

# Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests

Andrew N. Gray, Thomas A. Spies, and Mark J. Easter

**Abstract:** The effects of gap formation on solar radiation, soil and air temperature, and soil moisture were studied in mature coniferous forests of the Pacific Northwest, U.S.A. Measurements were taken over a 6-year period in closed-canopy areas and recently created gaps in four stands of mature (90–140 years) and old-growth (>400 years) Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest in the western Cascade Range of central Oregon and southern Washington. Gap sizes ranged from 40 to 2000 m<sup>2</sup>. Summer solar radiation levels and soil temperatures differed significantly among gap sizes and positions within gaps and were driven primarily by patterns of direct radiation. Nevertheless, effects on air temperature were slight. Soil moisture was more abundant in gaps than in controls, was most abundant in intermediate gap sizes, and tended to decline during the growing season in single-tree gaps and on the north edges of large gaps. However, there was substantial variation in moisture availability within individual gaps, primarily related to the variety of organic substrates present. Moisture in gaps declined over multiple years, likely caused by encroachment of vegetation within and around gaps. Low light levels probably limit filling of natural gaps in these forests, but the variety of microenvironments in large gaps may facilitate diverse plant communities.

**Résumé :** Les effets de la formation des trouées sur le rayonnement solaire, la température du sol et de l'air ainsi que l'humidité du sol ont été étudiés dans des forêts matures de conifères du Pacifique Nord-Ouest, aux États-Unis. Les mesures ont été prises pendant une période de 6 ans dans des endroits à couvert fermé et dans des trouées récemment créées dans quatre peuplements de forêt mature (90 à 140 ans) ou ancienne (>400 ans) de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco), située dans la partie ouest de la chaîne des Cascades du centre de l'Oregon et du sud de l'état de Washington. La taille des trouées variait de 40 à 2000 m<sup>2</sup>. Le niveau de rayonnement solaire estivale et la température du sol variaient significativement selon la taille des trouées et selon la position dans les trouées. Le rayonnement au sol était surtout fonction du rayonnement solaire direct. Les effets sur la température de l'air étaient toutefois minimes. L'humidité du sol était plus élevée dans les trouées que dans les zones témoins; elle était surtout importante dans les trouées de taille moyenne et tendait à diminuer pendant la saison de croissance dans les petites trouées causées par la chute d'un arbre et à la bordure nord des grandes trouées. Il y avait toutefois une variation substantielle de la disponibilité en eau à l'intérieur d'une même trouée, essentiellement en fonction de la variété de substrats organiques présents. L'humidité dans les trouées déclinait au cours des années, probablement à cause de l'empiètement de la végétation à l'intérieur et autour des trouées. Les faibles niveaux de lumière limitent probablement le repeuplement des trouées naturelles dans ces forêts mais la variété des micro-environnements dans les grandes trouées peut faciliter la présence de communautés végétales diversifiées.

[Traduit par la Rédaction]

## Introduction

Tree fall gap disturbances change the structure and composition of mature forests in many forest types (Pickett and White 1985; Platt and Strong 1989). Forest gaps can be sites of establishment of new plant species, increased growth of established plants, or specialized habitats for animals (Hibbs

1982; Phillips and Shure 1990; Vitt et al. 1998). Some studies suggest that timing of gap formation, variation in gap sizes, and differences in microsites within gaps contribute to the diversity of species within forests (Runkle 1982; Denslow 1987; Brandani et al. 1988), although the importance of microsite diversity is debated (Hubbell et al. 1999; Chazdon et al. 1999). The mechanisms of gap effects are the changes in environmental conditions and resources available for plant growth that occur when gaps are formed (Canham and Marks 1985). Resource levels vary with gap size and location within and around gaps, but these patterns are not consistent among studies and forest types.

Plants must make a fundamental tradeoff in allocation to structures that acquire aboveground and belowground resources, with no single species being able to maximize both relative to other species (Tilman 1988). The variation in abundance of different plant resources within and among gaps could facilitate the success of different species. Data concerning changes in abiotic environments and their vari-

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ability over succession are limited, which hampers our ability to understand the evolution of plant life-history attributes along successional gradients (Bazzaz 1987).

Microclimate and soil moisture are key attributes for understanding the distribution of plants and wildlife in forests, as well as for understanding forest ecosystem processes like photosynthesis and nutrient cycling. Different substrates on the forest floor create a variety of physical conditions and resource levels that can be critical to early plant establishment (Harper et al. 1965; Gray and Spies 1997). While the effects of forest openings on light are relatively well understood, it is not clear whether root "gaps" form below canopy gaps, and how their intensity varies with gap size. Soil moisture availability is particularly important in forests of the Pacific Northwest of the United States and Canada, where precipitation from June to September (i.e., most of the potential growing season) is usually less than 20 cm.

The microclimatic effect of canopy gaps is of considerable interest in the forests of the Pacific Northwest. Studies suggest that vegetation development is very slow in gaps in mature conifer stands, but the causes are unknown (Spies et al. 1990; Lertzman 1992). Forest managers in the region are investigating the use of group selection cutting to increase the rate of forest development and habitat diversity. At this point it is not clear which sizes of openings represent unfavorable conditions for biota of concern (e.g., amphibians requiring cool, moist habitats) or will provide sufficient resources to allow growth of desired plant species.

The objectives of this study were to examine the effects of gap formation on above- and below-ground resources in mature Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Pacific Northwest, U.S.A. The focus of this paper is on general patterns that were consistent among different stands, although differences were evaluated. Specifically, we (i) determined the effect of gap size on solar radiation and soil and air temperatures, (ii) determined the response of water content in soil and common forest-floor substrates to gap formation and the trends in soil moisture over several years, (iii) compared the effect of root trenching and gap formation on soil moisture, and (iv) determined the spatial patterns of soil moisture within gaps.

## Methods

### Site description

This study of experimental gaps was established in four forest stands on the west slope of the Cascade Mountains in 1990. Two stands were in old-growth forests (overstory trees approximately 500 years in age) dominated by *P. menziesii* and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in multiple canopy layers, and two stands were in mature forests (90–140 years in age) dominated by *Pseudotsuga* in a single canopy layer. One old-growth stand (HJA) was located in the H.J. Andrews Experimental Forest in the central Cascades of Oregon; the other three stands, Trout Creek old (TCO), Martha Creek young (MCY), and Panther Creek mature (PCM), were located in the Wind River Experimental Forest in the southern Cascades of Washington (Table 1). More detail on stand and soil characteristics of these sites can be found in Gray and Spies (1995, 1996). Climatic re-

gimes at the two Experimental Forests are similar, with mean annual air temperatures of 8.6 and 9.2°C and mean annual precipitation of 224 and 208 cm at the H.J. Andrews and Wind River, respectively.

Within each stand, experimental gaps and controls were located in areas with slopes less than 20%, with relatively dense tree canopies (to minimize interactions with recent gap events), and with similar understory and overstory plant species composition. Two replicates of control plots and four sizes of circular gaps were created in each stand. Gap size was scaled to the mean height of dominant trees in each stand to provide similar light environments, and potentially similar belowground environments, assuming belowground influence is correlated with tree size (heights are given in Table 1). The gap diameter (measured between tree crown edges) to tree height ratios for the four gap sizes were 0.2, 0.4, 0.6, and 1.0. Control plots were equal in area to the 1.0 gap size. Gaps were created in the fall of 1990 by cutting all trees over 2 m tall within the gap perimeter. Vine maple (*Acer circinatum* Pursh) were abundant in the mature stands, and although not purposely cut, many were damaged during logging. Trees were stage-felled into the northeastern or northwestern quadrants and winched from outside the gaps by skidders. Removal of most of the felled trees was necessary to allow sampling of vegetation, soils, and microclimate in intensive plots, and to study gap effects independently of tree bole effects. Branches and foliage trimmed from felled trees were removed from the gaps to avoid localized differences in nutrient input and shading.

Root trench plots were created at the same time as the gaps. The factorial design used a closed-canopy area and an open-canopy area (a natural gap ~0.4 in size) in each old-growth stand (HJA and TCO). Within each area two 3 × 3 m plots were left untrenched and two were trenched to a depth of 1 m, lined with heavy plastic (or 0.5 mm mesh stainless steel on any upslope or downslope sides), and backfilled. To examine the effect of understory plant roots, all vegetation was regularly clipped in one of each trenched and untrenched plot per area.

### Microclimate measurements

Measurements of photosynthetically active radiation (PAR) and soil temperature were made with microclimate stations at the centres and north and south edges of one replicate of each gap size and control in each stand. Mobile microclimate stations sampled each gap size simultaneously within a stand over 6–10 relatively sunny days during July and August of 1991. Each microclimate station sampled PAR at 1.5 m above the forest floor and soil temperature at 5 and 30 cm below the forest floor. An additional sensor measured air temperature at 2 m in gap and control centres. A few microclimate stations in the mature stands were partially shaded by *A. circinatum*, but most were not.

PAR photon flux density was measured with calibrated quantum sensors (model No. LI-190SZ, LI-COR Inc., Lincoln, Nebr.) and galium arsenide photodiodes (model No. G1738, Hamamatsu Corporation, Hamamatsu City, Japan). Temperatures were measured using thermocouple wire (model No. TT-E-24S chromel–constantan; Omega Engineering Inc., Stamford, Conn.) and a temperature reference

**Table 1.** Characteristics of the stands in the experimental gap study.

	Old-growth <sup>a</sup>		Mature <sup>a</sup>	
	HJA	TCO	MCY	PCM
Latitude (N)	44°15'	45°49'	45°47'	45°50'
Longitude (W)	122°15'	122°00'	121°57'	121°49'
Elevation (m)	900	550	550	850
Soil texture	Loam	Loam	Clay loam	Sandy loam
<i>Pseudotsuga</i> age (years)	350–500	350–500	90	140
Mean canopy height (m)	50	50	35	50
<b>Tree basal area (m<sup>2</sup>/ha)</b>				
<i>Abies amabilis</i>	0.1	4.0	—	—
<i>Abies procera</i>	—	2.8	—	—
<i>Pseudotsuga menziesii</i>	65.3	40.3	68.9	78.6
<i>Thuja plicata</i>	23.1	—	—	0.1
<i>Tsuga heterophylla</i>	27.5	44.9	0.1	0.2
Other <sup>b</sup>	0.2	0.2	0.7	0.3
Total basal area	116.2	92.3	69.7	79.2
<b>Vegetation mean cover (%)<sup>c</sup></b>				
Bryophytes	7.3	8.1	9.6	5.0
Herbs	4.9	9.3	0.8	26.7
Shrubs	9.4	26.8	46.9	35.6
Midcanopy trees	4.2	5.8	43.4	34.6
Total cover	25.8	50.0	100.7	101.9

<sup>a</sup>HJA, H.J. Andrews Experimental Forest in the central Cascades of Oregon; the other three stands were located in the Wind River Experimental Forest in the southern Cascades of Washington; TCO, Trout Creek old; MCY, Martha Creek young; PCM, Panther Creek mature.

<sup>b</sup>Other trees include *Abies grandis*, *Acer glabrum*, *Acer macrophyllum*, *Cornus nuttallii*, *Pinus monticola*, and *Taxus brevifolia*.

<sup>c</sup>Covers are sums of individual species' estimates, with midcanopy referring to tree vegetation 1–5 m in height (primarily *Acer circinatum*).

(thermistor) at the datalogger. Air sensors used single-stranded thermocouple wire ends to minimize solar heating. Soil sensors were crimped inside brass pieces, which were inserted into the ground at an angle with a rod. Dataloggers (model No. CR-10, Campbell Scientific Inc., Logan, Utah) sampled each solar radiation sensor at 10-s intervals and each temperature sensor at 1-min intervals and stored measurements as 30-min means.

Canopy openness was measured in 1991 with hemispherical photographs (Anderson 1964; Easter and Spies 1994) taken at 1.5 m above the forest floor along the north–south transects bisecting all gaps and controls, extending beyond the edges of each gap. These photos provided a more extensive examination of the solar radiation environment within and surrounding the experimental gaps than was possible with the microclimate stations. Photographs were analyzed with CANOPY software (Rich 1989), using a consistent protocol for setting image contrast and periodically checking results against standards. Variation of individual estimates was not formally assessed, but differences in light levels ranged within 5%. Data were summarized in terms of direct site factor (DSF) and indirect site factor (ISF), which are expressed as the proportion of the direct and indirect radiation received in an open site (Rich 1989). A global site factor (GSF) was calculated from ISF and DSF by assuming a 50:50% contribution of direct and indirect radiation to total radiation, which is a commonly used empirical average based on seasonal changes in solar declination, cloudiness, and atmospheric transmissivity (e.g., Canham et al. 1990).

While the PAR measurements sampled generally sunny summer days, hemispherical photography provided estimates of annual radiation.

Volumetric soil water content was estimated with time-domain reflectometry (TDR; model No. 1502C, Tektronix Inc., Beaverton, Oreg.), using site-specific calibrations developed for each stand (Gray and Spies 1995). TDR probes were placed in mineral soil along the north–south and east–west transects of one replicate of each gap size and control in each stand. “Shallow” probes were 30 cm long and placed at a 30° angle to sample the 0–15 cm depth (from the top of the litter layer). Additional 45 cm “deep” probes were placed vertically at gap centres and edges along the north–south transects to sample the 0–45 cm depth. Two measurements were taken in September and October of 1990, prior to gap creation. Subsequent to gap creation, measurements were taken at monthly intervals between May and October from 1991 to 1993 and at the driest time of the year (late August or early September) from 1994 to 1996.

Moisture in organic substrates was measured by placing shallow TDR probes in two decay classes of wood on the forest floor (class III and V; Maser et al. 1979) and in “skirts” of organic matter (e.g., bark, twigs and needles) that had accumulated around *Pseudotsuga* stems. A single TDR calibration equation for decayed wood (Gray and Spies 1995) was used. Three of each substrate were sampled in each control, 0.4, and 1.0 gap size in each old-growth stand (mature stands did not have the range of substrates available). Probes were sampled on the same schedule as the gap

soil probes during 1992 and 1993. Soil moisture was sampled in the root trench plots with three shallow and two deep probes on the same schedule from 1991 to 1994.

To characterize spatial patterns of soil moisture, spatially intensive surface moisture samples were collected in a control and a 1.0 size gap in stand TCO in July and September of 1993 and in September of 1995. Shallow probes were systematically placed at each 4-m grid point within a gap, regardless of substrate. Additionally, an 8 × 8 m portion at each site was sampled at a 1-m spacing, with the intention of using the fine-scale pattern to model moisture patterns at the coarser (4 m) scale (after Robertson et al. 1988).

### Statistical analyses

The PAR data were adjusted to account for changes in global radiation and cloudiness as stations were moved among stands during the sample period. Data from radiation sensors at the Wind River Nursery (J. Nelson, personal communication) and at the H.J. Andrews Experimental Forest (H.J. Andrews Long-Term Ecological Research Project (LTER) data set) were used, by dividing the mean daily solar radiation for the entire period by the means for the sample periods for individual stands. The PAR values for gap sensors were multiplied by the correction factors for the appropriate sample period from the nearest reference station.

A “standardized moisture response” (SMR) index to gap formation was calculated from the measured water content of each sample point as

$$[1] \quad \text{SMR} = (\theta_{ijk} - \theta_{ij(\text{pregap})}) - [\theta(0)_{jk} - \theta(0)_{j(\text{pregap})}]$$

where  $\theta$  was the volumetric water content,  $\theta(0)$  was the mean water content in a control plot, and  $i$ ,  $j$ , and  $k$  (or pregap) were subscripts for sample point, stand, and time, respectively. The first subtraction removed site-specific patterns present before gap creation, and the subtraction of the last two terms removed seasonal variation in moisture abundance within each stand. Gap centre  $\theta$  values were calculated by averaging the five shallow and three deep TDR probes within 4 m of the centre of each gap. The deep layer moisture content between 15 and 45 cm was calculated using side-by-side shallow and deep probes by accounting for differences in volume sampled (deep layer  $\theta = (3 \times \text{deep } \theta - \text{shallow } \theta)/2$ ).

Tests of statistical significance on solar radiation, temperature, and moisture data were conducted using a split-plot, mixed model analysis of variance (ANOVA; SAS Institute Inc. 1999). The model was

$$[2] \quad Y_{ij} = \mu + \alpha_i + \beta_j + \alpha_i\beta_j + \varepsilon_i + \delta_{ij}$$

where  $Y$  was the response variable (PAR, temperature, or soil moisture),  $\mu$  was the general mean,  $\alpha_i$  was the fixed effect of gap size  $i$ ,  $\beta_j$  was the fixed effect of position  $j$ ,  $\varepsilon_i$  was the random effect for variation between stands that received the same gap treatment, and  $\delta_{ij}$  was the random effect for variation of locations that received the same gap and position treatment. Because position was a nonrandom treatment within gap, it was modeled as a repeated measure of gap. Analyses of gap centre values (e.g., air temperature and mean moisture) used reduced models with just the gap effect. Initial analyses indicated that stand age was not a sig-

nificant factor in the measured variables; because the focus of this paper is on general patterns of gaps, stand age was not included in the final models. Results of ANOVA are shown as  $F_{[df_1, df_2]}$  values and  $P$  values where  $df_1$  and  $df_2$  are the degrees of freedom for the fixed and random effects, respectively. Residuals were examined after initial analyses, and only the solar radiation data were transformed (log) to remove increasing variance with predicted values. Effects in the models were considered significant if the probability of a type-I error was less than 0.05. When interactions were significant, results of main effects were not presented, since those means were artificial given the interaction. Differences among treatments were assessed with either preplanned contrasts (comparing controls and 0.2 gaps, or north and south positions of large gaps) or least-squares means with Tukey's adjustment for experimentwise error rates (SAS Institute Inc. 1999).

To examine whether gaps were getting drier over time, we modeled gap centre  $\theta$  for each gap size (averaged for the three stands at Wind River and the one stand at H.J. Andrews), on precipitation records from 1990 to 1996 from the H.J. Andrews and the Carson Fish Hatchery at Wind River. The time series data were tested with a mixed model relating soil moisture at the driest time of each year to the number of years since gap creation, cumulative precipitation over the water year, and cumulative precipitation over the 5 weeks prior to the sample time. The mixed model used Wind River and H.J. Andrews as replicates and avoided autocorrelation by predicting multiple  $Y$ 's (a matrix of moisture by year and location) based on the two precipitation variables and year. A compound symmetry covariance structure was selected as the best fit (Littell et al. 1996), and because no changes to the soil in the gaps, other than those introduced by the treatment effect, were expected to affect covariance.

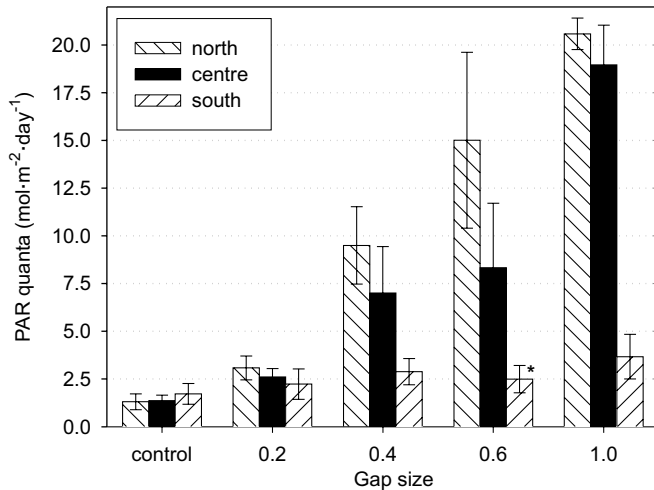
Analysis of the spatially intensive surface moisture data used semivariograms and Moran's  $I$  (Haining 1990) to determine whether there was any spatial correlation in moisture. Moisture patterns were interpolated across the TCO control and 1.0 size gap at each sample period using linear kriging at a 2-m scale (Haining 1990).

## Results

### Solar PAR levels

Measurements of sunny summer-day PAR varied significantly for the interaction of gap sizes and within-gap positions ( $F_{[8,29]} = 3.1$ ,  $P = 0.013$ ) (Fig. 1). Contrasts among control and 0.2 gap size positions indicated that only the north positions were significantly different ( $F_{[1,29]} = 6.3$ ,  $P = 0.018$ ;  $F_{[1,29]} = 2.4$ ,  $P = 0.133$ ;  $F_{[1,29]} = 0.4$ ,  $P = 0.553$  for north, centre, and south positions, respectively). The contrast testing the combined north positions in 0.4, 0.6, and 1.0 size gaps versus the combined south positions was also significant ( $F_{[1,29]} = 45.2$ ,  $P < 0.001$ ). Solar radiation levels were, on average, twice as high in 0.2 gaps as in controls and increased dramatically with gap size. PAR tended to decline from north to centre to south positions for all gap sizes. Given a mean daily flux of  $43.9 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  in the open during July and August at the Wind River Nursery meteorological station, mean solar radiation measurements in the

**Fig. 1.** Mean summer daily PAR quantum levels by gap size and within-gap position. Means and SEs of measurements over several sunny days are shown ( $n = 4$  stands, except  $n = 3$  for 0.6 south (\*)). Gap size is the ratio of the canopy opening diameter to the mean height of the dominant trees (heights are in Table 2).



gaps and controls ranged from 3.0 to 47% of full sunlight (the range for stand-level measurements was 1.4 to 58%).

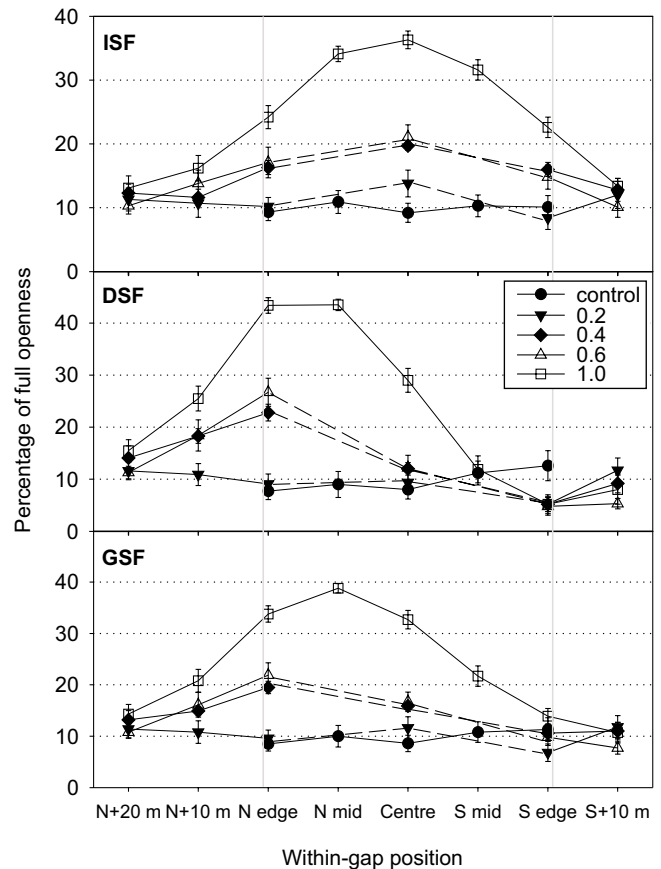
#### Hemispherical photography

Analysis of solar radiation derived from hemispherical photographs indicated significant differences for the interaction of gap sizes and within-gap positions for indirect, direct, and global site factors (ISF:  $F_{[19,177]} = 9.5$ ,  $P < 0.001$ ; DSF:  $F_{[19,177]} = 16.6$ ,  $P < 0.001$ ; and GSF:  $F_{[19,177]} = 11.7$ ,  $P < 0.001$ ). Contrasts among control and 0.2 gap size positions indicated that no positions were significantly different for any site factor (e.g., ISF:  $F_{[1,177]} = 1.2$ ,  $P = 0.274$ ;  $F_{[1,177]} = 3.5$ ,  $P = 0.064$ ;  $F_{[1,177]} = 0.01$ ,  $P = 0.942$  for north edges, centres, and south edges, respectively). The contrast testing the combined north edges in 0.4, 0.6, and 1.0 size gaps versus the combined south edges was not significant for ISF but was for the other site factors ( $F_{[1,177]} = 1.9$ ,  $P = 0.172$ ;  $F_{[1,177]} = 346$ ,  $P < 0.001$ ; and  $F_{[1,177]} = 151$ ,  $P < 0.001$  for ISF, DSF, and GSF, respectively). ISF increased predictably with gap size; was highest in gap centres; and declined symmetrically to, and beyond, gap edges (Fig. 2). DSF also increased with gap size, but intensity was shifted so that the highest levels were found at north edges of gaps and the lowest at south edges. Even 20 m to the north of the larger gaps, DSF levels appeared to be greater than those in controls and south ends of gaps. As a combined index of the symmetrical ISF and asymmetrical DSF, the GSF pattern also displays a shift to higher levels in northern portions of large gaps.

#### Temperature

Mean air temperatures in gap centres on sunny summer days were not significantly different among gap sizes ( $F_{[4,15]} = 0.8$ ,  $P = 0.542$ ) (Fig. 3). Maxima of the 30-min mean air temperatures were different ( $F_{[4,15]} = 4.8$ ,  $P = 0.011$ ), with comparison of means indicating the 1.0 gap size

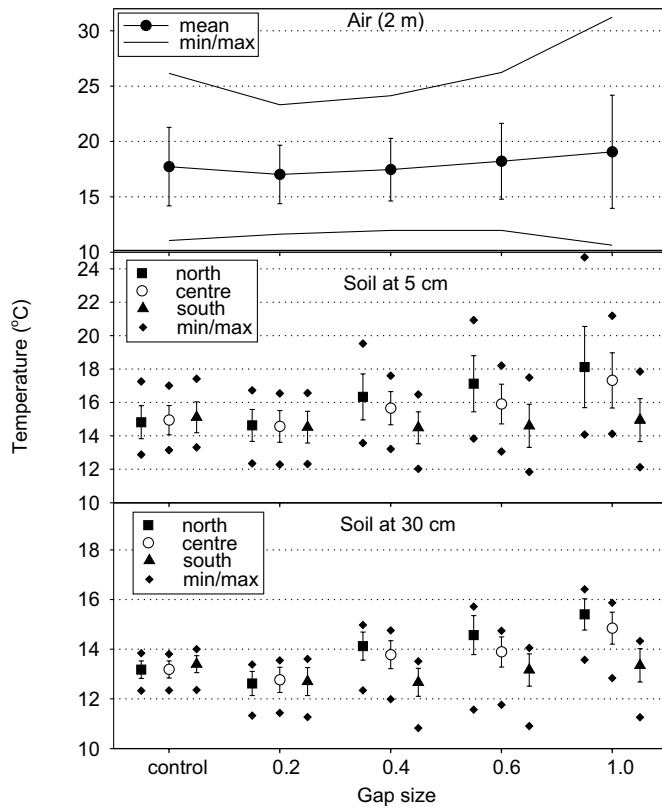
**Fig. 2.** Mean trends in indirect, direct, and global site factors (ISF, DSF, and GSF, respectively) along the north–south transects across different gap sizes in both replicates of four stands ( $n = 8$ ). Gap size is the ratio of the canopy opening diameter to the mean height of the dominant trees. Vertical lines indicate north and south edges of gaps. Broken lines connect points without intervening samples.



was greater than the 0.2 and 0.4 gap sizes. Minima of mean air temperatures among gaps were not different ( $F_{[4,15]} = 0.1$ ,  $P = 0.969$ ).

Soil temperatures at the 5-cm depth differed significantly for the interaction among gap sizes and positions ( $F_{8,27} = 6.0$ ,  $P < 0.001$ ) (Fig. 3). The 0.2 gap sizes tended to be cooler than controls, but contrasts among respective positions indicated that differences were not significant ( $F_{[1,27]} = 0.03$ ,  $P = 0.857$ ;  $F_{[1,27]} = 0.1$ ,  $P = 0.722$ ;  $F_{[1,27]} = 0.3$ ,  $P = 0.580$  for north, centre, and south positions, respectively). Temperatures within the larger gaps increased from south to centre to north, with a significant difference between the combined north positions in 0.4, 0.6, and 1.0 gaps versus the combined south positions ( $F_{[1,27]} = 92.3$ ,  $P < 0.001$ ). Temperature patterns were similar at the 30-cm depth as those discussed above, although absolute differences were smaller. The gap size by position interaction effect was significant ( $F_{[8,27]} = 2.3$ ,  $P = 0.048$ ). Contrasts among positions in controls and 0.2 gaps indicated no significant differences ( $F_{[1,27]} = 0.3$ ,  $P = 0.565$ ;  $F_{[1,27]} = 0.2$ ,  $P = 0.662$ ;  $F_{[1,27]} = 0.5$ ,  $P = 0.469$  for north, centre, and south positions, respectively). The difference between the combined north positions

**Fig. 3.** Comparison of summer sunny-day air and soil temperatures by gap size and by gap size and within-gap position, respectively, showing averages of means, standard deviations, minima, and maxima for measurements over several days ( $n = 4$  stands). Gap size is the ratio of the canopy opening diameter to the mean height of the dominant trees. Note changes in scale among panels.



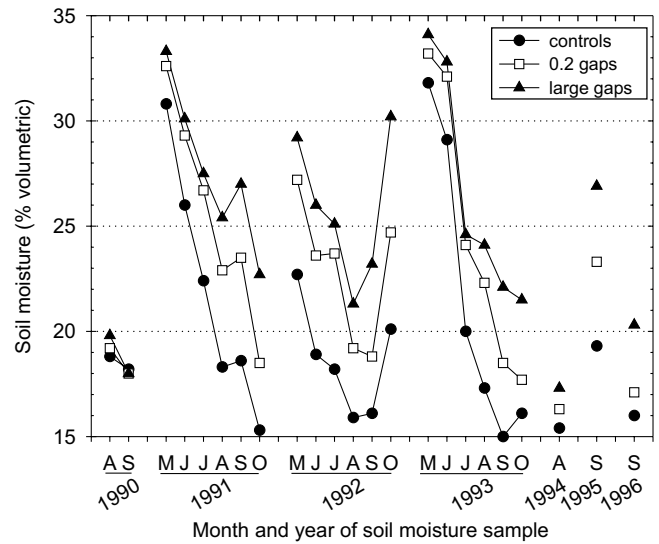
in 0.4, 0.6, and 1.0 gaps versus the combined south positions was significant ( $F_{[1,27]} = 31.1, P < 0.001$ ).

**Soil moisture**

Soil moisture levels changed dramatically in response to gap creation. Gaps and controls started the growing season with relatively similar shallow (0–15 cm) moisture values following wet winters and springs (1991 and 1993) and diverged during the summer (Fig. 4). Following a dry winter and spring (1992), gaps remained substantially wetter than controls all summer, although gap values were much closer to those in controls in a particularly warm and dry year (1994). The centres of 0.2 size gaps appeared to dry out more rapidly during summer drought than the larger (0.4, 0.6, and 1.0 size) gaps. The increase in soil moisture content seen in gaps and controls in September 1992 was caused by the onset of fall rains.

Significant differences among gap sizes tended to occur in late summer and were more common for shallow (0–15 cm) than for deep (15–45 cm) soil layers (Table 2). For the driest times of the year, examination of means and standard errors suggested that the standardized moisture response of the shallow layer in gap centres were usually greater for the 0.4 and 0.6 gap sizes than for the 0.2 size, which were in turn

**Fig. 4.** Seasonal trends in mean shallow (0–15 cm) soil moisture values for summer samples from centres of controls, 0.2 size, and large (0.4, 0.6, and 1.0 size) gaps ( $n = 4$  stands, each centre value was mean of five probes). Gap size is the ratio of the canopy opening diameter to the mean height of the dominant trees. Samples are shown from 1990 (just prior to gap creation) to 1996.



**Table 2.** Statistics for the gap size effect on standardized moisture response in gap centres at the driest time of the year by depth, taken from the full split-plot ANOVA tables.

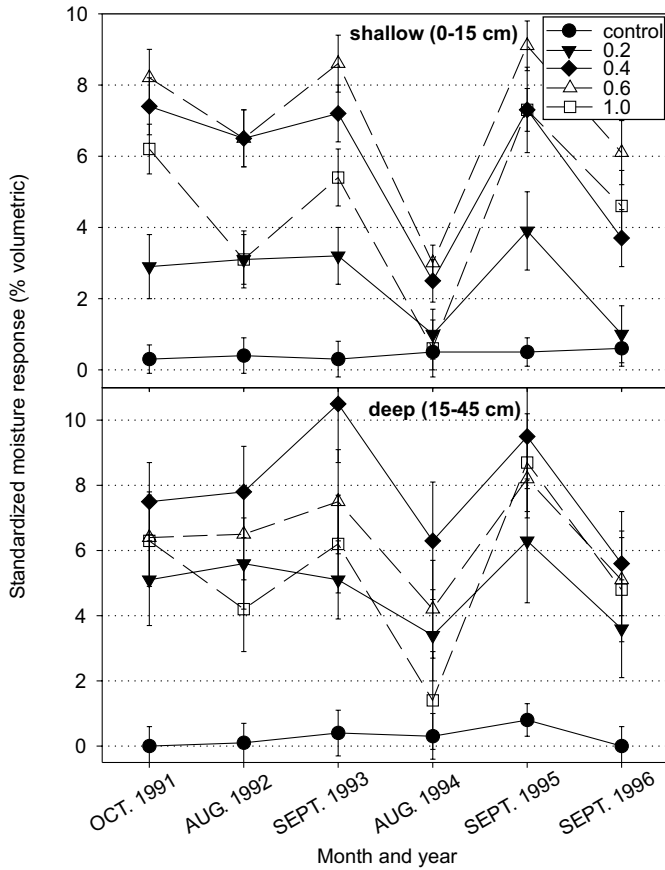
Date	Shallow (0–15 cm)			Deep (15–45 cm)		
	MS	F	P	MS	F	P
October 1991	198.6	22.6	<0.001*	93.0	4.6	0.033*
August 1992	131.1	16.1	0.001*	94.6	4.2	0.041*
September 1993	174.3	31.0	<0.001*	81.6	2.7	0.108
August 1994	26.1	3.2	0.075	62.1	2.0	0.183
September 1995	208.9	22.9	<0.001*	123.4	3.2	0.074
September 1996	93.0	5.0	0.025*	48.2	1.8	0.227

**Note:** In all cases, the degrees of freedom for the *F* test are 4 and 19 for the numerator and denominator. \*, significant *P* values.

greater than controls (Fig. 5). The response of the centres of the 1.0 gap size was usually between the 0.2 and other gap sizes. The means for the deep layer in gap centres suggested that controls were drier than gaps (Fig. 5). During the driest year of all those sampled, 1994, moisture in gaps was not different from controls, particularly for the 0.2 and 1.0 gap sizes. Similar to the shallow response, the deep response of 0.2 gap sizes tended to be lowest, and the response of 0.4 and 0.6 gap sizes tended to be greatest among the gaps.

Analysis of within-gap positions for the mean shallow moisture responses at the driest times of the 6 sample years indicated a significant gap size by within-gap position interaction effect ( $F_{[48,116]} = 1.67, P = 0.014$ ). Means and standard errors within gap sizes indicated shallow moisture response was highest in gap centres and lowest at gap edges (Fig. 6). There appeared to be no effect of gap formation on soil moisture 5 m beyond gap edges. Northern portions of large gaps (0.4, 0.6, and 1.0 sizes) were usually drier than

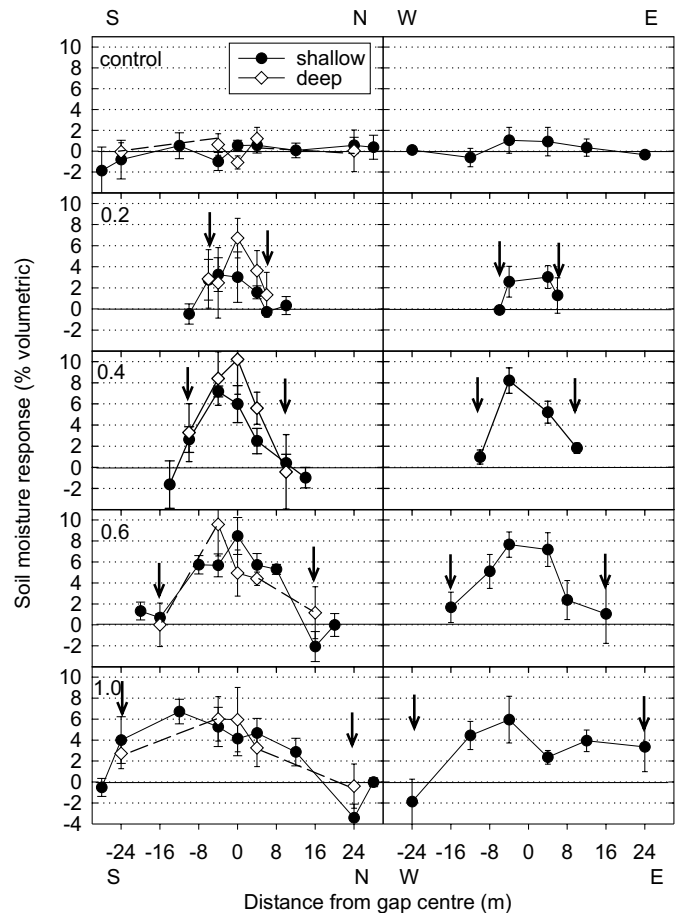
**Fig. 5.** Mean standardized moisture response in gap centres at the driest times of the year, for shallow (0–15 cm), and deep (15–45 cm) soil layers, by gap size, showing standard errors ( $n = 4$  stands; each centre value was mean of five shallow or three deep probes). Gap size is the ratio of the canopy opening diameter to the mean height of the dominant trees. Samples are shown from 1991 to 1996.



southern portions, with north edges exhibiting a negative response to gap formation and south edges a positive one. The gap size by position interaction was not significant for the deep moisture response values at the driest times of the 6 sample years ( $F_{[16,38]} = 1.23$ ,  $P = 0.294$ ), but the position term was ( $F_{[4,38]} = 6.73$ ,  $P < 0.001$ ). Separation of means indicated that the centre and 4 m south of centre positions were wetter than the edges, which appeared to be consistent across gap size (Fig. 6).

Determining whether gaps were drying out over time, as might be expected from root growth of plants within gaps and those bordering gaps, had to consider differences in precipitation among years. After considering precipitation effects, analyses indicated that shallow soil moisture in gap centres declined significantly with gap age, while no time effect was evident in controls (Table 3). The trend in the data for the first, third, and sixth years suggests that gap centres appear to be drying out, despite (i) increasing cumulative precipitation for the year and the 5 weeks prior to measurement, (ii) decreasing temperatures (i.e., evaporative demand) for the 2 months prior to measurement, and (iii) greater soil moisture in controls in year 6 (Table 4).

**Fig. 6.** Mean standardized moisture response from the driest period for each of 6 sample years, for shallow (0–15 cm) and deep (15–45 cm) soil, by gap size and within-gap position ( $n = 4$  stands; value for each position was the mean of 6 years). Gap size is the ratio of the canopy opening diameter to the mean height of the dominant trees. Error bars are SEs, and arrows show the location of gap edges. Panels on the left contain the south–north transects and panels on the right contain the west–east transects, with standardized distances from gap centre (gap sizes were not identical).



Analysis of different substrates by gap size in the old-growth stands over the summers of 1992 and 1993 indicated that substrates were significantly different at all times, with separation of means indicating that skirts were drier than class III and class V wood. At the driest time of 1993 (early September) the substrate by gap size interaction was significant ( $F_{[4,18]} = 3.1$ ,  $P = 0.043$ ). Examination of means and standard errors suggested that both types of decayed wood were wettest in 0.4 gaps, while skirt piles tended to be wettest in 1.0 gaps and very dry in controls (Fig. 7). In controls, class V wood tended to be drier than class III wood and tended to dry out more during the summer (e.g., loss of 18 vs. 14% moisture during 1993).

Soil moisture in trenched plots was significantly wetter than soil moisture in untrenched plots at the driest times of the year for both shallow and deep layers ( $F_{[1,6]} = 17.2$ ,  $P = 0.006$  and  $F_{[1,6]} = 40.2$ ,  $P = 0.001$ , respectively). The other factors (e.g., canopy cover and plant clipping) and the inter-

actions between them did not reach the  $P = 0.05$  level of significance (the degrees of freedom for the analysis were relatively low), except for the interaction between trenching and canopy cover for the deep layer ( $F_{[1,6]} = 9.5$ ,  $P = 0.021$ ). Examination of mean values indicated that trenching had a greater effect in closed-canopy conditions than in old gap openings. Values for the controls and 0.4 gap sizes in the same stands were quite similar to the control and open-trench treatments (Table 5).

The spatial analysis using 95% confidence intervals for Moran's  $I$  indicated no significant autocorrelation in surface moisture levels on either the 1- or 4-m grids in either the control or 1.0 size gap at any sample time. The contoured surface moisture levels in the 1.0 gap in September 1995 illustrates the great variation in moisture availability among nearby points, superimposed on the general trend of dry areas outside and to the north of the gap, and wet areas within the southern portion of the gap (Fig. 8). The wettest points in the gap and control tended to be the class III logs, while the driest points in the gap tended to be the skirt piles and mineral soil. Thus, despite the generalized moisture response to gap formation, any particular area in a gap generally had both wet and dry microsites.

## Discussion

Differences in gap size and within-gap position produced dramatic effects on microclimate and soil moisture in this study. The combination of these attributes produce a wide variety of microenvironments across the gap treatments. These measurements provide insights into the response of individual plants and animals, as well as ecosystem processes, to gap formation.

The experimental treatments that created the gaps in this study provided a controlled setting to examine the effects of disturbance size on above- and below-ground ecosystem attributes. The gaps were not perfect analogues to natural gaps in Douglas-fir dominated forests. Most of the trees in these forests die standing (Spies et al. 1990); increased shade from these snags would reduce radiation and soil temperatures from those we found. Some gaps are created suddenly by windstorms, which results in substantial soil disturbance and large amounts of wood on the ground, or slowly by root disease, which probably results in less dramatic resource changes within gaps. While commercial tree harvest does remove trees from cut areas, there is often considerable mechanical disturbance within openings, as well as damage and additional cutting of trees outside openings. Nevertheless, we feel that the results of this study accurately reflect the relative importance and direction of changes in microclimate and soil moisture in natural and created openings.

Solar radiation generally increased with gap size, but the increases varied among positions in gaps and among different radiation measurements. The 0.2 gap size is the most common in coastal *Pseudotsuga*-dominated forests (Spies et al. 1990) but measured PAR radiation levels on sunny summer days in these gaps averaged only 6% of full sunlight. Nevertheless, this was approximately double the radiation levels measured in control areas. In contrast, the hemispherical photographs in this study and the simulation study by Canham et al. (1990) indicated little or no light response in

**Table 3.** Results of mixed-model analysis of precipitation effects on gap centre shallow soil moisture values at the driest time of each year by gap size.

Fixed effect	Parameter estimate	<i>F</i>	<i>P</i>
<b>Control</b>			
Gap age	-0.059 (0.165)	0.1	0.732
Precipitation, 5 weeks	0.640 (0.111)	33.3	0.001*
Precipitation, year	0.005 (0.005)	0.9	0.376
<b>0.2</b>			
Gap age	-0.746 (0.267)	7.8	0.027*
Precipitation, 5 weeks	1.106 (0.179)	38.3	0.001*
Precipitation, year	0.013 (0.008)	2.6	0.151
<b>0.4</b>			
Gap age	-1.502 (0.201)	55.7	<0.001*
Precipitation, 5 weeks	1.327 (0.135)	96.7	<0.001*
Precipitation, year	0.026 (0.006)	17.6	0.004*
<b>0.6</b>			
Gap age	-1.538 (0.333)	21.3	0.002*
Precipitation, 5 weeks	1.297 (0.223)	33.8	0.001*
Precipitation, year	0.040 (0.010)	15.2	0.006*
<b>1</b>			
Gap age	-1.406 (0.508)	7.7	0.028*
Precipitation, 5 weeks	1.236 (0.341)	13.2	0.008*
Precipitation, year	0.035 (0.016)	5.2	0.057

**Note:** Parameter estimates (with SEs given in parentheses) and significance are shown for years since gap creation and cumulative precipitation for 5 weeks before the sample and since the prior October 1. Degrees of freedom for the *F* test are 1 and 7 for numerator and denominator. \*, significant *P* values.

the 0.2 gap size. Some of the discrepancy could be caused by comparing the summer measurements with annual estimates; reflected light off tree crowns and boles, and measurement error with the photographic technique, might explain the rest. Although low, the additional light levels could be important: conifer seedling growth was 50% greater in the 0.2 gaps than in the controls in this study (Gray and Spies 1996).

The largest differences in measured solar radiation appeared to be primarily determined by direct radiation, which was abundant in the largest gaps. Solar radiation in southern portions of gaps, determined primarily by diffuse light, also increased substantially with gap size. Formation of canopy gaps appeared to increase radiation levels by double or more up to 20 m beyond the north edges of the gaps. The effect was substantially higher for the same size gap than that simulated by Canham et al. (1990), possibly because actual canopy heights and layering are more variable than the single 70 m layer height used in the simulation. Thus, it is likely that effects of canopy gaps in Douglas-fir forests on forest processes (e.g., tree survival and growth) are not limited to the openings themselves (Van Pelt and Franklin 2000).

Temperature responses to gap creation were closely associated with direct radiation. Patterns of soil temperatures at 5- and 30-cm depths corresponded quite closely with DSF patterns derived from hemispheric photography. Temperature maxima tended to be relatively high at north edges of gaps, however, possibly caused by drier soil conditions. Once dry, exposure of forest floor materials (e.g., litter and duff) to di-

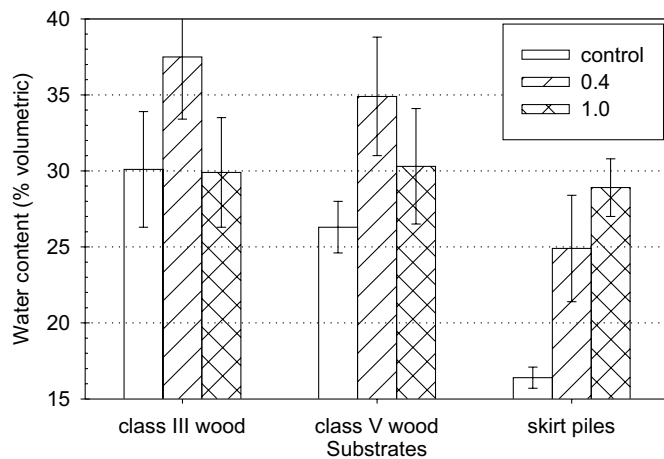


**Table 4.** Comparison of precipitation, temperature, time since gap creation, and gap centre shallow soil moisture values at the driest time of each year by gap size.

Gap age	Precipitation, year (cm)	Precipitation, 5 weeks (cm)	Temperature, 2 months (°C)	Soil moisture (% volume) by gap size				
				Control	0.2	0.4	0.6	1
1	199.9	0.1	17.1	15.3	18.5	23.9	22.8	21.3
2	157.3	2.1	18.2	15.9	19.2	23.5	21.6	18.7
3	215.5	0.5	16.4	15.0	18.5	23.4	22.8	20.1
4	150.1	0.1	19.1	15.4	16.3	18.9	17.5	15.5
5	247.9	6.0	15.5	19.3	23.3	27.6	27.3	25.9
6	306.8	0.9	15.8	16.0	17.1	20.0	21.1	19.8

**Note:** Parameters are the same as those in Table 3 with the addition of mean temperature for the 2 months prior to sample. Soil moisture in gaps (but not controls) decreases from gap age 1 to 3 to 6, despite increasing precipitation and decreasing temperature.

**Fig. 7.** Mean moisture values for organic substrates (0–15 cm depth) in September 1993 by gap size ( $n = 4$  gaps; value for each substrate was mean of three locations). Gap size is the ratio of the canopy opening diameter to the mean height of the dominant trees. Error bars are SEs.



rect radiation can lead to surface temperatures in excess of 60°C (Isaac 1938; Gray and Spies 1997), which then contributes to heating of soil and air. Gap size effects on mean air temperatures were quite modest compared with effects on soil temperatures, however. The difference suggests that substantial mixing of air occurred between the soil surface and 2 m. Chen et al. (1993) similarly found that turbulent mixing of air resulted in lower air temperatures in clearcuts than at forest edges, where wind speeds were lower. Soil and air temperatures tended to be lower in the 0.2 gap size than in other gap sizes or in controls. This may be caused by little direct radiation to lead to heating during the day and little vegetation to block radiative cooling during the evening. Other studies have found similar soil temperature gradients along the north–south axis of large gaps (Bauhus 1996; Wright et al. 1998). Zhang and Zak (1995) found increasing soil temperatures with gap size during the summer months in a subtropical forest but found that mean annual soil temperatures decreased with increasing gap size. Some long-term data from our study suggests that gaps might not be colder, on average, than closed-canopy control areas, possibly because of an insulating effect from winter snow cover.

Higher soil moisture levels in response to tree mortality indicate that belowground gaps were created at the same time as aboveground gaps. Belowground gaps were probably a result of reduced tree root density, which could have greatly reduced transpiration of soil water from gaps. The similarity of results from trench plots and the slow decline in moisture abundance over time (as vegetation established in gaps) also support this conclusion. In addition, data collected in the first growing season after gap creation in this study found few fine tree roots in mineral soil (Vogt et al. 1995). Fine-root density is usually lower in gaps than in closed-canopy forest (Brockway and Outcalt 1998), but differences can be small (Wilczynski and Pickett 1993) or variable among gaps (Denslow et al. 1998). One study in declining red spruce (*Picea rubens* Sarg.) forests, however, found greater root densities in gaps than in surrounding forest (Battles and Fahey 2000). Greater precipitation in gaps than in closed-canopy forest (Rothacher 1963; Geiger 1965) does not explain most of the moisture response in our study, because gaps and controls diverged in moisture content during extended periods without precipitation.

Studies in a wide variety of forest types have found increases in soil moisture in response to canopy gaps, including temperate hardwoods (Minckler and Woerhide 1965; Moore and Vankat 1986), pine forests (Ziemer 1964; Brockway and Outcalt 1998), tropical forest (Denslow et al. 1998), and temperate conifer forest (Wright et al. 1998). Despite greater exposure to evaporation, moisture is also initially more abundant in clearcuts than in uncut controls (Adams et al. 1991). Most studies that have found a moisture response were conducted in experimental treatments. Many studies that have not found a moisture effect were done in naturally formed gaps of various ages (e.g., Palik et al. 1997; Zhang and Zak 1998). These natural gaps may have been formed in edaphically dry areas or may have been old enough for belowground gaps to have closed from root encroachment by surrounding trees or roots of established vegetation within gaps. Most studies that have followed gaps over time have found a decline in moisture response with gap age (Ziemer 1964; Minckler et al. 1973; Moore and Vankat 1986), sometimes after only 1 year (Veenendaal et al. 1996).

Soil moisture in gaps is variable with distance from gap edge and orientation. Gap centres are generally wetter than gap edges, which are usually wetter (at least initially) than

**Table 5.** Soil moisture values for trench plots, showing the mean (and SE) from two stands and the driest period for each of the four sample years ( $n = 8$ ), for two sample depths.

Soil depth	Trenched plot results			Gap results	
	Canopy	Trench	Soil moisture	Gap size	Soil moisture
Shallow (0–15 cm)	Canopy	No trench	18.7 (0.33)	Control	18.3 (0.80)
	Canopy	Trench	25.6 (0.77)		
	Open	No trench	23.1 (0.74)		
	Open	Trench	26.4 (1.00)	0.4	
Deep (15–45 cm)	Canopy	No trench	25.7 (0.92)	Control	23.4 (0.48)
	Canopy	Trench	34.6 (1.36)		
	Open	No trench	30.7 (1.29)		
	Open	Trench	33.8 (1.24)	0.4	

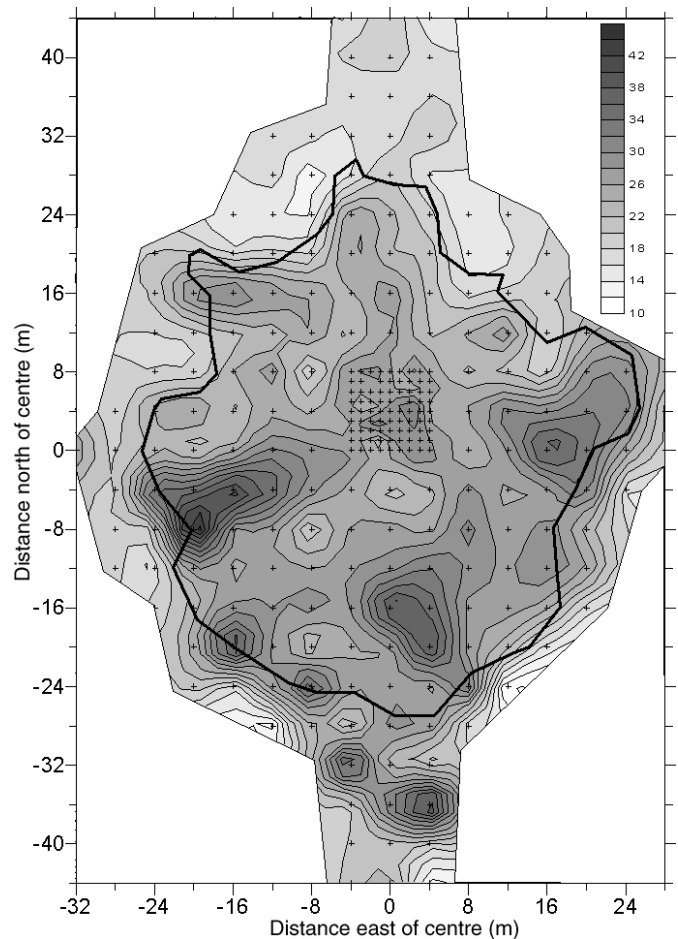
**Note:** Values for trenched and untrenched plots are shown by canopy condition (“canopy” and “open”). Moisture values for controls and 0.4 gap sizes for the same stands and sample periods are shown for comparison.

surrounding forest (Ziemer 1964; Minckler and Woerhide 1965). We found similar results, except that in our study north edges of large gaps were often drier than closed-canopy forest. This may have been caused by increased evaporation and transpiration in these areas under high levels of direct radiation. Chen et al. (1995) found analogous results for south-facing and north-facing forest edges next to clearcuts in similar forest types. The large seasonal and annual differences in moisture results suggest the importance of considering seasonal patterns of precipitation. Following periods of extended precipitation or drought, moisture tended to be very similar in gaps and controls.

Although consistent gradients in soil moisture were found related to gap size and within-gap position, surface moisture levels within any one gap can be highly variable. The general lack of spatial autocorrelation in surface moisture in the intensively studied gap and control appeared to be primarily related to the variation in surface substrates. This suggests that patterns of woody debris and litter accumulations, imposed on variation in vegetation and soil characteristics, produce a range of moist and dry microsite conditions in gap and control areas.

Microclimate responses to gap formation in this study have important implications for vegetation reproduction and growth. High surface temperatures at north edges of large gaps appeared to result in reduced tree regeneration in those locations (Gray and Spies 1996). However, annual variation in cloudiness and the onset of summer drought may allow opportunities for establishment in these zones in some years. The relatively cool, moist, diffuse light areas in the southern portions of large gaps were areas of abundant regeneration and growth of a wide range of plant species (Gray and Spies 1996; Van Pelt and Franklin 1999). Class III decayed logs in closed-canopy areas were high-moisture sites in otherwise dry surface conditions, which appears to be the critical factor for establishment of *T. heterophylla* in closed-canopy forests in this region (Harmon and Franklin 1989; Gray and Spies 1997). Drying of the more-decayed class V logs in controls, likely a result of occupation by roots of surrounding trees, may explain why they were a less-suitable substrate for seedling establishment than class III logs (Gray

**Fig. 8.** Contour map of shallow (0–15 cm) surface moisture content in September 1995 generated by kriging measured values in a 50 m radius gap in old-growth stand TCO (gap size ratio of canopy opening diameter to mean dominant tree height was 1.0).



1995). The results of this study suggest that the relatively slow canopy closure in natural gaps in coastal *Pseudotsuga* forests (Stewart 1986; Spies et al. 1990) is primarily caused by low levels of solar radiation within them. Although soil

moisture appears to be relatively abundant in these small gaps, growth rates of germinating and established trees are quite low (Gray and Spies 1996).

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