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Author(s): J. C. Hunter and V. T. Parker

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# The disturbance regime of an old-growth forest in coastal California

Hunter, J. C.<sup>1\*</sup> & Parker, V. T.

Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132, USA;

<sup>1</sup>Present address: Department of Botany, University of California, Davis, CA 95616, USA;

\*Corresponding author; Fax +1 916 7525410

**Abstract.** This study deals with the disturbance regime of an old-growth, mixed-evergreen forest with a canopy composed of *Arbutus menziesii*, *Lithocarpus densiflora*, *Pseudotsuga menziesii*, *Quercus chrysolepis*, *Q. wislizenii*, and *Sequoia sempervirens*. 80 canopy gaps were randomly selected from throughout a 230-ha watershed. Of the land area sampled, 11.1 to 16.6% was within gaps. Gap area had a mode of <50 m<sup>2</sup> and a range of 6–3437 m<sup>2</sup>. Gaps were formed by snags, snaps, tips, and slope failures. Although <10% of the gaps sampled were due to slope failures, these accounted for 43% of the total land area within gaps. All snags resulted from the death of a *Pseudotsuga* or *Arbutus* individual, the widely branched trunks of *Arbutus* individuals accounted for most of the irregularly shaped gaps, and larger gaps resulted from the death of *Pseudotsuga* and *Sequoia* individuals, averaging 119 and 111 m<sup>2</sup> respectively, than from the death of *Lithocarpus* or *Arbutus*, averaging 54 and 52 m<sup>2</sup>. Gaps were more frequent over concave sections of slopes and large gaps were more frequent on north-facing slopes. The creation of a gap increased disturbance to the adjacent canopy, with half of the gaps formed through more than one disturbance.

The relationship of disturbance regime to topography, the influence of canopy species biology on gap properties, and the repeated events involved in gap formation all indicate a fine scale variation in the pattern of gaps and their characteristics.

**Keywords:** Canopy gap; *Lithocarpus densiflora*; Mixed evergreen forest; *Pseudotsuga menziesii*; *Sequoia sempervirens*; Slope failure.

**Nomenclature:** Munz & Keck (1968).

## Introduction

All forests undergo a cycle of disturbance and regeneration. Canopy openings (gaps) created by the removal of limbs and trunks frees space and creates higher levels of some resources. Most studies of disturbance regimes have examined either fire or windthrow. Studies of fire regimes have often explicitly focused on variation in area, magnitude, and frequency, as well as the relationships between these parameters and topography (Minnich

1989; Bergeron & Brisson 1990). In contrast, most studies of windthrow regimes have focused only on variation in area, and very few have examined the relationships between disturbance regime and topography. The tendency to study small areas intensively (e.g. Putz & Milton 1982; Hartshorn 1978; Kanzaki & Yoda 1986; Liu & Hytteborn 1991) or only 'representative' stands (Runkle 1982; Aplet, Laven & Smith 1988) reduces topographic variation within samples, thereby obscuring the role of topography. Furthermore, the longevity of trees in the canopy and the interval between disturbances at one point in a forest are frequently derived by dividing the area disturbed per year into a unit area (Brokaw 1982; Runkle 1985). This method cannot distinguish sites with little variance in intervals between disturbances from sites with wide variances. It also does not distinguish between spatially homogeneous sites with basically one frequency of disturbance and spatially heterogeneous sites composed of areas with different frequencies of disturbance.

In this study, we sampled canopy gaps from throughout a 230-ha watershed. We describe not only the pattern of canopy gaps, but also the distribution of gaps over the landscape, variance within the cycle of disturbance and regeneration, and the formation of gaps with respect to location of pre-existing gaps.

## Study area

Our study area is the Maddock Creek watershed of Big Basin Redwoods State Park in the Santa Cruz Mountains of California's central coast (37° 10' N, 122° 15' W). The Maddock Creek watershed, 13 km from the Pacific Ocean, is 230 ha in size, and 340–535 m in elevation. It is underlain by Tertiary sandstones interbedded with siltstones and mudstones. Slopes are steep, 11–52°, and hummocky, with slope failures forming scarps, and benches. The main process of erosion is the down-slope movement of soil and rock by debris flow, landslide, and soil creep (McJunkin 1983).

Mixed evergreen forest covers most of the watershed,

but patches of chaparral exist along the ridgetop(s) and the upper south-facing slope. The forest has a two-tiered canopy: the conifers *Pseudotsuga menziesii* and *Sequoia sempervirens* form the upper tier while hardwood species *Arbutus menziesii*, *Lithocarpus densiflora*, *Quercus chrysolepis*, and *Q. wislizenii* dominate the lower tier. Neither tier forms a complete layer. Although each species is present throughout the watershed, distinct associations do exist. Nearly pure stands of *Sequoia* occur along creeksides and within concave swales on mesic slopes; an association dominated by *Lithocarpus*, *Pseudotsuga*, and *Sequoia* covers much of the slopes; and the hardwoods with *Pseudotsuga* predominate on xeric exposures and along secondary ridges and knobs.

Old-growth forest covers the study area. During the last 1000 yr, parts of the watershed have burned 12-15 times, with between-fire intervals of 5-261 yr (Greenlee 1983). Most of the study area last burned in 1904, but some locations burned in 1936 as well. These last two fires appear to have been surface fires causing little damage to the canopy.

California purchased 1012 ha of unlogged forest to form the park in 1902 (DeVries 1978). Bark strippers had previously removed cords of *Lithocarpus* bark for sale to tanneries and after the park's formation some *Sequoia* were illegally logged. We did not sample a small area at the mouth of the Maddock Creek watershed that apparently was impacted by these activities.

## Methods

We used the point-centered quarter method (Cottam & Curtis 1956) to obtain a random sample of canopy gaps and a measure of gap density. 20 points were randomly located 0-200 m up or down slope from a 6-km transect circling the watershed at about mid-slope. Thus points were located anywhere from streamside to ridgeline. However, due to the 'U'-shape of the transect, the lower slopes were oversampled relative to the upper slopes. From the points, we located the nearest gap within each compass quadrant (N, E, S, W). We considered a gap to be any break in the canopy  $> 1 \text{ m}^2$  due to tree or limb mortality and below which vegetation was less than  $2/3$  the height of the adjacent lower canopy tier. For each gap, we recorded distance from the random point to the gap center, area, shape, number of disturbance events, number of trees, the mechanism of gap formation and the species of tree that died and topographic characteristics (aspect, slope angle, slope shape, and position on slope). Within each compass quadrant, an additional point was randomly located. At each of these points, we recorded topographic position (aspect, slope angle, slope shape, and position on slope)

and point-centered quarter data for trees.

Openings were measured from the edge of the vegetation canopy as located with a periscope. Gap length and gap width were measured from the gap's center. For irregularly shaped gaps, such as Y- or L- shaped gaps, lengths and widths were measured from several points. Non-irregular gaps were considered circles or ellipses unless they had pronounced corners. Round gaps whose lengths were within 1 m of their widths were considered circles. Age of sprouts, plus position of logs and their state of decay were used to determine the species present in the canopy before the gap was created, the mechanism of formation (slope failure, wind thrown, wind snapped, snag) plus the number of trees involved and the probable minimum number of disturbance events (which are incidents removing one or more trees from the canopy). We measured slope aspect with a compass and slope angle with a clinometer. Slope shapes were characterized as concave, convex, and planar. We measured gap elevation with an altimeter and then relativized elevation as the difference between the gap's elevation and the creek's elevation divided by the difference in elevation between ridgetop and creekside.

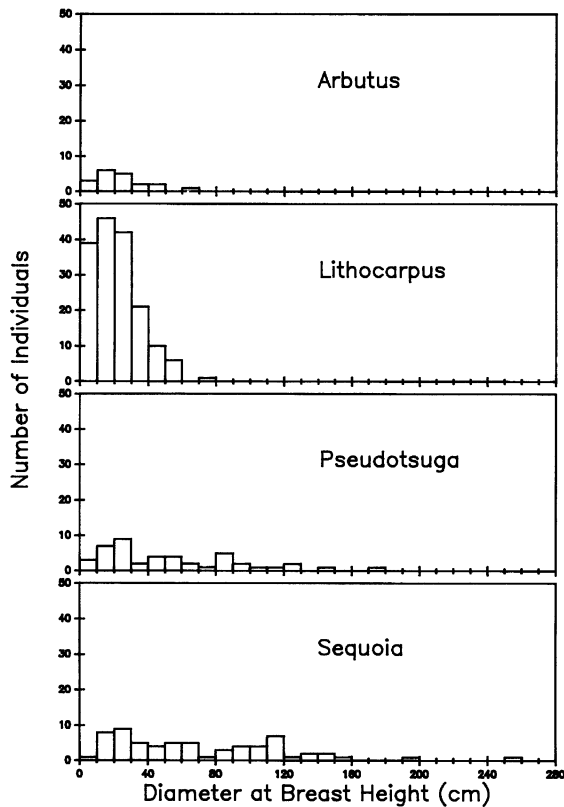
Additional data were collected on canopy structure and on large slope failures. For canopy structure, we recorded line intercept data with a periscope along six 90 m transects (Canfield 1941; Mueller-Dombois & Ellenberg 1974). Three transects each were located on a north-facing and a south-facing slope. They ran perpendicular to the slope at 80-m intervals up the slope with randomly located starting points. For large slope failures, we surveyed four adjacent old-growth watersheds and used aerial photographs to date the slope failures located in the survey.

To analyze the pattern of gaps, we calculated gap density and tabulated frequency distributions of gap area, number of trees involved, number of events, mechanism and tree species involved. We also examined interrelationships both among these characteristics and between characteristics and topography.

## Results

Based on 80 quarter points, tree density was 650.6 stems/ha and basal area was 124.2  $\text{m}^2/\text{ha}$ . *Lithocarpus* stems made up 54.6 % of the total density, while *Sequoia* and *Pseudotsuga* were represented by a smaller number of larger stems (relative densities of 21 % and 14.5 % respectively).

Each species was well represented across a range of diameters (Fig. 1). *Sequoia* in particular had an even distribution of individuals up to 120 cm dbh and a few larger individuals up to 260 cm dbh, although several of

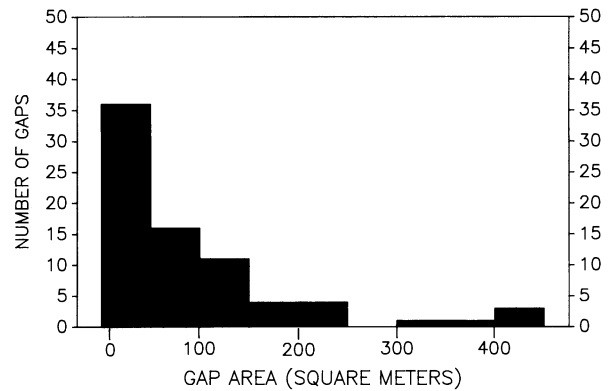


**Fig. 1.** Frequency distribution of diameters for trees sampled within the Maddock Creek Watershed, Santa Cruz County, California ( $n = 320$ ).

the smaller individuals were basal sprouts of previous trunks. Based on the age-diameter relationship for *Sequoia* determined by Viers (1982), the larger trees may be about 1200 yr old. In contrast, the maximum potential lifespan of *Lithocarpus* is only 300-400 yr (Jepson 1910). Therefore, a considerable range exists in the potential canopy residency times of the trees.

Based on the point-centered quarter gap data, 16.6% of the land area sampled was within canopy gaps, with an average gap size of 137 m<sup>2</sup>. If one exceptionally large slope failure is omitted, these numbers become 11.1% within canopy gaps with an average size of 91 m<sup>2</sup>. Gap density was 12.1/ha. The frequency distribution of gap size (Fig. 2) had a modal class size of <50 m<sup>2</sup>, but gaps ranged in size from 6-3437 m<sup>2</sup>.

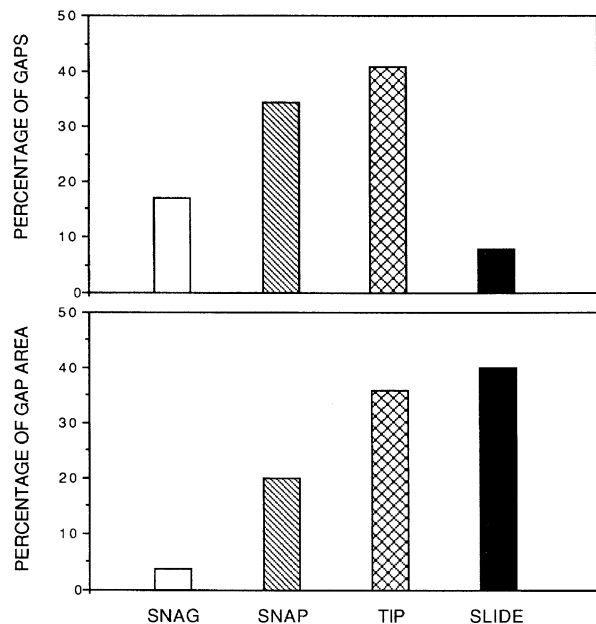
Gap size was, to some extent, a product of the mechanism of gap formation (Fig. 3). Gaps formed by slope failures ( $n=6$ , average 751 m<sup>2</sup>, range 79-3437 m<sup>2</sup>) were substantially larger than gaps formed by windthrows ( $n=31$ , average 131 m<sup>2</sup>, range 8-734) or snaps ( $n=26$ , average 87 m<sup>2</sup>, range 6-593), both of which had averages closer to the mean size. Although few gaps were formed by slope failures, these gaps accounted for 43%



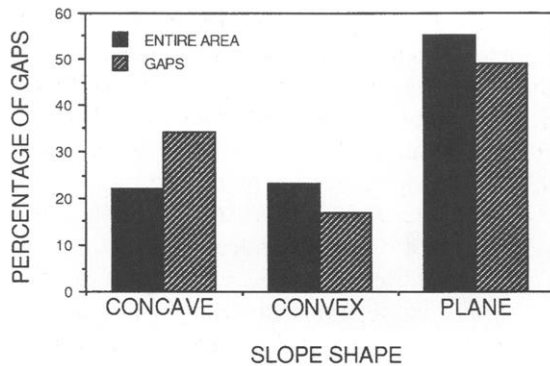
**Fig. 2.** Frequency distribution of area for gaps sampled within the Maddock Creek Watershed, Santa Cruz County, California ( $n = 80$ ).

of the total area within gaps. Gaps formed by snags ( $n=13$ , average 34 m<sup>2</sup>, range 10-103) were substantially smaller than gaps formed by other mechanisms. All snags were either *Pseudotsuga* or *Arbutus* individuals.

Gap size and shape were also related to the species involved. Most gaps were elliptical in shape and a few (20%) were highly irregular. *Arbutus* individuals growing with a single bifurcate trunk formed many of the irregularly shaped gaps. Gaps formed by *Sequoia* and *Pseudotsuga* (averaging 111 and 119 m<sup>2</sup> respectively) were ca. twice the size of gaps formed by *Lithocarpus* and *Arbutus* (averaging 54 and 52 m<sup>2</sup>). Gaps formed by



**Fig. 3.** Percentage of (A) number and (B) area of sampled gaps formed by four categories of disturbance mechanisms (snag = dead standing tree, snap = wind snapped, tip = wind thrown, slide = slope failure).



**Fig. 4.** Distribution of sampled openings and random points on three slope shapes within the Maddock Creek Watershed, Santa Cruz County, California. The distribution of the sampled openings is represented by the bars labeled 'gaps' and the distribution of the random points is represented by the bars labeled 'entire area' ( $n = 160$ ).

*Sequoia* were extremely long and narrow, and frequently a single fallen *Sequoia* formed more than one gap. The death of a *Pseudotsuga* also occasionally results in more than one gap. In both cases, the gap which we recorded represents only a portion of the total area of gap created by the fallen tree. If the full gap area formed by the fall of single trees were taken into account, there would be an even greater difference in size between gaps formed by *Sequoia* and *Pseudotsuga* and those formed by the lower canopy species. This difference results from individual size differences between species and probably from the greater likelihood that an upper canopy individual will fall on another tree than will a lower canopy individual.

The size of gaps varied with slope aspect. Gaps on the north-facing slope ( $205.6 \text{ m}^2$  average,  $n = 17$ ) were significantly larger (Mann-Whitney U,  $p < 0.05$ ) than gaps on the south-facing slope ( $48.5 \text{ m}^2$  average,  $n = 20$ ). The higher cover of the larger species (*Pseudotsuga*, *Sequoia*) and the reduction in the overlap of the two canopy layers on north-facing slopes accounts for the larger mean gap size on the north-facing slope: the upper canopy layer covered 71% of line intercept transects on the north-facing slope but only 58% of transects on the south-facing slope. Further, *Sequoia* comprised 87% of the north-facing slope's upper canopy but only 34% of the south-facing slope. The lower canopy was at its minimum beneath *Sequoia*. Consequently, nearly twice the area on the south-facing slope was covered by two canopy layers as compared with the north-facing slope. Where two canopy layers overlap, the death of a lower canopy tree does not form a gap and the death of an upper canopy tree may form a small gap, several smaller gaps, or a large gap, depending on how it dies and how many lower canopy trees it removes when it falls.

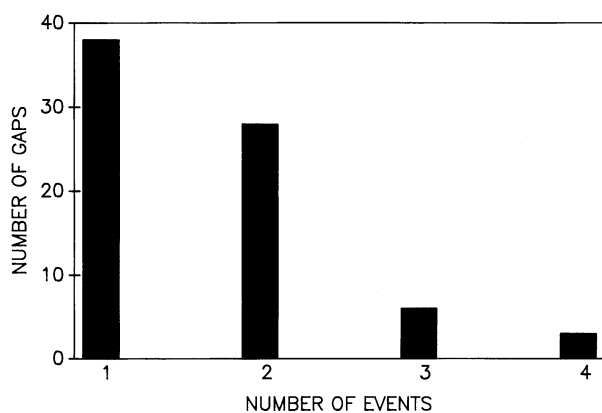
Canopy gaps were not distributed randomly with respect to slope shape. 36% of canopy gaps occurred on concave sections of slopes (Fig. 4), substantially more than expected from a random distribution over the sample area ( $\chi^2 = 8.75$ ,  $p < 0.05$ ). Gaps over concave sections of slope represent primarily two distinct categories, small gaps over narrow gullies or ravines and slope failures within broad swales.

Gaps may be more frequent over gullies and ravines because of a slower rate of gap closure or more frequent disturbance. Riparian shrubs occur within these gaps and may interfere with the establishment and growth of tree saplings which would fill the gap (Hunter 1989). The gullies are actively eroding, undercutting trees along their flanks and thus possibly contributing to windthrow. Windthrow accounted for significantly more gaps over gullies (53%,  $n = 15$ ) than elsewhere (38%,  $n = 61$ ).

During heavy rainfall, slope failures of soil and broken rock occur within the concave swales of the more mesic slopes. Within the coast ranges of N. California, steep slopes are frequently punctuated by concave sections. These topographic hollows contain 1-5 m of colluvium filling a U- or V-shaped depression within the bedrock (Lehre 1981). Water concentrates within the center and lower portions of these concave hollows and most slope failures occur within them. After a slope failure removes colluvium from a hollow, the hollow refills by soil creep, back wearing of the scarp, and sheet erosion from the sides, and eventually fails again.

These slope failures are episodes of disturbances rather than single disturbance events. A slope failure removes support from adjacent areas, destabilizing the slope and initiating subsequent failures. Soil creep and sheet erosion from the sides or backwearing of the scarp may undermine adjacent canopy trees, creating further disturbance. We surveyed three adjacent watersheds of old growth forest for large slope failures and located four. Three of these involved several successive events. The large slope failure within this study's random sample of 80 gaps appears on aerial photographs in 1973 as a smaller gap. Prior to 1985, an additional area upslope failed down onto the original gap.

Other disturbance mechanisms within this forest interact and also may promote episodes of repeated disturbance. Fire easily damages *Lithocarpus* and the trunks are weakened by decay around fire scars. Trees are subsequently felled by wind or ice (Roy 1957). For example, in portions of Big Basin State Park, a 1974 ice storm knocked down large numbers of *Lithocarpus* with trunks rotted as a result of fire scars (Greenlee 1983). Windthrows may damage other canopy individuals or expose adjacent individuals to stronger winds and these individuals may fall at a later date. Snags also involve a series of disturbances. Each snag involves at least two



**Fig. 5.** Frequency distribution of the probable minimum number of disturbance events involved in forming the gap for gaps sampled within the Maddock Creek Watershed, Santa Cruz County, California ( $n = 76$ ).

events, the initial death and defoliation of the canopy tree, and the eventual toppling of its trunk. *Pseudotsuga* snags involve a more protracted series of events: sloughing bark, dropping branches, and the trunk snapping one section at a time (Graham 1982). Some of these events may damage the adjacent canopy.

In this study, multiple disturbances were frequent: half of the sampled gaps resulted from at least two or more recognizable events (Fig. 5). Most involve repeated windthrows or snaps. Several gaps were formed by a series of at least four events involving wind-thrown and snapped individuals. In one of these gaps, the 1904 fire had charred the wood which was exposed after a tree had snapped during the first event. This dates gap initiation and indicates repeated disturbance during an 85-yr interval. This episodic nature of disturbance by windthrows, snags, fires, and slope failures indicates that disturbances are not randomly distributed with respect to prior disturbances nor are disturbances evenly rotating throughout a forest.

## Discussion

Our results illustrate the episodic nature of gap formation, the links between canopy tree biology and gap properties, and the relationship between topography and disturbance regime. The mechanisms of slope failure, fire, windthrow, and death of standing trees by disease or herbivory may all create intervals of repeated disturbance rather than single disturbance events: slope failures destabilize adjacent sections of slopes; fires damage trees mechanically, leaving them at risk to death by disease, herbivory, or windthrow; wind-thrown trees may damage their neighbors while falling and leave

them exposed to stronger winds; and snags may break apart gradually and drop debris on adjacent individuals and the understory for a prolonged period of time. In this study, half of the gaps resulted from more than one disturbance event. Studies of other forests have also found a high proportion of gaps formed by repeated events (e.g. Foster & Reiners 1986; Runkle & Yetter 1987; Taylor 1990; Taylor & Halpern 1991).

The biology of canopy species affects the characteristics of gaps resulting from their death. In our study, all snags resulted from the death of a *Pseudotsuga* or *Arbutus* individual, the widely branched trunks of *Arbutus* individuals accounted for most of the irregularly shaped gaps, and larger gaps resulted from the death of *Pseudotsuga* and *Sequoia* individuals (which are larger trees than the other canopy species). Other studies have found differences between species in their propensity to snap or tip up (Kanzaki & Yoda 1986), susceptibility to ice storm damage (Whitney & Johnson 1984; De Steven, Kline & Matthiae 1991), and in the size of gaps resulting from their deaths (Stewart 1986).

There is both a direct and an indirect relationship between topography and disturbance regime. Topography directly affects the disturbance regime. Slope aspect and position on a slope can affect the frequency of fires and the effects of windstorms (Kilgore & Taylor 1979; Foster 1988). Local physiographic features can serve as barriers to fire (Givnish 1981; Hemstrom & Franklin 1982). Geomorphic processes such as rockfalls (Hupp & Sigafos 1982), slope failures, and avalanches (Johnson 1987) are exogenous disturbances related to topographic features. Topography also indirectly affects the disturbance regime because resource availability varies with local topography, and hence so does the species composition and structure of the forest canopy. These differences in species composition and canopy structure result in differences in disturbance regime. In this study, the larger canopy species were less abundant on the south-facing slopes and a greater portion of the south-facing slopes' canopy had two canopy layers. As a consequence, gaps were smaller on these slopes.

The direct and indirect relationships of disturbance regime and topography, the influence of canopy species biology on gap properties, and the repeated events involved in gap formation all indicate the need to examine fine scale variation in the pattern of gaps and their characteristics within stands of forest vegetation.

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