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A Redwood Tree Whose Crown is a Forest Canopy

Abstract

Ancient redwood trees (*Sequoia sempervirens*) often have complex crowns consisting of multiple, resprouted trunks. This study focuses on a single redwood tree, which is known as the Redwood Creek Giant, growing in Tall Trees Grove of Redwood National Park, CA. It is the sixteenth tallest (109.8 m) known living tree and the twentieth largest (744.7 m³ wood volume) known living redwood. The main trunk, which is 5.6 m in diameter at the base and still over 3 m in diameter at 65 m, is devoid of branches for 54 m. Above this height, its crown becomes a forest; there are a total of 148 resprouted trunks arising from the main trunk, other trunks, or branches. Five of these trunks exceed 1 m basal diameter, and twelve of them are between 0.5 and 1 m basal diameter. The largest resprouted trunk is 40 m long. Many of the trunks are fused to other trunks and/or branches. The tree's crown, which begins above 50 m, is over 25 m diameter 100 m above the ground. A variety of vascular plant species grow as epiphytes in this tree, including two ferns (*Polypodium scolopendri* and *P. glycyrrhiza*), a shrub (*Vaccinium oxatum*), and two trees (*Lithocarpus densiflorus* and *Umbellularia californica*). The highest recorded epiphytic tree, an *U. californica*, grows from a knothole 98.3 m above the ground.

Introduction

The tallest and most massive forests on Earth are dominated by *Sequoia sempervirens* (D. Don) Endl. (hereafter 'redwood'). Individual redwood trees can reach 112 m in height, and individual redwood forest stands can have a biomass of over 3,000 metric tons per ha (Sawyer et al. 1999). Despite their impressive stature, however, very little was known about the biology of redwood forest canopies until the late 1990s, when rope-based canopy research began at Humboldt State University.

Like many other conifers, young redwood trees grow via a simple architectural model (sensu Hallé et al. 1978) consisting of a single vertically oriented trunk that supports numerous horizontally oriented branches. Older redwood trees, however, may have multiple resprouted trunks arising from other trunks and branches. These extra trunks are reiterations of the tree's architectural model, and each one supports its own system of branches. They appear to arise in response to increased light availability caused by either crown damage or the creation of nearby canopy gaps (Hallé et al. 1978, Sillett 1999). Reiterations in ancient redwood trees may account for over 10% of a tree's total wood volume (Sillett 1999).

Crown-level complexity promotes biological diversity in redwood forest canopies. A variety

of vascular plants, including ferns, shrubs, and trees normally found on the forest floor, flourish in deep humus accumulations in ancient redwood tree crowns (Sillett 1999). The crown humus is also home to a variety of animals, including arthropods, mollusks, earthworms, and salamanders that breed in the canopy (pers. obs., Welsh and Wilson 1995). Rotten wood in dead branches and hollow trunks also provides substrates for ericaceous shrubs, which are pollinated by bees and produce abundant crops of berries that are consumed and dispersed by birds (Sillett 1999).

In the course of our investigations of old-growth redwood forest canopies, we encountered a redwood with an astonishing crown. From a distance, its broad crown could easily be mistaken for several large trees standing close together. Using rope-based methods of access, we explored this tree in order to quantify its crown structure and to assess the distribution and abundance of resident vascular epiphytes.

Study Area

This study focused on a single 109.8-m tall redwood in Redwood National Park, Humboldt County, California. The tree is known as the Redwood Creek Giant (hereafter 'RCG'). It grows at 37 m elevation in Tall Trees Grove, which is on an alluvial terrace of Redwood Creek. The old-

growth forest canopy of the grove is overwhelmingly dominated by redwood. *Acer macrophyllum* Pursh, *Lithocarpus densiflorus* (Hook. & Arn.) Rehder, and *Umbellularia californica* (Hook. & Arn.) Nutt. occur in the understory and lower canopy. A few *Pseudotsuga menziesii* (Mirb.) Franco occur in the old-growth forest on the slope just east of the terrace. The forest across Redwood Creek was logged prior to Park acquisition in 1978. The RCG grows in a well-protected location at the northeastern edge of the terrace. Eighteen redwood trees over 90 m tall grow within a 100 m radius of it.

Methods

Tree Access

We accessed the RCG by shooting a rubber-tipped fiberglass arrow trailing 10 kg test strength Fireline® filament through a crotch formed by several reiterated trunks at 70 m with a compound bow mounted to a spinning reel. A 3 mm nylon cord, followed by an 11 mm static kernmantle climbing rope, was then hauled over the crotch. We anchored one end of the rope at ground level and climbed the other using mechanical ascenders. We used a 20 m long arborist's rope lanyard fitted with a double-end, split-tail system (Sherrill Arborist Supply, Inc.) to access progressively higher trunks and branches and to move laterally through the crown. A rescue pulley was secured near the top of the tree with a tubular nylon webbing sling. The climbing rope was lowered from the tree on nylon cord at the end of the day, and the pulley was used to haul the rope back into place for subsequent ascents. We explored the tree crown for seven days in December 1998 and January 1999.

Crown Mapping

We mapped crown structure of the RCG by measuring heights, diameters, and distances between reiterated trunks. The tree's total height was measured by lowering a graduated fiberglass tape from the topmost foliage to the forest floor with ground contact via radio. Numbered aluminum tags were attached to major trunks at 5 m intervals with 2 cm paneling nails. We used these tags as benchmarks for height measurements of smaller trunks, branches, and epiphytes. Aluminum tags were also used to label individual trunks for future refer-

ence. We recorded the following data for each reiterated trunk: top height, height of origin, basal diameter, and diameter at 5 m intervals along the length of the trunk. For reiterated trunks arising from branches, we also recorded horizontal distance to main trunk, branch height, branch basal diameter, and branch diameter at reiteration. Trunks were referenced to each other by recording azimuths and distances between them at 5 m height intervals. We used an Impulse® laser range finder (Laser Technology, Inc.) to measure vertical and horizontal distances between trunks. All other measurements were made with the aid of a compass, clinometer, and graduated fiberglass tape. Since large trunks often gave rise to complex arrays of smaller trunks, we sketched crown structure and noted physical connections between trunks and branches. We also noted whether trunks were monopodial (i.e., consisting of a single axis), sympodial (i.e., consisting of successive axes), or otherwise broken. All of this information was used to generate a tree crown diagram via DeltaGraph® and ClarisDraw® software for the Macintosh® computer.

Crown Illustration

In addition to mapping crown structure, we also made a detailed illustration of the entire tree as visible from Redwood Creek. Major branches, clumps of foliage, burls, and kinks were noted on a sketch, and heights to these landmarks were measured with the Impulse® laser. We then took photographs of all portions of the crown from as far away from the tree as possible. The illustration itself started with a 'skeleton,' which was based on the height and diameter measurements taken both from within the crown and from the ground. We used the photographs to provide details of foliage, branches, and bark texture. The illustration was drawn at 1/120 scale, and people were added for additional scale.

Epiphyte Sampling

We nondestructively measured sizes and locations of all vascular epiphytes occurring on the RCG. For each fern mat, we measured number of living fronds, maximum frond length, maximum frond order (i.e., rows of pinnae per frond), mat length, and mat width. For each shrub, we measured number of stems, maximum stem basal diameter, total length, and maximum crown width.

Similarly, we measured trunk basal diameter, total length, and maximum crown width for epiphytic trees. In addition to these variables describing epiphyte size, we measured height above ground, distance and azimuth to main trunk, and diameter of supporting branch beneath epiphyte (if present).

Data Analyses

We used linear regression analysis to explore relationships between crown structure variables (i.e., height of origin, total length, basal diameter, wood volume, distance from main trunk, branch basal diameter, and branch diameter at reiteration). Correlations were separately evaluated for all reiterated trunks and for the subset of reiterated trunks arising from branches. Wood volume was calculated by applying two different equations to the trunk diameter data. We used the equation for a parabolic frustum (i.e., $\text{volume} = \text{length}/2 * [A1 + A2]$, where A1 and A2 are the upper and lower trunk cross sectional areas) for reiterated trunks and upper sections of the main trunk that tapered rapidly. We used the equation for a regular conic frustum (i.e., $\text{volume} = \text{length} * \pi/3 * [(\text{lower diameter})^2 + (\text{lower diameter}) * (\text{upper diameter}) + (\text{upper diameter})^2]$) for sections of the main trunk that tapered slowly.

Results

Crown Structure

At 109.8 m (360.2 feet) tall and 744.7 m³ (26,298 feet³) wood volume, the RCG is the sixteenth tallest known living tree and the twentieth largest known living redwood (Figure 1, Sawyer et al. 1999). The most remarkable feature of the RCG, however, is neither its height nor its wood volume. There are a total of 148 reiterated trunks arising from the main trunk (n = 12), other trunks (n = 81), or branches (n = 55). Five of these trunks exceed 1 m basal diameter, and twelve of them are between 0.5 and 1 m basal diameter (Figure 2). The RCG's reiterations account for 14 percent of its total wood volume.

Trunk wood volumes in the RCG span seven orders of magnitude (Figure 3). Reiterated trunks arising from the main trunk are up to ten times larger than the largest trunks arising from other reiterations (Figure 3). Thirty-three of the RCG's trunks give rise to other reiterations, and wood

volume of the reiterations is positively correlated with the wood volume of the supporting trunk (Table 1). Trunk wood volume is also positively correlated with total length, basal diameter, and branch diameter at reiteration (Table 1).

In addition to those involving wood volume, there are several other significant correlations among the crown structure variables (Table 1). Longer trunks tend to occur lower in the crown; height of origin is negatively correlated with total length. Longer trunks also tend to occur on larger branches; branch diameter at reiteration is positively correlated with total length. Thicker branches support larger trunks than thinner branches; branch basal diameter and branch diameter at reiteration are positively correlated with trunk basal diameter. Finally, trunk basal diameter is strongly correlated with total length.

A more detailed description of the RCG proceeds with an examination of the crown illustration (Figure 4) and the crown diagram (Figure 5). Unlike most other tall (i.e., over 105 m) redwoods, whose upper crowns are usually thin and spindly, the RCG has a very top-heavy crown. The main trunk, which is 5.56 m diameter at the base and still over 3 m diameter at 65 m, is devoid of branches for 54 m. Above this height, its crown proliferates. Eleven trunks extend above 105 m, twenty trunks extend above 100 m, and the crown diameter between 70 and 100 m is over 25 m.

The first major reiteration (hereafter 'trunk I') emerges from the main trunk at 53.8 m (right side of Figure 5). A massive burl from the main trunk is fused with it between 57.2 and 59.4 m, and the diameters of both trunks are greater above the fusion than below it. Trunk I, which is 1.1 m basal diameter, 31.3 m long, and 14.8 m³ wood volume, supports 42 other reiterated trunks. Most of these trunks arise from a complex array of branches up to 6 m long and 74 cm basal diameter. The three largest branches in this array are fused together in several places.

Four reiterations emerge from the main trunk between 66.1 and 69.9 m (left side of Figure 5). Their precise origins are difficult to determine because a deep layer of crown humus supporting ferns and shrubs has accumulated in the crotch (hereafter 'main crotch') formed at the base of these trunks and the main trunk. The largest of the reiterations (hereafter 'trunk II') forming the

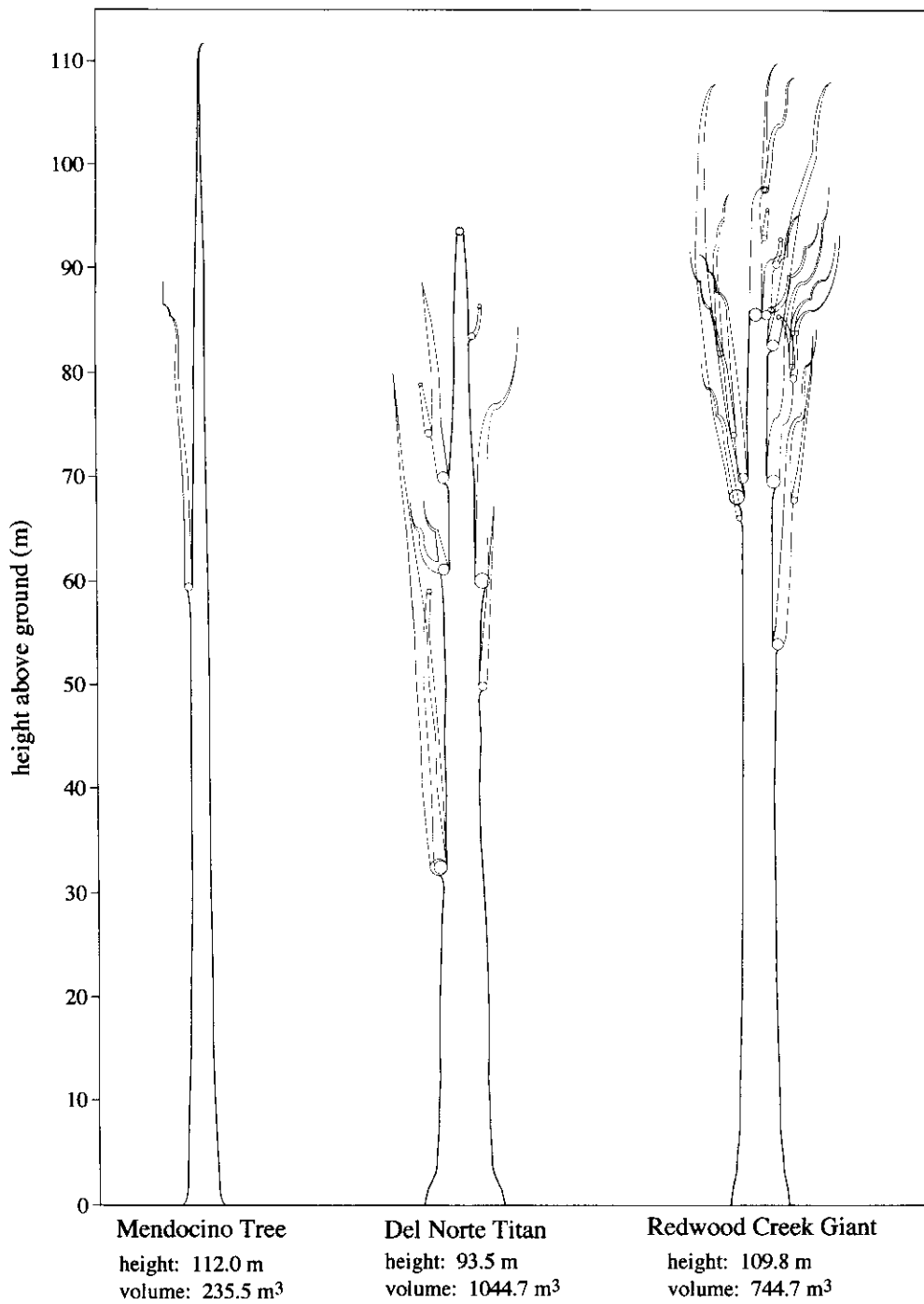


Figure 1. Scale diagram comparing crown structures of the tallest (Mendocino Tree, Montgomery Woods State Reserve, CA) and largest (Del Norte Titan, Jedediah Smith Redwoods State Park, CA) known living redwoods to the Redwood Creek Giant. Circles correspond to the basal diameters of reiterated trunks. Only trunks greater than 0.5 m basal diameter are shown. For each tree, distances between reiterated trunks are drawn relative to the presumed central axis of its main trunk. All distances are drawn to the scale of the y-axis.

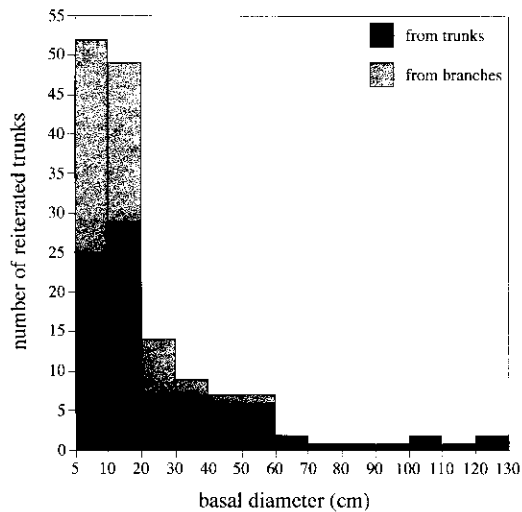


Figure 2. Size distribution of reiterated trunks on the Redwood Creek Giant by basal diameter. Trunks arising from other trunks are distinguished from those arising from branches.

main crotch is 1.3 m basal diameter, 40.0 m long, and 28.6 m³ wood volume. Trunk II is the largest reiteration on the RCG, and it supports 21 other reiterated trunks. Above 90 m, most of these trunks sweep to the south, having been sculpted by winds moving up Redwood Creek from the Pacific Ocean. Several of trunk II's reiterations are fused together, including two trunks that are fused to the same branch. Many of the lesser reiterations on trunk II and the other trunks emerging from the main crotch are sympodial, having lost successive leaders in storms. Another reiteration (hereafter 'trunk III') emerging from the main crotch is 1.0 m basal diameter, 20.7 m long, and 6.5 m³ wood volume. Trunk III and most of its 14 reiterated trunks extend out into the large canopy gap above the Tall Trees Grove loop trail.

Another major reiteration (hereafter 'trunk IV') emerges from the main trunk at 69.6 m (right side of Figure 5). Trunk IV is 1.3 m basal diameter, 28.8 m long, and 13.6 m³ wood volume. It supports

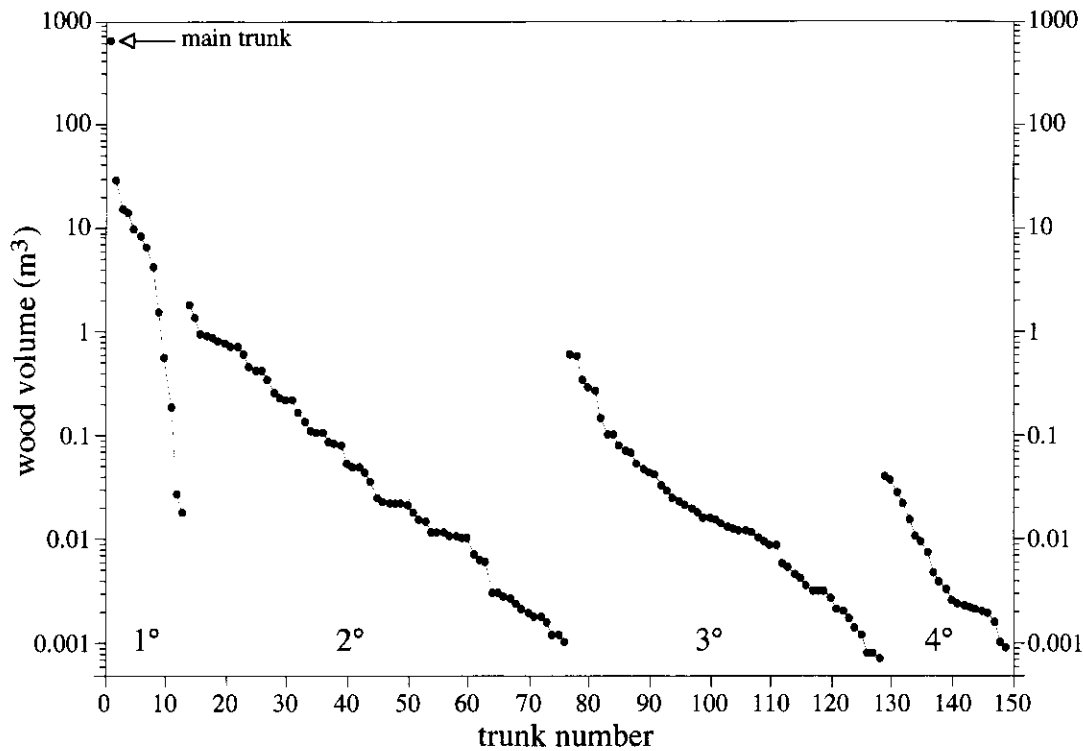


Figure 3. Ranked size distribution of trunks on the Redwood Creek Giant by reiteration hierarchy and wood volume. Trunks are separated into five classes (i.e., main, 1°, 2°, 3°, and 4°) on the basis of reiteration hierarchy. Reiterations arising directly from the main trunk are considered primary (1°) trunks, reiterations arising directly from 1° trunks are considered secondary (2°) trunks, and so on.

TABLE 1. Summary of product-moment correlation coefficients (r) between crown structure variables for reiterated trunks on the Redwood Creek Giant. Broken trunks ($n = 13$) were excluded from correlations for total length and volume. Correlations for supported wood volume were based only on unbroken trunks that supported other reiterated trunks ($n = 25$). Correlations statistically significant ($P \leq 0.01$) are highlighted in bold.

All reiterated trunks ($n = 148$)						
	Height of origin	Total length	Basal diameter	Wood volume		
Total length	-0.31					
Basal diameter	-0.14	0.92				
Wood volume	-0.20	0.84	0.81			
Supported wood volume	-0.46	0.82	0.87	0.86		

Reiterated trunks arising from branches ($n = 55$)						
	Height of origin	Total length	Basal diameter	Wood volume	Distance from main trunk	Branch basal diameter
Total length	-0.29					
Basal diameter	-0.20	0.89				
Wood volume	0.00	0.73	0.88			
Distance from main trunk	-0.28	-0.14	-0.28	-0.27		
Branch basal diameter	-0.32	0.29	0.41	0.31	-0.08	
Branch diameter at reiteration	-0.27	0.50	0.68	0.47	-0.28	0.67

27 other reiterated trunks, including three trunks with snapped tops. Trunk IV itself is sympodial with a complex history of breakage and reiteration. A dead, snapped trunk leads into a rotten hollow near its base. A 0.7 m diameter trunk arises from trunk IV at 79.5 m. It is forked at 83.9 m, and both lesser trunks reach almost 95 m. A branch from one of these lesser trunks is completely fused with the other trunk at 85.0 m (not shown in Figure 5). Remarkably, this 11.1 m long branch remains alive and vigorous despite the fact that it is now detached from its trunk of origin. An 8 cm gap now separates the branch from its original source of water and nutrients. Since breaking away, the diameter of this transplanted branch has increased by 2 cm.

At 82.7 m, yet another major reiteration (hereafter 'trunk V') emerges from the main trunk (right side of Figure 5). Trunk V is 1.1 m basal diameter, 25.9 m long, and 9.5 m³ wood volume. It supports five other reiterated trunks.

The main trunk is snapped at 85.4 m, where it gives rise to 3 major reiterations. The largest of these (hereafter 'trunk VI') is 1.1 m basal diameter, 12.3 m long, and 8.0 m³ wood volume. It supports 12 other reiterated trunks. At 97.7 m,

trunk VI is broken and gives rise to two reiterations, including the trunk bearing the highest foliage on the RCG. Two of trunk VI's reiterations are broken with snapped tops. Trunk VI is fused with another major reiteration (hereafter 'trunk VII') at 88.1 m. Trunk VII is 0.9 m diameter at the base, 1.0 m diameter above the fusion, and 8.2 m long with a broken top. It gives rise to 11 other reiterated trunks, including one broken and one sympodial trunk. An old raven (*Corvus corax*) nest is perched in the crotch formed by trunk VII and the other trunk (hereafter 'trunk VIII') arising from the snapped top of the main trunk. Just above the nest, a branch from trunk VII is fused with trunk V, although the branch is now dead. Trunk VIII is sympodial and extends out into a crown gap near the top of trunk IV.

Epiphyte Distribution

We found five species of vascular epiphytes growing on the RCG (Table 2). The shrub *Vaccinium ovatum* is the most numerous species with 10 individuals. Eight of the shrubs grow on dead branches, from the tops of broken trunks, or from rotten hollows in trunks that lacked crown humus accumulations. Two of the shrubs grow from

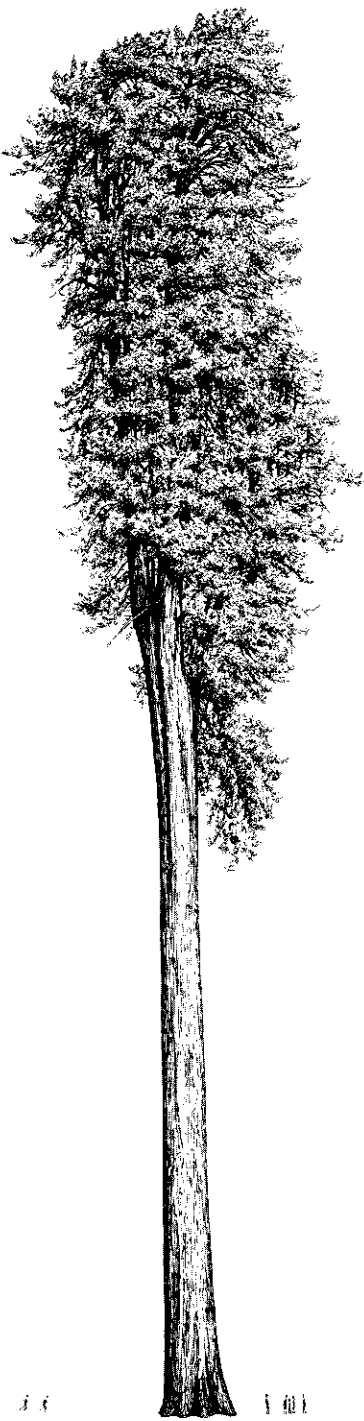


Figure 4. Illustration of the Redwood Creek Giant prepared by Dr. Robert Van Pelt on the basis of crown structure data and photographs taken from Redwood Creek.

deep (i.e., > 50 cm) humus in the main crotch. This crown humus is also exploited by ferns, including one of the largest epiphytes on the tree: a *Polypodium scolieri* fern mat with 36 fronds up to 75 cm long. A small *P. glycyrrhiza* fern mat also grows in the main crotch. Crown humus and epiphytes in the main crotch store water, some of which drips down the trunk to form a splash zone that is exploited by a lush growth of bryophytes. Two fern mats, one of each species, grow beneath the raven nest in the crotch formed by trunks VII and VIII. One *P. glycyrrhiza* mat grows on the top of a broken trunk at 92.1 m. Two *P. glycyrrhiza* mats grow on dead branches at 86.7 m and 83.2 m. Three epiphytic trees grow on the RCG. One *Umbellularia californica* grows on a dead branch at 84.8 m. Another *U. californica* grows from trunk II at 98.3 m. It may be the highest vascular epiphyte on Earth. Finally, a *Lithocarpus densiflorus* grows on a dead branch at 82.1 m.

Discussion

The RCG is neither the tallest nor the largest living redwood, but it certainly has one of the most complex crowns. No known redwood has as many reiterations as the RCG; the most complex redwood previously studied has only 62 reiterated trunks (Sillett 1999). The cause of the RCG's tremendous crown-level complexity is unknown, but repeated exposures to crown fires and high winds probably contributed to it. Evidence of crown fires is commonly observed in ancient redwood trees (Sillett 1999). Several fire scars are evident beneath the break in the RCG's main trunk at 85.4 m, suggesting that its original trunk may have been lost during a fire. The RCG's upper crown is exposed to high winds during storms, and wind-sculpting of the trunks and branches is evident, especially above 90 m. While exploring the upper crown in early December, we were suddenly hit by a storm with gale-force winds. The major reiterations swayed back and forth wildly. Such independent movement of reiterated trunks initiates wound responses as sections of the crown abrade one another in the wind. Ultimately, many such wounds lead to fusions between trunks and branches.

The prevalence of trunk-to-trunk ($n = 7$), trunk-to-branch ($n = 11$), and branch-to-branch ($n = 3$) fusions in the RCG indicate that the hydraulic architecture of its crown is convoluted. Fusions

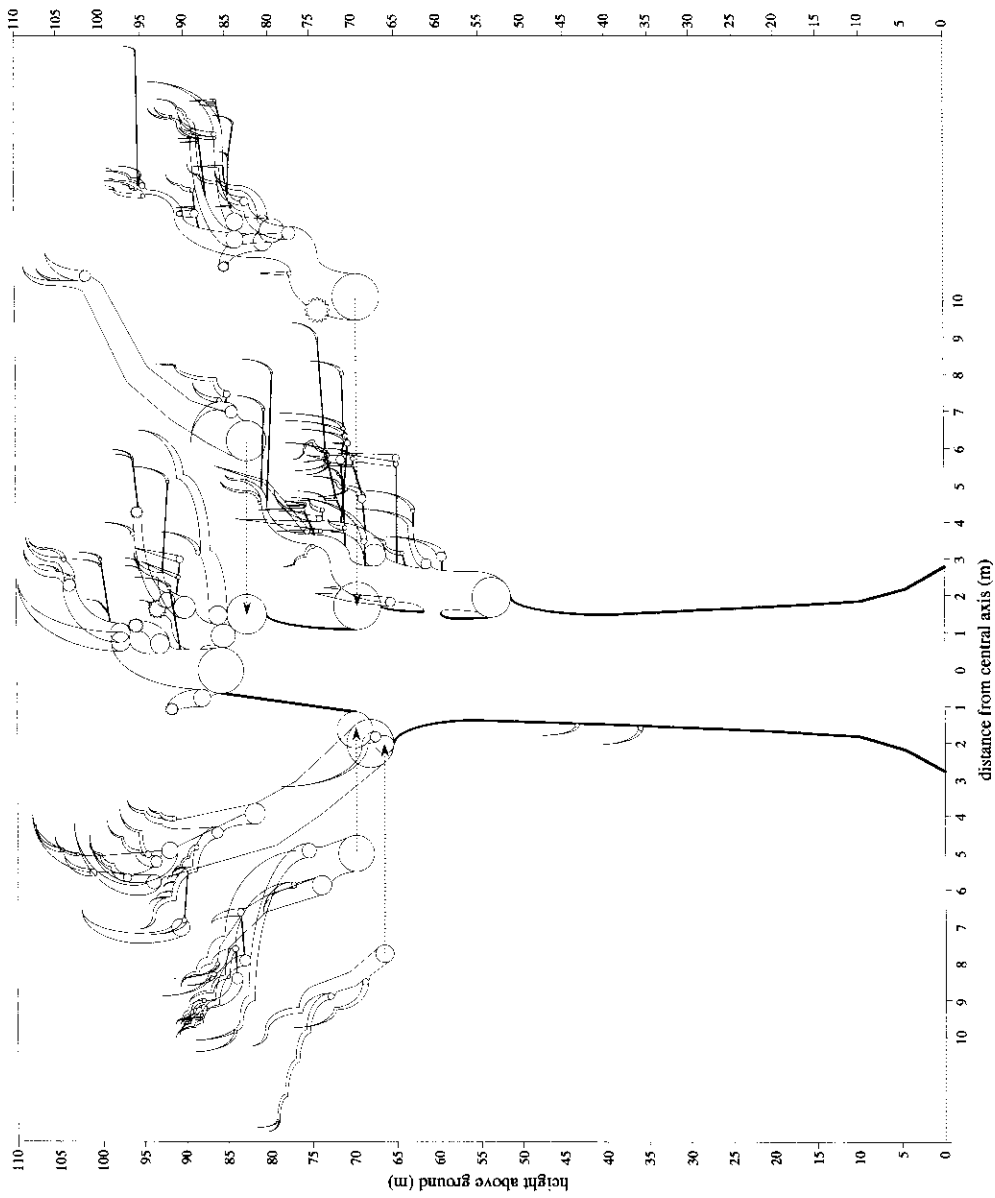


Figure 5. Crown diagram of the Redwood Creek Giant. Unlike Figure 1, all trunk diameters are drawn to the scale of the x-axis, which is expanded relative to the scale of the y-axis. Circles correspond to the basal diameters of reiterated trunks. Circles with serrated edges indicate broken trunks. Branches bearing reiterated trunks are depicted with single straight lines. No other branches are shown.

TABLE 2. Summary of vascular plants occurring as epiphytes in the crown of the Redwood Creek Giant. Mean values for each variable are listed along with ranges in parentheses.

Species	N	Height above ground (m)	Size of tree, mat. or shrub		Number of stems or fronds	Maximum stem diameter (mm)	Maximum frond length (cm)
			length (cm)	width (cm)			
<i>Lithocarpus densiflorus</i>	1	82.2	31.0	15.0	1.0	3.0	—
<i>Polypodium glycyrrhiza</i>	5	82.7 (66.5–92.1)	37.4 (15.0–80.0)	17.8 (1.0–45.0)	13.6 (3.0–23.0)	—	19.2 (9–27)
<i>Polypodium scolieri</i>	4	77.3 (66.7–89.8)	65.5 (20.0–180.0)	30.2 (5.0–70.0)	14.2 (3.0–36.0)	— (6–75)	35.0
<i>Umbellularia californica</i>	2	91.6 (84.8–98.3)	28.5 (22.0–35.0)	6.5 (5.0–8.0)	1	5.5 (3.0–8.0)	—
<i>Vaccinium ovatum</i>	10	84.0 (66.2–95.3)	80.2 (16.0–176.0)	89.4 (31.0–225.0)	8.5 (2.0–38.0)	12.6 (3.0–22.0)	—

divert the flow of water and nutrients through the tree's vascular tissues. Two pieces of evidence support this assertion. First, trunk diameters are consistently greater above fusions than below them (see also Sillett 1999). Second, the branch on trunk IV that fused with another trunk survives even though it is no longer attached to its original trunk. In addition to affecting the RCG's hydraulic architecture, crown fusions may increase the tree's architectural strength, thus reducing the severity of crown breakage during storms. They also provide platforms for humus accumulation and epiphytes.

The deepest crown humus accumulation, which occurs in the main crotch, supports the richest growth of vascular epiphytes on the RCG. Compared to many other large redwood trees, however, the RCG is rather depauperate in crown humus and vascular epiphytes. Most of the RCG's epiphytes occur close to the central axis of the tree either in crotches or on rotten wood above the break in the main trunk. Very few vascular epiphytes inhabit the massive reiterated complexes sprouting from the main trunk below 85 m; crown humus accumulations are completely lacking.

Crown humus and vascular epiphytes are often abundant far from the main trunk on reiterated trunks in large redwoods of Prairie Creek Redwoods State Park and Jedediah Smith Redwoods State Park (Sillett 1999). Occurrence of the RCG in a drier microclimate than these areas may account

for this difference. Tall Trees Grove lies in the rain shadow of a steep 400–800 m tall ridge that protects Redwood Creek from the ocean, while the groves studied by Sillett (1999) are more exposed to moisture-laden air coming directly from the ocean. Rarity of vascular epiphytes in the tall redwood forests of Humboldt Redwoods State Park and Montgomery Woods State Reserve (pers. obs.), both of which are located inland away from direct ocean influence, supports this hypothesis. Thus, despite its unrivaled complexity, most of the RCG's crown may be inhospitable to vascular epiphytes requiring year-round access to a moist substrate.

Only one species of vascular epiphyte growing on the RCG has not been previously observed on other redwoods. *Umbellularia californica* is a common understory tree in many redwood forests. Its fleshy drupes must have been dispersed high into the crown of the RCG by birds. The individual growing at 98.3 m had only four living leaves, and its roots were located 20 cm down inside a knothole that collects stemflow.

In conclusion, the RCG challenges our concepts of individual tree crowns and forest canopies. In normal usage, trees have crowns and forests have canopies. With 148 reiterated trunks, several of which are as large as full-size trees in other forests, the crown of the RCG can be viewed as a forest canopy. This tree and others like it dramatically illustrate that the distinction between trees and forests is a small one.

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