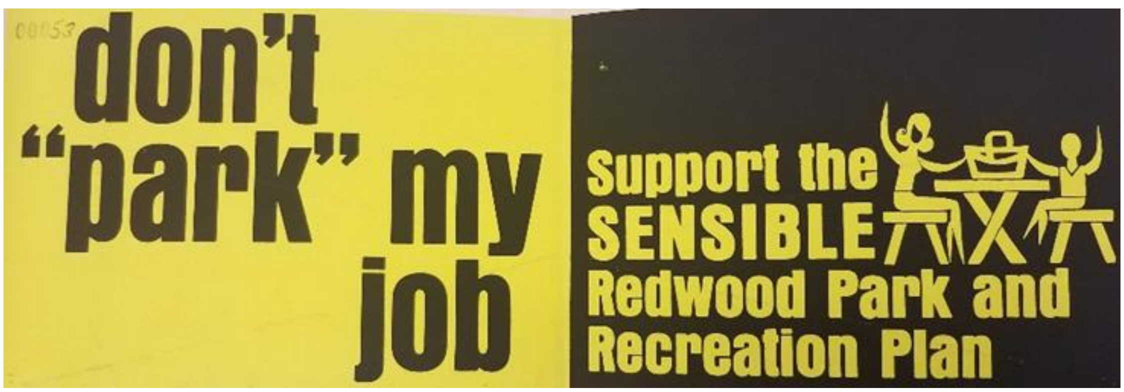

Figure 7. Bumper sticker advertising the timber industry's alternate plan, the *Redwood Park and Recreation Plan*.[82]

In addition to these tensions surrounding the effects of a national park on the local economy, there were also feelings of maliaise concerning the annexation of lands to form such a park. In September 1968, The Times-Standard, a local newspaper based out of Eureka, CA, featured a Yurok family's 120-acre property on the south spit of the Klamath River. The land was originally deeded to the family by the U.S. Calvary and by President Grover Cleveland. Later in 1907, President Theodore Roosevelt renewed the title. When the family learned that the proposed annexation included their land, they charged California Congressman Don H. Clausen as responsible. In his defense, Congressman Clausen explained that the clandestine move was made during a House-Senate conference without his prior knowledge.[83] Despite this, lawmakers and conservationists proceeded with efforts to create a redwood national park.

REDWOOD NATIONAL PARK IS ESTABLISHED (AND EXPANDED)

In the 1960s, President Lyndon B. Johnson strongly supported the establishment of RNP. In his 1965, 1966, 1967, and 1968 messeages on conservation affiars, he asked Congress to take action toward this goal. And, in his internationally broadcasted 1968 State of the Union address, he also voiced this support.[84] Even after his messages to Congress, old-growth redwood stands continued to be harvested, causing great concern among the public, government, and conservationists. In 1966, Secretary of the Department of the Interior, Stewart Udall, asked the five timber companies owning lands proposed for the annexation to agree to a logging moratorium on these lands. The president of Rellim Redwood Company, Harold Miller, initially refused to comply with Secretary Udall's request, and only abided after receiving a presidential appeal.

On September 19th, 1968, the Redwood National Park Conference, led by Senator Henry M. Jackson of Washington, presented the final text of bill S.2515. In his presentation of the bill's reallocation of land to form RNP, Senator Jackson sought to equally address the interests of logging companies, conservationists, and consumers.[85] Senators at this conference understood the extensive impacts that this'legislative taking,' when the federal government pays 'just compensation' to acquire lands, would have on timber companies, communities, and economies. A congressional agreement was reached for the park acquisition to be fixed at 23,472 hectares (58,000 acres) and a cost of $92,000,000 ($685,647,101 adjusted for inflation in 2019).[86] On October 2, 1968

President Johnson signed S.2515 into law and for the first time in U.S. history, ‘legislative taking’ of private land occurred.[87]

Immediately after the signing, Arcata Redwood Company, Georgia-Pacific, and Simpson Timber Company began harvesting their remaining tracts of old-growth within the Redwood Creek watershed, lands upslope of the soon-to-be Redwood National Park. The Sierra Club had repeatedly asked Secretary Udall to expand the proposed boundaries of RNP to include these upslope lands, but these requests had not been granted. As such, even though the new park would protect a 0.4 km-wide land strip on either side of Redwood Creek (‘the Worm’), the above hillsides were still free to be clearcut, creating substantial ecological problems in the watershed.

Thus, after RNP was established, conservationists lobbied to expand timber regulations to the vulnerable privately owned hillsides adjacent to the park ‘Worm.’ As popularity for environmentalism and ecological sustainability increased nationwide, activists and local communities pressured federal and state legistlation to stop destructive forestry practices. In an article titled “The Second Battle of the Redwoods,” the author describes tourists in the serene majesty of RNP being hauntingly dismayed by the sounds of chainsaws and falling timber on adjacent lands owned by timber companies.[88]

Many conservation groups including Save the Redwoods League and the Sierra Club invested time and money attempting to acquire additional land and stop forest harvesting on RNP-adjacent lands. In section 2a of S.2515, the Secretary of the Interior was given authority to modify RNP boundaries to “minimiz[e] siltation of the streams, damage on the timber, and assur[e] the preservation of the scenery within the boundaries of the national park as depicted on said maps”.[89] To move forward with RNP expansion under this guide, conservation groups pooled resources to study the effects of logging on RNP water quality, erosion, plant and animal biodiversity, forest health, and scenery aesthetics. In turn, timber companies retained Winzler and Kelly Consulting Engineers to conduct the same research from their perspective. Though the data gathered from both projects was similar, the conclusions were opposite. Upon the presentation of both sets of findings, the California Board of Forestry recruited an outside perspective. Henry A. Froelich of Oregon State University reviewed both party’s data and concluded that no significant damage to any of the above factors could occur due to clearcuts. This professional assessment ended a many-year campaign to expand RNP boundaries.

The Department of the Interior claimed that timber harvests on adjacent private lands did not jeopardize RNP. To back up this claim, they ordered two new studies of the Redwood Creek watershed. When completed in 1972 and 1973, both studies recommended a 244 meter (800 feet) no-harvest buffer zone around RNP and federal protection of the Redwood Creek watershed. These recommendations were not heeded by the Nixon Administration and the reports were never publicized.[90] Although conservationists perceived this legislative apathy as a major setback, the courts were full of environmentalist victories.

One of those victories was *Bayside Timber v. San Mateo County*, 1971. Bayside Timber, a logging company, wanted to build a road connecting its timber stands to a state highway in San Mateo County. The San Mateo Board of Supervisors declined the permit on the grounds of increased risk of watershed damage. Bayside sued and the case went to court where the permit was declined again. The California Court of Appeals ruled in favor of the Board of Supervisors, deeming the 1945 Forest Practice Act unconstitutional due to the fact that the Board of Forestry was made up of timber industry executives, a notable conflict of interest.[91] Rebutting this view, the North Coast Timber Association stated in a January 1972 memo that the State legislature "wisely decided in 1945 that the industry itself could best determine what practical actions should be taken to leave the land in a productive condition after logging and to prevent present and future forest crops from destruction."[92] The timber industry was dealt a major setback when this era of self-regulation ended and conservationists could use the legal system to their advantage.

Further support for conservation in forestry came in January 1973 when California passed the Z'Berg-Nejedly Forest Practice Act. With it came a set of Forest Practice Rules created to assure that "maximum sustained production of high-quality timber products is achieved while giving consideration to values related to recreation, watershed, wildlife, range and forage, regional economic vitality, employment, and aesthetic enjoyment."[93] Private timber companies were now required to complete a Timber Harvest Plan (THP), which would be reviewed by multiple agencies, before harvesting any timber on their land and private citizens were allowed to review those plans.

This new law was well-received by the Sierra Club, Governor Ronald Reagan, and the forest industry. Feeling pressure from a Sierra Club lawsuit, the National Park Service requested stricter enforcement of the new Forest Practices Law and water quality standards in the Redwood Creek watershed. Their requests were denied and permits for logging in the watershed continued to be issued through 1974. As a result of *Bayside Timber v. Board of Supervisors*, on January 19th, 1975 the State Supreme Court ruled the new Forest Practices Act was subject to the recently passed California Environmental Quality Act (CEQA). This Act required the Board of Forestry to amend and more strictly enforce logging regulations for increased timber sustainability. The following year, the First District Court of Appeal, Division 2 ruled in *Natural Resources Defense Council, Inc. v. Arcata National Corp.*, 1976 that THPs are projects under CEQA[94]. Because projects are discretionary actions by a government agency that will cause direct or indirect environmental impacts, they require multi-agency reviews and cumulative impacts analyses.

In January 1977, President Jimmy Carter was sworn into office and his pledge for governmental environmental stewardship was quickly acted on by the Sierra Club. An Act to extend the boundaries of RNP was introduced in February and subsequent hearings took place in April. The fears of another economic downturn were realized when the Department of the Interior stated that 1,000 jobs would be lost (the timber industry estimated 2,000) in Humboldt County where unemployment already ranged between 14 and 18%. In an effort by the North Coast Timber Association to gain nationwide support against RNP expansion, a convoy of 23 logging trucks, led by a truck carrying a nine metric-ton redwood log carved as a peanut (Figure 8), left Eureka and headed for Washington, D.C. On May 23, while President Carter delivered his environmental message to Congress,[95] the logging truck convoy drove by the U.S. Capitol with a sign attached to the peanut-log that read “It may be peanuts to you, but it’s jobs to us.”[96] The peanut-log was a gift for the president, which The White House turned down, and was in reference to Carter’s upbringing as a peanut farmer in Georgia.

Figure 8. A nine metric-ton redwood log carved as a peanut loaded on a flatbed semi-trailer with a sign reading, “It may be peanuts to you, but it’s jobs to us.” Credit: Associated California Loggers.[97]

The Office of Management and Budget also opposed the proposed RNP expansion as this would become the most-costly land acquisition in history, costing taxpayers an estimated $359 million ($1,426,810,418 adjusted for inflation in 2019)[98] for 19,425 hectares (48,000 acres). Nevertheless, Americans overwhelmingly supported the Act and after many debates, testimonies, and hearings, on March 27, 1978 President

Carter signed The Redwood National Park Expansion Act, thereby enacting Public Law 95-250.[99] The law enlarged RNP boundaries to include the entire Redwood Creek watershed, ridge to ridge, to protect resources from damage resulting from upstream and upslope land use activities. Furthermore, a small piece of legislation within this Act provided the foundation for all future restoration efforts in RNP:

> (6) In subsection 3(e)…the Secretary, in consultation with the Secretary of Agriculture, is further authorized, pursuant to contract or cooperative agreement with agencies of the Federal Executive, the State of California, any political or governmental subdivision thereof, any corporation, not-for-profit corporation, private entity or person, to initiate, provide funds, equipment, and personnel for the development and implementation of a program for the rehabilitation of areas within and upstream from the park contributing significant sedimentation because of past logging disturbances and road conditions, and, to the extent feasible, to reduce risk of damage to upstream areas adjacent to Redwood Creek and for other reasons…

Sec. 104 (b) stated that RNP must submit a comprehensive general management plan to the Committee on Interior and Insular Affairs of the House of Representatives, and to the Committee on Energy and Natural Resources of the Senate by January 1, 1980 that would include:

> (1) the objectives, goals, and proposed actions designed to assure the preservation and perpetuation of a natural redwood forest ecosystem;
> (2) the type and level of visitor use to be accommodated by the park, by specific area, with specific indications of carrying capacities consistent with the protection of park resources;
> (3) the type, extent, and estimated cost of development proposed to accommodate visitor use and to protect the

> resource, to include anticipated location of all major development areas, roads, and trails; and
> (4) the specific locations and types of foot trail access to the Tall Trees Grove, of which one route shall, unless shown by the Secretary to be inadvisable, principally traverse the east side of Redwood Creek through the essentially virgin forest, connecting with the roadhead on the west side of the park east of Orick.[100]

In 1994, Humboldt Redwoods State Park, Prairie Creek Redwoods State Park, Del Norte Coast Redwoods State Park (RNSP), and RNP merged into one cohesive unit, Redwood National and State Parks, to be cooperatively managed. In 2002, Save the Redwoods League purchased the Mill Creek watershed (north of the Redwood Creek watershed); in 2005 they donated the land to Del Norte Coast Redwoods State Park, thereby expanding RNSP boundaries by 10,117 hectares (25,000 acres) to a total size of 53,412 hectares (131,983 acres).[101, 102] All four parks follow the same management guidelines for natural and ecocultural resources, with lands divided into 11 management zones.

MODERN IMPLICATIONS

Because many of the forests acquired in RNSP were previously industrial timberlands, much of the RNSP consists of dense second-growth redwood forests with unnaturally high representations of Douglas-fir (largely from aerial seeding following clearcut harvests). Low tree vigor and low biodiversity are the results of these overly dense conditions in RNSP. Forest managers at RNSP have therefore utilized many different restoration treatments over the last 40 years, encouraging restoration on other state and federal lands as well. One of the first projects following the 1978 expansion was a large-scale thinning treatment across several 25-year old stands. The objectives were to increase redwood dominance by removing Douglas-fir and to reduce overall stand densities. Following these treatments, stands were still above desired densities, and even though Douglas-fir representation was reduced to roughly 40% of all trees, greater redwood dominance was still needed to regain historical stand composition.[103] In the 1990s and 2000s, similar thinning treatments were replicated across RNSP lands.

In 2017, RNSP experimented with a more holistic approach to forest restoration using variable density thinning (Carey, 2003). This treatment creates a mosaic of varying tree densities across the landscape to mimic natural mortality patterns and create suitable wildlife habitat. Interestingly, RNSP negotiated an arrangement where excess biomass (predominantly Douglas-fir) generated from thinning operations was awarded to contractors to help finance the costs of restoration. This project highlights the potential for private industry and the federal government to work together in mutually beneficial ways.[104] Coming full circle, this working relationship also reflects what proponents of the *Redwood Park and Recreation Plan* had envisioned decades earlier: a dual use of land for preservation and perpetual timber extraction. Another RNSP restoration project involves decommissioning1,046 kilometers (650 miles) of failing logging roads. Approximately 402 kilometers (250 miles) have been restored since 1978, but another 161 kilometers (100 miles) of high-priority road removal still exists. The cost of logging road restoration is costly, ranging from about $128,747 to $643,736 per kilometer ($80,000 - $400,000 per mile).[105]

Redwoods Rising, a collaborative effort between RNSP and Save the Redwoods League, is trying to finance these expensive restoration projects by pooling resources, federal and state budgets, and private donations. Their goal is to raise $120 million by 2022 to further restoration of second-growth redwood stands impaired from past disturbances and to acquire additional redwood forests for protection. To accomplish the restoration goals, they will provide support needed to foster healthy watersheds and streams, create suitable wildlife habitat, and remove invasive species.[106] These collaborative efforts among all stakeholders will help to accelerate the development of old-growth characteristics in impaired redwood forests.

As anticipated, in the years following the creation of RNP, the logging community of Orick experienced a remarkable loss of livelihood. Located one mile south of town, the Freshwater Spit had been a popular recreation location for RV-goers, campers, and local commercial fishermen. Money spent by these groups provided the

Orick community with much-needed revenue after the collapse of the logging industry. However, in the summer of 2001, the National Park Service closed the Spit, deeming it environmentally hazardous to have people camping on ecologically fragile land, and consequently that revenue disappeared. Additionally, in the early 2000s commercial fishing permits were no longer being issued or renewed by the National Park Service, thereby ending another local livelihood. In July 2001, the community hosted an event, the Freedom Rally, to build support against federal land closures like what happened at the Freshwater Spit. Confirming their sense of minimal importance, they had hoped this event would attract a few thousand people, but only about 200 people attended.[107] With minimal employment opportunities related to resource extraction, this tiny logging town suffers from a depressed economy; the 2017 median household income in Orick, $37,500, was far below the county ($43,718), state ($67,169), and national ($57,672) medians.[108]

In addition to RNSP restoration efforts, legislators have recently proposed federal bills to revive traditional indigenous land management practices on state and federal park lands. Agencies such as the U.S. Forest Service and National Park Service are earnestly trying to incorporate indigenous governance in public land management programs. By advocating for the cultivation and maintenance of plants important to indigenous people, agencies can protect and preserve valuable ecocultural resources.[109] Since European settlement, the indigenous tribes of the redwood region have continuously sought to preserve their spiritual, cultural, physical, and ancestral connections to the land. From the expansion of reservations and the continuation of sacred traditions such as basketry, indigenous peoples of this area have strived to regain sustainable management of their ancestral homeland. Tribal council websites for the Yurok and Karuk show their continued commitment to sustainable land stewardship via publications of their own management plans and programs.[110,111]

As a recent bill proposed by Representative Jared Huffman, the Yurok Land's Act of 2019, requires continued cooperation between federal, state, and tribal agencies[112] and continued access to park lands for research, these tribal management plans provide important indigenous perspectives to be included in RNSP management policies moving forward. Continued access to RNSP lands for research like the scientific study presented in the second chapter of this thesis is essential for adaptive and effective forest management. Future use of holistic, multidisciplinary forest science to examine management effects on forest productivity, biodiversity, and ecocultural resources, could assist management practices that support the interests of indigenous peoples, conservationists, scientists, timber companies, and local communities.

CHAPTER 2: EFFICACY OF FOREST RESTORATION TREATMENTS ACROSS A 40-YEAR CHRONOSEQUENCE AT REDWOOD NATIONAL PARK

INTRODUCTION

Although the iconic coast redwood (*Sequoia sempervirens* [D.Don.] Endl.) is currently restricted to a narrow natural range along the coast of northern California and southern Oregon, ancestors of this species were once dominant and widespread around the Northern Hemisphere. The most ancient redwood clade fossils are from northern France and northeastern China and date back 146 million years to the Jurassic era (Fliche and Zeiller, 1904; Endo, 1951; Scott et al., 2016). Redwood first showed up in the North America fossil record approximately 66 mya in Wyoming, 58 mya in Nevada and Idaho, and 24 mya in Oregon (Noss, 2000). Coast redwood has been in California for approximately 20 million years, although approximately 1 myr ago advancing ice sheets reduced this species to its current range – a thin belt along the coasts of northern California and southern Oregon (Dewitt, 1982).

Within this restricted range, redwood persistence has been threatened by numerous factors. Soon after European settlement in California, redwood became prized for its giant size and rot-resistant, red heartwood and commercial logging began in 1856 (Nixon, 1966). Following redwood harvests, eradication methods such as repetitive burning and grass-seeding were used to convert prior forestlands to grasslands for ranching and farming (Dewitt, 1982), further reducing redwoods' range. Due to over 150 years of commercial logging and ranching, today less than 5% of the original old-growth redwood forest remains (Noss, 2000; Sillet and Van Pelt, 2014). Further, redwood's narrow range restricted to the foggy coast is vulnerable to climate change, as over the last century, the frequency of summer fog, an important water input, has reduced by 33% (Johnstone and Dawson, 2010), and over the last 50 years, mean temperature has increased by approximately 0.5º C (Koopman et al., 2014). There is therefore a need to restore the current matrix of young second-growth stands surrounding the few remaining old-growth patches to serve as habitat corridors for wildlife and act as buffers against forest edge effects (O'Hara et al., 2010).

Compared to old-growth redwood forests, second- and third-growth forests, typically established after industrial timber practices, support unnaturally high tree densities, low redwood dominance, low biodiversity, and relatively low tree vigor (Teraoka and Keyes, 2011). Due to this shade-tolerant forest type, exceptionally high tree densities can preclude the development of old forest features for decades (Veirs and Lennox, 1982; Thornburgh et al., 2000). It is therefore important for land managers to use active restoration techniques in overly dense second-growth stands to accelerate natural thinning, improve forest health, and promote the development of old-growth characteristics. While the re-introduction of fire has the potential to return lands to historical conditions, prescribed burning is often not a feasible option due to numerous logistical, bureaucratic, and political barriers (Berrill et al., 2013) as well as increased annual precipitation over the last century (Woodward et al., 2020), and relatively wet fuel loads in this forest type. Alternatively, forest managers can use thinning to prevent stand stagnation (Oliver and Larson, 1996; O'Hara et al., 2010) and increase forest biodiversity, the latter a fundamental guiding principal for ecologically sustainable forest management (Carey, 2003; Larsson and Dannell, 2010; Lindenmayer and Franklin, 2002).

Redwood National Park (RNP) is centrally located within redwood's range and is comprised of over 20,000 ha of second-growth forests (Sarr et al., 2004), the majority in need of active restoration. Annexed in 1968 and 1978, these lands were largely impaired due to former use as industrial timberlands (Teraoka and Keyes, 2011). Since annexation, these lands have been largely unmanaged and today exhibit a high degree of even-aged trees with homogenous stand structure, and a disproportionate amount of Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) and tanoak (*Notholithocarpus densiflorus* [Hook and Arn.] Manos, C.H. Cannon, & S. Oh) (Chittick and Keyes, 2007). In 1978, RNP began actively managing the second-growth trees to rehabilitate the inherited impaired ecosystems.

For over 40 years, RNP has sought to use restoration to accelerate the development of old-growth conditions in second-growth forests (Chittick and Keyes, 2007) and in 1999 this goal became formally included in the Redwood National and State Parks' General Management Plan (California State Park and Recreation Commission and Service, 2000). As such, since 1978 there have been numerous restoration treatments implemented across the park. Notably, in 2017 RNP conducted a variable density thinning (VDT) trial experiment across 22 ha on Holter Ridge (Figure). On this same ridge, earlier thinning treatments were conducted in 1978 (Veirs and Lennox, 1982) and 2009 (Teraoka, 2012). Thus, although RNP has been investigating the effectiveness of thinning prescriptions to restore second-growth forests for decades, circumstances such as climate change, increasing catastrophic wildfires, forest pathogens, and urban development highlight the need to increase the scale of these practices (Burns et al., 2018).

Given the resource-intensive costs of forest restoration, it is important to monitor the efficacy of treatments to improve adaptive management efforts (Teraoka, 2012). Growth (Kerhoulas et al., 2013; King et al., 2013) and, less commonly, physiology (Skov et al., 2004) are two ways to evaluate and monitor forest responses to management treatments. Growth is often evaluated using tree-rings to measure radial increments and basal area increments (BAI); these metrics can also be calculated using repeated diameter measurements. While most investigations of forest tree responses to treatments rely on breast height diameter growth (Skov et al., 2005), this growth-based approach can take approximately four years to detect (Roberts and Harrington, 2008; Dagley et al., 2018) and can fail to detect a response if newly available carbon is allocated to fine roots, leaf area, or sugar reserves rather than to diameter growth. In complement to long-term growth-based evaluations, physiological measurements such as water potential (Ψ) and stomatal conductance of water vapor (g_s) can provide useful information about shorter-term tree responses (Skov et al., 2004). Predawn Ψ (Ψ_{pd}) is a surrogate for plant available water and represents the most hydrated daily status, while midday Ψ (Ψ_{md}) represents the most stressed daily water status.

Plants exchange gases through stomata. Photosynthesis involves CO_2 uptake through these stomata and is positively correlated with the rate of water transpired out of these pores. Thus, g_s measurements can serve as a proxy measurement for photosynthesis. Physiological measurements also have the potential to identify adverse initial responses to thinning, 'thinning shock' (Harrington and Reukema, 1983), which could be useful information when formulating prescriptions and predicting short- and long-term forest responses. Despite these appeals, physiological measurements can be time consuming to conduct and require specialized equipment and skills. Unsurprisingly, few studies have investigated leaf-level physiological responses to restoration. Given the lack of published measurements of redwood physiology in these forest types, knowledge about redwood physiology in suppressed forests would provide useful baseline data for long-term monitoring of forest responses to treatments.

Fostering healthy understory vegetation (e.g., forbs, grasses, and shrubs) supports wildlife diversity, as these plants provide essential food sources and habitat for animals. Under closed canopies, understory vegetation is minimal and can take decades to re-establish as it requires increased light originating from the formation of canopy gaps (Oliver and Larson, 1996). In Pacific Northwest forests, although herbaceous understory cover can initially increase following treatments, these responses are often short-lived and can frequently cause vegetation to shift towards shrub dominance (Cole et al., 2017;

Goodwin et al., 2018). Furthermore, while thinning can accelerate the development of old-growth conditions capapble of supporting a wide array of animals, the short-term loss of understory vegetation following thinning operations can reduce reduce wildlife diversity (Hayes et al., 1997; Carey, 2003). More specifically, treatments such as VDT that increase stand heterogeneity seem particularly effective at creating suitable habitat for a variety of fauna (Carey, 2003; Verschuyl et al., 2011). As such, silvicultural treatments such as low thinning and VDT are often used in forest restoration treatments (Carey, 2003; Teraoka and Keyes, 2011). Low thinning treatments remove smaller trees and retain larger trees, while VDT treatments increase spatial variability by creating a mosaic of different tree densities across the landscape. Although low thinning has been a popular prescription, investigations indicate that VDT is a more effective approach to holistic forest restoration (Carey, 2003) and the use of VDT is becoming increasingly widespread (Chittick and Keyes, 2007; O'Hara et al., 2010).

In this study I examined physiological, growth, and biodiversity responses to restoration treatments applied across a chronosequence of sites in RNP that range in years-since-thinning from 40 to 1, as well as untreated sites to serve as a control. To improve our understanding of ecosystem-scale responses to restoration treatments, I investigated three questions and hypotheses. First, does treatment affect redwood physiology (Ψ and g_s), and if so, how persistent are these responses? I hypothesized that in response to thinning, redwood Ψ would decrease due to greater evapotranspirational water losses, redwood g_s would increase due to greater light availability, and that these responses would decrease with time-since-treatment. Second, does treatment affect tree growth (as measured by BAI), and if so, and how long does this response persist? I hypothesized that thinning would increase growth, that this increase would be delayed a few years following treatment, and that this response would be relatively short-lived due to quick canopy reclosure in this temperate forest. And finally, does treatment affect biodiversity, and if so, how persistent are these responses? I hypothesized that while treatments increase understory plant diversity due to increased light availability, wildlife diversity would be slow to respond due to the loss of understory vegetation resulting from thinning operations.

MATERIALS AND METHODS

Study Site and Design

The coast redwood range extends approximately 724 km along the Pacific Ocean from southwestern Oregon to Monterey County, CA (Stuart and Sawyer, 2001). Centrally located within redwood's range, this study occurred approximately 13.2 km east of Orick, CA, USA on the top of Holter Ridge in RNP. This region has a Mediterranean climate with cool, wet winters and warm, typically rainless, foggy summers. Based on 1981-2010 climate data at the Orick Prairie, CA Weather Station, the average annual temperature and average annual precipitation are 10.6º C and 168.6 cm, respectively (NOAA: https://www.ncdc.noaa.gov/cdo-web/datatools/normals).

Historically an upland coast redwood old-growth forest (Veirs, 1986), Holter Ridge now consists of dense, second-growth stands largely dominated by Douglas-fir and supporting low biodiversity (Chittick and Keyes, 2007). In 1978, RNP experimentally thinned several 25-year-old second-growth stands on Holter Ridge with goals to reduce competition for residual trees, promote redwood dominance, and increase biodiversity (Veirs and Lennox, 1982). In 1978, average stand density on Holter Ridge averaged 2,400 stems ha^{-1} with some stands having 7,400 stems ha^{-1} (Veirs, 1986; Chittick and Keyes, 2007). For comparison, stand density in redwood-dominated old-growth stands typically ranges from 25 to 90 trees ha^{-1}, with a minor representation of Douglas-fir (typically 3 to 10 trees ha^{-1}) (Chittick, 2005). Other less common tree species found in the

Holter Ridge area include western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.), tanoak, and Pacific madrone (*Arbutus menziesii* [Pursh.]). The understory vegetation is comprised mainly of evergreen huckleberry (*Vaccinium ovatum* [Pursh.]), red huckleberry (*Vaccinium parvifolium* [Sm.]), salal (*Gaultheria shallon* [Pursh.]), rhododendron (*Rhododendron macrophyllum* [D.Don], and sword fern (*Polystichum munitum* [Kaulf.] C. Presl) (Veirs, 1986; Chittick and Keyes, 2007).

Due to past experimental thinning treatments in RNP, this study was able to use nine existing 0.25 ha plots that ranged in time-since-thinning from 40 years to one year and were otherwise comparable in most respects: two unthinned control plots, two plots thinned in 1978, two plots thinned in 2009, and three plots thinned in 2017 (Table 2, Figure 9). Plots thinned in 1978 were treated using a low-thinning prescription that reduced Douglas-fir numbers to 60% of redwood numbers (Veirs and Lennox, 1982); this treatment reduced stand basal area (BA) density by approximately 40%. Similarly, plots thinned in 2009 were also treated with a low-thinning prescription that targeted Douglas-fir removal and reduced stand BA density by approximately 40%. Plots thinned in 2017 were treated using a variable density thinning (VDT) prescription that removed approximately 0, 25, 40, 55, and 75% of BA density, with each reduction treatment randomly applied in 0.10 ha cells across 22 ha of Holter Ridge (Figure 10). To monitor VDT treatment efficacy, RNP established three permanent 1 ha plots, each with a 0.25 ha central subplot that was predominantly thinned to a 40% BA reduction. Thus, to compare tree responses to 40% BA reduction treatments across time (1978 to 2017), these inner 0.25 ha VDT plots were compared against the 0.25 ha plots thinned in 1978 and 2009. In all plots, Douglas-fir was targeted for removal to promote redwood dominance.

Table 2. Plot-level attributes of the nine study plots on Holter Ridge in Redwood National Park (RNP). Each plot is 0.25 ha and was treated using a low-thin prescription that targeted Douglas-fir removal. Plots were treated in 1978, 2009, and 2017, with control plots untreated. The 1978 and 2009 plots were thinned to a target basal area (BA) reduction of 40%. The 2017 plots were treated using variable density thinning (VDT) with five BA reduction treatments: 0, 25, 40, 55, and 75%. The VDT plots used in this study were predominantly thinned using a 40% BA reduction treatment.

Plot	**RNP Name**	**Elevation (m)**	**Aspect**	**Slope**	**Treatment Year**	**DBH (cm)**	**BA (m^2 ha^{-1})**
Control-A	Control-3	501	NE	10º	n/a	29 ± 2	111 ± 10
Control-B	Control-4	504	E	14º	n/a	40 ± 4	96 ± 8
1978-A	IB2-2	522	SW	10º	1978	48 ± 4	62 ± 5
1978-B	IB2-4	515	SW	15º	1978	44 ± 2	73 ± 7
2009-A	40L1-1	679	NNW	14º	2009	37 ± 2	73 ± 8
2009-B	40L1-3	631	NNW	8º	2009	42 ± 2	70 ± 9
2017-A	VDT-1	512	E	9º	2017	45 ± 7	61 ± 19
2017-B	VDT-2	511	N	12º	2017	52 ± 15	81 ± 8
2017-C	VDT-3	504	NE	8º	2017	27 ± 4	76 ± 9

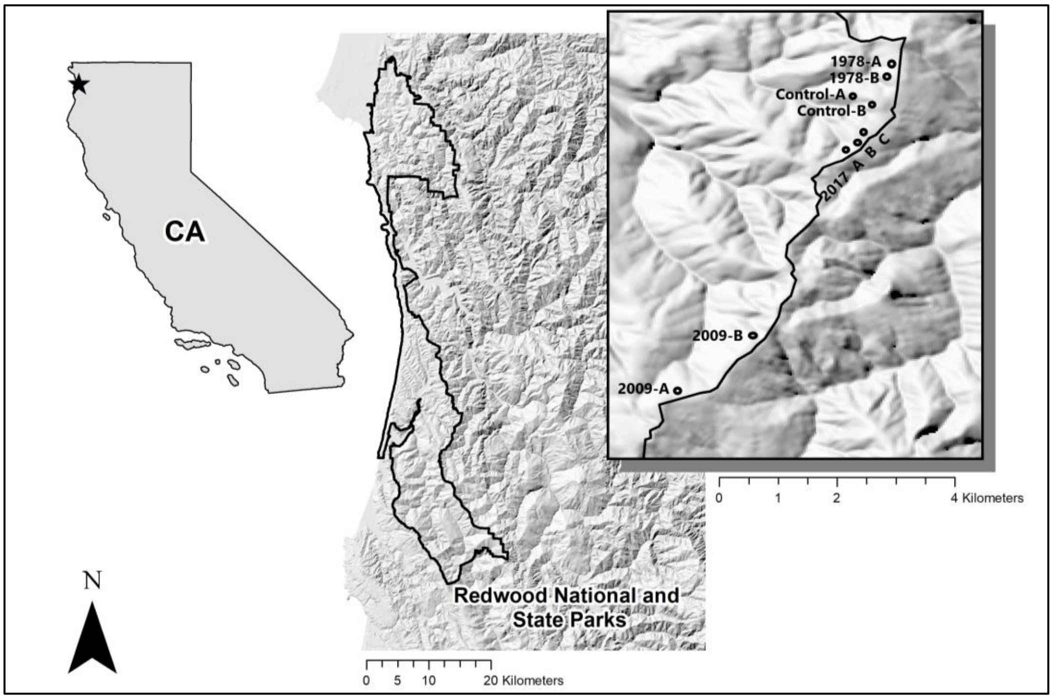

Figure 9. Locator map of the nine 0.25 ha study sites on Holter Ridge in Redwood National Park. Years indicate when stands were thinned using a 40% basal area reduction treatment; control stands were untreated.

Moving forward, these nine study plots will enable long-term evaluations of treatment efficacy in RNP. Within each plot, the 10 redwood trees closest to plot center that were healthy and had a live crown base accessible via a pole pruner (no higher than 14 m) were selected as study trees for physiological and dendrochronological analyses. For each study tree, diameter at breast height (DBH) and local competition (as measured with a prism, basal area factor 9.184) were recorded in 2018.

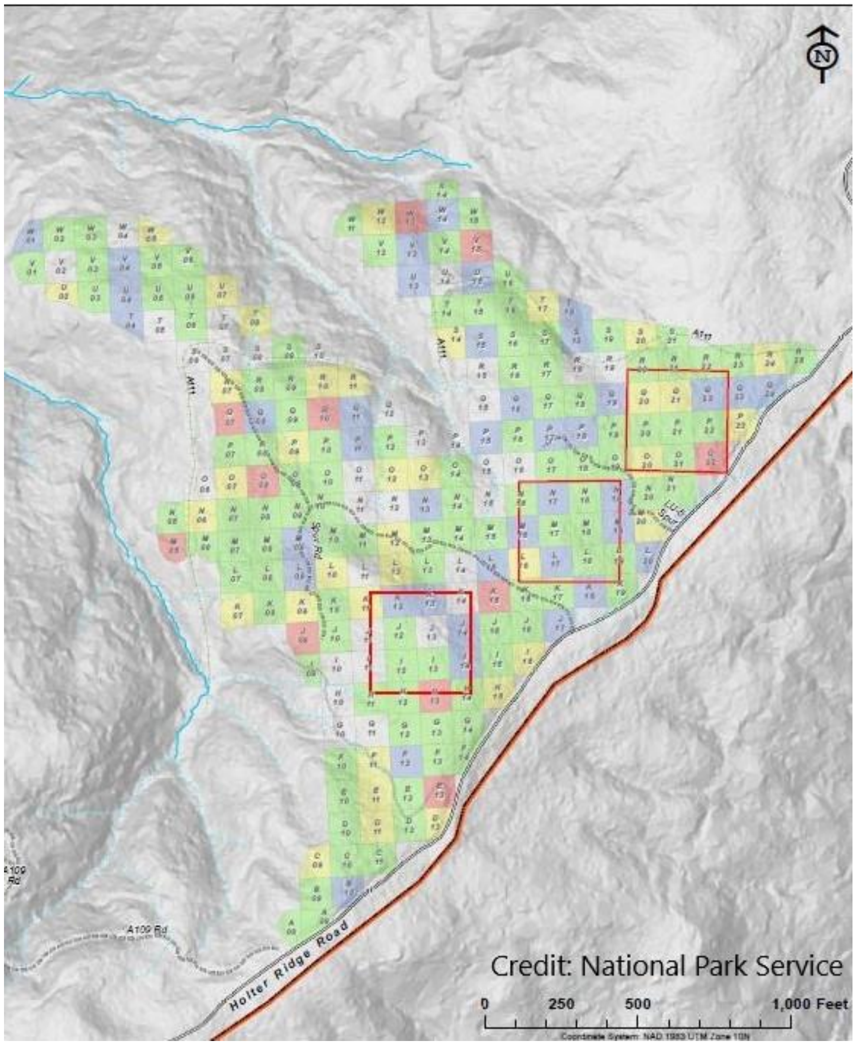

Figure 10. Credit: National Park Service. The Middle Fork of Lost Man Creek variable density thinning (VDT) unit map on Holter Ridge in Redwood National Park. Treatments were applied in the fall of 2017 across this 22 ha area. Each basal area (BA) reduction treatment (0, 25, 40, 55, and 75%) was randomly applied to 0.10 ha subplots. Within each of the 1 ha permanent plots (red boxes), there is a 0.25 ha central plot. This study used these three central 0.25 ha plots for comparison with other stands on Holter Ridge that were thinned in 1978 and 2009. The three central plots were thinned in 2017 predominantly using the 40% BA reduction treatment.

Physiological Measurements

In 2018 and 2019, leaf-level physiological measurements occurred across two consecutive sunny days in July, a time of high productivity and low precipitation input.

Leaf water potential (Ψ_l) was measured using a pressure chamber (Model 600, PMS Instruments, Corvalis, OR) and g_s was measured using a leaf porometer (Model SC-1, Decagon Devices, Pullman, WA). For leaf Ψ and g_s measurements, a pole pruner was used to clip one small branch from the lower crown of each study tree at predawn (Ψ_{pd}) and at midday (Ψ_{md}). Leaf Ψ_{pd} was only measured in 2018, not 2019. At midday, care was taken to collect the branch from a well illuminated portion of the crown. From each predawn branch, three Ψ_{pd} measurements were immediately taken from three different branchlets cut from the collected branch and averaged into a single Ψ_{pd} value for that tree. Similarly, from each midday branch, three Ψ_{md} and g_s measurements were immediately taken and averaged into single values for that tree.

In 2019, stem psychrometers (Model PSY1, ICT International, Australia) were used to continuously measure xylem Ψ during the last week of August and first week of September. For these measurements, one study tree per plot was instrumented and measured every 30 minutes for 17 consecutive days from August 22 to September 8; trees were chosen such that the nine study trees were comparable in size and local competition (BA density). Unfortunately the stem psychrometers in two plots (2009-A and 2017-C) did not function properly; data from these two plots were therefore not included in my analyses or results. For each instrumented tree, on each monitoring day, the highest Ψ value occurring between 00:00 – 05:00 hours was identified as xylem Ψ_{pd} and the lowest Ψ value occurring between 11:00 hours – 16:00 hours was identified as xylem Ψ_{md}. Due to instrument noise, I only used a seven-day window (August 31 to September 6) for analysis of xylem Ψ.

To evaluate the relationships among xylem Ψ, leaf Ψ, and g_s, I measured these three variables at midday (between 11:00 – 16:00 hours) on August 25, 2019 on each tree instrumented with a stem psychrometer. Stem psychrometers were used to measure xylem Ψ, a pressure chamber was used to measure leaf Ψ, and a leaf porometer was used to measure g_s. On each study tree, all three measurements were obtained within a 10-minute window of time.

Dendrochronological Measurements

To evaluate tree growth responses to thinning treatments using dendrochronological analyses, growth was measured in trees from the control plots, plots thinned in 1978, and plots thinned in 2009. The VDT plots, thinned in 2017, were omitted from this analysis as it was deemed that insufficient time had passed since treatment (< 2 years) to reliably detect a radial growth response. Within the 1978 plots, the pre- and post-treatment years were 1971-1977 and 1980-1986, respectively. The pre- and post-treatment years for the 2009 plots were 2002-2008 and 2011-2017, respectively. Treatment year and the year immediately following treatment were excluded from growth analyses to avoid the influence of any thinning shock on residual trees (Reukema, 1959).

In March 2019, two breast height increment cores (5 mm diameter) were taken at 90º angles from each other on the upslope side of each study tree used for physiological measurements (n = 10 trees per plot). Ten more redwood trees from each included plot were added for this growth analysis to make a total of 20 trees per plot. These additional trees were selected based on randomly chosen azimuths from plot center. For all study trees in my dendrochronological analyses, DBH and BA (as measured with a prism, basal area factor 9.184) were recorded.

In spring 2019, following standard dendrochronology techniques (Stokes and Smiley, 1968), cores were mounted, sanded to 600 grit, and scanned at 2400 dpi (Epson America, Inc., Long Beach, CA). Cores that were damaged or had unreadable tree-rings were excluded from analysis (n = 16 out of 240 cores). Attempts were made to cross-date cores using COFECHA software, but these efforts were unsuccessful, likely due to complacent growth across all plots as well as short time series (< 50 years on most trees). Thus, cores were visually measured and cross-dated using WinDendro (Régent Instruments Inc., Québec, Canada) and a list of marker years. Using this method, cores were reliably cross-dated from 1960 to 2017. On each study tree, annual radial growth measurements from the two cores were averaged into a single value. These radial growth measurements were then used with tree DBH measurements and bark thickness (BT) estimates to calculate basal area increment (BAI) using the dplR statistical package with the *bai.out* function in R. To calculate an estimate of BT for each tree, a locally-derived regression equation for coast redwoods on Holter Ridge (Lalemand, 2018) was used:

$$\text{coast redwood BT} = 9.939 + 0.722 * \text{Diameter} \qquad (1)$$

where Diameter is tree breast height diameter (including bark). To evaluate the magnitude and persistence of growth responses to treatment, I used a ratio of mean annual post-treatment BAI (n = 7 years, excluding treatment year and first post-thinning year) over mean annual pre-treatment BAI (n = 7 years).

Biodiversity Measurements

To investigate understory plant diversity, understory plants were inventoried in June (peak flowering season) of 2018 and 2019. Five circular subplots (radius = 1.78 m; 10 m^2) were installed within each of the nine 0.25 ha study plots. Subplots were systematically placed within each plot: one per corner (NW, NE, SW, SE) and one directly over plot center. Within each subplot, species present, slope, aspect, and percent cover per species were recorded. Percent cover was recorded using the Daubenmire cover class scale (1 = 0-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-95%, 6 = 95-100%).

Wildlife diversity (IACUC No. 17/18.FWR.37-A) was inventoried in 2018 and 2019, largely following protocols established by California State Park wildlife biologists. In both years, mammalian diversity was quantified using camera traps in October, a period of high mammalian activity. Camera traps (three per plot placed at 0°, 120°, and 240° orientations 10 m from plot center) recorded wildlife activity on the forest floor for three weeks during each sampling period. Incidental observations of mammal scat were also recorded but not included in species diversity estimates. In 2018, the use of Sherman live traps baited with peanut butter and oats was attempted, but due to bear activity and poor capture rates, this method of sampling was aborted. To evaluate bird abundance in each plot, three consecutive 10-minute point counts were conducted within 90 minutes before or after sunrise across two consecutive sunny days in June (a period of high bird song activity) in 2018 and 2019. All avian species were identified by sight and/or sound.

For each of the nine study plots, understory plants, birds, and mammals were evaluated via three diversity metrics: species richness (S), species evenness (D) calculated using the following equation:

$$\mathrm{D} = 1 - \frac{\sum_{i=1}^{S} n_i(n_i - 1)}{N(N - 1)} \tag{2}$$

and the Shannon-Wiener diversity values (H’) calculated using the following equation:

$$\mathrm{H}' = -\sum_{i=1}^{S} \frac{n_i}{N} * \ln \frac{n_i}{N} \tag{3}$$

where n_i = relative cover of each species and N = total number of species.

Statistical Analyses

Using R software version 3.5.1 (R Core Team, 2016), one-way ANOVAs were used to determine the influence of treatement (control, 1978, 2009, 2017) on tree physiology and growth. Paired *t*-tests were used to test for differences in Ψ_{md} and g_s between years (2018 and 2019). Understory plant diversity, avian diversity, and mammalian diversity were analyzed with two-way ANOVAs using treatment and sampling year as effects. To test the assumption of equal variances among groups, Levine and Bartlett tests were used; when this assumption was violated, Welch tests were used to determine whether or not groups significantly differed. To test the assumption that data were normally distributed, Shapiro-Wilk goodness-of-fit tests were used; when this assumption was violated, Kruskal-Wallis tests were used to determine whether or not groups significantly differed. If groups significantly differed, Tukey's HSD multiple means comparisons were used to identify significant differences among groups. Regression analyses were also conducted to investigate relationships among xylem Ψ, leaf Ψ, and g_s. For all statistical analyses, an α level of 0.05 was used.

RESULTS

Physiology

Across all plots used in my physiology analysis (control, 1978, and 2009, each with two replicates, and 2017 with three replicates), there were 87 study trees. On average, these trees had DBH 41 ± 3 cm and BA density was 79 ± 3 m^2 ha^{-1}. Among all physiology plots, DBH was not statistically different (p = 0.48) however BA density was significantly higher (p < 0.0001) in the control as compared the 1978, 2009, and 2017 plots.

In 2018 and 2019, water potential (Ψ) was measured on a pressure chamber (leaf Ψ) and with stem psychrometers (xylem Ψ), respectively. In 2019, leaf Ψ_{md} was also measured in July using a pressure chamber to enable interannual comparisons. Both xylem and leaf Ψ measurements were consistently high, not dropping below -2 MPa in 2018 or 2019. Across seven days in September 2019, continuous stem psychrometer measurements showed that the 1978 and 2009 plots generally experienced the highest and lowest xylem Ψ, respectively (Figure 11). In 2018, leaf Ψ_{pd} was significantly higher in the 2009 plots compared to all other plots (p = 0.0002, Figure 12A, Table 4). In 2019, xylem Ψ_{pd} was highest in the 1978 plots compared to all other plots, although not significant (p = 0.15, Figure 12A, Table 3). Due to differing methods of Ψ_{pd} collection, Ψ_{pd} between 2018 (leaf Ψ_{pd}) and 2019 (xylem Ψ_{pd}) could not be compared.

At midday, the 2017 plots experienced lower leaf Ψ_{md} than all other plots in 2018 (p < 0.0001) and in 2019 (p < 0.0001, Figure 12B, Table 3). Between years, leaf Ψ_{md} was significantly higher in 2019 than 2018 for all plots: control (p = 0.0001), 1978 (p < 0.0001), 2009 (p < 0.0001), and 2017 (p = 0.006). Regression analyses found no significant relationships between xylem Ψ_{md} and leaf Ψ_{md} (p = 0.92, R^2 = 0.002, Figure 13A), xylem Ψ_{md} and g_s (p = 0.35, R^2 = 0.17, Figure 13B), or between leaf Ψ_{md} and g_s (p = 0.10, R^2 = 0.02, Figure 13C).

In 2018, g_s was significantly higher in the 2017 plots compared to the 2009 plots (, Figure 12C, Table 3). Similarly, in 2019, g_s was significantly higher in the 2017 plots compared to the control plots (p = 0.01). Compared to 2018, g_s values in 2019 were significantly higher in the 1978 (p = 0.01), 2009 (p < 0.0001), and 2017 (p = 0.001) plots, but not in the control plots (p = 0.59).

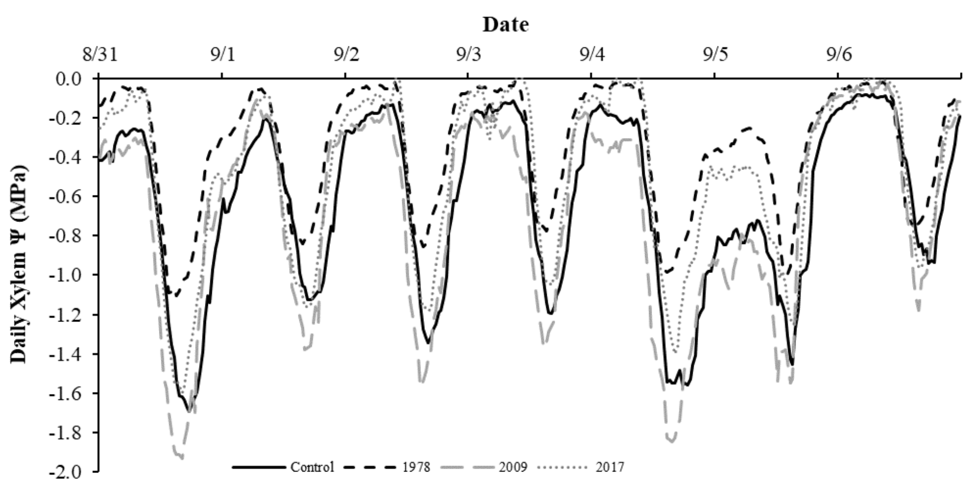

Figure 11. Daily xylem water potential (Ψ) for redwood trees in the control (black line), 1978 (black dots), 2009 (gray line), and 2017 (gray dashes) treatment plots. Measurements were taken with a stem psychrometer every 30 minutes from August 31 through September 6, 2019 in Redwood National Park. The anomalous drop in Ψ on September 5 at all plots was likely due to an issue with data retrieval from the psychrometer data box on September 4.

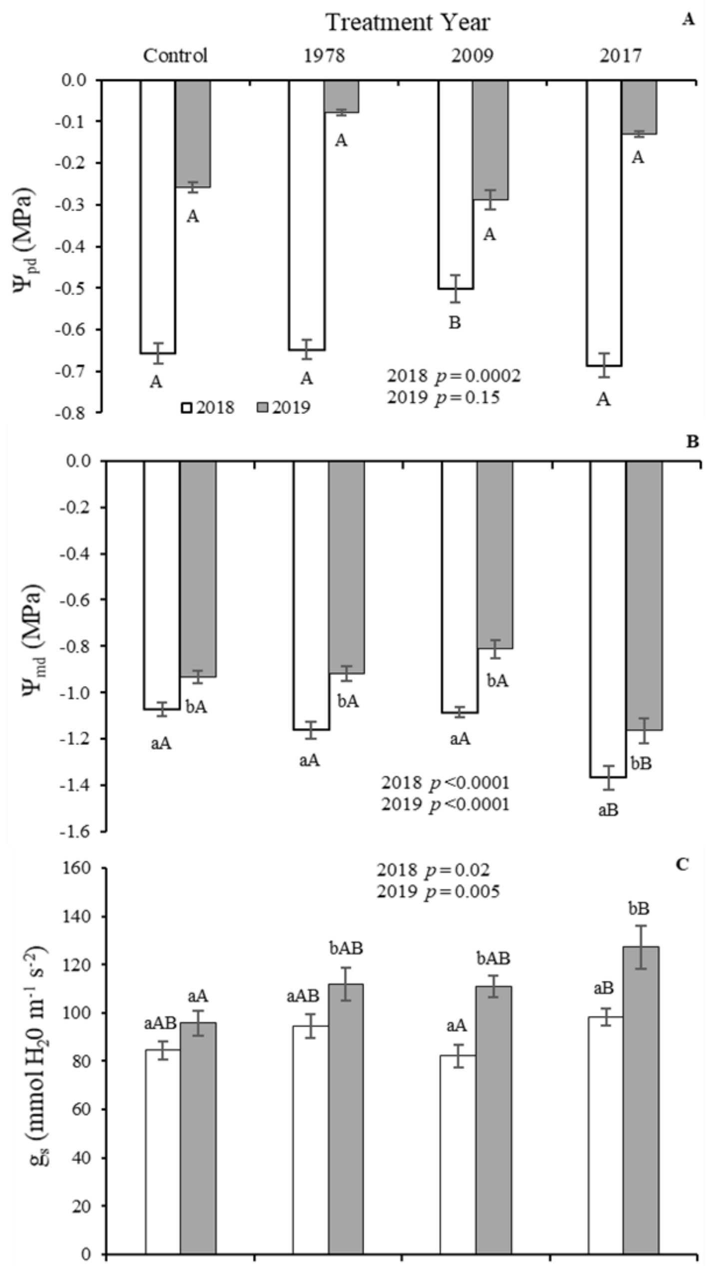

Figure 12. Mean (± SE) water potential (Ψ) and stomatal conductance (g_s) in 2018 (white) and 2019 (gray) in Redwood National Park in control plots and plots thinned in 1978, 2009, and 2017. A) Leaf predawn water potential (Ψ_{pd}) measured in July 2018 with a pressure chamber and xylem Ψ_{pd} measured in September 2019 with stem psychrometers. B) Leaf midday water potential (Ψ_{md}) measured in July 2018 and July 2019 with a pressure chamber. C) g_s measured in July 2018 and July 2019 with a leaf porometer. For each panel, treatments within a year not sharing the same uppercase letter are significantly different. For the Ψ_{md} and g_s panels, within a treatment, years not sharing the same lowercase letter are significantly different. In each panel, *p*-values for one-way ANOVAs comparing treatment means within each year are provided.

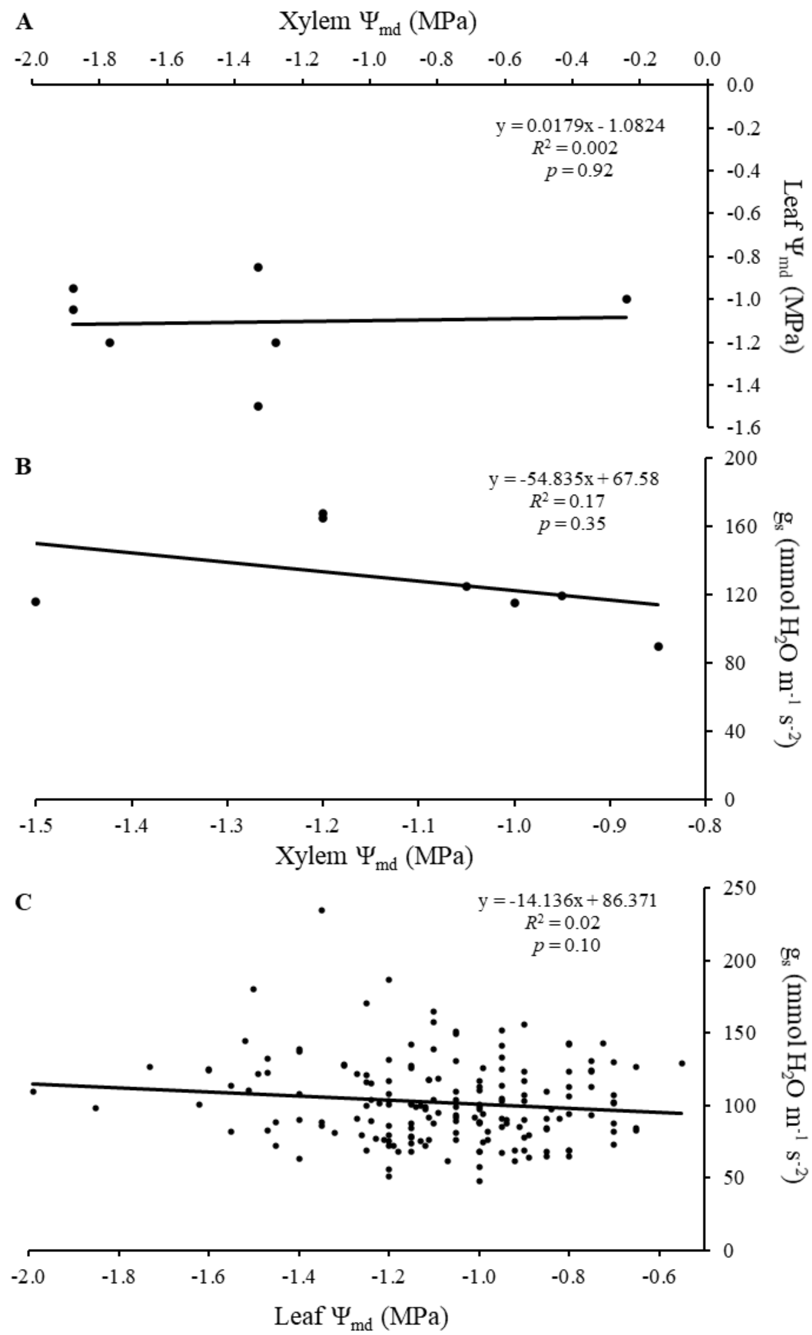

Figure 13. Redwood physiological relationships between A) xylem Ψ and leaf Ψ, B) xylem Ψ and g_s, and C) leaf Ψ and g_s. On each tree, these midday measurements of xylem Ψ (using a stem psychrometer), leaf Ψ (using a pressure chamber), and g_s (using a leaf porometer) were taken within a 10-minute window of each other in Redwood National Park. Panels (A) and (B) show measurements from August 25, 2019 using seven trees instrumented with stem psychrometers. Panel (C) shows all measurements taken in July 2018 and 2019.

Table 3. Mean (± SE) predawn water potential (Ψ_{pd}), midday water potential (Ψ_{md}), and stomatal conductance (g_s) for redwood trees in the control plots and plots thinned in 1978, 2009, and 2017 in Redwood National Park. In 2018, leaf Ψ_{pd} and Ψ_{md} measurements were made in July using a pressure chamber. In 2019, xylem Ψ_{pd} measurements were made in September using stem psychrometers and leaf Ψ_{md} measurements were made in July using a pressure chamber. In 2018 and 2019 g_s measurements were made in July using a leaf porometer. For each variable, treatments not sharing an uppercase letter are significantly different, with the one-way ANOVA statistics provided. For Ψ_{md} and g_s, within each treatment, years not sharing the same lowercase letter are significantly different.

Variable	**Control**	**1978**	**2009**	**2017**	***p*-value**	***F*-stat**	***df***
Leaf Ψ_{pd} 2018	-0.67 ± 0.03^{A}	-0.64 ± 0.03^{A}	-0.59 ± 0.05^{B}	-0.69 ± 0.03^{A}	0.0002	7.50	82
Xylem Ψ_{pd} 2019	-0.12 ± 0.08^{A}	-0.02 ± 0.02^{A}	-0.16 ± 0.10^{A}	-0.03 ± 0.00^{A}	0.15	1.95	24
Leaf Ψ_{md} 2018	-1.07 ± 0.03^{aA}	-1.16 ± 0.04^{aA}	-1.09 ± 0.02^{aA}	-1.37 ± 0.05^{aB}	<0.0001	14.94	81
Leaf Ψ_{md} 2019	-0.93 ± 0.03^{bA}	-0.92 ± 0.03^{bA}	-0.81 ± 0.04^{bA}	-1.16 ± 0.04^{bB}	<0.0001	16.65	83
g_s 2018	85 ± 4^{aAB}	94 ± 5^{aAB}	82 ± 5^{aA}	98 ± 3^{aB}	0.02	3.55	83
g_s 2019	96 ± 5^{aA}	112 ± 7^{bAB}	111 ± 5^{bAB}	127 ± 7^{bB}	0.01	4.58	83

Growth

Across all plots used in my growth analysis (control, 1978, and 2009, each with two replicates), there were 115 study trees (20 trees per plot minus five trees that were not cross-datable). On average, these trees had DBH 44 ± 1 cm, BA density 86 m^2 ha^{-1} ± 3, and annual BAI (based on 1960 – 2015) 16.6 ± 0.3 cm^2 yr^{-1} (Table 4). Among plots, although DBH ($p = 0.32$) and annual BAI ($p = 0.054$) did not differ significantly, BA density was significantly higher ($p < 0.0001$) in the control plots compared to the 1978 and 2009 plots. Overall, there was a general trend in all plots of increasing BAI starting around 1990, with BAI generally being highest in the 1978 plots and lowest in the control plots (Figure 14). However, an analysis of post-/pre-treatment growth responses evaluating mean BAI seven years before and after treatment found no significant differences among plots ($p = 0.39$, Figure 15).

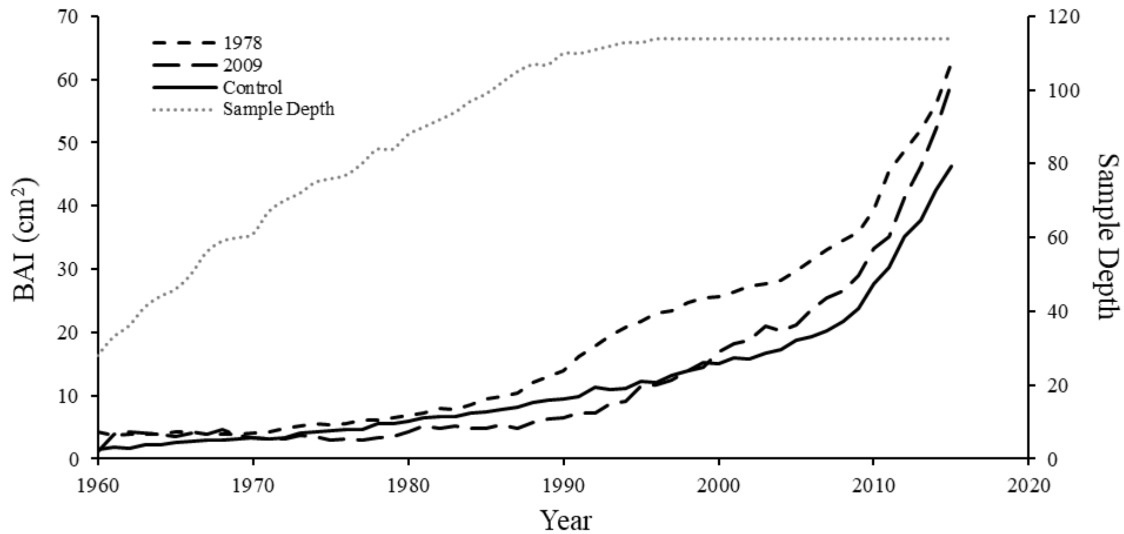

Figure 14. Mean annual growth, as measured by basal area increment (BAI), for redwood trees in each treatment: control (black solid line), 1978 treatment (small black dashes), and 2009 treatment (large black dashes) across 55 years (1960-2015) in Redwood National Park. Tree sample depth (gray dots) is also shown on the right vertical axis.

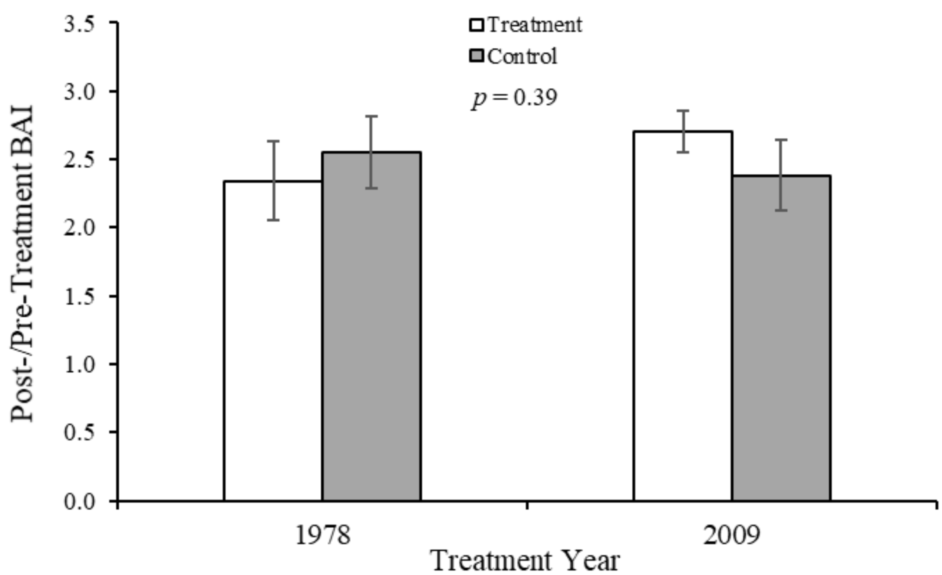

Figure 15. Mean (± SE) post-/pre-treatment basal area increment (BAI) for redwood trees in control plots and plots treated in 1978 and 2009 in Redwood National Park. Within the 1978 plots, pre-and post-treatment years were 1971-1977 and 1980-1986, respectively; pre- and post-treatment years for the 2009 plots were 2002-2008 and 2011-2017, respectively. These same time periods were used for comparison with the control plots.

Table 4. Mean (± SE) plot-level growth metrics of the six study sites used for growth analysis in Redwood National Park in 2019, including diameter at breast height (DBH), basal area density (BA), and basal area increment (BAI) for redwood growth study trees. BAI calculations are based on 1960 – 2015 tree ring data.

Plot	**DBH (cm)**	**BA (m^2 ha^{-1})**	**BAI (cm^2)**
Control-A	38 ± 3	112 ± 7	17.6 ± 0.7
Control-B	40 ± 2	101 ± 6	15.9 ± 0.6
1978-A	51 ± 3	65 ± 4	22.3 ± 0.8
1978-B	45 ± 2	76 ± 5	20.3 ± 0.8
2009-A	42 ± 4	75 ± 6	19.9 ± 1.2
2009-B	43 ± 3	82 ± 6	20.5 ± 0.8
All Plots	44 ± 1	86 ± 3	16.6 ± 0.3

Biodiversity

Across all nine plots in 2018 and 2019, 24 different understory plant species were observed: 14 herbaceous plants, three ferns, four shrubs, and three trees (Table 5). Across the two sampling years, plot-level plant species richness (S) ranged between six and 20, Decies evenness (D) ranged from 0.28 to 0.81, and the Shannon-Wiener diversity Indes (H’) ranged from 0.45 to 2.29 (Table 6); neither D (p = 0.074) or H’ (p = 0.054) were significantly different among treatments. Treatment had a significant effect (p = 0.01) on understory S but sampling year (p = 0.19) was not. Compared to all other plots, understory S was significantly higher in the 2009 plots (p = 0.003), with these plots supporting 22 different species: 15 forbs, three ferns, one shrub, and three trees. Between 2018 and 2019 in the 2017 plots, there were dramatic increases in percent cover for tanoak (2 to 33%), Douglas-fir (0 to 8%), and stream violet (*Viola glabella* [Nutt. in Torr. & A. Gray], 1 to 4%) (Table 7). Understory diversity was lowest in the control plots, with these plots only supporting five different species, supporting no ferns, and having cover dominated by forest litter (55%).

Across all nine study plots in 2018 and 2019, there were 29 avian species observed, all of which are federally protected under the Migratory Bird Treaty Act (Table 8). Generally, avian diversity was relatively comparable among all plots based on S, D, and H'. Across the two-year period, plot-level S ranged between 16 and 18, D ranged from 0.87 to 0.92, and H' ranged from 2.30 to 2.57 (Table 5). Among treatments, neither S (p = 0.74), D (p = 0.38), nor H' (p = 0.85) differed significantly. Notably, in 2019, a marbled murrelet (*Brachyramphus marmoratus*), a species federally listed under the Endangered Species Act as Proposed Threatened, was observed in the 1978 plots.

Among all study plots in 2018 and 2019, a total of nine identifiable mammals were observed (Table 9). Across the two-year period, plot-level S ranged from 6 to 8, D ranged from 0.73 to 0.83, and H' ranged from 1.52 to 2.00 (Table 5). Similar to the trends observed for birds, neither S (p = 0.90), D (p = 0.07), nor H' (p = 0.56) differed significantly among treatments for wildlife diversity. Although H' was lower in 2019 compared to 2018 for all treatments, two new species were observed: Roosevelt elk (*Cervus canadensis roosevelti*) in the 2009 plots and fisher (*Pekania pennanti*), a species federally listed under the Endangered Species Act as Proposed Threatened, in the 1978 and 2009 plots

Table 5. List of vascular plants observed across the nine study sites in Redwood National Park in July 2018 and 2019 in control plots and plots thinned in 1978, 2009, and 2017. Growth forms: herbaceous forb (H), fern (F), shrub (S), and tree (T). "X" Denotes presence.

Species	**Common Name**	**Growth Form**	**Control**	**1978**	**2009**	**2017**
Achlys triphylla	deer's foot	H			X	
Agrostis spp.	grass	H			X	
Asarum caudatum	western wild ginger	H			X	
Berberis nervosa	little Oregon-grape	H	X		X	X
Claytonia sibirica	spring beauty	H			X	X
Corallorhiza maculata	spotted coralroot	H			X	
Polypodium glycyrrhiza	licorice fern	F			X	
Galium aparine	cleavers grass	H			X	X
Gaultheria shallon	salal	H	X	X	X	X
Iris douglasiana	Douglas' iris	H			X	
Listera cordata	heart-leaf twayblade	H			X	X
Lilium bolanderi	Bolander's lily	H		X	X	X
Notholithocarpus densiflorus	tanoak	T	X	X	X	X
Polystichum munitum	sword fern	F		X	X	X
Pseudotsuga menziesii	Douglas-fir	T			X	X
Pteridium aquilinum	bracken fern	F		X	X	
Rhododendron macrophyllum	rhododendron	S	X			X
Rubus ursinus	California blackberry	S		X	X	
Sequoia sempervirens	coast redwood	T			X	X
Trichostema ovatum	San Joaquin blue curls	H			X	
Trientalis latifolia	Pacific starflower	H			X	X
Vaccinium ovatum	evergreen huckleberry	S	X	X	X	X
Vaccinium parvifolium	red huckleberry	S		X		X
Viola glabella	stream violet	H			X	X

Table 6. Species richness (S), species evenness (D), and Shannon-Wiener diversity index (H’) for plants, birds, and mammals among the control, 1978, 2009, and 2017 plots in 2018 and 2019 in Redwood National Park. In both years, understory plant surveys were conducted in May, bird point count surveys were conducted in June, and mammals were inventoried for three weeks in October using trail cameras.

Sampling Year		2018				2019			
Diversity Metric	**Biodiversity**	**Control**	**1978**	**2009**	**2017**	**Control**	**1978**	**2009**	**2017**
Species Richness (S)	Plants	5	6	17	11	5	6	20	15
Species Evenness (D)	Plants	0.28	0.68	0.81	0.48	0.28	0.68	0.72	0.72
Shannon-Wiener Diversity Index (H')	Plants	0.45	1.22	2.29	1.14	0.45	1.22	2.15	1.96
Species Richness (S)	Birds	17	17	17	16	18	17	17	18
Species Evenness (D)	Birds	0.89	0.92	0.87	0.90	0.88	0.91	0.91	0.91
Shannon-Wiener Diversity Index (H')	Birds	2.36	2.57	2.27	2.37	2.34	2.30	2.43	2.40
Species Richness (S)	Mammals	6	7	7	8	7	8	8	8
Species Evenness (D)	Mammals	0.83	0.80	0.73	0.77	0.82	0.81	0.65	0.71
Shannon-Wiener Diversity Index (H')	Mammals	1.73	1.72	1.52	2.00	1.63	1.63	1.48	1.36

Table 7. Change in percent cover (based on Daubenmire cover classes) of understory vegetation from 2018 to 2019 in the variable density thinning (2017) plot in Redwood National Park.

Species	**Common Name**	**Change in Cover (%)**
Berberis nervosa	little Oregon-grape	0
Claytonia sibirica	spring beauty	-1
Galium aparine	cleavers grass	5
Gaultheria shallon	salal	3
Lilium bolanderi	Bolander's lily	-1
Listera cordata	heart-leaf twayblade	7
Notholithocarpus densiflorus	tanoak	31
Polystichum munitum	sword fern	-1
Trientalis latifolia	Pacific starflower	2
Pseudotsuga menziesii	Douglas-fir	8
Rhododendron macrophyllum	rhododendron	0
Sequoia sempervirens	coast redwood	5
Vaccinium ovatum	evergreen huckleberry	1
Vaccinium parvifolium	red huckleberry	1
Viola glabella	stream violet	3

Table 8 List of avian species observed in Redwood National Park in June of 2018 and 2019 in control plots and plots thinned in 1978, 2009, and 2017. "X" Denotes presence. Species denoted with an asterisk (*) are federally listed under the Endangered Species Act.

Species	**Common Name**	**Control**	**1978**	**2009**	**2017**
Bombycilla cedrorum	cedar waxwing		X		
*Brachyramphus marmoratus**	marbled murrelet		X		
Calypte anna	Anna's hummingbird	X			
Catharus guttatus	hermit thrush	X	X	X	X
Catharus ustulatus	Swainson's thrush		X		X
Certhia americana	brown creeper	X	X	X	X
Chaetura vauxi	Vaux's swift				X
Contopus cooperi	olive-sided flycatcher				X
Corvus brachyrhynchos	American crow			X	
Corvus corax	common raven	X		X	X
Dryobates villosus	hairy woodpecker		X		
Dryocopus pileatus	pileated woodpecker		X	X	X
Empidonax difficilis	Pacific-slope Flycatcher	X	X	X	X
Ixoreus naevius	varied thrush	X	X	X	X
Junco hyemalis	dark-eyed junco	X		X	X
Patagioenas fasciata	band-tailed pigeon	X	X	X	X
Pheucticus melanocephalus	black-headed grosbeak	X			
Piranga ludoviciana	western tanager			X	X
Poecile rufescens	chestnut-backed chickadee	X	X	X	X
Regulus satrapa	golden-crowned kinglet	X	X	X	X
Selasphorus sasin	Allen's hummingbird		X		
Setophaga coronata	yellow-rumped warbler	X	X	X	X
Setophaga sp.	warbler spp.	X	X	X	X
Sialia mexicana	western bluebird		X		
Cardellina pusilla	Wilson's warbler	X	X	X	X
Troglodytes hiemalis	winter wren	X	X	X	X
Turdus migratorius	American robin		X		X
Vireo huttoni	Hutton's vireo	X	X	X	X
Zenaida macroura	mourning dove			X	

Table 9. List of mammals observed in Redwood National Park in October of 2018 and 2019 in control plots and plots thinned in 1978, 2009, and 2017. "X" Denotes presence. Species denoted with a double asterisk (**) are federally listed under the Endangered Species Act as Proposed Threatened.

Species	**Common Name**	**Control**	**1978**	**2009**	**2017**
Cervus canadensis roosevelti	Roosevelt elk			X	
Glaucomys oregonensis	Humboldt flying squirrel	X	X		X
*Pekania pennanti***	fisher		X	X	
Odocoileus hemionus	black-tail deer	X	X	X	X
Sciuridae sp.	squirrel sp.	X	X	X	X
Tamias sp.	chipmunk sp.	X	X	X	X
Tamiasciurius douglasii	Douglas squirrel	X	X	X	X
Ursus americanus	American black bear	X	X	X	X
Rodentia sp.	rodents	X	X	X	X

DISCUSSION

This study's assessment of forest restoration efficacy based on tree physiology (Ψ and g_s), annual growth (BAI), and biodiversity (understory vegetation, birds, and mammals) metrics produced findings comparable with other studies (Thomas et al., 1999; Chittick and Keyes, 2007; Verschuyl et al., 2011; O'Hara et al., 2015; Sohn et al., 2016; Cole et al., 2017; Goodwin et al., 2018; Lalemand, 2018). In second-growth redwood forests, the standard approach to evaluate treatment efficacy is typically to assess breast height radial growth (Veirs, 1986; Lalemand, 2018). However, responses to treatment can take years to detect when relying on these growth-based metrics (Dagley et al., 2018). Thus, this study measured both physiology and growth to evaluate forest responses to treatment in both the short- and long-terms, respectively. In support of the hypotheses, restoration treatments on Holter Ridge in Redwood National Park (RNP) elicited positive forest responses, as measured by redwood physiology, redwood growth, and biodiversity of plants, birds, and mammals. Redwood physiological responses to treatment were greatest in the most recently thinned plots and were otherwise relatively homogenous across the 1978, 2009, and control plots. Similarly, redwood growth also responded to treatment, with the time between thinning and increased growth ranging from four to 10-years and the responses persisting for many years. Finally, treatments promoted understory plant biodiversity through increased species richness and percent cover, although this increased diversity was not detected for birds or mammals. Overall, these findings realize this study's objective to inform on the capacity of second-growth redwood forest restoration to accelerate the development of old-growth characteristics.

Physiology

Physiological responses to treatments were detectable in the 2017 plots but were relatively muted in the 1978, 2009, and control plots, demonstrating that these types of measurements can be useful to evaluate tree responses to treatments in the short-term. Previous physiology-based studies, many based in arid environments such as the U.S. Southwest, have shown that thinning treatments can increase leaf Ψ_{pd} in residual trees during drought conditions (Skov et al., 2004; Sohn et al., 2016). In these dry, water-limited ponderosa pine forests, Ψ_{pd} and Ψ_{md} are often negatively correlated with stand density (Kolb et al., 1998), although in some stands density does not seem to affect Ψ (Schmid et al., 1991). In RNP, thinning did not meaningfully affect leaf Ψ_{pd} (almost all values > 0.75 MPa), suggesting that in this coastal, wet, temperate rainforest, soil water availability is ample throughout the year regardless of stand density. Corroborating this speculation of ample water availability in this forest, redwood growth on Holter Ridge was highly resistant to the recent 2012-2015 California drought (Williams et al., 2015; Lalemand, 2018). Thus, this study and others collectively suggest that in its northern range, substantial precipitation inputs of winter rain and summer fog (Litvak et al., 2011) provide sufficient water for coast redwood.

While Ψ_{pd} indicated ample soil water availability regardless of treatment history in this study, recent treatments did affect leaf Ψ_{md}. The decreased leaf Ψ_{md} measured in the 2017 plots may result from increased evapotranspirational water loss due to increased light availability (Gauthier and Jacobs, 2009). By contrast, in the 1978 and 2009 plots, post-treatment times were likely sufficient to allow canopy re-closure such that light, evapotranspiration, and resulting leaf Ψ_{md} were indistinguishable from the controls.

Although leaf Ψ largely indicated that water status was invariable with treatment, Ψ_{md} in recently thinned plots being the exception, xylem Ψ suggested that treatments might quantifiably affect tree water status, even in the long-term. Among treatments, xylem Ψ was consistently lowest in the 2009 plots and highest in the 1978 plots. In the 2009 plots, it is possible that greater post-treatment light availability stimulated an increase in the leaf area to sapwood area ratio in residual trees (Simonin et al., 2006), thereby causing the measured reduction in xylem Ψ. Alternatively, because only one tree per plot was instrumented, it is also possible that the relatively consistent ranking of xylem Ψ from high to low in 1978, 2017, control, and 2009 plots, respectively, is the result of differences in microclimate, growing space, and/or physiology of the instrumented trees. Nevertheless, on the whole, xylem Ψ values (all > -2 MPa) generally supported leaf Ψ findings, together indicating that redwoods at this site are not water-limited.

In July 2019, paired midday measurements showed that xylem Ψ was typically lower than leaf Ψ and that there was not a strong relationship between the two metrics. Previous studies using stem psychrometer and pressure chamber measurements of Ψ have found strong (Milliron et al., 2018) and weak (Wright et al., 1988) correlations between the data resulting from these two methods. It is possible that the pressure chamber overestimated leaf Ψ due to issues with apoplastic solutes (Duniway, 1971; Milliron et al., 2018). Interestingly and somewhat surprisingly, my measurements also yielded weak relationships between Ψ_{md} (xylem and leaf) and g_s. My synchronized measurements of xylem Ψ, leaf Ψ, and g_s highlight that further work with a larger sample is needed to better understand the dynamic relationships among these three metrics in redwood trees.

Increased g_s in the 2017 treatments indicates that thinning can enhance carbon assimilation rates in second-growth redwood forests for at least the first few years following treatment. In 2019, g_s was greatest in the 2017 plots that were thinned just two years earlier. This finding, likely due to increased light availability increasing transpiration in residual trees, showcases how thinning can rather immediately stimulate g_s. Similarly, in second-growth ponderosa pines of northern Arizona, g_s often increases within one- to three-years post-thinning (Kolb et al., 1998; Skov et al., 2004). Additionally, black walnut (*Juglans nigra* L.) physiology responds to thinning via higher photosynthetic rates resulting from increased light availability just one year after treatment (Gauthier and Jacobs, 2009). Thus, in thinned second-growth redwood forests, elevated g_s in residual trees can be expected in the short-term. In the longer-term however, it is likely that this increase will relatively quickly recover to pre-treatment rates due to canopy re-closure. In temperate forests of the United Kingdom (Valverde and Silvertown, 2019) and forests of the eastern U.S. (Runkle et al., 2018), for example, the canopy can re-close within just ten years of treatment. Given the results of these studies coupled with muted g_s rates in the 2009 plots (treated 10 years prior to this study), it seems likely the 2017 plots will have muted g_s responses by 2027. It would be informative for future studies of the VDT treatments to include canopy openness measurements to possibly quantify a correlation with g_s rates.

Overall, these physiology measurements collectively demonstrate that this redwood forest is not water-limited and that increased light availability following thinning therefore has the potential to increase tree productivity until canopy re-closure again limits light. Continued monitoring of Ψ and g_s in the 2017 plots over the next five to seven years would provide useful information about how long enhanced gas exchange persists following thinning in this forest type. Given current projections for regional climate change and widespread efforts to restore second-growth redwood forests in northern California (Burns et al., 2018), these physiological measurements can serve as useful baseline data to help land managers tailor thinning treatments for desired short- and long-term responses and monitor forest responses to treatment and climate over time. For example, the knowledge that leaf Ψ_{md} is reduced immediately following thinning could help minimize negative responses to treatment such as ‘thinning shock’ (Harrington and Reukema, 1983), particularly in a future with projected increases in mean annual temperatures and decreased summer fog (Johnstone and Dawson, 2010).

Growth

Given that increased leaf-level gas exchange is a typical short-term response to reductions in stand density for multiple forest types, it reasons that growth should also increase following thinning treatments. This type of ‘release effect’ has been detected for ponderosa pine growth in Oregon and northern Arizona, with the response persisting for four (O’Hara et al., 2010), 10 (Kerhoulas et al. 2013), and 20 (Latham and Tappeiner, 2002) years following treatment. In Sierra Nevada mixed-conifer forests, thinning was observed to immediately promote increased tree growth (Callahan, 2019). In second-growth redwood forests of northern California, this same type of response to thinning has also been observed with the time between treatment and the onset of increased growth varying from four (Dagley et al., 2018), to five (Roberts and Harrington, 2008), to 10 years post-treatment (O’Hara et al., 2010).

In agreement with these previous studies of redwood restoration, my work found that treatment increased growth. This can be seen in the 1978 and 2009 treatments as delayed departures from the controls (Figure 13). Remarkably, these increases in growth have persisted through 2015 in both the 1978 and 2009 treatments, suggesting that the benefits of thinning can be impressively long-lived in this system. Interestingly, although not included in this study’s analyses, trees in the 2009 plots had detectable 2019 radial growth when cored in early February, whereas trees in the control and 1978 plots did not yet have any detectable growth at this time. This early onset of growth in recently thinned plots indicates that young residual redwoods are vigorous and respond favorably to treatments.

As typically occurs in many forest systems, there was a delay between treatment and a release in growth at this site. Trees in the 1978 and 2009 plots experienced a growth-based departure from the control about 10- and four-years post-treatment, respectively (Figure 13). This difference in lag time between treatment and release could relate to tree age, as the single cohort of trees in the 1978 plots were approximately 25-years-old at the time of treatment and the single cohort of trees in the 2009 plots were approximately 45-years-old when thinned (Teraoka and Keyes, 2011; Veirs and Lennox, 1982). Only 25 years after clear-cutting, it is likely that in 1978 trees were not yet light limited and thinning therefore did not immediately meaningfully increase a limiting resource. Furthermore, because redwood prolifically sprouts in response to disturbance after thinning (O'Hara et al., 2015), increased photosynthate likely was allocated to basal sprout production rather than diameter growth. Diameter growth therefore likely did not increase in the 1978 plots until the canopy had sufficiently closed over to suppress sprouting, possibly explaining the 10-year delay between treatment and release. More generally, reasons for the common lag between treatment and increased breast height growth are variable, most notably including thinning shock (Harrington and Reukema, 1983) and the fact that newly available photosynthate from increased leaf-level carbon uptake might first be allocated to numerous competing sinks other than breast height diameter growth (Lagergren et al., 2019). Examples of alternative carbon sinks following treatment include increased leaf area to take advantage of greater light availability

(McDowell et al., 2003) and increased structural roots for improved stability under more severe wind exposure (Thornburgh et al., 2000).

Likely due to the four- to 10-year lag that I detected between thinning and increased growth, I did not detect a significant release effect when evaluating seven-year-average post-/pre-treatment growth. Additionally, this failure to detect a release in growth using this common post-/pre-treatment approach could indicate that the 40% BA reductions used in 1978 and 2009 were insufficient in these stands with tree densities on Holter Ridge of approximately 2,400 trees per hectare (TPH), compared to the historical old-growth reference conditions of 25 – 90 TPH, and Douglas-fir continuing to be overrepresented (Chittick, 2005). In fact, previous work in 40- to 50-year-old second-growth redwood forests suggests that to foster the greatest increase in growth, BA reductions ranging from 50 to 75% should be used (Oliver et al., 1994; O'Hara et al., 2015). Thus, these physiology- and growth-based analyses as well as multiple other studies on second-growth redwood forests all suggest that heavy basal area reductions, or possibly silvicultural methods other than low thinning, are needed to elicit a large release in residual trees.

Biodiversity

While common objectives for restoration treatments include increasing vigor in residual trees, increasing biodiversity is another important goal. This is particularly true in second-growth redwood forests where impenetrably dense thickets of suppressed trees stalled in the stem exclusion phase of stand development can blanket extensive swaths of the landscape. Previous work in redwood forests (Chittick, 2005; Chittick and Keyes, 2007) and in mixed-conifer forests of the Sierra Nevada Mountains (Goodwin et al., 2018) and Oregon (Cole et al., 2017) has shown that thinning treatments can help spur a shift towards understory reinitiation with increased plant diversity (Oliver & Larson, 1996). However, in these studies, initial increases in understory plant diversity were often followed by shrub dominance and a corresponding decrease in herbaceous cover. In RNP, this shift from understory herbaceous dominance to shrub dominance can occur within three years of a clearcut (Chittick, 2005; Muldavin et al., 1981), suggesting that heavy thinnings should be avoided, if maximizing understory plant diversity is a high priority of treatment. On the other end of the spectrum, low-intensity restoration treatments (e.g., the 40% BA reductions implemented on Holter Ridge) also typically accelerate the development of large shrub thickets that can persist beyond canopy closure (Chittick, 2005; Thomas et al., 1999) and perhaps indefinitely (Teraoka, 2012).

Similar to previous work, restoration treatments in RNP promoted the development of understory vegetation, as measured by increased species richness, species evenness, Shannon-Wiener diversity indices, and percent cover compared to control plots. In the 2017 plots, understory herbaceous cover dramatically increased from 2018 to 2019, as did all other biodiversity metrics, indicating a positive short-term response to treatments. In 2019, the 2009 and 2017 plots supported markedly higher plant species richness and herbaceous cover compared to the 1978 and control plots, which were dominated by evergreen huckleberry and overstory litter, respectively. Plant community structure in the 2009 and 2017 plots will likely follow this trajectory towards shrub dominance near the time of canopy re-closure due to decreased light availability. Pacific Northwest plant communities can begin to recover pre-disturbance conditions after 20-30 years (Halpern and Spies, 2008; Jules et al., 2008) and for redwood forests, after about 55 years post-thinning (Jules et al., 2008). Thus, because in many forest types this initial pulse of understory plant diversity following thinning seems to diminish relatively quickly due to increasing shrub dominance, if promoting the development of understory vegetation is an objective of management, then multiple treatment entries to keep the upper canopy open for light availability may be needed to stall shrub dominance (Hayes et al., 1997) without having to wait decades for pre-disturbance vegetation communities to re-establish.

Research in diverse western forest types have reported positive effects of thinning treatments on avian communities (Verschuyl et al., 2011). Contrastingly, there was no detectable influence of restoration on birds in this study, as evidenced by relatively homogenous species richness and diversity across all plots. This trend may continue until old-growth features such as large trees, large diameter branches, and multiple canopy layers are present to create habitats suitable for a wider array of avian life. Based on the diversity of birds detected in this study, it seems that Holter Ridge stands are developing these characteristics. For example, the federally threatened marbled murrelet (Hayes et al., 1997), a species dependent on large diameter branches for viable nesting platforms, was observed in the 1978 plots. And, in addition to the commonly-observed mixed-conifer-dependent bird species, the chestnut-backed chickadee (*Poecile rufescens*), a species dependent on hardwoods, likely tanoak in this study, was recorded in all plots during both sampling years (Hayes et al., 1997). The presence of this species confirms the existence of suitable habitat and forage for hardwood-dependent avian species at this site and verifies that the management objective to create tanoak codominant redwood forests has been met. Additional evidence that these stands are on track to support rich bird diversity, the Pacific-slope flycatcher (*Empidonax difficilis*), a species typically less abundant in treated stands (Hagar et al., 1996; Hayes et al., 1997), was observed in all study plots, suggesting that despite treatments, suitable habitats and forage existed. Thus, while thinning treatments can quicken growth in residual trees and increase herbaceous plant diversity, it seems that these treatments are slow to quantifiably boost bird diversity. Nevertheless, the treated and untreated second-growth stands on Holter Ridge do appear to support a rich mixture of bird species.

Similar to bird diversity, mammal diversity was also relatively homogenous across all plots, suggesting that animals may be slow to respond to changes in forest structure in the wake of thinning treatments. In hardwood and mixed pine-oak forests in West Virginia (Muzika et al., 2004), ponderosa pine forests in the Southwestern U.S. (Converse et al., 2006), and mixed-conifer forests in Washington (Carey, 2003), research has shown thinning generally has a positive influence on small mammal abundance. Although mammal species detections suggest low diversity across Holter Ridge, sensitive species such as the fisher, Roosevelt elk, and the Humboldt flying squirrel (*Glaucomys oregonensis*) were observed in the 2009 plots. The latter species is typically associated with old-growth forests and is also the primary prey for the northern spotted owl (*Strix occidentalis caurina*), a threatened species (Carey, 1991). Additionally, by feeding primarily on truffles and spreading truffle spores throughout the forest, flying squirrels promote mycorrhizal networks that enhance plant absorption of water and nutrients (Carey, 2003). Still, wildlife diversity has been shown to positively correlate with the complexity of understory vegetation in eastern Canadian boreal (Desrochers and Major, 2013) and Pacific Northwest (Hayes et al., 1997; Thysell and Carey, 2001) forests, therefore, it could be decades before biodiversity of birds and mammals are restored.

Thus, while old-growth features such as nesting cavities and large branches to support birds and arboreal rodents are necessary to support high levels of wildlife diversity, it appears that second-growth redwood forests can nevertheless support a diverse collection of bird and mammal species. However, despite the presence of sensitive species, the Holter Ridge 40-year chronosequence suggests that although treatments can accelerate old-growth features beneficial for wildlife habitat (Noss, 2000; O'Hara et al., 2017), animals can be slow to respond to these changes. Compellingly, crown manipulations in second-growth redwood trees, while time-consuming and requiring specialized training to implement, may be an effective way to accelerate the development of wildlife habitat in developing canopies (Sillett et al., 2018).

CONCLUSIONS

In forests of the Pacific Northwest, restoration treatments can open the upper canopy to accelerate the development of old-growth forest features (Carey and Curtis, 1996; Hayes et al., 1997; McComb et al., 1993). The lower Redwood Creek basin and the Little Lost Man Creek subbasin in Redwood National Park have been identified as reference ecosystems for historical old-growth redwood conditions (Fritschle, 2009; Russell and Jones, 2001). Managers at RNP are currently focused on accelerating the development of these features in overly dense and impaired second-growth forests using prescribed thinning as a tool for restoration. Results from this study verify that restoration treatments in this forest type can improve growth conditions for residual trees in both the short- and long-term. Importantly, this work also demonstrates the usefulness of physiological measurements for short-term assessments of treatment efficacy when increases in breast height growth are often delayed numerous post-treatment years.

Given the complexity of redwood ecosystems, managers must balance not only forest, watershed, and landscape management but also logistical, social, and bureaucratic challenges to achieve their objectives. Objectives could be achieved with a simplified restoration process involving multiple-entries at regular intervals (e.g., six- to 10-year cycles) with low-severity basal area reduction (10 – 25%) treatments that terrace down stand density until historical old-growth conditions are reached. Canopy gaps created in the overstory could provide light for patches of herbaceous understory to develop, potentially benefiting wildlife, yet most of the stand would remain shaded, possibly suppressing Douglas-fir, a restoration objective of RNP for over 40 years (Veirs and Lennox, 1982). The logistical reality is that each thinning cycle would require its own series of consultations with regulatory agencies, fish and wildlife surveys, and possibly Environmental Assessments. Thus, multiple-entry low-severity thinning treatments would be expensive and time consuming to plan, prepare, and execute. Furthermore, RNPs watershed management program is actively removing existing logging road systems, accessing stands in need of restoration in the future may become difficult once these roads are restored. Therefore, restoring areas of RNP concurrently with road removal could reduce future ecosystem impacts and costs of building new skid roads and/or having to use lop-and-scatter slash treatments.

Given the widespread need for restoration across RNP, managers are limited to prescribing one-time single-entry treatments. Although VDT is complex and requires a tremendous amount of time and resources to plan, prepare, and execute (O’Hara et al., 2012), this treatment is a more holistic approach to restoration, fostering tree growth and biodiversity of plants and animals (Carey, 2003). To realize RNPs objective to accelerate the development of old-growth features in impaired second-growth forests, VDT seems to be best-suited approach. Therefore, a future study of long-term tree growth and biodiversity responses to the VDT treatment would help determine if the greater effort, cost, and implementation-time are warranted as compared to traditional low-thin treatments.

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