TRUNK REITERATION PROMOTES EPIPHYTES AND WATER STORAGE IN AN OLD-GROWTH REDWOOD FOREST CANOPY

STEPHEN C. SILLETT[1,3] AND ROBERT VAN PELT[2]

[1]*Department of Biological Sciences, Humboldt State University, Arcata, California 95521 USA*
[2]*College of Forest Resources, University of Washington, Seattle, Washington 98195 USA*

Abstract. *Sequoia sempervirens* (redwood) is a long-lived, shade-tolerant tree capable of regeneration without disturbances and thus often present in all sizes within a single forest. In order to evaluate functional linkages among structures, plant distribution, and biodiversity in the canopy, we quantified all vascular plants from ground level to the treetops in an old-growth redwood forest (Prairie Creek Redwoods State Park, California, USA). This involved mapping terrestrial and epiphytic trees, shrubs, and ferns as well as climbing 27 trees up to 101 m tall within a 1-ha plot. We monitored canopy microclimates using sensor arrays that collected hourly data for up to 30 months. The plot held 4283 Mg/ha of aboveground dry mass in living plants, 95.4% of which was contributed by redwood. A high degree of structural complexity and individuality was evident in the crowns of the 14 largest trees in the form of reiterated trunks arising from main trunks, other trunks, and limbs. Thirteen species of vascular plants occurred as epiphytes in the plot, and all but one of these were restricted to the 14 largest trees. The evergreen shrub *Vaccinium ovatum* had the highest biomass of any epiphyte (212 kg/ha) followed by the evergreen fern *Polypodium scouleri* (196 kg/ha). The spatial aggregation of reiterated trunks was highly coincident with epiphyte masses, explaining 92% of the variation in fern and 75% of the variation in woody plant distribution along the vertical gradient. In addition to epiphyte biomass, there were 2366 kg/ha of soil in the canopy. Soils in crotches held 2–4 times as much water as soils on branches or limbs, and deeper layers held more water than shallower layers. During two years of monitoring, the volume of water stored in dead wood and soils in the canopy fluctuated between 24.7 m^3 and 53.4 m^3/ha. The vast majority of the plot's structure and arboreal habitats was held in the crowns of the 14 largest trees. Reiterated trunks and limbs on a small number of trees have important ecological functions in old-growth redwood forests, and it may be feasible to accelerate the development of structural complexity and biodiversity in maturing redwood stands.

Key words: canopy-soil epiphytes; old-growth redwood forest structure; Prairie Creek Redwoods State Park, California, USA; Sequoia sempervirens; structural complexity; trunk reiteration.

INTRODUCTION

Important components of forest communities, including mammals, birds, arthropods, and epiphytes, often increase in abundance and diversity late in stand development because they require structures or substrates that emerge slowly as trees grow (Kelly et al. 1993, Ralph et al. 1995, Lindenmayer 1997, Winchester et al. 1999, Rosso et al. 2000, Sillett and Antoine 2004). Since the perennially exposed surfaces of trees expand with radial growth, there tends to be more surface area available for colonization by arboreal species on old compared to young trees. Having survived more disturbances, old trees also possess a greater diversity of arboreal habitats than young trees, because non-lethal injuries stimulate new growth from damaged regions of the crown (Hallé et al. 1978). Despite these obvious consequences of tree size and age, understand-

ing how tree structure promotes biodiversity has been hampered by the complex three-dimensional nature of forest canopies. Advances in techniques to access and quantify tree crowns (e.g., Van Pelt et al. 2004) now allow detailed examinations of tree structures and the habitats they create. Old-growth forests provide the best opportunities to study these functional linkages.

Much of our knowledge of old-growth forest ecology in western North America comes from forests dominated by shade-intolerant members of the Pinaceae (e.g., *Pseudotsuga*, *Picea*, or *Pinus*). Even before European colonization, forests containing living trees over 700 years old were rare in this region, because the dominant species are vulnerable to insects, fire, and wood-decay fungi and rarely reproduce beneath their own canopy (Franklin and Waring 1980). A major exception among North American coniferous forests is provided by *Sequoia sempervirens* (hereafter 'redwood'), a member of the Cupressaceae. Redwood is shade-tolerant, highly resistant to fungi, and capable of living more than 2000 years (Sawyer et al. 2000c). This longevity enables redwood to produce considerably larger branches,

limbs, and reiterated trunks than exist in forests dominated by Pinaceae. Redwood also regenerates with or without fire, replacing itself during stand development (Van Pelt and Franklin 2000, Busing and Fujimori 2002). Catastrophic, stand-replacing fires are unknown in northern redwood forests (sensu Sawyer et al. 2000c), but nearly all large redwoods in these forests show signs of having survived fires capable of killing other tree species (S. C. Sillett, *personal observation*). Even if the main trunk is heavily damaged or killed by fire, redwoods readily produce new foliage through epicormic branching or basal sprouts from lignotubers (Stuart 1987, Del Tredici 1998, 1999). This adaptation to fire, unusual in Cupressaceae (Farjon 2005), allows genetic individuals of redwood to persist indefinitely even in fire-prone forests.

Early growth of many conifers, including redwood, proceeds according to a genetically determined architectural model characterized by a single, orthotropic, and monopodial main trunk bearing numerous, plagiotropic, and monopodial branches. Trees retaining this simple growth form are known as "model conforming." Breakage of the main trunk stimulates the production of reiterated trunks that arise from the broken main trunk at or below the break (Hallé et al. 1978). Some of these originate as plagiotropic shoots that bend upward, becoming orthotropic, and others arise directly as orthotropic shoots. Regardless of their initial orientations, these reiterated trunks grow orthotropically and each produce new plagiotropic branches. In some cases, a single reiterated trunk will reestablish apical control of the crown, and the tree continues to resemble one that is model conforming except that it now has a kink between the main and the reiterated trunk. In other cases, multiple reiterated trunks arise and compete with each other. The crowns of tall, old conifers often contain dozens of reiterated trunks emerging from the main trunk, other trunks, and limbs (Sillett and Van Pelt 2000, 2001, Van Pelt 2001; R. Van Pelt and S. C. Sillett, *unpublished manuscript*). Trees possessing reiterated trunks are no longer considered model conforming and can be highly individual in form.

Some ecological consequences of tree individuality became apparent during the earliest rope-based scientific investigations of old-growth forests, when it was noted that epiphytes were nonrandomly distributed on tree surfaces (Denison 1973, Pike et al. 1977). Many epiphyte species exhibit preferences for particular structures in tree crowns. For example, mosses are often best developed on the thickest tree branches (Clement and Shaw 1999), and other epiphytes, notably certain rare cyanolichens (Sillett 1995, Sillett and McCune 1998), occur most frequently amidst moss mats. Over 200 species of lichens and bryophytes occur in the crowns of large redwoods where main trunks, reiterated trunks, and limbs support distinctive communities (Williams and Sillett 2007). Despite high species richness, nonvascular epiphytes are sparsely distributed on redwoods compared to adjacent and much younger *Acer*, *Picea*, *Pseudotsuga*, *Tsuga*, and *Umbellularia* trees (Ellyson and Sillett 2003; S. C. Sillett, *personal observation*). Even so, large redwoods can support hundreds of kilograms of epiphytic ferns and several species of epiphytic shrubs and trees (Sillett and Bailey 2003) in water-holding canopy soils developing beneath ferns on limbs and in crotches at the bases of reiterated trunks (Enloe et al. 2006). Lush growth of ericaceous shrubs is associated with pockets of decaying wood (Sillett 1999).

Moisture availability has been implicated as the primary factor limiting the distribution of epiphytes in forests worldwide (Zotz and Hietz 2001, Sillett and Antoine 2004), and a variety of desiccation-sensitive organisms appear to depend on the water stored within epiphyte mats in redwood forest canopies. For example, lungless salamanders (*Aneides vagrans*; Spickler et al. 2006) and aquatic crustaceans (harpacticoid copepods; Jones 2005) inhabit fern mats up to 80 m above the ground in old redwoods. Other microclimatic variables, notably light and temperature, also influence arboreal biota in forest canopies (Parker 1995), and vascular epiphytes themselves affect air temperature and humidity within tree crowns (Freiberg 1997, 2001, Ambrose 2004). The extent to which microclimatic gradients of moisture, light, and temperature co-vary with gradients of structural complexity in forests and the degree to which these two sets of factors influence species distributions in the canopy remain poorly explored.

Understanding the role of tree structures in creating canopy habitats has become increasingly important, as little old-growth forest remains. Over 95% of old-growth redwood forests have been logged (Noss 2000, Sawyer et al. 2000a). Protection of the few remaining stands in State and National Parks is essential for conservation, but the long-term effectiveness of this strategy is uncertain. Landscapes dominated by plantations with small reserves may be inadequate for maintaining regional biodiversity (FEMAT 1993). The vast majority of redwood forests that grew up in the wake of early logging have been logged again. Today, second-growth forests originating before 1930 are scarce, and nearly all of the forests within the redwood region are younger than rotation age (~50 years), with canopies <40 m tall. Redwoods in these forests almost always lack reiterated trunks; they are model-conforming trees with dense, conical crowns and small branches. As a consequence of their simple structure, the biological diversity of young redwood forests is extremely low. Epiphytic vascular plants, canopy soils, and many animals associated with old-growth forests are now virtually restricted to the Parks (Cooperrider et al. 2000, Sawyer et al. 2000b). Our present study was motivated by recognition of these profound differences between old-growth and younger redwood forests.

We undertook a detailed investigation of a very old and complex redwood forest to elucidate functional relationships among structures and habitats within the

canopy and to quantify the distribution and diversity of plant species. Our research addressed three main questions: (1) How do individual trees contribute to whole-forest structure and diversity of arboreal habitats? (2) To what extent does the distribution of epiphytes depend on forest structures along the vertical gradient? and (3) How much do vascular epiphytes and their substrates affect biodiversity through modification of canopy microclimates? To answer these questions we quantified the distributions and dimensions of all vascular plants within a 1-ha plot and measured the light, moisture, and temperature regimes of epiphyte habitats in large tree crowns. The research proceeded in three phases: (1) establishing the plot and mapping vegetation at ground level, (2) climbing trees and mapping every reiterated trunk, limb, and vascular epiphyte in the canopy, and (3) installing sensor arrays to monitor canopy microclimates.

METHODS

Site selection and description

The study plot was located between 52 and 60 m elevation in Prairie Creek Redwoods State Park (41°22′ N, 124°1′ W), California, USA. Forests along the gently sloping valleys of this 5700-ha reserve are dominated by redwood but also contain several other tall conifers, including *Picea sitchensis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*, as well as a wide variety of angiosperm trees and shrubs. A rectangular plot was centered on a very large redwood known as Atlas Tree, which was the site of the earliest work on crown structure, epiphytes, and microclimates in redwood forests (Sawyer et al. 2000*b*). The plot extended eastward and westward from Atlas Tree to include exactly 1 ha (320 × 31.25 m).

The stand we selected for this investigation is not typical of large tracts of forest; it was chosen to represent particularly well-developed, low-elevation redwood forest on the north coast of California. Comparable redwood forests now occur elsewhere only in this reserve and in parts of Jedediah Smith Redwoods State Park (41°47′ N, 124°6′ W). In 2003 and 2004, which were similar to the long-term mean, annual rainfall in these forests ranged from 1503 to 2080 mm with 97% occurring from November to May. During the same period, air temperatures ranged from 0° to 21°C during the winter and 7° to 33°C during the summer (see *Monitoring canopy microclimates*, below).

Stand mapping

The 1.0-ha reference stand was established by stretching a fiberglass tape 320 m east to west to establish a central axis. Distances perpendicular to the tape were measured, using a survey laser (Impulse 200LR [Laser Technology, Centennial, Colorado, USA]) and compass, for all trees ≥1.37 m tall (breast height). The *x* and *y* coordinates (easting and northing) were measured to the presumed center of every trunk,

and the *z* coordinate (elevation) of every tree base was measured with a survey laser relative to ground level at the base of Atlas Tree. Trees were excluded if trunk centers were beyond the ends of the tape or >15.625 m from the tapeline. Diameter at breast height (dbh) was measured relative to average ground level (the midpoint between the highest and lowest ground levels around the base of the trunk). For every tree in the plot we used a survey laser and compass to measure total height, crown depth, crown radius, and lean. Total height was determined by measuring both the vertical distance from the laser to the treetop and from the laser to average ground level, where the laser was held in a fixed position near ground level. Crown depth is the difference between total height and height to crown base, defined as the height above which live foliage occupied more than a 120° arc around the trunk. Crown radii on trees ≥5 cm dbh were measured from trunk center to the outermost branch along the cardinal directions with trees >400 cm dbh receiving supplemental measurements in the subcardinal directions. Tree lean is the horizontal displacement and azimuth of the treetop relative to trunk center; with total height, these data allowed calculation of trunk length. *Corylus* and *Vaccinium* shrubs, and all trees <5 cm dbh yet taller than 50 cm, were quantified over the whole plot with measurements of basal diameters, crown depths, crown diameters, and total heights. The same measurements were made for *Rubus* and all remaining shrubs and trees <50 cm tall but only within a 1.6 m × 320 m subplot centered on the whole plot. Crowns of shrubs, *Tsuga*, and model-conforming redwoods were modeled as paraboloids, angiosperms and *Pseudotsuga* were modeled as 2/3 ellipsoids, and highly reiterated redwoods were modeled as 1/3 ellipsoids based on a visual assessment of crown shapes and the proven utility of this approach in other studies (Van Pelt and North 1996; R. Van Pelt and S. C. Sillett, *unpublished manuscript*).

These measurements were used to estimate aboveground component masses of every angiosperm and model-conforming conifer in the plot by applying regression equations and ratios derived from this or previous studies (Appendix A). Components estimated for model-conforming conifers were trunk surface area (in square meters), trunk volume (in cubic meters), trunk mass (in kilograms), branch mass (in kilograms), leaf mass (in kilograms), and projected leaf area (in square meters). To improve estimates of trunk areas and volumes for redwoods, a taper model was developed by measuring trunk diameters at many heights throughout 20 model-conforming trees with a Criterion 400 (Laser Technology). Whole-tree leaf area was calculated as a multiple of sapwood cross-sectional area at the base of the live crown (SA_{BLC}, Stancioiu and O'Hara 2005). The taper model was used to estimate trunk diameter at the base of the live crown (D_{BLC}, Appendix A). Estimates of bark and sapwood thicknesses at the base of the live crown (BT_{BLC} and ST_{BLC}, respectively) were

then used to calculate sapwood area using the following equation:

$$SA_{BLC} = \pi(D_{BLC}/2 - BT_{BLC})^2$$
$$- \pi(D_{BLC}/2 - BT_{BLC} - ST_{BLC})^2 \quad (1)$$

where BT_{BLC} and ST_{BLC} were estimated from published equations (Appendix A). Redwood branch mass was estimated by applying the equation for *P. menziesii* since we found that this equation accurately predicted the branch mass of a 112-m-tall redwood whose branches had been surveyed in previous studies (Sawyer et al. 2000*b*; R. Van Pelt and S. C. Sillett, *unpublished data*). Redwood leaf mass was calculated by dividing each tree's estimated projected leaf area by the specific leaf area (4.893 m^2/kg; Jennings 2002). For angiosperm trees, leaf mass was calculated as the difference between crown mass and stem mass. Total mass of *Rubus* shrubs was calculated as the sum of stem mass and leaf mass, while stem mass of *Corylus* and *Vaccinium* shrubs was calculated as the difference between total mass and leaf mass. We were unable to find or to develop equations for the evergreen *Vaccinium ovatum*, so its leaf mass was conservatively estimated by an equation for *V. alaskense*, and its total mass was estimated by combining equations for *V. alaskense* and *V. parvifolium* (Appendix A).

Stand-level biomass of the nonwoody terrestrial plants *Oxalis* and *Polystichum* was estimated from measurements within 1-m-diameter subplots sampled at 1-m intervals along the tapeline of the whole plot. Aboveground dry mass (in kilograms) of *Oxalis* was estimated from percent cover (mass = [0.4625 × % cover]/1000; Means et al. 1994) and converted to projected leaf area (in square meters; area = 43.342[mass]; $n = 41$ plants). Aboveground dry mass (in kilograms) of *Polystichum* was estimated by one of two regression equations (for densely covered plots, mass = [−4.577 + 0.0644 × frond height × no. fronds]/1000, or, for sparsely covered plots, mass = [0.6209 + 1.9256 × percent cover]/1000; Means et al. 1994) and converted to projected leaf area (in square meters; area = 8.644[mass]; $n = 7$ fronds).

The volume of dead wood on the ground was estimated as the sum of two size classes. Ends of logs >1 m in diameter were mapped along with the original stand map, and end diameters were measured to the nearest centimeter. Volumes were calculated as conic frusta using lengths and end diameters. Pieces of wood <1 m in diameter were surveyed along the plot tapeline by recording the length of tape overlaying each piece as well as its diameter. Lengths of transect covered were summed for five diameter classes of dead wood (5–10, >10–25, >25–50, >50–75, and >75–100 cm). Cross-sectional areas of each class were estimated as π(midpoint radius)^2. For each diameter class, wood volumes (in cubic meters) were calculated as the product of cross sectional area (in square meters), proportion of transect

covered by the class, and the ratio of total plot area to midpoint diameter (in meters). All pieces of wood were further categorized by species (if possible) and decay stage (1–5, with higher numbers being the more advanced stages of decay; Harmon et al. 1986).

Crown mapping

Mapping of trees and other vegetation began in 1996 and continued through 2003. Tree climbing was used to map crowns of all conifers possessing reiterated trunks ($n = 27$ trees, all redwood). While on rope within these 27 trees, we examined all remaining trees in the plot for presence of reiterated trunks or epiphytic vascular plants other than *Polypodium glycyrrhiza*. A rubber-tipped fiberglass arrow trailing Fireline filament was shot with a compound bow over sturdy branches up to 89 m above the ground, and the filament was used to haul a nylon cord followed by an 11-mm-diameter rope over the branches. One end of the rope was anchored at ground level, and the other end was climbed with mechanical ascenders. Once within the crown, access to the treetop and horizontal movement were achieved by standard arborist-style (Jepson 2000) or other specialized (Dial et al. 2004) climbing techniques. A pulley was secured near the treetop with a nylon sling, safe climbing paths were established on opposite sides of the crown, and nylon cord was used to lower the rope from the tree at the end of each day as well as to haul it back into place for subsequent ascents. After completion of field work in 2003, pulleys, cords, and ropes were removed from the forest.

The total height of each tree was determined to within 10 cm by lowering a weighted tape from the treetop to average ground level. Within trees, trunks were identified by origin (ground, trunk, limb) and classified hierarchically by growth history (main trunks give rise to first-order reiterated trunks, which give rise to second-order trunks, and so on). A limb was defined as a branch segment connecting a higher-order trunk to a lower-order trunk. We counted segments of sympodial trunks (reiterated segments linked below a single leader). Diameters were recorded to 1 mm at intervals no greater than 5 m along main trunks and reiterated trunks of basal diameter ≥ 4 cm. All reiterated-trunk diameter measurements were accompanied by measurements of height above ground and distance and azimuth (horizontally, pith to pith) to the main trunk. For limb segments connecting trunks, we measured height of origin, basal diameter, distal diameter, and path length (distance along limb between trunks). Trunks and limbs were sketched, recording details of crown form including fusions, buttresses, burls, and regions of dead wood (estimated as percentage of total volume).

Crown measurements were used to develop a three-dimensional Cartesian coordinate system within which all trunks and limbs were mapped (Appendix B). Each trunk and limb segment was modeled as a cone or conical frustum using basal and distal diameters. For

each reiterated trunk arising from another trunk, the portion of the main trunk directly beneath its measured base was modeled as an inverted cone (hereafter "buttress") sharing the trunk's basal diameter. This required calculation of the x, y, z coordinate where the lower tip of the buttress touched the perimeter of the supporting trunk. For most reiterated trunks, buttress z values were estimated by subtracting a distance equal to trunk basal diameter from the trunk's height of origin. For reiterated trunks with enlarged buttresses, buttress z values were estimated as the height where the supporting trunk's diameter was no longer influenced by the reiteration (i.e., where its cross-section became circular). These calculations were used to adjust the supporting trunk's diameter and avoid overestimation of its volume and surface area. When necessary, supplemental x, y coordinates and diameters were calculated by linear interpolation of existing data. On leaning trees, all x, y coordinates were adjusted by the main trunk's displacement from vertical at every z value.

Mistakes made during field measurements or data entry were screened prior to final calculations by two successive error-checking procedures (Appendix B). The first procedure corrected errors in basal and buttress x, y coordinates of every reiterated trunk arising from another reiterated trunk. This involved an iterative search for the coordinates that forced the distance between modeled trunk centers to equal the sum of their radii at the height of the reiterated trunk's origin (i.e., where its basal diameter was measured). The second procedure corrected other errors and involved the development of a rotating computer model for each tree using Microsoft Excel. In these models, x, y coordinates of trunks were offset by adding and subtracting trunk radii at every z value to depict them as separate polygons in two-dimensional plots viewed from an angle perpendicular to the x, z plane. Limb segments were depicted as line segments. Visual inspection of the full plot of every tree as it was rotated through 360° permitted quick identification of errors (e.g., free floating or overlapping trunks or limbs), which were then corrected on a case by case basis.

Error-checked data from crown mapping were used to estimate dimensions of a tree's trunks, limbs, and branches. The x, y, z coordinates were used to calculate the length, surface area, and volume of each trunk and limb segment, treating segments as frusta of cones. For limb segments, path length was substituted for length in calculations of surface area and volume. Values for segments were summed to derive totals for each trunk and limb. Trunk surface areas were then used to estimate the mass and volume of each trunk's branches. Crown correction factors (range: 0–1), which were used to reduce the estimated mass of branches on a trunk in proportion to the occupancy of its crown space by reiterated trunks, were calculated as trunk surface area/(trunk surface area + reiterated trunk surface area). The branch mass of each main trunk was calculated by multiplying its crown correction factor by the estimated branch mass for a model-conforming *P. menziesii* of equivalent size (i.e., 0.626 + 0.00079[dbh]^2[length]; Means et al. 1994). The branch mass of each reiterated trunk was calculated by multiplying its crown correction factor by half the estimated branch mass for a model-conforming *T. heterophylla* of equivalent size (i.e., 0.00134[basal diameter]^2[length]; Means et al. 1994), because *T. heterophylla* was the only shade-tolerant conifer for which such an equation was available, and both *T. heterophylla* and redwood reiterated trunks have branches extending nearly to their bases. Halving the values avoided overestimation of branch masses on reiterated trunks, which are highly asymmetrical by virtue of their nested positions with the larger tree crown. Thus, our estimates of redwood branch masses were conservative. Branch volume of each trunk was calculated as dry mass divided by density, and dry masses of trunks and limbs were calculated as volume times density. The density of limbs and branches was conservatively estimated as 125% of the trunk wood density reported for redwood (400 kg/m^2; Wood Density Database [*available online*])[4] based on unpublished data. As with model-conforming redwoods, projected leaf area of reiterated redwoods was assumed to be proportional to SA_{BLC}.

We used Ripley's K, a spatial statistic that defines the type and scale of pattern among groups of objects (Ripley 1981), to quantify the distribution of trunks (including reiterated trunks) at different heights in the forest. This univariate measure considers all trunk-pair combinations at each horizontal distance and compares observed patterns to random patterns generated by Monte Carlo simulations. We used the shifting-torus method described by Lotwick and Silverman (1982) to calculate K values at 0.2-m distance intervals from stem maps prepared for the whole plot. Trunks of all species were included in the analysis. Unlike previous uses of Ripley's K to define the scale of understory and overstory plant interactions at ground level (Moeur 1993, Van Pelt and Franklin 2000), we performed this analysis on 20 different stem maps at 5-m height intervals up to 90 m above the ground.

Epiphyte mapping

After crown mapping, all epiphytic vascular plants were mapped and measured. We recorded height above ground and substrate (branch, limb, crotch, or trunk) for each epiphyte. For epiphytic shrubs, crown radius (in meters) and crown depth (in meters) were measured with a tape and used to calculate crown volume as a paraboloid. A functional basal diameter (in centimeters) of each shrub was then estimated with the following equation using data collected from terrestrial shrubs:

$$\text{diameter} = (\text{crown volume}/\alpha)^{\beta} \qquad (2)$$

where $\alpha = 0.0816$, $\beta = 0.4057$, and volume is expressed in cubic meters ($n = 23$ shrubs, $R^2 = 0.874$). This procedure was necessary because epiphytic shrubs often consisted of a dozen or more stems of widely varying diameters emanating from the substrate. Leaf and stem masses of epiphytic shrubs were estimated using functional basal diameters. For epiphytic trees, trunk length and basal diameter were measured with a tape and used to calculate stem volume as a paraboloid. All other calculations for epiphytic shrubs and trees were identical to those for terrestrial plants (Appendix A). For *Polypodium scouleri* ferns, which occur in discrete clumps (hereafter "mats"), mat length (in meters), mat width (in meters), and substrate type (branch, limb, or trunk) were recorded. A metal probe was used to assess soil depth (in meters) beneath ferns by inserting the probe through the mat perpendicular to the substrate and taking the average of several measurements. These measurements were used to calculate the elliptical surface area and volume (area × depth) of each mat. Maximum frond length and maximum frond order in each mat were also measured, where frond length (in centimeters) was the distance from surface of the mat to the tip of the farthest pinna and frond order was calculated as $0.5(1 + \text{number of pinnae})$. The following regression equations, modified from Sillett and Bailey (2003), were used to estimate component dry masses (in kilograms) of each fern mat:

$$\text{total mass} = 32.912(\text{mat volume})$$
$$+ 0.0250(\text{maximum frond length}) \qquad (3)$$

$$\text{frond mass} = 1.274(\text{mat volume})$$
$$+ 0.00257(\text{maximum frond order}) \qquad (4)$$

$$\text{rhizome mass} = 1.257(\text{mat volume})$$
$$+ 0.00146(\text{maximum frond length}) \qquad (5)$$

where volume is expressed in cubic meters and length is expressed in centimeters ($n = 18$ fern mats, $R^2 = 0.995$, 0.983, and 0.846, respectively). Soil and root mass was calculated as total mass minus frond mass minus rhizome mass. Projected leaf area (in square meters) of *P. scouleri* was calculated as $4.653(\text{frond mass})$ (in kilograms, $n = 10$ fronds). Mats of canopy soils not associated with *P. scouleri* were also quantified by measuring their lengths, widths, and depths, and their dry masses (kg) estimated as $10.397(\text{mat volume})$ (Bailey 2000). To facilitate calculations of soil water content, mat volumes were partitioned into 30-cm-deep strata, where the volume of each stratum was calculated as a proportion of soil depth.

Monitoring canopy microclimates

Microclimatic conditions within tree crowns were quantified by a combination of continuous monitoring and periodic spot measurements. Five large redwoods, three in Prairie Creek Redwoods State Park in or near the study site and two in a comparable forest along Mill Creek in Jedediah Smith Redwoods State Park, were equipped with solar-powered sensor arrays (Fig. 1) with readings taken at hourly intervals. Stored data were periodically downloaded from dataloggers via radio.

Light sensors, air temperature/humidity probes, and tipping-bucket rain gauges were attached to branches, limbs, or trunks throughout the crown, at the treetop, and near vascular epiphytes (Fig. 1). The internal temperature and moisture regimes of epiphytic substrates were also quantified. Temperatures of canopy soil beneath *P. scouleri* mats and of decaying wood supporting *V. ovatum* or *T. heterophylla* were measured with temperature probes embedded in the center of the substrate.

Volumetric water contents of canopy soil and dead wood were measured via time-domain reflectometry (TDR). Each probe was connected to a reflectometer housed inside a waterproof enclosure in the crown. In soil mats, TDR probes were inserted either vertically through the substrate ($n = 21$ probes) or parallel to the surface of a supporting limb at 15 cm ($n = 2$ probes), 45 cm ($n = 2$ probes), and 75 cm ($n = 1$ probe) depths such that probes were centrally embedded in 30-cm-deep strata. Since TDR is influenced by the dielectric properties of the substrate being monitored, laboratory calibration was required to convert the waveform output to a direct measure of volumetric water content (Appendix C). The final regression coefficients and intercepts were then included in the datalogger program to automatically convert the waveform output from the probes into volumetric water content.

Hourly light data were expressed as transmittance fraction and estimated as the proportion of photosynthetically active radiation (in micromoles of photons per square meter per second) received at each within-crown sensor compared to the sensor mounted 1 m above the highest leaves on Atlas Tree. Canopy light environment was also measured by hemispherical photography and a balloon-launched sensor. Within-crown light availability was quantified via digital photography on overcast days. Forty-four hemispherical photographs were taken directly above leaves in the inner and outer crowns of five large redwoods trees using a camera with a fisheye lens on a self-leveling mount (Jennings 2002). Additional photographs were taken at ground level and directly above the six light sensors in the crown of Atlas Tree (see Fig. 1). Hemispherical photographs were analyzed using WinScanopy (version 2002a, Régent Instruments [Quebec City, Quebec, Canada]) to calculate light availability expressed as canopy openness. Canopy openness was converted to transmittance fraction using the following equation derived from the sensors in Atlas Tree that collected hourly data for exactly one year:

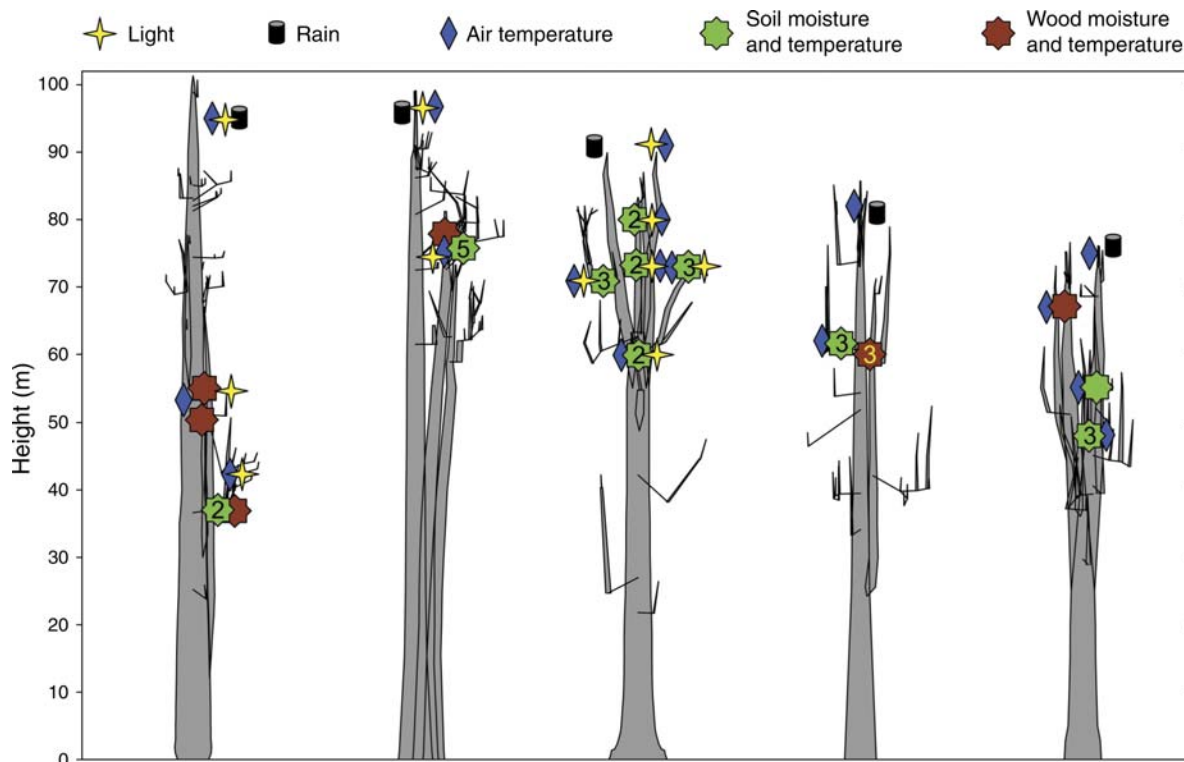$$\text{transmittance} = 0.0106(\text{canopy openness}) \qquad (6)$$

Fig. 1. Locations of microclimate sensors in crowns of five *Sequoia sempervirens* trees in Prairie Creek (three on left) and Jedediah Smith (two on right) Redwoods State Parks, California, USA. In each tree, a rain gauge and one or two other sensors were mounted as high as possible. Only those in Atlas Tree (center) were completely above all leaves. Within tree crowns, light and air-temperature sensors were located 1 m above vascular epiphytes. Soil and wood sensors were embedded in substrates beneath these epiphytes. The numbers inside the symbols for moisture and temperature sensors indicate replication. All sensors were connected to dataloggers and powered by solar panels. Systems consisted of the following: CR23X (datalogger), AM16/32 (multiplexer), LI190SB-L (light), HMP45C-L (air temperature), TE525WS-L (rain), TDR100 (reflectometer), SDMX50 (TDR multiplexer), CS610-L (soil/wood moisture), 107-L (soil/wood temperature), and RF400 (spread-spectrum radio; Campbell Scientific, Logan, Utah, USA). Tree diagrams show main trunks, reiterated trunks, and limbs as seen from one view angle.

where transmittance ranges from 0 through 1 and canopy openness is expressed in percentage ($n = 6$ sensors, $R^2 = 0.993$). Validity of this transformation was tested by calculating the average hourly transmittance fraction of five independent sensors in two other trees, which also collected hourly data for exactly one year, and plotting transmittance fraction vs. height for all data combined. Between-crown light availability was quantified within one hour of solar noon and one week of equinox on calm, cloud-free days by attaching a light sensor to the top of a large helium-filled balloon (Parker et al. 1996). In 10 independent locations within the plot and nearby forest of Prairie Creek Redwoods State Park, the balloon was allowed to drift upwards from ground level through gaps between trees to above the canopy, and light availability was measured at 1-m height intervals. Light data from each balloon launch were expressed as transmittance fraction and estimated as the proportion of photosynthetically active radiation received at each height within the canopy compared to the value observed above the canopy.

Sensor arrays in the five trees were deployed at different times over a three-year period and maintained for up to 30 months. The array in Atlas Tree yielded data from March 2000 through March 2001 (Ambrose 2004), arrays in two other trees in Prairie Creek Redwoods State Park yielded data from September 2002 through the end of 2004, and arrays in two trees in Jedediah Smith Redwoods State Park yielded data from September 2002 through March 2005. Power shortages, damage from storms, and periodic hardware failures resulted in some missing data. Despite these problems, over 1.58 million hourly measurements were collected, which represented 91.9% of the total sensor hours.

Analyzing canopy microclimates

Seasonal and hourly air temperatures at the treetop and within 1 m of vascular epiphytes were compared to internal temperatures of canopy soil and dead wood supporting these epiphytes. Maximum, minimum, and mean temperatures were calculated using two complete years' data from the sensor arrays in four trees (Fig. 1, excluding Atlas). Values were summarized as four-tree

TABLE 1. Average volumetric water contents (expressed as proportions), regression equations, substrate correction factors, and replication used to model empirically the water-storage dynamics of dead wood and canopy soil supporting vascular epiphytes in *Sequoia sempervirens* trees, Prairie Creek and Jedediah Smith Redwoods State Parks, California, USA.

	Volumetric water content in dead-wood regions (average)	Regression equations and substrate correction factors for 0–30 m deep canopy soil†	Correction factor		
				Depth	
			Crotch	30–60 cm	60–90 cm
Season					
Winter					
Maximum	0.371	0.382 − (0.00204 × height)	1.848	1.535	1.459
Minimum	0.242	0.270 − (0.00199 × height)	2.394	1.588	1.665
Mean	0.300	0.345 − (0.00249 × height)	2.020	1.561	1.577
Spring					
Maximum	0.358	0.390 − (0.00226 × height)	1.774	1.533	1.487
Minimum	0.233	0.127	2.340	1.728	1.664
Mean	0.277	0.174	2.140	1.599	1.639
Summer					
Maximum	0.241	0.139	2.308	1.720	1.730
Minimum	0.183	0.064	4.087	2.125	1.760
Mean	0.207	0.089	3.203	2.118	1.650
Fall					
Maximum	0.312	0.363 − (0.00247 × height)	2.227	1.638	1.448
Minimum	0.174	0.061	4.233	2.174	1.750
Mean	0.203	0.120 − (0.00615 × soil volume)	3.356	1.842	1.635
Replication (sample size)					
No. TDR probes‡	8	21	12	4	2
No. crown locations	6	9	5	2	1
No. trees	4	5	1	2	1

Note: See *Methods: Analylzing canopy microclimate* for further explanation.

† Units of the terms in the regression equations, all of which were statistically significant ($P < 0.05$), are meters (height) and cubic meters (soil volume).

‡ TDR = time-domain reflectometry.

averages for eight seasons (winter 2003 through fall 2004) and each hour of the day.

Water storage dynamics of epiphytic substrates were modeled empirically by calculating maximum, minimum, and mean volumetric water contents for each season using all of the available sensor data (Table 1). This resulted in 12 dependent variables for each substrate type that were then regressed against height and, in the case of canopy soil, substrate volume. If these relationships were statistically significant ($P < 0.05$), the resulting equations were used to estimate volumetric water contents of every substrate unit in the plot (346 soil mats and 116 regions of dead wood); otherwise, means were used. Volumetric water contents of canopy soils were adjusted for substrate context (crotch vs. other position) and depth by multiplying estimated values for the 0–30 cm strata by empirically derived correction factors (Table 1). The crotch correction factors were calculated by dividing volumetric water contents of a crotch soil mat (pedon 1, Enloe et al. 2006) by the average volumetric water contents of four other soil mats in Atlas Tree (Ambrose 2004). The 30–60 cm depth-correction factors were calculated by dividing average volumetric water contents of 30–60 cm strata by those of 0–30 cm strata for two soil mats on limbs in Prairie Creek and Jedediah Smith Redwoods State Parks. The 60–90 cm depth- correction factors were

calculated by dividing volumetric water contents of the 60–90 cm stratum by those of the 30–60 cm stratum for a 100-cm-deep soil mat on a limb in Jedediah Smith Redwoods State Park (pedon 2, Enloe et al. 2006). The total water content of each soil mat was calculated as the product of estimated volumetric water content and substrate volume for each stratum. To avoid overestimation, crotch corrections were applied only to soil mats >30 cm deep ($n = 18$ mats), and volumetric water contents were assumed to reach a maximum at the saturation points measured for crotch soils (0.66 to 0.81) and other soils (0.45 to 0.76) in the laboratory (Enloe et al. 2006). For each season, total water storage in epiphytic substrates was estimated by summing values for all soil mats and regions of dead wood in each tree and in the plot as a whole. Stand-level values were further partitioned into 5-m-height strata to examine the vertical distribution of stored water.

Evaluating linkages among tree structures and arboreal habitats

Potential effects of tree structure on arboreal habitats were examined by indirect ordination analysis and linear regression. A primary matrix of 13 tree-level structural variables (i.e., total aboveground dry mass, percentage mass in reiterations, height, dbh, crown spread, crown volume, number of reiterated trunks, number of limbs,
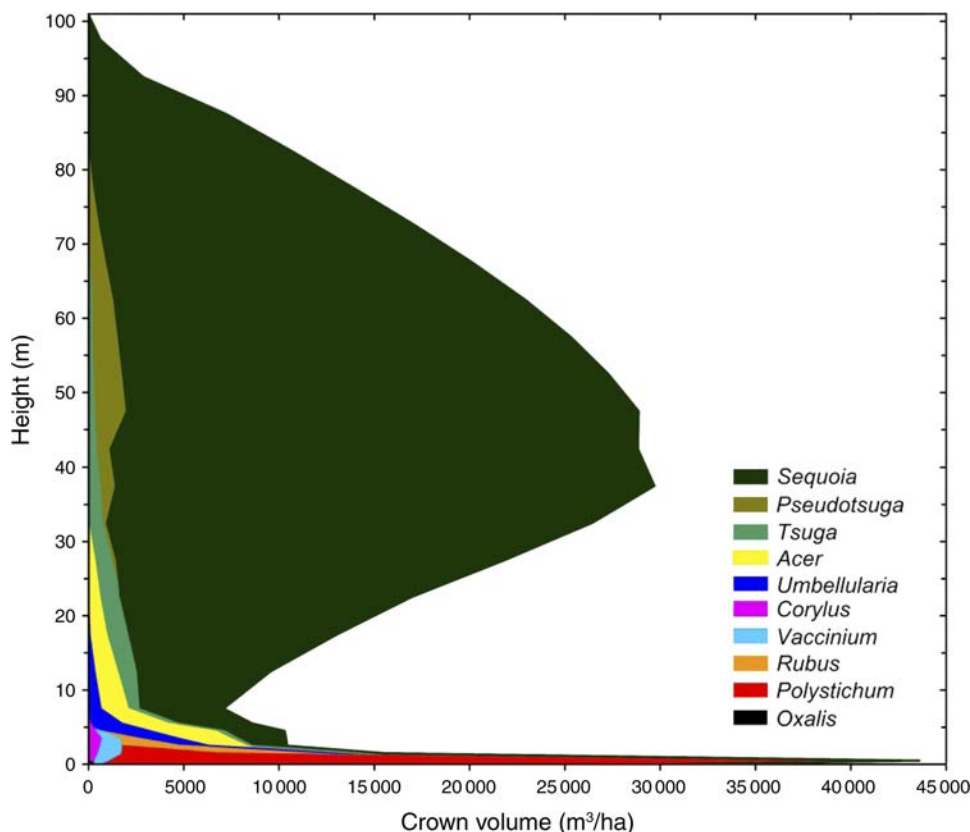
FIG. 2. Vertical distribution of crown volumes in the 1-ha plot. Values are for 5-m height strata. The area covered by each genus is equivalent to its proportion of total crown volume in the plot. Note that individuals of a number of genera were too small or infrequent to be shown, including *Athyrium*, *Chamaecyparis*, *Gaultheria*, *Lithocarpus*, *Picea*, *Rhamnus*, *Ribes*, and *Sambucus*.

crown spread, volume of main trunk, volume of reiterated trunks, volume of dead wood in trunks, volume of limbs, and leaf dry mass) representing the full range of information derived from crown mapping each redwood supporting vascular epiphytes in the plot ($n = 14$ redwoods) was subjected to principal components analysis using PC-ORD (McCune and Mefford 1999). Multivariate normality among the structural variables was improved by cube-root transforming three variables exhibiting excessive skewness or kurtosis (i.e., volumes of reiterated trunks, dead wood in trunks, and limbs). In the final matrix, skewness of the variables ranged from −0.78 to 1.24 and kurtosis ranged from 0.52 to 2.11. The cross-products matrix consisted of Pearson correlation coefficients among the structural variables. The resulting principal components were interpreted by regressing them against variables describing tree-level arboreal habitats (i.e., dry masses of epiphytic ferns, shrubs, and trees; percentage of soil in crotches; dry mass of soil; mean annual water content of soil and dead trunks; and number of epiphytic vascular plant species).

Finally, we examined potential effects of whole-forest structure on arboreal habitats. Results of the stand-level spatial pattern analysis were combined into a matrix of Ripley's K values distributed across the grid defined by 90 m of height and 20 m of horizontal distance in the canopy. These values were regressed against dry masses of plants and soil at 5-m height intervals to examine potential effects of trunk spatial distribution on accumulation of epiphytes.

RESULTS

Forest structure

Crowns of vascular plants in the 101-m-tall, 1-ha reference stand occupied 453 000 m³ (44.9%) of the total possible canopy volume, 312 900 m³ (69.1%) of which was attributed to redwood. The remaining tree species were stratified along the vertical gradient in the following sequence from top to bottom: *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Acer macrophyllum*, and *Umbellaria californica* (Fig. 2). A dense understory including shrubs (*Corylus cornuta*, *Rubus spectabilis*, *Vaccinum ovatum*, and *V. parvifolium*), ferns (*Polystichum munitum* and *Athyrium felix-femina*), and an herb (*Oxalis oregana*) occurred beneath the trees to a height of about 5 m.

Logs contributed 1258 m³ (69.0%) of dead wood per hectare and covered 11.8% of the ground (Fig. 3). Over 90% of the log volume was derived from redwood, and it occurred in all stages of decay. Snags and living trees
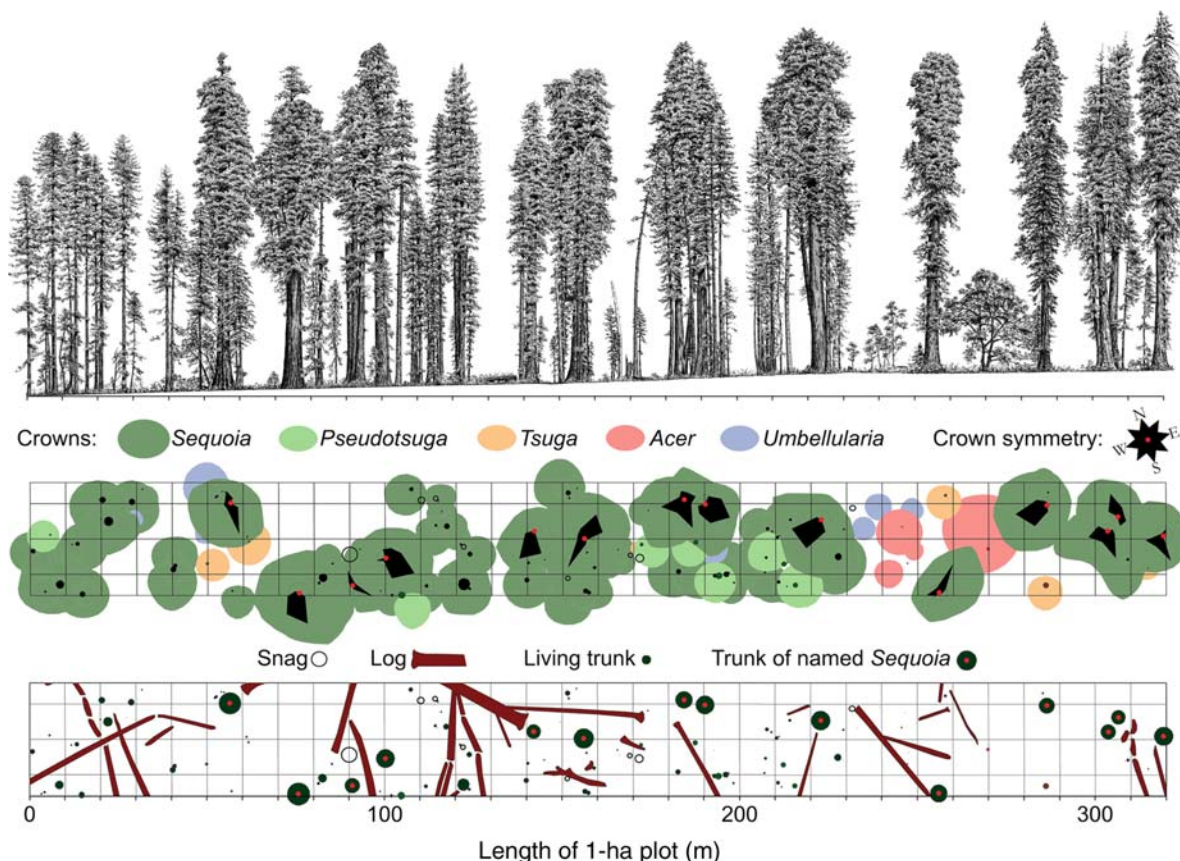
Fig. 3.   Profile diagram, crown projections, and trunk locations of the 1-ha plot. (Upper panel) An undistorted profile from view angle perpendicular to the long axis of the plot. Sketches were superimposed on error-checked structural diagrams and based upon field notes and photographs taken at ground level and from tops of trees outside the plot. Note that the ground level rises 7.8 m from left to right in the diagram. (Middle panel) Crown profiles of trees as viewed from above the plot. Solid red circles indicate the main trunk centers. Black polygons represent radial frequency distributions of reiterated trunks for 14 named *Sequoia* individuals. (Lower panel) Locations and sizes of living main trunks, standing dead trees (snags), and fallen dead trees (logs).

contributed 498 m³ (27.3%) and at least 67 m³ (3.7%) of the total dead wood volume per hectare, respectively.

The stand held an estimated 4283 Mg of aboveground dry mass, excluding snags and logs (Table 2). Over 95.4% of this total was contributed by redwood. The total leaf mass of redwood was greater than the mass of all non-conifers in the forest combined, and the largest redwood carried more leaf mass (1.5 Mg) than the entire plot's fern mass (1.4 Mg).

The total leaf-area index of the stand was approximately 14.2, 59.3% of which was attributed to redwood (Table 2). This estimate is preliminary. Redwood branches were not sampled directly, and the sapwood area–leaf area ratio used to calculate whole-tree leaf area of redwood was based on only 11 trees up to 45 m tall (Staniciou and O'Hara 2005).

The stand included 14 redwoods over 400 cm dbh and 99 other redwoods up to 250 cm dbh (Fig. 4). The 14 largest redwoods were named to facilitate their recognition during field work and data analyses. Only one standing redwood was dead, a thoroughly fire-scarred

426-cm-dbh snag. Most (86 of 99) of the smaller redwoods were model conforming, including individuals up to 91 m tall. In addition to redwood, the plot contained living *P. menziesii* up to 82 m tall, *T. heterophylla* up to 69 m tall, angiosperms up to 29 m tall, and 9 non-redwood snags (Fig. 4).

Redwood crown structure

Reiteration in redwoods contributed greatly to forest structure. There were nearly twice as many trunks, including reiterations, 60 m above the ground as at ground-level ground (Fig. 5). Reiterated trunks and limbs contributed 20.2 % (4290 m²) of total bark surface and 6.4 % (641 m³) of total stem volume in the plot, and 86% of these stems occurred between 35 and 85 m above the ground (Fig. 5).

Structurally, the 14 named redwoods were complex and highly individual (Table 3). Several of these trees possessed over 100 reiterated trunks up to 260 cm diameter and dozens of limbs up to 231 cm diameter. The largest tree (Iluvatar; see also Van Pelt 2001) had a

TABLE 2.   Summary of vascular plant characteristics in the 1-ha plot, listed in descending order by total dry mass of species (excluding roots).

| Species | Density (no./ha) | Basal area (m²/ha) | Mass | | | Leaf-area index |
			Total dry mass (kg)	Epiphytic mass (%)	Leaf dry mass (kg)	
Trees						
Sequoia sempervirens	113	363.2	4 084 408.7	0	17 191.6	8.41
Pseudotsuga menziesii	7	10.9	145 113.6	0	961.3	0.62
Tsuga heterophylla	18	3.4	39 005.7	>0	863.7	0.50
Acer macrophyllum	5	0.9	5633.7	0	264.4	0.40
Umbellularia californica	16	0.7	3857.4	>0	273.3	0.35
Rhamnus purshiana	2	>0.0	144.2	1	17.8	0.03
Picea sitchensis	1	0.0	1.1	0	0.1	>0.00
Chamaecyparis lawsoniana	1	0.0	1.0	0	0.1	>0.00
Lithocarpus densiflorus	1	0.0	0.1	100	>0.0	>0.00
Shrubs						
Rubus spectabilis	2033	1.7	2659.9	>0	686.3	2.11
Vaccinium ovatum	189	0.3	552.4	38	25.9	0.12
Corylus cornuta	9	0.1	289.4	0	5.8	0.01
Vaccinium parvifolium	56	0.1	98.7	1	4.2	0.02
Gaultheria shallon	1	>0.0	0.5	100	0.4	>0.00
Sambucus callicarpa	1	>0.0	0.3	100	0.1	>0.00
Ribes laxiflorum	1	>0.0	0.1	100	>0.0	>0.00
Non-woody plants						
Polystichum munitum	152×10^3	0.0	1270.8	0	1270.8	1.10
Polypodium scouleri	38×10^3	0.0	196.3	100	88.8	0.04
Oxalis oregana		0.0	112.0	0	112.0	0.49
Polypodium glycyrrhiza		0.0	15.4	100	7.0	>0.00
Athyrium felix-femina		0.0	12.2	1	12.2	>0.00

crown volume of almost 24 000 m³ and possessed 209 reiterated trunks, 61 limbs, 958 m³ of wood, 143 m³ of bark, and a total aboveground dry mass over 440 Mg, 18.4% of which was carried in its reiterations. Fusions between reiterated trunks, limbs, and branches were common, and dense mats of adventitious roots (endomycorrhizal with *Glomus*; S. C. Sillett, *unpublished data*) frequently occurred amid canopy soils in crotches formed by the bases of trunks.

Reiterated trunks were not randomly distributed within redwood crowns; accelerated growth in high-light environments and negative interactions among adjacent crowns were evident in their nonuniform radial distributions around main trunks. Most of the reiterated trunks occurred toward the south and southwest sides of the crowns (Fig. 6). However, large trees standing side by side tended to reiterate away from each other's crowns regardless of direction (Fig. 3).

Biomass and distribution of epiphytes

Thirteen species of vascular plants occurred as epiphytes on trees in the plot (Table 2). Aside from the deciduous fern *P. glycyrrhiza*, whose primary habitats were branches of *P. menziesii*, *T. heterophylla*, and angiosperm trees, epiphytic vascular plants were restricted to the 14 named redwoods (Table 3). No vascular epiphytes occurred on the 86 model-conforming redwoods in the plot. The 13 unnamed redwoods with reiterated trunks also lacked vascular epiphytes. Six species were clearly accidental epiphytes (1% or less of

species' stand-level biomass was epiphytic). Of these, only *T. heterophylla* and *V. parvifolium* were observed reproducing in the canopy. Three others (*Gaultheria shallon*, *Lithocarpus densiflorus*, and *Sambucus callicarpa*) were also considered accidental epiphytes, because only a few epiphytic individuals were found and the species occurred abundantly as terrestrial plants outside the plot boundary in nearby slope forests. Three species appeared to be obligate epiphytes whose only known habitats in the stand or nearby forest were epiphytic (both *Polypodium* ferns and the shrub *Ribes laxiflorum*). The evergreen shrub *V. ovatum* was a facultative epiphyte, occurring and reproducing abundantly both in the canopy and on the ground. This species had the highest biomass (212 kg) among epiphytes.

The evergreen fern *Polypodium scouleri* had the second highest biomass (196 kg) among epiphytes. Limbs were the preferred substrate of *P. scouleri* (Fig. 5), accounting for 42.8% of its biomass even though limb volume represented only 28.4% of branch volume. About 19.5% of limb surfaces were covered by *P. scouleri* mats, and limbs supporting ferns were, on average, twice as thick as branches supporting ferns (46.4 vs. 22.3 cm, $P < 0.0001$). Small *P. scouleri* mats that were apparently plastered to the sides of trunks always had a dead branch or limb stub buried within the mat.

In contrast to *P. scouleri*, 94.7% of *V. ovatum* biomass occurred on trunks or in crotches formed by the bases of trunks (Fig. 5). Shrubs arising directly from trunks were
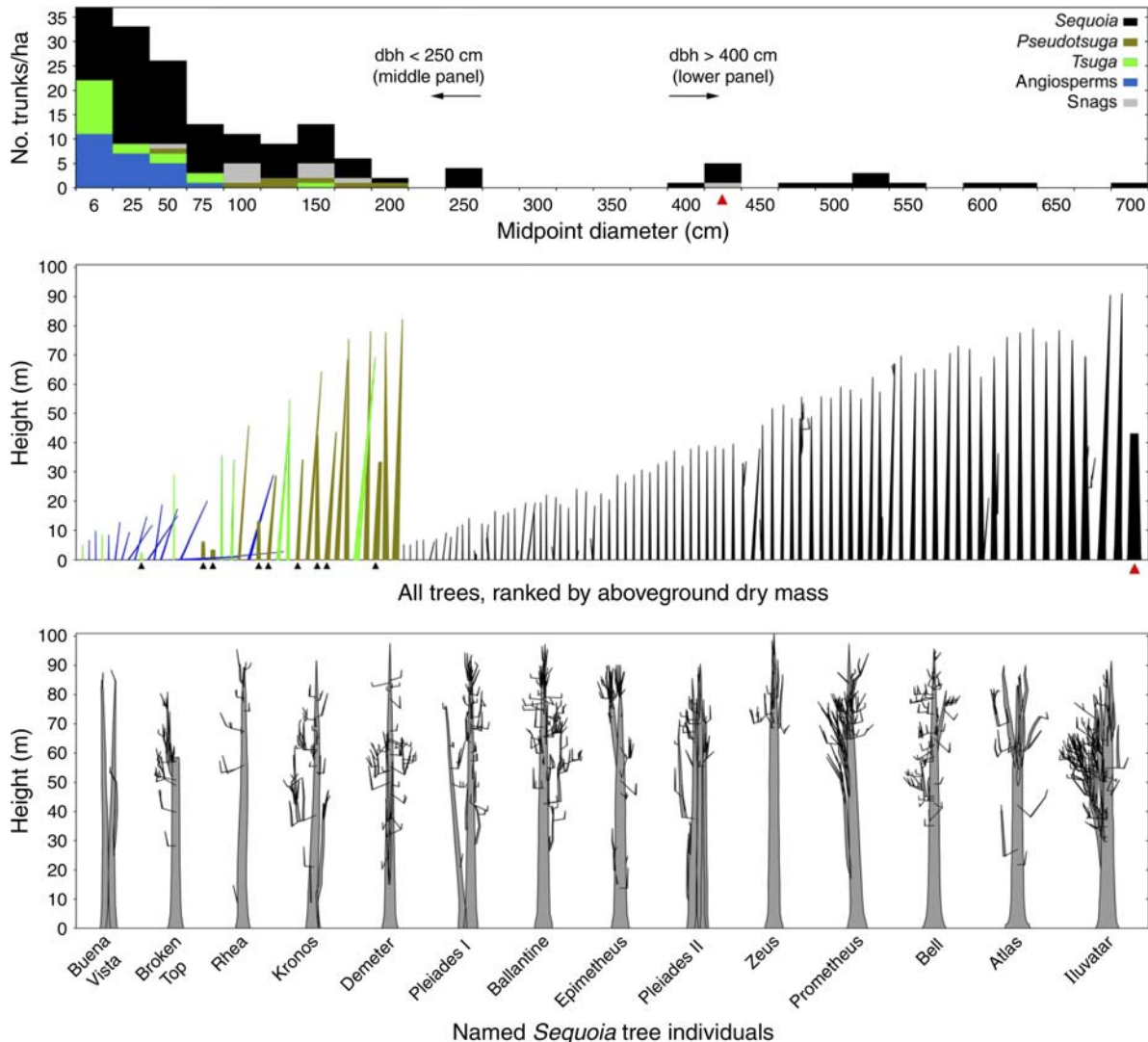
Fig. 4. Trunk diameter distribution and tree structure in the 1-ha plot. (Upper panel) Frequency distribution of trunk diameters at breast height (dbh, cm) for all trees; values on x-axis represent midpoint diameters. (Middle panel) All trees between 5 and 250 cm dbh (the red triangles in the upper and middle panels indicate single dead *Sequoia*; black triangles in the middle panel indicate other dead trees). (Lower panel) The 14 named individual *Sequoia* trees, all of which exceed 400 cm dbh. In the middle and lower panels, trees are ranked by aboveground dry mass and are depicted in diagrams showing main trunks, reiterated trunks, and limbs from the view angle best illustrating their individuality. No branches are shown. Angiosperms include *Acer*, *Rhamnus*, and *Umbellularia*.

invariably associated with pockets of decayed heart-wood. On average, though, *V. ovatum* in crotches were larger (5.2 kg) than those on trunks (2.2 kg), limbs (0.7 kg), or branches (0.3 kg, $P < 0.002$). Heartwood decay was often evident in the limbs and branches on which *V. ovatum* grew, although we were unable to quantify heartwood decay in these situations.

In addition to substrate effects, light availability may have affected epiphyte distribution along the vertical gradient. For example, crown volume of *V. ovatum* was strongly correlated with dead-trunk volume above 60 m ($r = 0.86$, $P < 0.01$) but poorly correlated below 60 m ($r = 0.37$, $P > 0.20$). Similarly, crown volume of *P. scouleri* was strongly correlated with limb volume above 60 m (r

$= 0.97$, $P < 0.0001$) but more weakly correlated below 60 m ($r = 0.59$, $P > 0.03$). Light availability within the forest sharply declined from above the canopy to around 60 m where it could be lower (1% transmittance) than near the ground (>10% transmittance, Fig. 7).

Soil and dead-wood habitats in the canopy

Canopy soil consisted mostly of dead fern roots (Sillett and Bailey 2003, Enloe et al. 2006), and 97.7% of all the canopy soil in the plot (78.8 m³, 2366 kg) occurred beneath *Polypodium scouleri* ferns. Crotch soils were best developed between 50 and 75 m, extending down to 30 m and up to 90 m. The deepest soils occurred between 55 and 65 m (Fig. 5). The largest soil
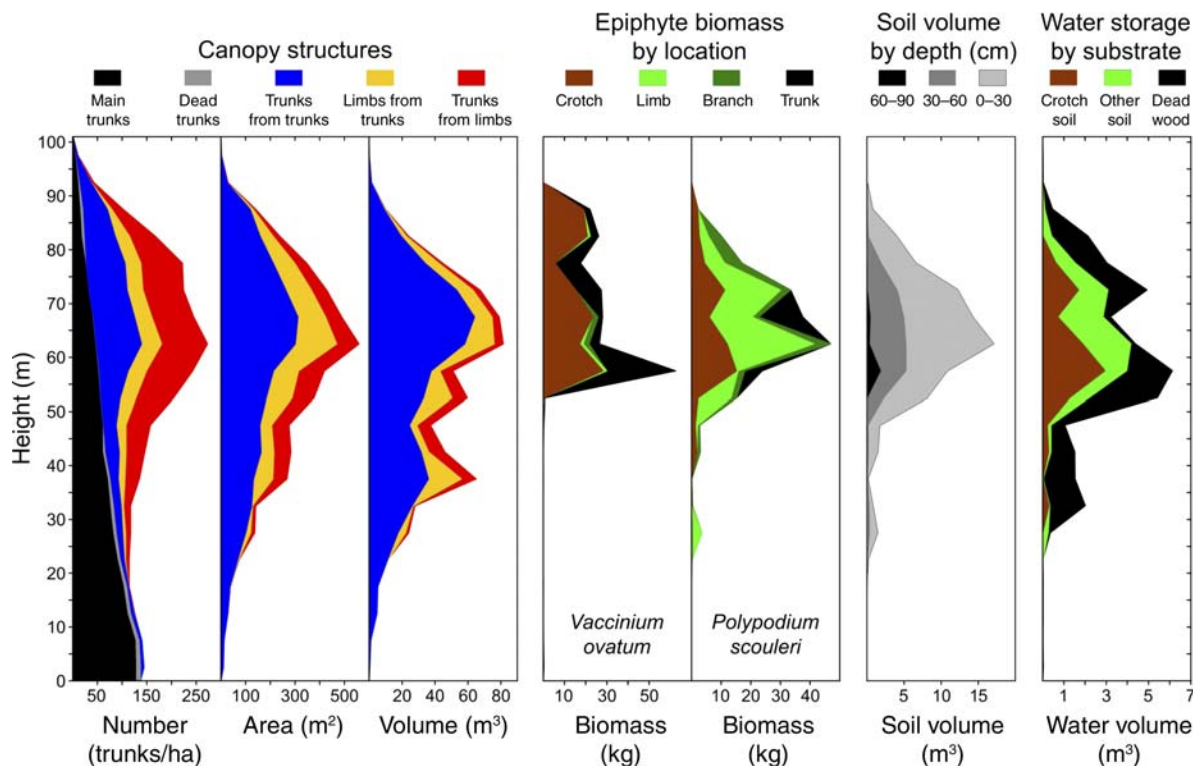
Fig. 5. Summary of canopy structures and habitat characteristics along the height gradient in the 1-ha plot. Values are 1-ha totals for ground level (0 m), highest treetop (101 m), and 5-m height intervals. Canopy structures were derived from x, y, z coordinates and diameters collected during crown mapping (see Appendix B). Number of canopy structures is the total number of trunks/ha in each 5-m height stratum. Epiphyte biomass is dry mass of stems and leaves for each species. Water storage is mean annual water content during the 2000–2005 monitoring period. The area covered by each category is equivalent to its proportion of the 1-ha plot total.

accumulations, which were on limbs supporting *P. scouleri*, stored over 1 m³ of water (see below). Shallow soils receiving adequate stemflow occasionally supported small epiphytic *Rhamnus* and *Tsuga* (Ambrose 2004).

Compared to soil, the vertical distribution of dead wood in the canopy was difficult to quantify. Our estimate of dead wood volume in the crowns of living trees was conservative, because we did not quantify dead branches or dead regions of limbs. Moreover, since trees were not cored, internal "pocket rot" caused by the basidiomycete *Poria sequoiae* was often not visible. The largest observed volumes of dead wood in the canopy were the sun-bleached spires of main trunks and regions of decaying heartwood extending below the tops of thick, broken trunks. Fire damage appeared responsible for much of the dead wood in the canopy. Scorched bark and wood were evident high in the crowns of all 14 named trees, although fire origins were difficult to discern.

Functional linkages between forest structures and arboreal habitats

Strong spatial aggregation of trunks between 50 and 90 m was highly coincident with the vertical distribution of epiphytic vascular plants (compare Figs. 5 and 8). Up

to 92% of the variation in fern and soil distribution along the vertical gradient was explained by degree of trunk aggregation, with the highest correlations between Ripley's K and epiphyte mass occurring at a scale of 20-m horizontal distance ($P < 0.0001$, Fig. 9). The distribution of epiphytic woody plants along the vertical gradient was also correlated with degree of trunk aggregation, with the highest correlation ($R^2 = 0.75$, $P < 0.0001$) occurring at 10-m horizontal distance. Stepwise multiple regression revealed that dead-wood volume explained an additional 14% of the variation in distribution of epiphytic woody-plant biomass along the vertical gradient ($P < 0.0004$).

Redwood crown structure affected epiphyte biomass, mass and water content of canopy soil, and epiphyte species richness. The best whole-tree correlate of epiphytic fern mass ($r = 0.69$, $P < 0.01$), soil mass ($r = 0.68$, $P < 0.01$), and average soil water content ($r = 0.68$, $P < 0.01$) was the percentage of a tree's total mass in reiterations. The best correlate of woody-epiphyte mass was dead-trunk volume ($r = 0.77$, $P < 0.002$). Trees with larger crown spread had a larger proportion of canopy soil in crotches ($r = 0.54$, $P < 0.05$), and trees with thicker main trunks (higher dbh) supported more species of vascular epiphytes ($r = 0.81$, $P < 0.001$). Principal-

TABLE 3.　Summary of tree-level structure and arboreal habitat characteristics for *Sequoia sempervirens* in the 1-ha plot, for each of the 14 named trees as well as all other trees collectively.

	Iluvatar	Atlas	Bell	Prometheus	Zeus	Pleiades II	Epimetheus
Tree structure							
dbh (cm)	614	710	602	559	520	527	509
Height (m)	91.5	90.0	95.7	97.4	101.0	90.5	90.1
Crown spread (m)	28	28	21	24	19	21	20
Crown volume (m^3)	23 764	23 692	15 063	17 840	13 865	12 506	13 419
No. main trunks	1	1	1	1	1	3	1
No. reiterated trunks	209	34	119	123	32	45	82
Limbs	61	9	45	11	7	16	10
Volume (m^3)							
Main trunk	874.0	637.9	633.1	598.5	608.4	589.6	567.5
Reiterated trunk	162.5	115.1	13.6	63.1	7.2	28.0	32.3
Dead trunk	11.8	0.0	0.0	1.9	0.1	0.9	2.3
Limb	24.6	11.0	11.6	3.2	3.2	8.6	3.6
Branch	28.0	26.9	97.0	24.9	38.2	22.6	27.2
Total aboveground dry mass (Mg)	442	321	314	280	268	263	256
Mass in reiterations (%)	18.4	17.0	3.7	10.1	1.8	6.4	6.0
Leaf dry mass (kg)	1462	1101	1043	1086	954	878	1029
Arboreal habitats							
Dry mass (kg)							
Fern	20.0	61.7	5.3	24.7	0.6	11.2	>0.0
Shrub	27	24	2	54	0	7	11
Tree	>0.0	>0.0	>0.0	0.9	0.2	0.1	>0.0
Soil	229	719	67	327	12	144	>0
Soil in crotches (%)	39	26	0	71	0	18	0
Water storage, mean (L)							
Soil	1908	5932	303	4416	52	986	1
Trunk	2905	3	3	460	14	230	556
No. epiphytic vascular plant species	5	6	5	5	2	5	3

components analysis revealed two dimensions of tree structure that had independent effects on epiphytes. Trees were clearly ordered along the first principal-component axis (PC1) by variables describing both stature and extent of reiteration (Table 4). The number of vascular epiphyte species was correlated with tree scores along PC1 ($r = 0.67$, $P < 0.01$). Trees were ordered along the second principal-component axis (PC2) by dead trunk volume (Table 4). The mass of epiphytic trees and the mass of *V. ovatum* on dead trunks were both correlated with tree scores along PC2 ($r = 0.67$ and 0.64, respectively; $P < 0.01$).

Internal temperatures of dead wood and soil in the canopy were more stable seasonally and diurnally than air temperatures at the treetop and within 1 m of vascular epiphytes (Fig. 10). Epiphytic substrates remained cooler during the day and warmer at night than air within or above tree crowns. Soil was consistently warmer than dead wood in the spring and summer, but dead wood was warmer than soil during daytime in the fall and winter. Deeper layers of soil (>30 cm) had virtually no diurnal fluctuations in temperature, whereas shallower layers fluctuated by up to 3°C.

Microclimatic differences between epiphytic substrates were also evident in water contents. Soils in crotches had the most stable water content (coefficients of variation for seasonal weighted mean volumetric

water contents were 8.0, 20.0, and 27.5 for crotch soils, dead wood, and other soils, respectively) and held 2–4 times more water than other canopy soils (Table 1). Deeper soil layers held more water than shallower layers (Fig. 11, Table 1). Water contents of the soils spiked during rain events. These spikes were followed by relatively brief periods of drainage and prolonged periods of evapotranspirational water loss, especially after the last spring storms (Fig. 11). The lowest substrate water contents occurred prior to the first major fall storms, and the highest water contents occurred during major storms in winter. During the 2000–2005 monitoring period the total water content of dead wood and soils in the canopy fluctuated between 24.7 and 53.4 m^3/ha (Table 5).

Discussion

In old-growth redwood forests, the dominant tree species is decay- and fire-resistant, long-lived, shade-tolerant, and thus often present in all sizes from saplings through emergents within a single stand. The 1-ha plot surveyed in this study was placed in the midst of giant trees on alluvial soil to capture as full an expression of structural development as possible among remaining redwood forests. This forest stand has the highest basal area (381 m^2), highest standard deviation of dbh (153 cm) (an index of forest structure: Spies and Franklin

TABLE 3. Extended.

Ballantine	Pleiades I	Demeter	Kronos	Rhea	Broken Top	Buena Vista	99 other live redwoods	Precision
523	481	434	428	405	424	425	0–249	1
97.2	94.4	97.5	91.6	95.5	80.9	88.4	1.4–90.8	0.1
21	18	23	22	17	18	17	1–19	0.1
12 434	8904	18 002	17 125	10 626	6623	8799	110 256	1000
1	2	1	1	1	1	2	99	1
141	83	63	63	21	49	6	23	1
50	31	29	21	8	9	0	4	1
554.9	456.0	389.7	335.4	359.3	327.3	322.1	1669.6	0.1
19.1	9.3	27.7	30.5	1.2	12.0	8.7	2.7	0.1
5.0	2.8	0.0	4.1	0.2	17.1	0.0	20.9	0.5
11.8	3.9	6.4	14.5	1.5	3.2	0.0	0.3	0.1
22.4	21.7	20.1	10.1	11.0	10.3	17.1	84.4	>5
248	200	181	159	151	143	141	715	1
5.7	3.0	8.5	12.8	0.8	4.7	2.6	0.2	0.1
1085	762	769	597	691	730	518	4485	>100
10.2	15.0	2.2	23.4	15.9	6.2	>0.0	0.0	<1
11	20	0	5	20	33	1	0	>1
0.0	0.0	0.0	0.3	0.0	82.1	0.0	0.0	<1
129	165	36	252	190	95	>0	0	10
48	24	16	6	4	4	0	0	1
1088	1168	437	1561	1003	835	0	0	100
1239	694	0	1020	44	4210	3	5158	100
2	2	1	3	2	3	2	0	<1

1991), and among the highest aboveground masses (4283 Mg) and volumes (10 448 m^3, including bark and wood of living trees) ever reported for a single hectare (see also Van Pelt and Franklin 2000). Only a few hectares of redwood forest on alluvial soils in other protected areas (Jedediah Smith and Humboldt Redwoods State Parks, California, USA) may have higher mass accumulations (Sawyer et al. 2000c). Because we quantified microclimates and vascular-plant distribution and biomass from ground level to treetops in a forest of extreme size and complexity, our results reveal a number of functional linkages between tree structures and arboreal habitats that may apply broadly to other forests.

Tree individuality

The formation of reiterated trunks, also known as sprouting, is a common response to injury among trees in many temperate and tropical forests (Putz and Brokaw 1989, Clark and Clark 1991, Bellingham et al. 1994, Bond and Midgley 2001, Del Tredici 2001). Trunk reiteration drives the development of structural complexity and individuality in redwood. Wind-induced breakage removes tops and creates gaps in otherwise dense, model-conforming crowns. Several of the named trees in the plot lost their tops long ago and have rebuilt their crowns with reiterated trunks. A few of the smaller

redwoods apparently reiterated after losing their tops when large pieces fell from the canopy, the wreckage of which is still visible on the ground at their bases and traceable to broken sections of named trees. Indeed, crushing damage from falling debris has recently been implicated as a major driving force in forest stand dynamics (Lutz and Halpern 2006). The largest redwood log in the plot was one of two main trunks in a double tree, the other half of which still stands (Broken Top). The same severe storm that felled this trunk seems also to have shattered the top of its twin (Fig. 4). Smaller-scale damage from wind or falling debris appears to stimulate reiteration, too; nearly every limb measured in the plot ($n = 311$ limbs) had an obviously broken main axis beyond its reiterated trunk(s). By killing portions of crowns, fire may also stimulate reiteration. For example, main trunks of the three trees (Iluvatar, Pleiades II, and Kronos) with the largest limbs (196, 214, and 231 cm diameter, respectively) in the plot terminate in long-dead spires whose bases are covered with scorched bark and wood.

Spontaneous formation of reiterated trunks has been observed in tree species from both temperate and tropical forests (Koop 1987, Cao and Peters 1998; Woolley et al. 2007), but the extent to which redwood can reiterate without prior damage from wind, falling debris, or fire is unclear. The existence of two model-
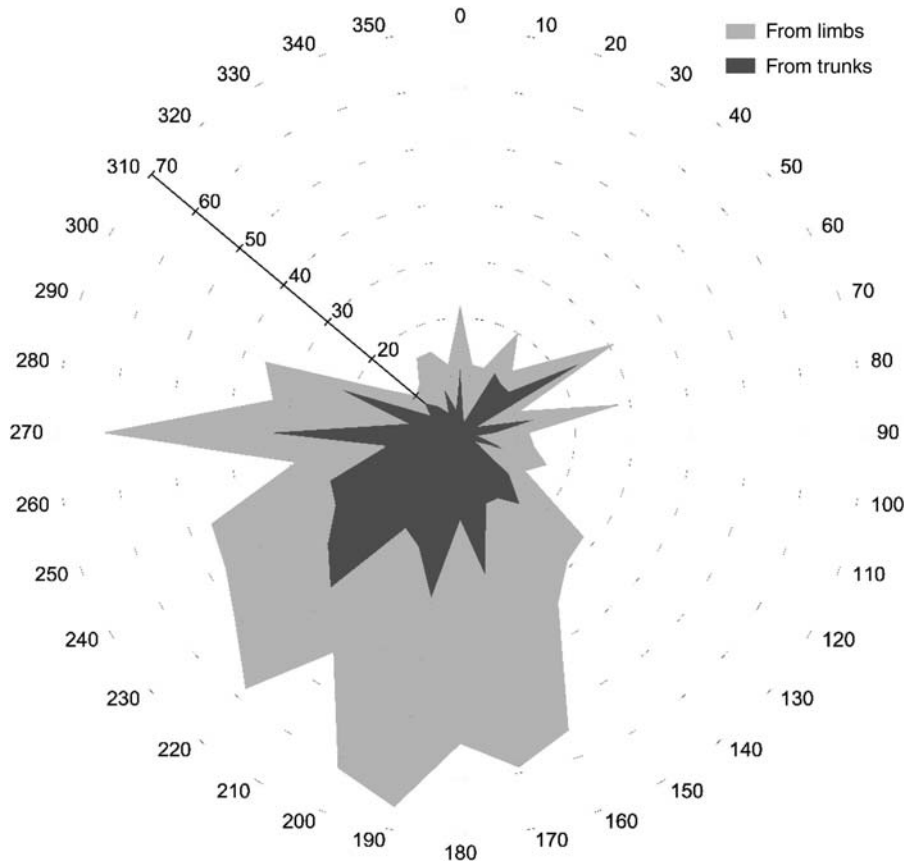
FIG. 6. Radial frequency distribution of reiterated trunks arising from other trunks and limbs in the 1-ha plot. Radial values are cumulative counts within 10° arcs radiating from the centers of all *Sequoia* main trunks in the plot. The "0" represents true north.

conforming trees over 90 m tall in the plot implies that rates of reiteration are slow in the absence of injuries, perhaps not occurring for centuries. After an injured tree has begun reiterating, new trunks might form spontaneously from other trunks. The frequent occurrence of stair-stepping, sympodial trunks in the broad crowns of large redwoods is consistent with the hypothesis that a deeply shaded leader can be replaced by a more rapidly growing subterminal branch, which bends upward, continues the trunk's growth, and gives rise to a branch that may, in turn, replace the new leader without any physical damage.

Regardless of the underlying causes, reiterated trunks and their associated limbs become the largest appendages on the main trunks of redwoods and other conifers (e.g., *Pseudotsuga menziesii*; R. Van Pelt and S. C. Sillett, *unpublished manuscript*). These structures expand canopy habitats in the form of sloping bark surfaces channeling litterfall and stemflow, bowl-shaped crotches between trunks, and horizontal platforms. Moreover, sapwood exposed by injuries is susceptible to a plethora of saprotrophic fungi and quickly decays (S. C. Sillett, *personal observation*). As a result, troughs form on the upper surfaces of limbs wounded by falling debris, facilitating the retention of litterfall and absorption of

precipitation, and likely hastening decomposition of the underlying wood. Redwood trees occasionally send adventitious roots into these areas of decayed sapwood and canopy soil. Thick limbs weakened by injury and decay can maintain flourishing reiterated trunks for many years, because cambial growth continues to produce high-density compression wood on uninjured lower surfaces (buttresses). Branches and small limbs lacking sufficient buttressing readily break after sustaining injuries to their upper surfaces (S. C. Sillett, *personal observation*).

Unlike sapwood, heartwood exposed by injuries persists for centuries in dead spires, overhung ledges, or slowly decaying cavities. Two specialized fungi (*Poria sequoiae* and *P. albipellucida*) are the only documented significant agents of heartwood decay in redwood (Bega 1978, Olson et al. 1990). The decay resistance of heartwood likely contributes to the slow turnover of trees observed in old-growth redwood forests (Busing and Fujimori 2002). Wood decay was directly responsible for the only two disturbances affecting >1 m^3 of redwood volume in the plot since 1996. The uppermost main trunk of one named tree (Kronos), which was dead above 80 m, collapsed in 2003, obliterating many underlying branches, limbs, and their epiphytes on its
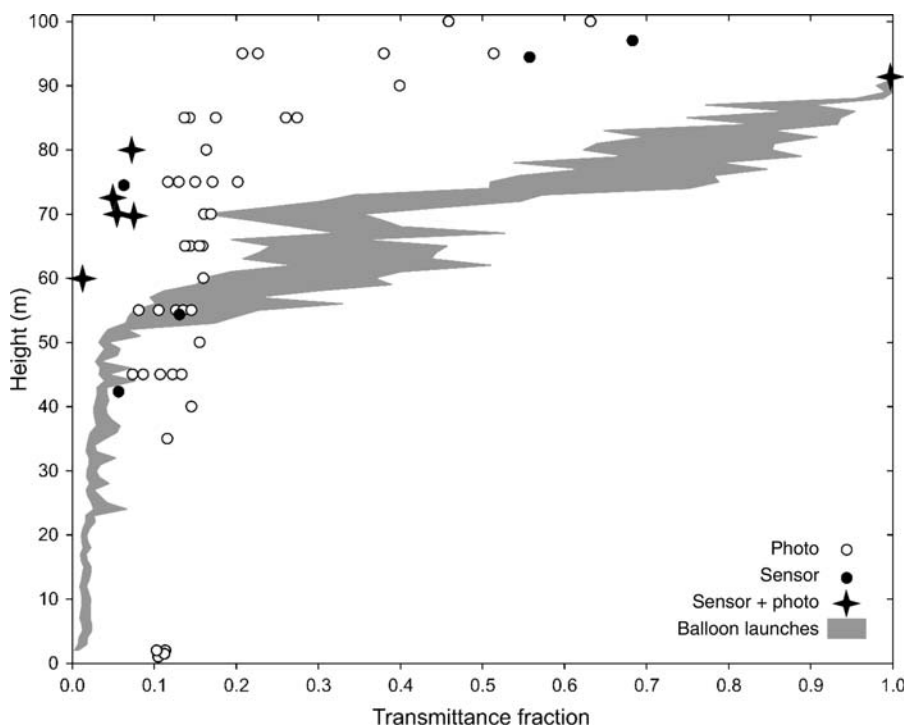
Fɪɢ. 7. Vertical distribution of light availability, expressed as transmittance fraction, in the 1-ha plot. Stars indicate locations within tree crowns where light sensors were deployed for one year and where hemispherical photographs were also taken. Solid circles indicate locations within tree crowns where light sensors were deployed for one year but no hemispherical photographs were taken. Open circles indicate locations within tree crowns where only hemispherical photographs were taken. The gray shaded area indicates mean ± SE ($n = 10$ balloon launches) derived from a light sensor mounted to a helium balloon launched between tree crowns. See Fig. 1 for sensor information.

way to the ground. Investigation of the broken top revealed an extensive internal cavity filled with decaying heartwood and basidiomata of *P. sequoiae*. The other event was not caused by redwood decay but by a *P. menziesii* snag decayed by *Phaeolus schweinitzii* and other fungi. In 2001 the snag toppled, shearing a 69-cm-diameter reiterated trunk from a 134-cm-diameter limb in the lower crown of Atlas Tree, which has since reiterated.

Factors limiting vascular epiphytes

The degree to which biotic vs. abiotic factors determine the distribution of vascular epiphytes in this forest canopy can be assessed by comparing epiphyte biomass to quantitative measures of both sets of factors. The two dominant epiphytes, *Polypodium scouleri* and *Vaccinium ovatum*, produce copious quantities of propagules that enable them to disperse readily from tree to tree via wind-borne spores and animal-borne seeds, respectively. Despite prolific reproduction, both species are rare as epiphytes on model-conforming redwoods, even those standing next to highly reiterated trees with heavy epiphyte loads. A similar dependence on particular structural features or moist substrates also occurs among epiphytes in other forests. The vascular epiphytes *P. glycyrrhiza* and *Selaginella oregana* require the initial development of bryophyte mats before

colonizing branches of *Picea*, *Acer*, and *Populus* in western Washington (USA) rain forests (R. Van Pelt, *unpublished data*). Strangler figs, which begin life as epiphytes, produce enormous crops of figs, the seeds of which are widely dispersed by animals (Laman 1996). Epiphytic figs, however, are sparsely distributed because successful germination and establishment depend upon the availability of moist substrates (e.g., canopy soil, knotholes) with adequate illumination, which are scarce even in primary rain forest (Laman 1995). Like these epiphytes in other forests, *P. scouleri* and *V. ovatum* may require particular substrates or microclimatic conditions that are seldom found on model-conforming redwoods.

Desiccation-sensitive gametophytes of *P. scouleri* commonly occur in drip zones beneath thick accumulations of canopy soil on redwood. A closely related, deciduous species, *P. glycyrrhiza*, is uncommon on redwoods but abundant on several of the other trees in the plot. Its gametophytes establish almost exclusively amidst thick, sponge-like mats of bryophytes that maintain high water-vapor pressures near tree surfaces (Lovelace 2003). Substrates with sufficient water-holding capacities are usually lacking on model-conforming redwoods, whose branches are often too narrow to permit accumulations of the litterfall or bryophytes required for colonization by either species of *Polypodium*.
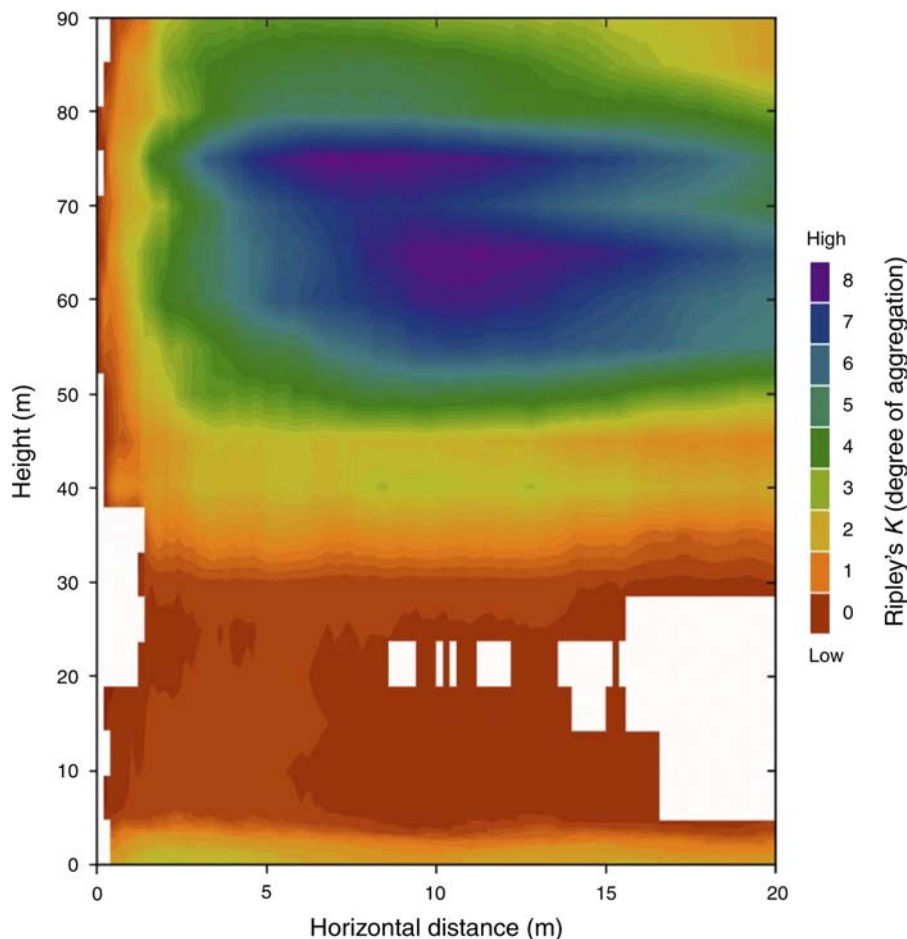
STEPHEN C. SILLETT AND ROBERT VAN PELT

FIG. 8. Spatial aggregation of trunks along vertical and horizontal gradients in the 1-ha plot. Values of Ripley's *K* are depicted as colors on a grid covering 90 m of height and 20 m of horizontal distance. Regions with no color in the grid are those where the spatial distribution of trunks was not statistically different from random ($P > 0.05$).

Even if sufficient moisture is available for fern establishment, other microclimatic factors, notably light, may limit fern growth. Light availability is often very low below 60 m in the redwood canopy, and few ferns occur there. However, *P. scouleri* exhibits low light compensation points (5–10 µmol photons·m^{-2}·s^{-1}) and low maximum rates of net photosynthesis (2–4 µmol CO_2·m^{-2}·s^{-1}), which are characteristics of shade plants, even though it has relatively high light-saturation points (>500 µmol photons·m^{-2}·s^{-1}; S. C. Sillett and M. E. Antoine, *unpublished data*). It is thus well equipped to exploit heterogeneous light environments throughout the canopy. Large *P. scouleri* mats do occur occasionally on limbs in the lower canopy, although they may have established there under a different light regime than currently exists. The scarcity of *P. scouleri* in the lower canopy and its absence from model-conforming trees can both be attributed to a dependence on structural features that simultaneously increase moisture availability and promote fern growth.

The vertical distribution of *V. ovatum* also suggests light limitation, as there is virtually no epiphytic biomass of this species below 50 m in the plot despite plentiful water storage in dead trunks down to 30 m (Fig. 5). Over 84% of dead-trunk volume in this region of the canopy is contributed by a dead-topped redwood standing in deep shade beneath the crown of the plot's largest redwood (Fig. 3; 82 m). Light availability near the ground is often higher than inside large crowns (Fig. 7), and >60% of the stand-level *V. ovatum* biomass and the three largest individuals grow on terrestrial woody debris. Like *P. scouleri*, epiphytic *V. ovatum* is abundant in crotch soils, but tree- and stand-level correlations suggest a dependence on decaying wood. Thus, absence of *V. ovatum* (and other ericaceous shrubs) on model-conforming trees may be attributed to a lack of decaying-wood substrates. It remains an intriguing possibility that prior heartwood decay by *Poria* may be necessary to facilitate the mycorrhization of *V. ovatum* roots and, ultimately, its colonization of redwood crowns.
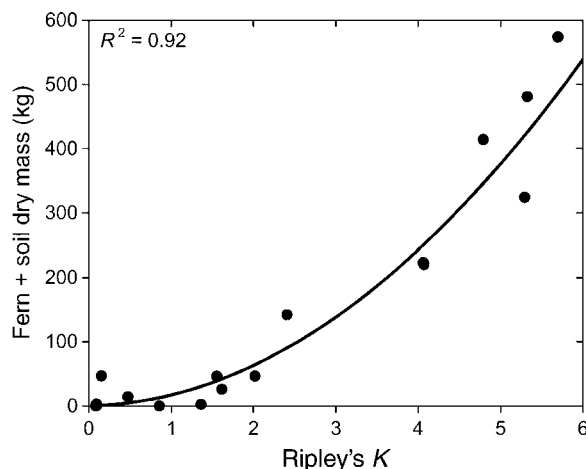
FIG. 9. Correlation between dry mass of ferns plus underlying canopy soil and spatial aggregation of trunks (including reiterations) as measured by Ripley's K. Mass values are totals for 5-m height strata, and Ripley's K values are calculated at 20-m horizontal distance for midpoints of height strata. The coefficient of determination (R^2) is derived from linear regression of square-root-transformed mass data.

Vascular epiphytes and canopy biodiversity

Vascular epiphytes enhance arboreal habitats through their contributions to decaying wood and canopy soils. The frequent emergence of *Vaccinium* shrubs directly from the sides of redwood trunks, without any visible soil, may be related to pockets of decaying wood providing water and mineral nutrients via symbioses with mycorrhizal fungi (Read 1996). Other shrubs in the Ericaceae are widespread as epiphytes in tropical forests and possess ericoid mycorrhizae (Rains et al. 2003). These fungi possess saprotrophic capabilities and may utilize decaying wood (Haselwandter et al. 1990) as well as the chitin in other fungal mycelia (Kerley and Read 1997) as sources of nitrogen for their hosts. The water and nutrients stored in dead redwood trunks are clearly sufficient for reproduction of *Vaccinium*, as many epiphytic shrubs produces an annual crop of berries, even during years with below average rainfall (S. C. Sillett, *unpublished data*). The largest region of dead wood in the canopy (Fig. 4, Broken Top) supported the largest epiphyte observed in the study, an 8.5-m-tall *Tsuga heterophylla* tree ectomycorrhizal with *Rusulla* (Agaricales) growing 58 m above the ground.

Canopy soils, which can be up to 1 m deep, are a major source of water for epiphytes and may hold more water per hectare than decaying wood in redwood trunks. *Polypodium scouleri* ferns are responsible for nearly all soil formation in redwood forest canopies (Sillett and Bailey 2003). With increasing depth, soils beneath these ferns become more decomposed, and their ability to retain nutrients and water increases (Enloe et al. 2006). Soils in crotches are particularly important as water reservoirs, accounting for more than a third of the water stored in epiphytic substrates during the dry

season, despite representing only 17% of substrate volume. The water supply of crotch soils is supplemented by stemflow (Ambrose 2004), perhaps explaining why the largest *P. scouleri* mats and epiphytic shrubs occur in crotches. Crotch soils hold so much water because, unlike branch and limb soils, drainage is restricted and standing water can accumulate in the lower horizons. Water and nutrients stored in canopy soils allow vascular plants normally restricted to the forest floor to survive as epiphytes in old-growth forests (Sillett and Neitlich 1996). Many of the vascular plants inhabiting large redwoods are accidental epiphytes that rarely, if ever, reproduce in the canopy. The low bulk densities and freely draining properties of canopy soils contribute to low water potentials (−1.0 to −6.7 MPa, Enloe et al. 2006) in shallow horizons that probably preclude the ability of most forest species to maintain turgor during the dry season. Only specialized, drought-adapted epiphytes, like *P. scouleri*, which has water-storing rhizomes, are likely to persist on canopy soils unless they are deep, occur in crotches, or cover hidden pockets of decaying wood. Indeed, adaptations to drought are rampant among vascular epiphytes in many forests, especially in the tropics (Zotz and Hietz 2001, Benzing 2004).

A rich animal community shares canopy soil habitats with epiphytic plants in large redwood crowns. Pitfall traps, litterbags, and cores from soils on five of the named redwoods in the plot sampled 85 species of mites and many other invertebrates, including spiders, insects, copepods, centipedes, millipedes, nematodes, annelids, and gastropods (Jones 2005). Redwood leaves and other plant material deposited on the surfaces of canopy soils are processed by a variety of saprotrophic fungi whose fruiting bodies are frequently observed after the first fall rains (S. C. Sillett, *unpublished data*). The top predator of these communities appears to be a salamander,

TABLE 4. Pearson correlations (r) between structural variables and tree scores along the first and second ordination axes (PC1 and PC2) derived from principal-components analysis of 14 named *Sequoia sempervirens* trees in the 1-ha plot.

Structural variable	PC1	PC2
Aboveground dry mass	0.930	−0.150
Crown spread	0.925	−0.108
Leaf dry mass	0.909	−0.048
Reiterated trunk volume	0.892	0.090
Volume		
Main trunk	0.888	−0.179
Crown	0.854	−0.274
Limb	0.828	0.229
dbh	0.822	−0.309
Percentage mass in reiterations	0.810	0.161
No. reiterated trunks	0.771	0.322
No. limbs	0.644	0.276
Volume of dead trunks	0.224	0.924
Height	0.150	−0.685

Note: PC1 accounted for 61.2% and PC2 accounted for 14.1% of total variation in the primary matrix of 13 tree-level structural variables.
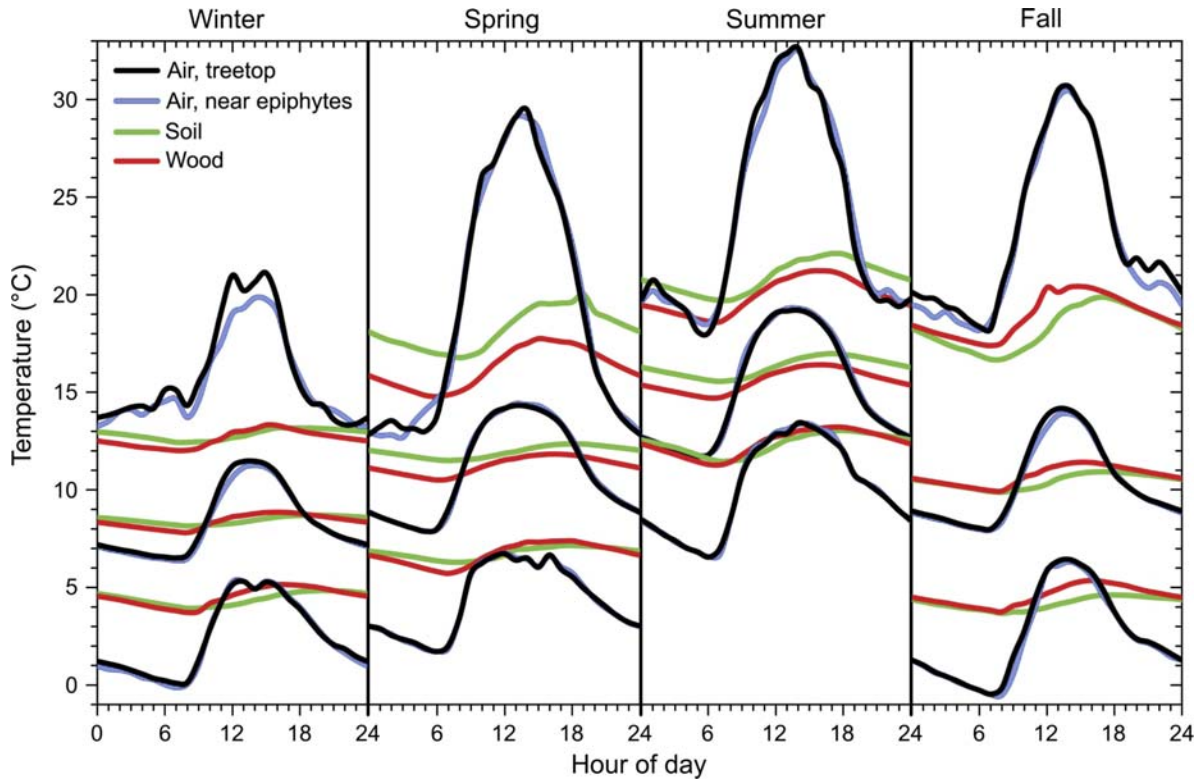
STEPHEN C. SILLETT AND ROBERT VAN PELT

FIG. 10. Summary of diurnal and seasonal temperatures for air at treetop, air near epiphytes, and soil or wood beneath epiphytes. Values are hourly maxima (upper curves), means (middle curves), and minima (lower curves) for each season.

Aneides vagrans, whose tree-level abundance is strongly correlated with the water content of canopy soils (Spickler et al. 2006). Since this lungless species must maintain moist skin for respiration and lays its eggs in humid cavities inside *P. scouleri* mats (Welsh and Wilson 1995), moisture availability is critically important to its survival. The relatively stable temperatures of canopy soils and decaying wood may also influence habitat use
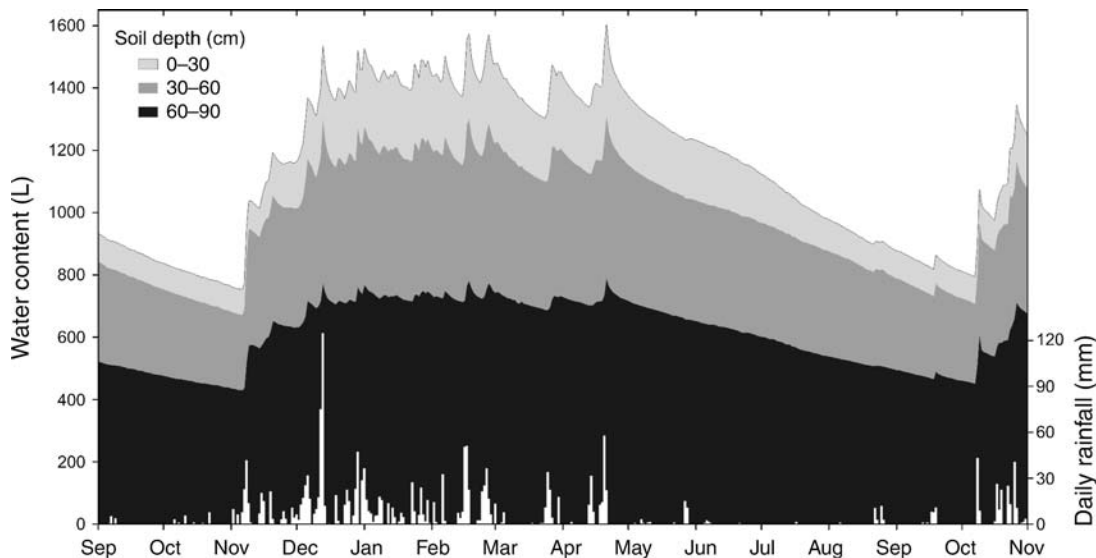
FIG. 11. Summary of water-storage dynamics of a 1-m-deep canopy soil (pedon 2; Enloe et al. 2006) beneath a *Polypodium scouleri* fern mat on a 1.8-m-diameter limb 47 m high in a large *Sequoia sempervirens* tree, Jedediah Smith Redwoods State Park, California, USA, from September 2003 to November 2004. The vertical white bars indicate daily rainfall totals (right-hand axis). The area covered by each depth stratum is equivalent to its proportion of the total water content.

TABLE 5.   Seasonal water contents of canopy soils and dead trunks in the 1-ha plot.

Substrate	Volume of stored water (m³/ha)				
	Winter	Spring	Summer	Fall	Mean annual storage
Crotch soil	9.3–11.9	8.3–11.3	8.2–8.9	8.2–12.1	9.9
Other soil	9.6–16.6	8.9–16.2	4.9–9.8	4.7–13.8	9.8
Dead wood	16.2–24.9	15.6–24.0	12.3–16.2	11.7–20.9	16.5
Total	35.1–53.4	32.9–51.5	25.4–34.9	24.7–46.7	36.2

Note: Seasonal range data are minima and maxima during the 2000–2005 monitoring period.

by arboreal salamanders (Waldron and Humphries 2005). The richness of animal life in canopy soils is not unique to redwood forests, but only a few studies (e.g., Nadkarni and Longino 1990, Winchester et al. 1999) have directly assessed this hidden component of biodiversity in other forests.

In addition to associated soil and decaying wood, vascular epiphytes and the living tree structures beneath them provide habitats and food resources for many organisms in redwood forest canopies. The bark of woody epiphytes serves as substrate for lichens and bryophytes that rarely, if ever, occur on redwood bark (Williams and Sillett 2007). Yellow-cheeked chipmunks (*Tamias ochrogenys*) as well as Band-tailed Pigeons (*Columba fasciata*) frequently feed on *Vaccinium* berries in redwood crowns. A nest of the Sonoma tree vole (*Arborimus pomo*), which feeds primarily on leaves of *P. menziesii* (Johnson and George 1991), was observed on a
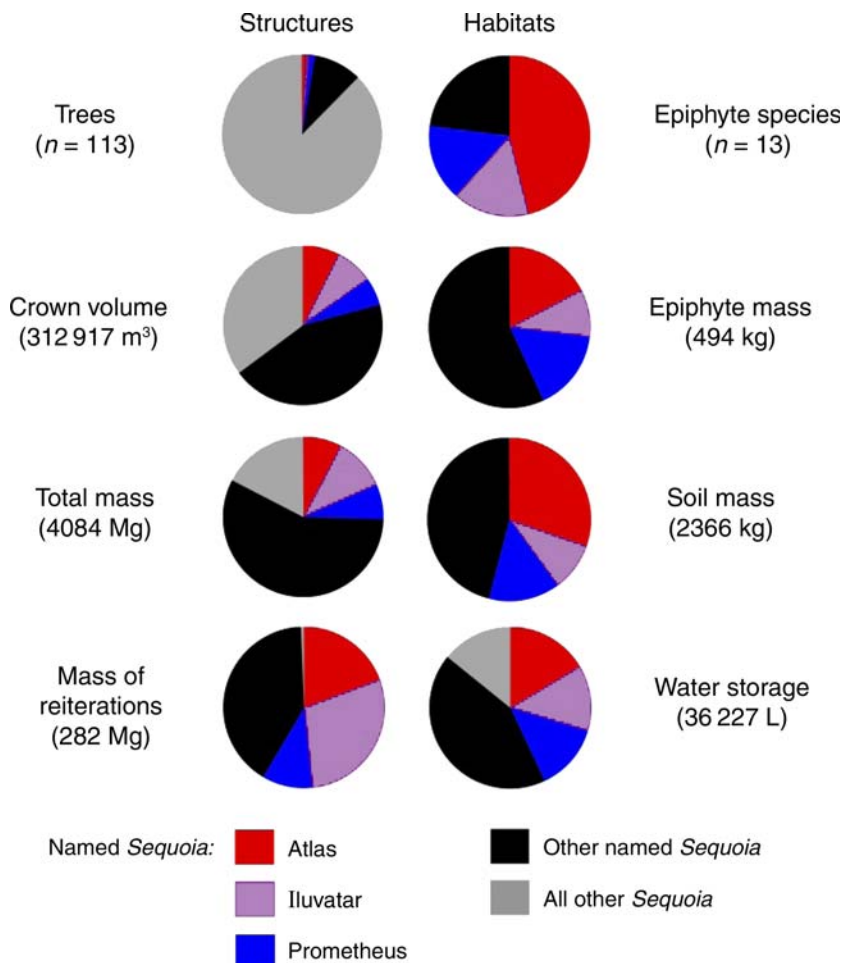

FIG. 12.   Summary of tree structures and arboreal habitats associated with living *Sequoia sempervirens* trees in the 1-ha plot. Pie charts show the relative proportion of trees (named and other) in each category. Mass values are estimated dry masses. Mass values of reiterations include trunks and limbs. Proportions of epiphyte species are expressed as cumulative richness beginning clockwise with the individual tree named Atlas. Water storage is mean annual water content of canopy soil and dead wood.

PLATE 1.   A ground-level view of the study plot in Prairie Creek Redwoods State Park, California (USA), showing a profusion of sword fern (*Polystichum munitum*) in the understory beneath towering redwoods (*Sequoia sempervirens*) with reiterated trunks. Photo credit: R. Van Pelt.

limb complex in the middle crown of a redwood projecting into the crown of an adjacent *P. menziesii*. Finally, the endangered Marbled Murrelet (*Brachyramphus marmoratus*), a seabird whose closest relatives nest on rocky cliffs, nests on thick horizontal tree surfaces (Hamer and Nelson 1995), including two redwood limbs in the plot between 1998 and 2002.

Future research directions

Results from this intensive investigation of a 1-ha plot indicate that restoration of redwood forests may be feasible. The majority of the plot's structure was held in the crowns of 14 trees, the largest and most complex of which carried the bulk of habitats for vascular epiphytes

and other arboreal organisms (Fig. 12). Thus, manipulation of a relatively small number of trees could have important ecological consequences for the forest as a whole. If redwood responds like other conifers, a variety of techniques may be effective in stimulating trunk reiteration and accelerating limb formation. Many conifers exhibit strong apical control in which the intact treetop suppresses reiteration and regulates the export of assimilate from branches (Cline 1997), so treetop removal can result in more rapid branch growth, upward bending, and trunk formation (Wilson 1998, 2000). What is not clear, however, is whether treetop removal will stimulate formation of multiple trunks within the crown or merely a single replacement of the

leader trunk. Moreover, if the treetop exerts apical control over lateral branches from the main trunk, branch tips may also exert apical control over branchlets stemming from the main axis of the branch. If this occurs in redwood, branch-tip removal might stimulate limb formation, especially when apical control of the main trunk is disrupted, too.

In addition to the effects of apical control, branch growth is also controlled by light availability, and branches compete with each other for light within the crown (Stoll and Schmid 1998). Thus, pruning branches from tree crowns may reduce shade within the crown and lead to higher rates of growth in the remaining branches. Branches also compete for assimilates they export to the main trunk, which are stored and then re-allocated at the beginning of the growing season. Well-illuminated higher branches are more competitive sinks than shaded lower branches, leading to self-pruning even when there is adequate light for positive net photosynthesis (Sprugel 2002).

A factorial experiment involving treetop and branch-tip removal as well as branch pruning would be necessary to demonstrate whether or not such arbori-cultural manipulations stimulate trunk reiteration and limb formation. If they do, it may be possible to accelerate the development of structural complexity in forest trees, which has long-term implications for conservation. Ultimately, we envision a two-stage strategy for restoration of structural complexity to young redwood forests. The first stage utilizes well-established silvicultural techniques to promote tree growth (e.g., thinning). When trees reach a sufficient height to maintain reiterated trunks and limbs induced by injury (~60 m; Fig. 4), they are ready for the second stage, which would involve crown-level manipulations suggested by experimental results.

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APPENDIX A

Equations used to estimate structural components of woody plants in the 1-ha plot (*Ecological Archives* M077-011-A1).

APPENDIX B

Measurements and calculations used to derive a Cartesian coordinate system connecting all structures in mapped tree crowns and to error-check the resulting models in Microsoft Excel (*Ecological Archives* M077-011-A2).

APPENDIX C

Description of the calibration procedure used to convert waveform output of time-domain reflectometry (TDR) to volumetric water contents of soil and dead-wood substrates beneath vascular epiphytes in old-growth redwood forest canopies (*Ecological Archives* M077-011-A3).

ERRATUM

In the recent paper by Stephen C. Sillett and Robert Van Pelt (2007) entitled "Trunk reiteration promotes epiphytes and water storage in an old-growth redwood forest canopy," *Ecological Monographs* 77(3):335–359, an error was introduced by the printer in the last sentence of the last full paragraph on p. 337. Highly reiterated redwoods were modeled as 3/4 ellipsoids (not 1/3 ellipsoids, as published). Thus, the sentence should read "Crowns of shrubs, *Tsuga*, and model-conforming redwoods were modeled as paraboloids, angiosperms and *Pseudotsuga* were modeled as 2/3 ellipsoids, and highly reiterated redwoods were modeled as 3/4 ellipsoids based on a visual assessment of crown shapes and the proven utility of this approach in other studies. . . ."