Understanding *Sequoia sempervirens*[1]

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> "Scattered as the leaves of the forest are the printed references to the Redwoods of California."
> – Joseph Grant, Save the Redwoods League, 1935

Humans have no doubt observed the coast redwood, *Sequoia sempervirens* (D. Don) Endl., in wonder for thousands of years. It is no small task to seek understanding of a species whose sheer size cannot readily be assessed from the ground and whose generation time can exceed that of humans by 100 times. Fortunately, the scientific method has provided a steadfast approach to study, describe, and explore many aspects of *S. sempervirens* ecology in recent centuries.

This review focuses on select aspects of coast redwood ecology that illustrate how redwood research has progressed and proliferated over time. Redwood research developed slowly after the first botanical description of the species in 1824, but in recent decades the pace of ecological investigation has accelerated. Major methodological innovations including molecular genetics, canopy-access rope techniques, and dendrochronology have resulted in profound discoveries that shape our contemporary understanding of Earth's tallest tree and the forest it defines.

First roots of redwood research trace back to European discovery of coast redwoods in California. On October 10, 1769, Franciscan missionary Fray Juan Crespi documented the first historical observation of redwood in his diaries of the Portolá Expedition near Monterey Bay (Bolton 1927). He writes of the party traveling in an area likely along Soquel Creek, "over plains and low hills, well forested with very high trees of a red color, not known to us. They have a very different leaf from cedars, and although the wood resembles cedar somewhat in color, it is very different, and has not the same odor; moreover, the wood of the trees that we have found is very brittle. In this region there is a great abundance of these trees and because none of the expedition recognizes them, they are named redwood from their color."

Another 22 years passed before the first known botanical collections of redwood occurred which led to formal botanical description of the species in the 19th century. In 1791, the Czech botanist Thaddeus Haenke planted the first redwood seeds in Europe near Granada, Spain that were collected during the Malaspina Expedition (Jepson 1910). In 1795, Archibald Menzies brought additional specimens from the Santa Cruz region back to England from the Vancouver Expedition and these specimens were used by the English botanist Aylmer Bourke Lambert in 1824 to name the coast redwood *Taxodium sempervirens*, in recognition of its morphological similarities to bald cypress (Jepson 1910). Stephen Endlicher subsequently changed the genus in 1847 to *Sequoia*, a name with unknown and debated origin (Lowe 2012).

The evolutionary relationship of *S. sempervirens* to other conifers remained dependent on morphological trait assessments and therefore highly unresolved until the late 20th century. For many decades, botanists debated the phylogenetic arrangement of *S. sempervirens* within the conifer lineage until R. Pilger assigned *S. sempervirens* to the Taxodiaceae in 1926 on the basis of ovulate cone similarities (Brunsfeld et al. 1994, Eckenwalder 1976). It remained there for nearly 50 years until a strong case to merge the Taxodiaceae and Cupressaceae families was made on the basis of vegetative and reproductive traits from all life cycle stages (Eckenwalder 1976). Brunsfeld et al. (1994) confirmed through a cladistic analysis of genetic markers that including *S. sempervirens* and the other

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Taxodiaceae species (except *Sciadopitys*) in the Cupressaceae indeed created a monophyletic conifer lineage.

The application of genetic markers not only resolved the long-standing mystery of *S. sempervirens* evolutionary relationships with other species, but also enabled a new field of research to begin on inheritance and intraspecific diversity. Through neutral genetic marker studies (including allozymes, restriction length polymorphisms, and microsatellites) it has been shown that both chloroplast and mitochondrial DNA in *S. sempervirens* are paternally inherited (Neale et al. 1989) and there is evidence for an autoallopolyploid origin for this hexaploid species (Douhovnikoff et al. 2004, Rogers 1997). Genetic marker studies have further revealed a high frequency of clonality within stands, ramet distances of up to 40 m (Douhovnikoff et al. 2004), and common genetic diversity within fairy rings (Rogers 2000). In addition, genetic investigations have revealed a disjunction between northern and southern *S. sempervirens* populations (Brinegar 2011, Douhovnikoff and Dodd 2011). These findings demonstrate a need to integrate contemporary forest management and conservation practices with genetic screening so that forestry techniques can be used in the future with enhanced understanding of how stand manipulation directly impacts genetic diversity within stands and across the ecosystem range.

As the field of molecular genetics was developing in the late 20th century, a new field of research was beginning in the coast redwood forest. Ascension into *S. sempervirens* crowns with rope access techniques catalyzed the study of epiphytes, plants growing on tree crowns. Stephen Sillett's pioneering first investigations of species inhabiting the canopy transformed the world's perspective of biodiversity in the coast redwood forest, revealing a lush ecosystem more than 50 m above the ground. Structurally complex *S. sempervirens* crowns with reiterated trunks, massive limbs, and dead wood were found to support as much as 742 kg of epiphytic biomass in a single crown (Sillett 1999, Sillett and Van Pelt 2007). Numerous vascular plants, bryophytes, lichens, and microorganisms grow in the canopy (Carrell and Frank 2015, Sillett and Van Pelt 2000, Williams and Sillett 2007), but the most common species found in temperate rainforest sites was the leather leaf fern, *Polypodium scouleri*, a perennial epiphyte that grows extensive mats of succulent rhizomes and fibrous roots over branches (Sillett and Bailey 2003). Fern mats were shown to trap organic matter, rain, and fog, facilitating the development of arboreal soils that can form a layer up to 1 m deep and are characterized by low pH and low soil moisture content during the dry season (Enlow et al. 2006, Enlow et al. 2010, Sillett and Bailey 2003). These organic soils support a diverse arthropod community (Jones 2005) and cryptic vertebrates including the wandering salamander, *Aneides vagrans* (Spickler et al. 2006).

Within a few years of rope methods providing redwood canopy access, physiological research on *S. sempervirens* also expanded into the treetops. A common theme among these studies was the investigation of how climate influences redwood growth. Dendrochronology was applied to study whole-tree wood production by sampling cores from *S. sempervirens* crowns. Contrary to the long-standing assertion that growth rates decline as redwoods age (Fritz 1929), Sillett et al. (2015) showed unequivocally that old trees produce more wood than younger, smaller trees because of their higher leaf and cambium surface area for growth. By sampling wood cores and measuring bole volume at multiple heights, Sillett et al. (2015) documented the distribution of whole-tree wood production and important contribution of the tree crown to total wood volume which explained past observations of small annual growth increments at the tree base. In a complementary study, Carroll et al. (2014) decoded climatic signals embedded in *S. sempervirens* tree rings throughout the ecosystem range. Carroll and colleagues created the longest dendrochronological record for the species spanning 1,685 years, overcoming numerous obstacles including commonly missing rings that plagued coast redwood tree ring studies in the past. With the benefit of this new dendrochronological record and detailed whole-tree volume measurements across sites, Sillett et al. (2015) discovered that wood production in old-growth *S. sempervirens* forests throughout the ecosystem range has increased in recent decades, especially since the 1970s in the northern extent of the range.

Environmental changes in the 20th century caused this redwood growth surge, but the relative influence of abiotic factors is unknown (Sillett et al. 2015). Proposed climate changes affecting *S. sempervirens* include warming temperatures, increasing atmospheric carbon dioxide, and reduced air particulates from burning restrictions (Fernández et al. 2015, Sillett et al. 2015). In addition, declining fog in the 20th century (Johnstone and Dawson 2010) may contribute to the recent redwood growth surge because fewer foggy days increases solar radiation and promotes photosynthesis (Sillett et al. 2015).

The assertion that fog decline could stimulate *S. sempervirens* growth contrasted with more than 60 years of research that demonstrated the benefits of fog. Fog interception in the redwood forest and use as a water resource by *S. sempervirens* was first measured at ground level (Azevedo and Morgan 1974, Dawson 1998, Oberlander 1956), but once the canopy became accessible, Stephen Burgess and Todd Dawson made the remarkable discovery of sapflow reversal in *S. sempervirens* crowns during fog inundation (Burgess and Dawson 2004). This documentation of foliar uptake and direct atmospheric hydration in the canopy inspired a new cohort of researchers to study the benefits of fog for *S. sempervirens*. Specifically, it was shown that fog both raised the water status of *S. sempervirens* when soil moisture is low (Earles et al. 2016, Limm et al. 2009, Simonin et al. 2009) and delivered significant nitrogen to the forest (Ewing et al. 2009, Templer et al. 2015).

The short-term benefits of fog have not been refuted, but the recently documented redwood growth surge illustrates the challenge the scientific community faces to integrate our understanding across disciplines of how *S. sempervirens* responds to its complex environment. After nearly 250 years of botanical and ecological investigation into this iconic species, there is still compelling need to advance conservation and restoration science for the coast redwood forest. We know that the remarkable growth, longevity, and environmental resilience of redwood has allowed ancient *S. sempervirens* forests to accumulate record-breaking aboveground biomass of more than 5100 mg ha^{-1} over the millennia (Van Pelt et al. 2016), but the next centuries will be markedly different. The ecosystem's future depends on how the forest responds to anthropogenic forces of climate change, habitat fragmentation, and biodiversity loss in the years ahead.

To prepare ourselves for managing a vibrant coast redwood forest through the 21st century, we must strive to invest more in critical research fields that will improve our ability to sustain *S. sempervirens* and the ecosystem it defines. First, we need enhanced understanding of genetic adaptations in *S. sempervirens* to anticipate the species' ability to withstand further environmental change. With a majority of the coast redwood ecosystem undergoing continual forest management, it is critical to assess the genetic conservation status of the species and seek to sustain or restore genetic diversity throughout the ecosystem range to bolster *S. sempervirens* population resilience as conditions change. Second, we need better understanding of biodiversity in the forest to develop conservation strategies that recognize and support a broad range of interdependent native taxa. While there has been recent progress identifying macroepiphytes in the canopy, microbial diversity from the treetops to belowground and food web ecology is still poorly studied in the coast redwood forest. Third, we need to better understand the ecological cycles of fire, carbon, and nutrients that sustain ancient forest conditions so that we can restore vital processes on the landscape. Coast redwood forests today have dramatically reduced carbon storage from past logging activities and experience heavily modified fire and flood regimes, alterations that may further degrade the structure and function of this iconic ecosystem over time unless mediated.

To advance these frontiers of redwood research, we need continued public and private investment in science and a diversified scientific community to accelerate the field forward. Redwood research has proliferated most quickly in the past when new perspectives and methodological innovations entered the scientific community and we must facilitate the same opportunities in the century ahead.

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