

UNDERSTORY LIGHT AND GAP DYNAMICS IN AN OLD-GROWTH FORESTED WATERSHED IN COASTAL CALIFORNIA

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ABSTRACT

This paper describes the understory light environments and gap dynamics of forests in the watershed of Maddock Creek, Big Basin Redwoods State Park, Santa Cruz County, CA. Most of this 230 ha watershed is covered by old-growth forests representative of upland redwood forests and the *Pseudotsuga*-hardwood forests which intergrade with them. Species of canopy trees include *Sequoia sempervirens* (D. Don) Endl., *Lithocarpus densiflorus* (Hook. & Arn.) Rehder, *Pseudotsuga menziesii* (Mirbel) Franco, *Arbutus menziesii* Pursh, and *Quercus chrysolepis* Liebm., in descending order of cover. In the understory of these forests, total light was about 12% of that incident upon the canopy. Understory light levels differed between aspects and were influenced by canopy species composition and gaps. Except for *Lithocarpus*, regeneration of canopy species was associated with higher understory light levels and the species less tolerant of shade (*Arbutus*, *Pseudotsuga*, and *Quercus*) filled more gaps on the south-facing slopes, where light levels were higher. In contrast, *Lithocarpus* was abundant throughout the understory, present in most gaps at a high cover, and filling twice as many canopy gaps as it had formed. In the presence of surface fires, we suggest that *Lithocarpus* would not increase in dominance. However, in the absence of fire, our results indicate an increasing dominance by *Lithocarpus*, and suggest that interspecific differences in shade cast and shade tolerated are contributing to the dynamics of forests in central coastal California.

In north coastal California, upland redwood and *Pseudotsuga*-hardwood forests are the predominant forest types (Barbour and Major 1988). These forests have a two-layered canopy: an upper layer (to 70 m high) dominated by gymnosperms, and a lower layer (to 40 m) dominated by angiosperms (Whittaker 1960; Sawyer et al. 1988; Zinke 1988). The most important gymnosperms are *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir, Pinaceae) and *Sequoia sempervirens* (D. Don) Endl. (redwood, Taxodiaceae), and the most important angiosperms are *Arbutus menziesii* Pursh (madrone, Ericaceae) and *Lithocarpus densiflorus* (Hook. & Arn.) Rehder (tanoak, Fagaceae).

The dynamics of these forests involve both fire and tree falls. Prior to the twentieth century, fires typically burned through these forests at intervals of 5–50 yr (Greenlee 1983; Jacobs et al. 1985; Rice 1985; Agee 1991; Finney and Martin 1992). For most of this century, however, fires have been suppressed, and tree falls have dominated the dynamics of older stands. Because the dominant species differ in longevity and shade tolerance (Burns and Honkala 1990), species composition and structure could

be changing substantially. If so, these on-going changes generally have not been documented, and are not well understood (but see Sugihara 1992; Hunter 1997a).

This paper contains two components of an investigation into the dynamics of an old-growth forested valley which has not experienced fire for 60–80 years. The first examines understory light as a potentially significant factor affecting recruitment of saplings. The second examines canopy gaps from throughout the watershed, and for each gap documents the species of the canopy tree(s) that formed the gap and of the understory tree(s) filling it.

The study area is Maddock Creek Watershed in the Santa Cruz Mountains of California's central coast (37°10'N, 122°15'W). This watershed is 13 km from the coast, 230 ha in size, and at 340–535 m in elevation. Ridgelines run northwest to southeast, and have steep slopes of 11–52°.

Most of this watershed is covered by old-growth forest, portions of which last burned in 1904 and 1936 (Greenlee 1983). These forest stands are representative of upland redwood forests and the *Pseudotsuga*-hardwood forests that intergrade with them (Hunter 1989). They have a two-tiered canopy: the conifers *Pseudotsuga menziesii* and *Sequoia sempervirens* form an upper tier, while the angiosperms

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Arbutus menziesii, *Lithocarpus densiflorus*, *Quercus chrysolepis* Liebm., and *Quercus wislizeni* A. DC. form a lower layer dominated by *Lithocarpus*. (Nomenclature follows Hickman 1993.) Neither tier forms a complete layer: each covers about two-thirds of the forest floor. Canopy gaps (breaks in both canopy layers) occupy approximately 11% of the land area with an average size of 91 m² (Hunter and Parker 1993). In species composition and structure, the understory vegetation beneath canopy gaps is similar to that at canopied locations (Hunter 1989). The shrub layer (0.5–3 m) typically has 25–50% cover and is dominated by *Vaccinium ovatum* Pursh and juvenile *Lithocarpus*. The herb layer (<0.5 m) typically has <1% cover.

METHODS

Understory light environments. We used computer analysis of hemispherical photographs to estimate light levels at the forest floor relative to light levels above the forest canopy (Percy 1989). This technique allows a reasonably precise comparison of the light environments at different locations (Chazdon and Field 1987; Becker et al. 1989). It is outlined below and described in more detail by Anderson (1964), Becker et al. (1989), Percy (1989), and Rich (1989).

In hemispherical photographs, the distance from the image's center is proportional to the angle from the zenith of the hemisphere which was above the camera. Therefore, the photograph can be divided into regions corresponding to ranges of zenith and azimuth angles, and the sun's path can be plotted across these regions. Each region can be weighted by the proportion of total irradiance coming from that section of sky. This procedure is done separately for direct and indirect components of light. Direct light is received only from those regions of sky along the sun's path, whereas indirect light (diffuse light which has been scattered by the atmosphere) is received from all regions of the sky but is more intense towards the zenith. For each region of sky, the fraction of light reaching the understory is assumed to equal the fraction of sky unobscured by foliage.

We used the "Canopy" computer program to analyze the photographs (Rich 1989). For calculating the percentage of indirect light, the program divides the image into 160 regions, and weights these assuming a standard overcast sky. For calculating the percentage of direct light, it divides the sun's annual path across the sky into monthly paths, each of which gets sub-divided into half-hour intervals.

We took photographs of the canopy at 80 points randomly located throughout the watershed. A Telestar hemispherical lens on a Pentax K1000 body was used with ASA-64 slide film. (The slide images had very sharp contrasts between sky and foliage, partially due to ideal weather.) The camera was positioned on a level surface 1 m above the forest

floor and a white pole used to mark true north in the photograph. We took photographs only when the sky was uniformly overcast and no wind was blowing.

At each point, we recorded slope aspect, understory species, and canopy characteristics. Within a radius of 2 m from the camera, all species in the herb and shrub layers (0–0.5 m and 0.5–3 m high, respectively) were recorded and total cover visually estimated. All canopy species within approximately 30 m of the camera were listed in order of estimated cover. We also noted if the camera was below a gap.

Gap dynamics. To obtain a random sample of 80 canopy gaps, we randomly located 20 points within the watershed. From these points, the nearest gap within each compass quadrant (N, E, S, W) was located. We defined a gap as any break in both canopy tiers due to tree or limb mortality and below which vegetation was less than two thirds the height of the adjacent lower canopy tier (minimum diameter 4 m). The edge of the adjacent crowns of canopy trees was considered the gap edge, and was determined with a canopy densitometer. The canopy densitometer has a mirror, level and cross-hairs allowing the user to determine the point directly overhead (GRS 1992).

For each gap, we recorded slope aspect, area, understory vegetation, gap-forming species, and gap-filling species. Within the gaps, species cover was visually estimated for herb, shrub and sapling layers (0–0.5, 0.5–3 and >3 m respectively).

We used position of logs and their state of decay to determine the species present in the canopy before the gap was created (the gap-forming species). Ten of the sampled gaps had been formed by more than one canopy species. In all cases, the removal of one species created most of the gap's area, and this species was considered the gap-forming species.

We considered the tree species present in a gap's uppermost vegetation layer to be the species filling that gap. (For 78 of the 80 gaps, the sapling or shrub layer was uppermost.) Twenty gaps had more than one tree species in the uppermost layer. In these gaps, the species with the greatest cover in the upper layer, we identified as the species filling the gap. Where an angiosperm and a conifer species were both in the uppermost layer, the conifer could have been considered the gap-filling species, even if at a lower cover, because of its greater maximum size and potentially faster growth (McArdle et al. 1949; Porter 1965). However, in no gap was *Sequoia* both in the uppermost layer and at a lower cover than an angiosperm in that layer, and in only three gaps was *Pseudotsuga* both in the uppermost layer and at a lower cover than an angiosperm species. If *Pseudotsuga* had been considered the species filling those three gaps, the results would have

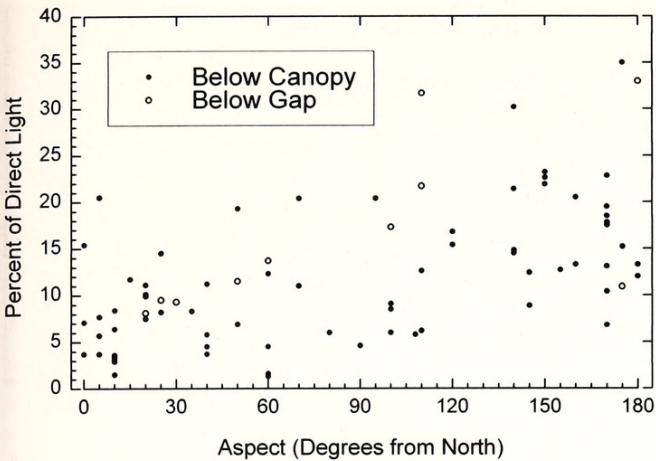


FIG. 1. Aspect and direct light reaching the understory for 80 locations in the watershed of Maddock Creek, Santa Cruz Co., CA. Percent direct light is percent of light incident upon canopy that reaches understory.

remained similar, and their interpretation would not have been altered.

RESULTS

Understory light environments. For the year and the watershed as a whole, total light reaching the understory was about 12% of that incident upon the canopy. Direct light averaged $12.5 \pm 7.3\%$ and ranged from 0.1 to 35%. Indirect light had a comparable average (11.8%), but less variation (1 SD = 3.6, range 4.8–21.0%).

More light reached points beneath canopy gaps ($n = 10$, direct light mean $16.7 \pm 9.2\%$, indirect light mean 13.7 ± 3.6) than beneath the canopy ($n = 70$, direct light mean $11.9 \pm 6.9\%$, indirect light mean $11.6 \pm 3.6\%$; Mann-Whitney U, $P = 0.03$ and 0.02 , respectively). However, light levels at gap locations were not disjunctly higher than light levels at canopied locations. The range of light levels within gaps fell within the range of light levels at canopied locations (8.1–33% and 0.1–35% direct light, respectively).

Understory light environments also differed between aspects (Fig. 1). Twice as much direct light reached the understory of south-facing slopes (90–270°, $n = 38$, mean = $16.9 \pm 7.1\%$) than of north-facing slopes (270–0–90°, $n = 42$, mean = $8.4 \pm 5.3\%$; Mann-Whitney U, $P < 0.001$). Twenty-two percent more indirect light reached the understory of south-facing slopes ($13.8 \pm 3.4\%$) than of north-facing slopes ($10.8 \pm 2.9\%$; Mann-Whitney U, $P < 0.001$). The higher indirect light levels on south-facing slopes indicate a more open canopy.

Interestingly, species composition of the canopy also influenced understory light levels. On south-facing slopes, canopy species composition was patchier and separated into two distinct canopy types: (1) a *Pseudotsuga*-hardwood type with emergent *Pseudotsuga* above a layer of angiosperms dominated by *Arbutus* and the *Quercus* species, and (2) an upland redwood type with emergent *Sequoia* above a layer of *Lithocarpus*. Light levels beneath the *Pseudotsuga*-hardwood canopy ($22.4 \pm 8.4\%$, $n = 7$) were substantially higher than beneath the *Sequoia*-*Lithocarpus* canopy ($12.6 \pm 6.4\%$, $n = 7$; Mann-Whitney U, $P = 0.05$). This difference between canopy types was comparable to that between canopied and gap locations, and indicates that local variation in canopy composition can affect understory light environments significantly. These two canopy types covered 37% of south-facing locations, and the remaining locations were intermediate in canopy structure and light environment.

There was a correspondence between light levels and distribution of tree species in the understory. For *Arbutus*, *Pseudotsuga*, and *Quercus*, understory saplings in the shrub layer occurred at significantly high light levels (Table 1). *Sequoia* saplings in the shrub layer were not found at high light levels, but established seedlings in the herbaceous layer were found at significantly high light levels (mean = $20.5 \pm 7.0\%$ direct light). This result is consistent with the species' biology: saplings of *Sequoia* are

TABLE 1. MEAN LIGHT ENVIRONMENTS FOR UNDERSTORY INDIVIDUALS OF CANOPY TREE SPECIES. N is the number of locations (out of 80) at which species were present in a given vegetation layer. Means (± 1 SD) are of percent of light incident upon the canopy that reaches the understory. Asterisks denote an average significantly higher than locations without the species; * $P < 0.05$, ** $P < 0.01$ (Mann-Whitney U test).

Species	N	Direct light ave.	Indirect light ave.
Shrub layer			
<i>Arbutus menziesii</i>	2	$25.6 \pm 8.6^*$	$17.4 \pm 1.2^*$
<i>Quercus chrysolepis</i>	4	$22.3 \pm 9.1^{**}$	$16.0 \pm 2.9^*$
<i>Pseudotsuga menziesii</i>	6	$19.6 \pm 7.6^{**}$	$14.5 \pm 3.6^*$
<i>Lithocarpus densiflorus</i>	69	11.7 ± 7.3	11.7 ± 3.7
<i>Sequoia sempervirens</i>	22	10.9 ± 7.0	10.0 ± 3.4
Herbaceous layer			
<i>Sequoia sempervirens</i>	5	$20.5 \pm 7.0^*$	17.0 ± 14.7
<i>Quercus chrysolepis</i>	9	$19.1 \pm 11.3^*$	14.2 ± 4.5
<i>Pseudotsuga menziesii</i>	5	14.5 ± 7.5	12.6 ± 2.4
<i>Lithocarpus densiflorus</i>	24	12.0 ± 8.1	11.6 ± 3.5

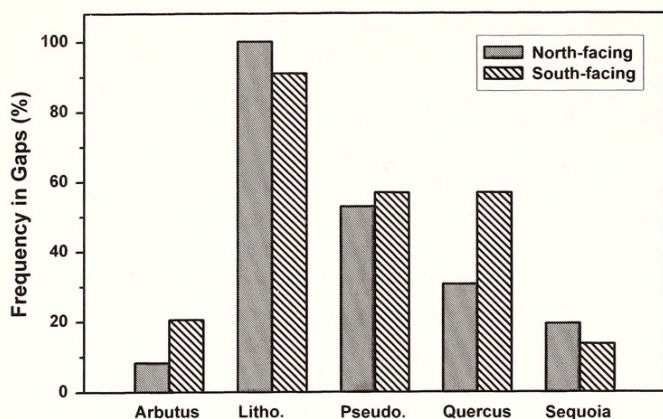


FIG. 2. Frequency of tree species beneath canopy gaps on north-facing ($n = 36$) and south-facing ($n = 44$) aspects of Maddock Creek's watershed, Santa Cruz Co., CA. *Arbutus* = *Arbutus menziesii*, *Litho.* = *Lithocarpus densiflorus*, *Pseudo.* = *Pseudotsuga menziesii*, *Quercus* = *Quercus chrysolepis* and *Sequoia* = *Sequoia sempervirens*.

shade-tolerant and persist in the understory for decades, but establishment of seedlings is strongly affected by light levels (Jacobs 1987). Only *Lithocarpus*, by far the most abundant and widespread tree in the understory, had no correspondence between light levels and seedling or sapling distribution.

Gap dynamics. Most tree species were absent from a large portion of gaps (Fig. 2). Only *Lithocarpus* was present in almost all gaps (95%), and at a high cover (mean = $36.4 \pm 27.4\%$). *Pseudotsuga* and *Quercus* were in a large portion of gaps (49 and 45% respectively) but when present were at a low cover (5.5 ± 9.4 and $6.1 \pm 11.6\%$), while *Arbutus* and *Sequoia* were rarely present (15 and 16% respectively) and were at a low cover (mean = 7.5 ± 11.2 and $12.3 \pm 19.5\%$).

Lithocarpus also was filling the most gaps (Fig. 3). Of 80 gaps, *Lithocarpus* was filling 68%, *Pseudotsuga* 15%, *Quercus chrysolepis* 9%, *Sequoia* 5%, and *Arbutus* 4%. Because *Lithocarpus* had formed significantly less of the gaps (38%) than it was filling, it was increasing in importance within the canopy (χ^2 test, $df = 1$, $P = 0.0001$). *Pseudotsuga* and *Arbutus* had formed significantly more of the gaps (35 and 14% of gaps, respectively) than they were filling, and thus were declining in importance within the canopy (χ^2 test, $df = 1$, $P = 0.004$ and 0.025 respectively). *Sequoia* and *Quercus* did not have significant differences between the number of gaps formed and the number filled, though an increase in *Quercus* is suggested ($P = 0.086$).

There was also a relationship between gap-forming and gap-filling species. Of gaps formed by *Lithocarpus* ($n = 30$), *Lithocarpus* filled 90%, significantly more than expected (χ^2 test, $df = 1$, $P = 0.001$). This result may be due in part to a significantly lower presence of other species in gaps

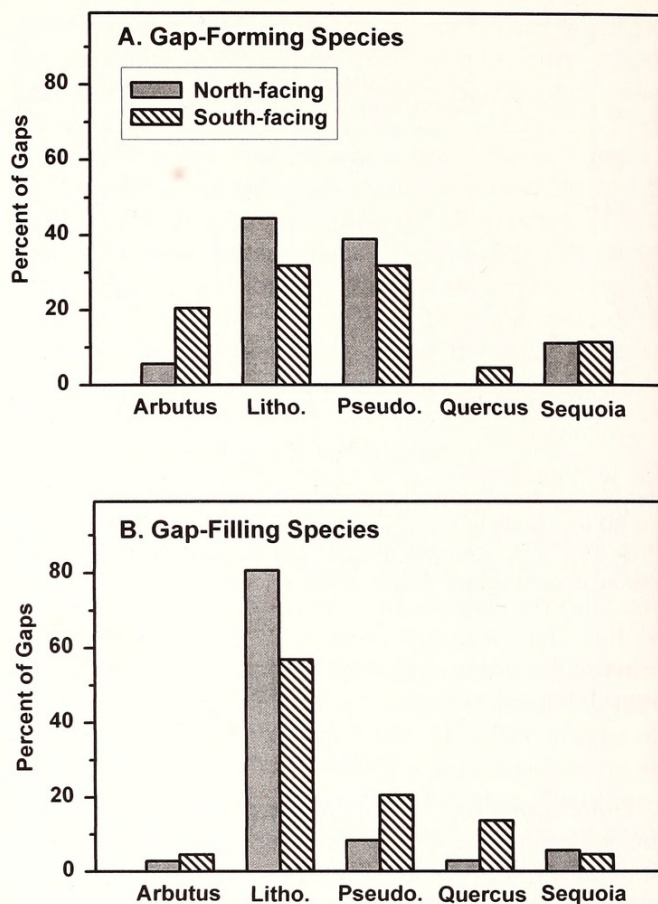


FIG. 3. Species forming and filling gaps on north-facing ($n = 36$) and south-facing ($n = 44$) aspects of Maddock Creek's watershed, Santa Cruz Co., CA. Species abbreviations as in Figure 2.

formed by *Lithocarpus* (χ^2 test, $df = 1$, $P = 0.002$). Gaps formed by *Lithocarpus* ($n = 30$) averaged 1.8 ± 0.8 tree species versus 2.4 ± 0.9 present below gaps formed by other species (Mann-Whitney U, $P = 0.003$). Also, *Lithocarpus* was the only tree species present below 43% of gaps formed by *Lithocarpus*, while just 10% of gaps formed by other species had only *Lithocarpus* present beneath them (χ^2 test, $df = 1$, $P < 0.001$). The data also suggest self-replacement by *Sequoia*. Three of four gaps formed by *Sequoia* were being filled by basal sprouts of the same tree(s) that had formed the gap.

Although there was no relationship between gap area and species filling the gap, there was a relationship between slope aspect and gap-filling species (Fig. 3). Species less tolerant of shade (*Arbutus*, *Quercus chrysolepis*, and *Pseudotsuga*) filled significantly more south-facing gaps (39%) than north-facing gaps (14%; χ^2 test, $df = 1$, $P = 0.014$). As a consequence, succession differed between north and south-facing slopes. On north-facing slopes, *Pseudotsuga* formed significantly more gaps than it filled (χ^2 test, $df = 1$, $P = 0.002$) and therefore declined in importance, while on south-facing slopes there was no significant difference in the number of gaps formed and filled by *Pseudotsuga* ($P = 0.23$). The data also suggested differences be-

tween aspects in the dynamics of *Lithocarpus* and *Quercus*.

DISCUSSION

In upland redwood and *Pseudotsuga*-hardwood forests, tree species differ in shade-tolerance. For example, *Quercus* species, *Arbutus* and *Pseudotsuga* are clearly less tolerant than *Lithocarpus*, *Sequoia* and *Umbellularia californica* (Hook. & Arn.) Nutt. (Waring and Major 1964; Unsicker 1974; Tappiener et al. 1986; Burns and Honkala 1990; Sugihara 1992; Hunter 1997a and 1997b). Together with the influence of fire, these interspecific differences in shade-tolerance probably determine most patterns of sapling recruitment into the canopy.

Prior to fire suppression, surface fires would have removed most understory regeneration, including *Lithocarpus* saplings (Kauffman 1986). This effect would have limited the successful recruitment of understory *Lithocarpus* into the canopy, while creating seedbed and understory conditions favorable for the other canopy species (Jacobs 1987; Hermann and Lavender 1990; Hunter 1994). Currently, however, *Lithocarpus* saplings accumulate in forest understories (Tappiener and McDonald 1984; Hunter 1997a).

By affecting sapling establishment prior to gap formation, the transmission of light through canopies can influence substantially the species composition of regeneration (Canham et al. 1994). This was the case in this watershed's forests. Here, most gaps were filled by saplings that had established prior to the gap's formation. As a consequence, the most abundant species throughout the understory, the shade-tolerant *Lithocarpus*, was also the species filling the majority of canopy gaps.

Because forest canopies vary on a fine scale in species composition, leaf area and height, light reaching the understory is also variable (Baldocchi and Collineau 1994). In this study, canopied locations received from 0.1 to 35% of the direct light incident upon the canopy. This range of light levels had ecological significance because four of the five canopy species had understory regeneration associated with higher understory light levels, and because the less shade tolerant species were filling more gaps on south-aspects, where light levels were higher.

Interestingly, much of the variation in understory light seems to be due to interspecific differences in shade cast. In this study, on south-facing slopes, light levels beneath a *Pseudotsuga*-mixed hardwood canopy were nearly twice those beneath a *Sequoia-Lithocarpus* canopy (ave. 20.7% vs. 12.6%), a difference comparable to that between gaps and canopied locations (16.7% vs. 11.9%). In other studies, there is also evidence that the more shade-tolerant species can develop a denser crown and therefore allow less light to pass through to the understory (Waring & Major 1964; Unsicker 1974; Minore 1986; Harrington et al. 1984).

If much of the variation in understory light is due to interspecific differences in transmission of light through the crown, then this attribute could be an important cause of observed patterns in the stand dynamics in California's coastal forests. For example, the self-replacement of *Lithocarpus* (observed in this study) may be promoted by low levels of light passing through the crowns of canopy-sized *Lithocarpus*, allowing advance regeneration of the shade-tolerant *Lithocarpus* but not of less tolerant species. Similarly, relatively high levels of light passing through the crowns of *Quercus* species and *Arbutus* may contribute to their replacement by *Pseudotsuga* and *Umbellularia*, which occurs in several types of forest and woodland vegetation (McBride 1974; McDonald and Littrell 1976; Hunter 1995; Safford 1995; Barnhart et al. 1996).

For the dominant trees of California's coastal forests, the magnitude of interspecific differences in shade cast, and the influence of these differences upon succession both deserve further investigation.

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