Redwood Burls: Immortality Underground

Peter Del Tredici

The California coast redwood, *Sequoia sempervirens*, is famous for many reasons, not least for being the tallest tree in the world, reaching heights over three hundred feet under optimal growing conditions. Indeed, the tree is so spectacular that it has come to symbolize the grandeur and uniqueness of California itself. Since the earliest days of statehood, the redwood tree has played a major role in the lives of California's citizens. No one has described the importance of that role better than Willis Linn Jepson in his famous *Silva of California:*

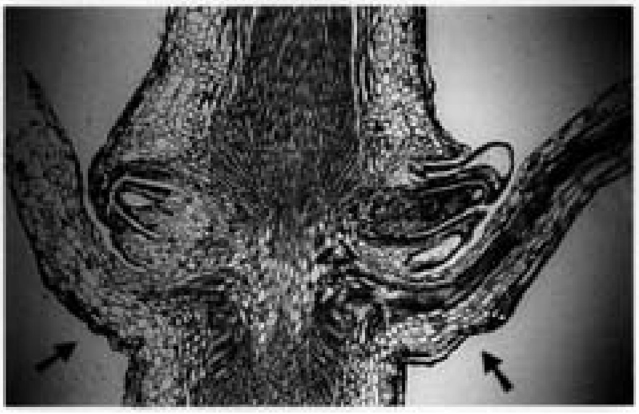
> The writer of these lines is a Californian. He was rocked by a pioneer mother in a cradle made of Redwood. The house in which he lived was largely made of Redwood. . . . He went to school in a Redwood schoolhouse, sat at a desk made of Redwood and wore shoes the leather of which was tanned in Redwood vats. Everywhere he touched Redwood. Boxes, bins, bats, barns, bridges, bungalows were made of Redwood. Posts, porches, piles, pails, pencils, pillars, paving-blocks, pipe lines, sometimes even policemen, were made of Redwood. . . .

From the tree's perspective, the love affair with the early Californians was perhaps a bit too intense, leading to the logging of over ninety percent of the tree's original range by the late 1950s. It is only through the efforts of private conservation groups, beginning in the 1920s, later by the State of California, and finally the National Park Service, that any of the original, uncut stands of trees exist today. As spectacular as these old-growth forests are, with their trunks disappearing into the fog that enshrouds the forest much of the year, they do not present a complete picture of the species. For that, one must visit redwood stands that were logged fifty to one hundred and fifty years ago. It is here that one finds the multi-trunked specimens that have sprouted from around the stumps of the original trees. In some redwood forests, the second generation of trunks have also been cut, leading to a third generation of sprout growth. Among conifers, the redwood is unique in its remarkable power of basal regeneration. To my mind it is the redwood's ability to resprout—its great vitality—that makes the tree worthy of admiration and study.

My own interest in the coast redwood goes back to my childhood in Marin County, California, where redwoods grow naturally on the slopes of nearby Mt. Tamalpais. Quite literally, I grew up with the tree in my backyard and spent a week every summer vacationing in their midst, along the banks of the Eel River. Even as a child it was hard not to recognize something special about the redwood tree, something that made it different from other trees. Had you asked me about it then, I'm sure I would have said something about their huge size or about the solemnity I felt in their midst, almost like being in church. Such quasi-religious feelings are expressed by nearly everyone who visits an old-growth redwood forest, but few people think about or are even aware of the tree's extraordinary powers of survival.

Studies of Tree Regeneration

Given my long personal connnection with the redwood tree, it's not surprising that I chose to study it later in life. Nor is it surprising that I chose to focus on the tree's ability to resprout following traumatic disturbance. I have been studying the regenerative powers of trees for many years, most notably in *Ginkgo biloba*, and it seemed only natural that I should turn to *Sequoia sempervirens* as a research subject, to see whether the redwood behaves similarly. With generous support from the Highsted Foundation in Redding, Connecticut, I was able to visit the center of the "redwood empire," near Eureka, California, to conduct a week of field



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A cross section of a 133-day-old redwood seedling clearly showing the well developed bud clusters in the axils of the cotyledons (indicated by arrows). The stem of the seedling, above the cotyledonary node, is about two centimeters in diameter.

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A five-year-old greenhouse-grown seedling showing the proliferation of suppressed buds at and above the cotyledonary node. Bar = 1.0 centimeter.

studies on vegetative regeneration and to collect seeds for cultivation in the Arnold Arboretum's greenhouses.

There are numerous reports in the literature of woody plants, primarily angiosperms, that possess the ability to resprout from underground burls, technically known as lignotubers. Anatomical studies of lignotuber formation in a number of species, including *Eucalyptus* in Australia (Carr et al. 1984), the cork oak *(Quercus suber)* of the southern Mediterranean (Molinas and Verdagues 1993), and *Ginkgo biloba* (Del Tredici 1992, 1997), have established that they form in seedlings as part of the trees' normal development. Lignotubers originate in buds located in the axils of the seed leaves (cotyledons) and a few of the leaves immediately above them.

At first these cotyledonary bud swellings are small, but over time they can become quite large and contribute to the survival of the tree in several ways: Primarily they are a site for the production and storage of suppressed buds that can sprout following traumatic injury to the primary stem. They are also a site for the storage of carbohydrates and mineral nutrients, which facilitate the rapid growth of these suppressed buds following stress or damage to the primary trunk. And finally, in the case of plants growing on steep slopes, the lignotuber can function as a kind of clasping organ that anchors the tree to the rocky substrate (Sealy 1949, Del Tredici et al. 1992). In general, lignotuber-producing species are most commonly found in Mediterranean-type ecosystems that are characterized by hot, dry summers and periodic fires.

Early Stages of Lignotuber Development

The forestry literature on *Sequoia* is clear about the commercial and ecological importance of the tree's ability to resprout after logging, but very little has been written about the precise origin of these sprouts in young plants. My observations on greenhouse-grown *Sequoia* seedlings indicate that lignotuber formation starts with the precocious development of buds located in the axils of the two cotyledons, just as it does in *Ginkgo* and *Eucalyptus*. Within the first six months of life, these buds proliferated to form distinct clusters that protruded from the

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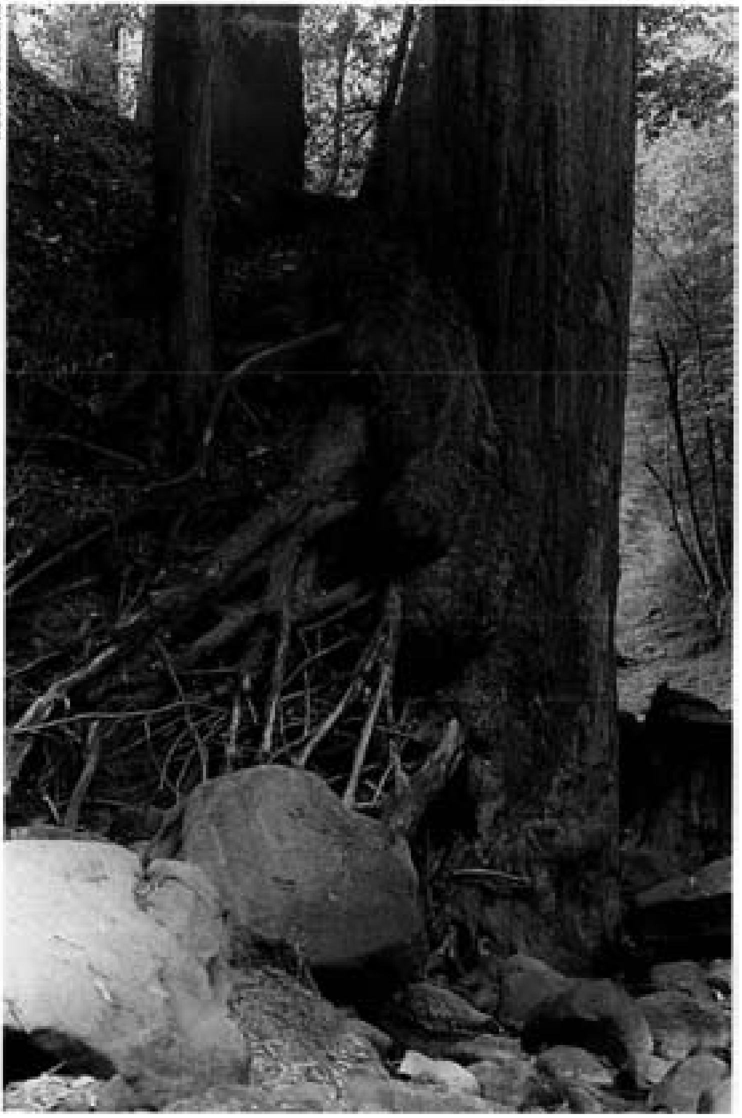


A large Sequoia *growing along a streambank in the Humboldt Redwoods State Park. It shows extensive root and trunk development from its exposed, downward-growing lignotuber*

stem and were clearly visible to the naked eye. In a few cases, one or two of these buds produce tiny leafy shoots within six months.

After a few years of cultivation in the greenhouse, nearly all of the young lignotubers were producing leafy shoots and the swelling of the stem associated with lignotuber formation had spread upward to engulf several nodes above the cotyledons.

With redwood seedlings growing in nature, the process of lignotuber development proceeds more slowly than it does in the greenhouse, mainly because the tiny plants are under severe environmental stress. In the wild, one typically finds redwood seedlings growing in areas that have experienced some form of disturbance, such as flooding or road maintenance, that had disturbed the topsoil, leaving the subsoil exposed. Under field conditions, most redwood seedlings do not form visible bud swellings at the cotyledonary nodes until they are between three and six years old. Interestingly, these tiny lignotubers often produce adventitious roots as well as leafy shoots in response to the partial burial that they experience following the heavy rains and erosion characteristic of the region.

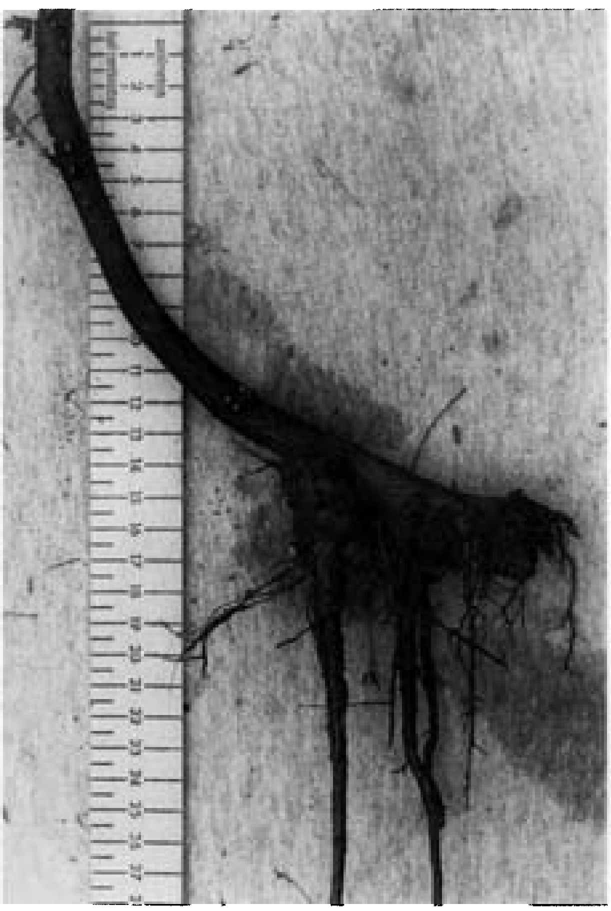
Lignotuber Development in Mature Trees

Lignotubers continue to expand throughout the life of a *Sequoia* tree, eventually forming massive swellings at or just below ground level, and their outer surface is literally covered with suppressed shoot buds. On undamaged trees, the lignotuber typically gives rise to clusters of small leafy shoots that ring the base of the trunk. On trees that have experienced damage, either from logging or erosion, the lignotuber can produce large secondary trunks that equal or exceed the primary trunk in size. Mature trees that were logged 90 to 100 years ago develop lignotuber sprouts well over a meter in diameter. When such second-generation trees are found growing on a steep slope near a stream or a roadcut, the woody lignotuber is readily recognized as a massive "plate" of downward-growing tissue that follows the contours of the ground and extends up to ten feet from the nearest trunk. On such sites, the lignotuber often develops into a kind of clasping organ that completely envelops large rocks, further stabilizing the tree. As well as giving rise to new shoots, such exposed lignotubers are also the source of new roots that help to anchor trees to the eroding slopes. Indeed, preliminary observations suggest that all of the roots that support a second-generation *Sequoia* sprout, regardless of its size, are generated by the lignotuber.

Induced Lignotubers on Layered Branches

Only once have I observed "layering" in *Sequoia.* Rudolf Becking, a retired ecologist from Humboldt State University, had taken me to see what he assumed was a group of "seedlings" that had germinated following a particularly severe flood in the 1960s. Closer examination showed that they were not seedlings at all. Rather, they were lateral branches of very weak, spindly saplings that had been bent over by limbs falling from the nearby canopy trees and had taken root and reestablished a vertical orientation. Typically, a single, downward-growing lignotuber had developed along the side of the branch in contact with the soil, although in a few cases several lignotubers had formed along the length of the buried stem. On such layered branches, the original connection to its parent trunk had mostly withered away, leaving only the bowed shape of the stem and the off-center lignotuber as evidence of its origin in a branch.

As is the case with lignotubers derived from the cotyledonary node, those formed by layered branches possess the ability to generate both buds and roots. How long it takes for a branch to develop a lignotuber after it has been pinned to the ground is not known, but it is probably at least a year or two. From the ecological perspective, the layering ability of redwood seedlings appears to give them some flexibility in



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A layered lateral branch of Sequoia. *Note that the downward-growing, induced lignotuber has produced both roots and a vegetative shoot Bar = 1 0 centimeter*

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An ancient Sequoia *in Big Basin Redwoods State Park showing massive burl development on its trunk.*

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A trunk burl purchased in a Eureka, California, gift shop that is producing both roots and shoots after six months in the greenhouse

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A fallen redwood tree resprouting from its basal lignotuber.

responding to environmental conditions by migrating from areas of shade into areas with better light.

Redwood Burls

The large lignotuber-like structures that are sold in redwood country gift shops are commonly called burls. They develop not below ground, as true lignotubers do, but on the lower portions of the trunks of old redwood trees in response to injury from fire, wind, or flooding. Typically, trunk burls form above the point of injury to the stem and eventually grow out and down to cover the wound. In some cases, particularly when damage to the tree is extensive, great tongues of tissue project from the trunk—two feet or more—creating bizarre structures that resemble the gargoyles on medieval cathedrals. When these structures come in contact with the ground, they can develop both roots and shoots. Indeed, there has long been a cottage industry in the redwood region based on the harvesting of burls for sale to tourists. When placed in a dish of water with the cut side down, they will produce leafy shoots within a week or two. They can even be induced to produce roots after six months to a year if kept in a warm greenhouse with plenty of light and water. Interestingly, only when the orientation of the burl on the tree is reversed—putting the cut side down—will buds sprout out.

My preliminary observations of wild trees suggest that these burls originate on the trunks of old redwoods as wound-induced callus tissue that incorporates nearby buds into its ever-expanding mass. There appear to be two distinct types of burls on *Sequoia* trunks. The "gargoyle" type, usually located on the lower portions of the trunk, is irregular in shape, grows outward and downward, and is covered with sprouts or buds. The second type occurs higher on the trunk; it is nearly hemispherical in shape, does not grow downward, and produces comparatively few sprouts or buds.

In general, trunk burls can be interpreted as a case of uncontrolled bud and cortex proliferation induced by old age, traumatic injury, or environmental stress. The ecological function

A forest of redwoods in Korbel, California, resprouting from their lignotubers three years after clear-cutting.

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A postcard showing what is believed to be the largest Sequoia *lignotuber ever reported. It was 41 feet across, weighed approximately 525 tons, and supported at least seven large trunks The burl was uncovered in 1977 at Big Lagoon near Eureka, California.*

COURTESY OF THE BURL BROTHERS

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A ring of "second generation" redwoods that sprouted from the lignotuber after the primary trunk was logged approximately one hundred years ago

of trunk burls is to produce new shoots and adventitious roots on trees that have been partially buried under silt from flooding or that were leaning such that they come in contact with the soil (Stone and Vasey 1968). While trunk burls with basal lignotubers are similar, it is important to keep in mind that the lignotuber formed at the cotyledonary node is under strict genetic control, while burls that develop on the stem are under environmental control. In this regard, *Sequoia* is similar to *Ginkgo biloba*, which also produces lignotubers from the cotyledonary node as well as burls on its trunk and branches (Del Tredici 1992, 1997).

The Economics of Lignotubers

Regardless of the age or size of the parent tree, redwood lignotubers can resprout within two to three weeks of logging. While most of these sprouts die before reaching maturity, enough of them survive to regenerate the forest. A study of an old-growth forest that had been clearcut five to ten years earlier showed that the rate of resprouting was greatest in trees that had been between 200 and 400 years of age at the time of cutting and it decreased rapidly thereafter, such that trees more than 1,000 years old resprouted at only 20 to 25 percent of the peak rate (Powers and Wiant 1970). The researchers found that 92 percent of all surviving sprouts grew from the lignotuber, 6 percent from the remains of the trunk, and 2 percent from the cut, horizontal surface of the stump. For trees growing on a slope greater than 20 percent, the sprouts were more numerous on the downhill side of the trunk than on the uphill.

The remarkable ability of redwood trees to resprout from lignotubers, regardless of age, is clearly the basis for the redwood's vitality in the face of massive over-harvesting by the timber industry. Essentially, logging has transformed *Sequoia sempervirens* into a clonal organism that slowly expands its range by lignotuber sprouting. The potential dimensions of the redwood lignotuber were first suggested by W. L. Jepson, who described a clump of 45 large redwoods that formed a third-generation "fairy ring" fifty feet by fifty-six feet across. The photo on page 19 shows a giant lignotuber that has been exposed by erosion near the city of Eureka, California.

The Ecology of Lignotubers

The importance of lignotuber sprouting to the forestry industry has been abundantly documented, but very little information is available on its ecological significance in the absence of

Unlike most redwoods that sprout from the basal lignotuber, this unusual specimen has sprouted along the entire length of its prostrate trunk, producing a linear grove of trees

logging. In a 1987 study of an uncut *Sequoia* forest, J. D. Stuart found that basal sprouting in redwood is closely associated with fire. By correlating fire scars on the primary trunk of the tree with basal sprouts from its lignotuber, the author determined that during the presettlement period (between 1775 and 1875), fires occurred regularly at the site, at an interval of about 25 years. Other studies on the cut stumps of old-growth trees also support the idea that fires were common prior to European settlement and that redwood trees are well adapted to survive them (Fritz 1931, Jacobs et al. 1985, Finney and Martin 1992).

These findings from California redwood forests are consistent with studies in other Mediterranean-type climates, which indicate that lignotuber-producing angiosperms are common in areas where fire or other types of frequently recurring disturbances (for example, grazing) are common (James 1984, Mesleard and Lepart 1989). These studies also suggest that, in the absence of logging, sprouting from the lignotuber probably has much greater ecological significance for seedlings and saplings growing in dense shade or on exposed slopes than it does for mature trees (Canadell and Zedler 1994).

It is also worth noting that the trunk of a redwood tree above the basal lignotuber has the ability to resprout following damage from wind, fire, or flooding. At the turn of the century, when fire was commonplace in the redwood region, there were frequent reports of large trees whose foliage had been entirely burned off vigorously sprouting to form lush "fire columns"(Jepson 1923, Fritz 1931). Similarly, I have seen one wind-felled tree sprout new growth along the entire length of the fallen trunk.

Rejuvenation

Both morphologically and physiologically, the lignotuber-generated shoots produced by mature redwoods are considered "juvenile" relative to the shoots on the rest of the tree. This conclusion is supported by *in vitro* studies that demonstrated that tissue cultures started with lignotuber shoots from the base of a 90-year-old *Sequoia* were more vigorous and rooted more readily than those started with shoots from the crown of the same tree (Bon et al. 1994). The researchers also identified numerous membrane-associated proteins that were synthesized in greater abundance in cultures derived from lignotuber shoots than those derived from the upper portions of the tree.

In light of this and other similar studies, it is not surprising that as long ago as 1950 *Sequoia* should have been the first conifer to be successfully cultured using *in vitro* techniques, by Ernest Ball, and that these cultures were started from lignotuber sprouts. Quite literally, the *Sequoia* lignotuber can produce physiologically juvenile shoots continually throughout most of its long life. This ability endows the tree with a kind of ecological immortality—by which I mean that as long as environmental conditions remain constant, the tree can live forever, or at least until it's uprooted.

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