

Canopy gaps affect long-term patterns of tree growth and mortality in mature and old-growth forests in the Pacific Northwest

Andrew N. Gray^{a,*}, Thomas A. Spies^a, Robert J. Pabst^b

^a USDA Forest Service Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, United States

^b Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, United States

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ABSTRACT

Canopy gaps created by tree mortality can affect the speed and trajectory of vegetation growth, species' population dynamics, and spatial heterogeneity in mature forests. Most studies focus on plant development within gaps, yet gaps also affect the mortality and growth of surrounding trees, which influence shading and root encroachment into gaps and determine whether, and how quickly, a gap becomes occupied by recovering vegetation. The objective of this study was to determine the effect of canopy gap size on mortality and growth of surrounding trees over a 16-year period in mature and old-growth Douglas-fir dominated forests in the coastal Pacific Northwest, USA. Replicates of four sizes of experimental gaps and controls were created in two mature stands (90 and 145-years old) and two old-growth stands (overstory trees 350–525-years old); mortality and diameter of surrounding trees were measured periodically over 16 years. A subset of trees was cored to compare growth increment before and after gap creation. There was no difference between mortality rates of trees within 8 m of gaps and trees in closed-canopy controls, although mortality causes did differ for understory trees. Mortality of understory trees was higher at gap edges than in controls, but lower several meters into the forest, suggesting a shift from negative to positive effects with the gradient in exposure. Diameter growth rates of trees were greater next to gaps than in controls, with the greatest difference ranging from 39% for overstory trees to 111% for understory trees in mature stands. Growth rates of trees in old-growth stands differed by crown class and position around gap, suggesting an effect of direct solar radiation. Growth rates of trees in mature stands were relatively insensitive to gap size and position, suggesting that increased soil moisture drove responses in these stands. Somewhat unexpectedly, there were rapid increases in growth in some old-growth trees, but not in the largest gap sizes. Results suggest canopy gaps can create heterogeneity of ecosystem function through spatial variation in effects on growth and mortality across mature and old-growth stands.

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1. Introduction

Mortality of mature trees creates canopy gaps, and the conditions found within gaps have lasting effects on newly-establishing vegetation and the development of the stand as a whole (Watt, 1947; Pickett and White, 1985). Gaps in mature forests profoundly affect species composition and stand structure in tropical, temperate, and boreal forest types (e.g., Runkle, 1982; Brokaw, 1985; Kneeshaw and Bergeron, 1998). Although the importance of gaps in forest succession is well-recognized the effects of gaps on forest succession and spatial heterogeneity of related forest processes (e.g. mortality and growth) are not well-understood. Canopy gaps can function as agents of succession by enabling establishment of

tree cohorts in the understory, enhancing the growth of established understory trees, and providing space for overstory trees to develop the large sizes found in old-growth stands (Peet and Christensen, 1980; Franklin et al., 2002). Indeed, gap creation is being used by some forest managers to accelerate development of late-successional characteristics in relatively young (30–80-years old) stands in the Pacific Northwest (USDA Forest Service and USDI Bureau of Land Management, 1994; Poage and Anderson, 2007). Since most gap studies are based on retrospective analysis of natural gaps and not controlled experiments, it is often not clear how growth of understory and overstory trees, and subsequent tree mortality, affect stand development and the process of gap closure. In contrast, controlled long-term experiments using created gaps of different sizes and in stands at different stages of successional development permit this examination.

Most gap research is focused on vegetation responses within gaps, yet gaps can have significant and long-term effects on trees

* Corresponding author. Tel.: +1 541 750 7252; fax: +1 541 758 7742.

E-mail address: agray01@fs.fed.us (A.N. Gray).

in surrounding stands. For instance, initial gap events can become loci for further gap expansion as surrounding trees succumb to increased exposure or root disease (Sprugel and Bormann, 1981; Runkle and Yetter, 1987; Rizzo and Slaughter, 2001). Canopy gaps can also affect surrounding vegetation by increasing solar radiation, moisture, and nutrients (Denslow, 1987; Poulson and Platt, 1989). Solar radiation levels increase with increasing gap size; and while indirect radiation increases more or less uniformly around gap perimeters, direct radiation increases on one side of a gap in temperate latitudes and can penetrate several meters into the surrounding stand (Canham et al., 1990; Gray et al., 2002). In contrast, soil moisture increases are found across a range of gap sizes, are generally uniform with position around gap, and appear to be exploited by adjacent trees (Minckler et al., 1973; Brockway and Outcalt, 1998; Gray et al., 2002). The varied levels of above- and below-ground resources associated with gap size and position around gaps result in a spatial mosaic of resource availability and growing conditions.

The environmental changes experienced by trees next to gaps of different sizes or in comparable thinning treatments do not always result in predictable increases in growth. Sudden exposure in heavily-disturbed stands can result in “thinning shock” and reductions in growth that can last 10 years or more (Harrington and Reukema, 1983; Garber et al., 2011). In contrast, vigorously-growing trees in dense early- and mid-successional stands can respond quickly to reductions in neighbor density (Pedersen and Howard, 2004; York and Battles, 2008). Growth of vigorously-growing trees may not change, however, for canopy dominants or for treatments with low levels of density reduction (Poage and Peart, 1993; Maguire et al., 2006). Overstory trees in late-successional old-growth stands may not increase growth at all in response to gap formation, since it is speculated that widely-spaced trees may either be capturing the resources they need, or are physiologically incapable of responding to the increases in resource availability (Oliver and Larson, 1990; Ryan et al., 2006). However, we would expect that in old-growth forests the shade-tolerant understory trees would exhibit the greatest response to adjacent gaps (McDonald et al., 1996; Jones and Thomas, 2004). Knowledge of response of old trees to gap-created resources could help us understand causes of recent increases in mortality rates of old conifer trees in old-growth forests of the western US (van Mantgem et al., 2009).

Vegetation growth in gaps in conifer forests of the Pacific Northwest of the United States is remarkably slow, with gaps taking 50–100 years to close with tree cover (Spies et al., 1990; Lertzman, 1992). In contrast, canopy closure in gaps may take as little as 2 years in moist tropical forests (Lorimer, 1989) or 5 years in temperate deciduous forests (Runkle, 1990). Slow development in gaps in the Pacific Northwest may be a result of relatively low light levels associated with low sun angles in the temperate latitude combined with tall trees with deep crowns (Canham et al., 1990). Alternatively, reduced availability of soil moisture in gaps during the dry summers due to uptake by roots of surrounding trees may limit vegetation growth as well. Because the growing season coincides with low precipitation levels in this region, soil moisture availability is an important determinant of plant community composition and tree growth (Zobel et al., 1976; Littell et al., 2008). We anticipated that the diversity of above- and below-ground resource levels associated with a long-term gap size experiment would provide insights into the limiting factors of stand development.

The objectives of this study were to determine growth and mortality of trees surrounding gaps of different sizes in mature and old-growth stands over a 16-year period after gap formation. We investigated the effects of gap size, location around gap, and time since gap formation in an experimental gap study.

2. Methods

2.1. Stand description

This study was conducted in four forest stands on relatively flat ground (slopes < 20%) in the *Tsuga heterophylla* zone (Franklin and Dyrness, 1973) on the west slope of the Cascade Range, USA. A common developmental sequence in this zone begins with young stands dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) in a single canopy layer, which develop into multi-layer old-growth forests containing increasing amounts of shade-tolerant *T. heterophylla* (Raf.) Sarg. (western hemlock), *Abies amabilis* (Dougl.) Forbes (Pacific silver fir), and *Thuja plicata* Donn. (western redcedar) (Munger, 1940; Spies and Franklin, 1991). Two of the stands were in the old-growth age class (overstory tree ages ranged from 350–525-years) and dominated by *P. menziesii* and *T. heterophylla* in multiple canopy layers; the other two stands were in the mature age class (90 and 145-years of age) and dominated by *Pseudotsuga* in a single canopy layer. Statistics of tree density by species and crown class for each stand and stand codes are found in online Appendix A, Table A. One old-growth stand (coded HJA) was located in the Andrews Experimental Forest in the central Oregon Cascades, and the other three stands were located in the Wind River Experimental Forest in the southern Washington Cascades. Four sizes of circular gaps were created in the fall of 1990 with two replicates of each size and two closed-canopy control plots in each stand. The ratios of gap diameter to tree height for the four gap sizes were 0.2, 0.4, 0.6, and 1.0, while the control plots were equal in area to the 1.0 gap size (gap diameters were measured between edges of surrounding tree crowns, and mean dominant tree heights were 50 m in three of the stands and 35 m in mature stand MCY). The 0.2 gap size corresponded to the removal of a single dominant tree. Details of stand characteristics and gap creation methods are provided in Gray and Spies (1996).

2.2. Tree selection

A 4 m by 4 m grid was surveyed within the gaps, and extended to at least 2 m beyond the canopy gap edges along the gap perimeter (Fig. 1). The grid extended 6 m beyond the boundary on the east–west center line, and 12 m beyond the gap boundary on the north–south center line and on the two parallel lines 4 m to the east and west. All trees greater than 5 cm diameter at breast height (DBH, 1.37 m) located between the outermost grid points and the planned gap, or with crowns that projected vertically onto a grid point, were measured and tagged in the summer of 1990. Trees with boles within 8 m of the gap edge at the time of gap creation (fall of 1990) were identified as “edge trees”. The location of each tagged tree was mapped and digitized, and the edges of tree crowns defining each gap were sketched and digitized. DBH, crown ratio (percent of bole length occupied by leafy material extending at least 1/3 around the bole horizontally), species, and crown class (estimated degree of shading by neighboring trees; Oliver and Larson, 1990) were recorded for each tree. Annual mortality checks were conducted through 2000, and likely cause of mortality was estimated from tree condition and evidence of damaging agents. Tree DBH and status were remeasured in 1997, 2002, and 2006.

A subsample of trees was selected for extraction of increment cores to compare individual tree growth rates before and after gap creation. The sample design was a cross of 4 tree classes by 4 levels of growth by 3 gap sizes by 3 trees (reps). The four classes were based on species, size, and crown position: (1) *Pseudotsuga* > 100 cm DBH in old-growth stands, (2) *Pseudotsuga* 50–100 cm DBH in mature stands, (3) *Tsuga* in dominant and co-dominant crown classes, and (4) *Tsuga* in intermediate and suppressed

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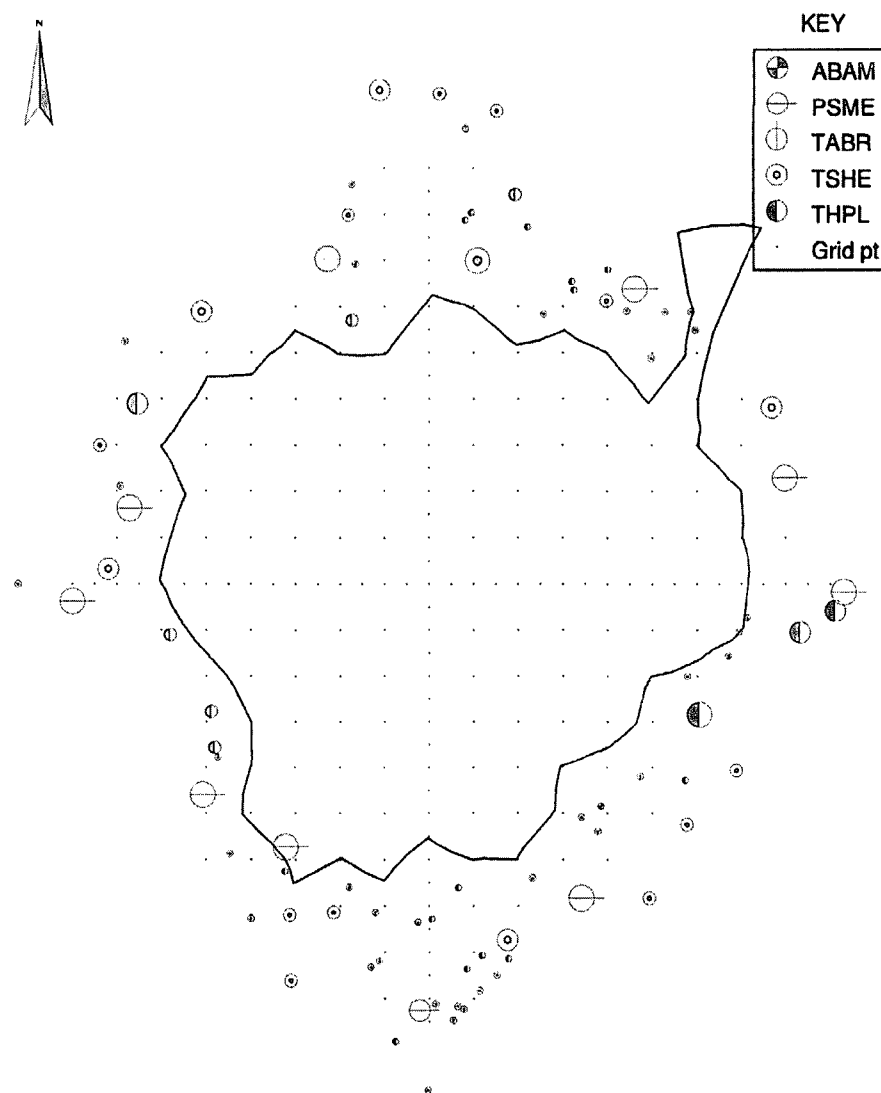


Fig. 1. Stem map of one of the 1.0 gaps in old-growth stand HJA after gap creation, showing gap outline defined by live tree crowns, 4 m grid, and tree species. Symbols vary by tree size (smallest = 0–25 cm, largest > 100 cm DBH).

crown classes. *Tsuga* were only sampled in old-growth stands due to rarity in mature stands. The four growth-rate groups were delineated using quantiles of tree basal area growth between 1990 and 1997. Cored trees were selected from controls and 0.4 and 1.0 gap sizes with an attempt to distribute samples across stands and gap replicates. There were not enough trees surrounding 0.4 gaps to find all desired replicates of growth groups, resulting in a total sample size of 142 out of 144 possible combinations. Two increment cores were extracted in the fall of 1999 from each selected tree: one facing the gap opening and one on the opposite side of the tree (or north side and south side in controls), of sufficient depth to get at least nine years of pre-gap growth to compare to the nine years of post-gap growth.

2.3. Statistical analyses

We analyzed mortality and growth with different models to assess the effects of: (1) gap size using all trees in controls and only edge trees in each gap (i.e. within 8 m of the gap edge) and (2) distance from and position relative to gap edges using all trees measured around each gap (no controls). Initial examination of the data indicated that tree crown classes could be collapsed into two groups with little loss of information: “overstory” trees (dominant

and co-dominant crown classes) and “understory” trees (intermediate and suppressed crown classes). All analyses included crown class group as a fixed effect. Results were considered significant if the probability of a Type I error was less than 0.05. Significant differences among means were determined for significant effects with either Tukey’s studentized range test or contrast statements for simple effects (SAS Institute, 2008).

The gap-size analysis of mortality was done with generalized linear mixed models (SAS MIXED procedure) for a split-split-split-plot design, with stand age, gap size, and crown group as categorical fixed effects; stand(age) and gap replicate as random effects; and time period as a repeated effect. The split-plot design placed a compound-symmetric structure on the covariance matrix. Mortality was calculated for each crown group in each replicate of gap size within each stand before calculation of statistical tests. Annualized rates of tree mortality for each period and population of interest were calculated as $r = 1 - (N_t/N_o)^{1/t}$, where N_o = number of trees at the beginning of the interval, N_t = number of living trees at the end of the interval, and t = number of years (Sheil et al., 1995). Causes of mortality were examined using proportional mortality by cause with the arcsin-square-root transformation and separate models for gap size, time period, and crown group, since the sample size was too small for a multi-factorial analysis.

The gap-distance analysis of mortality was done with a logistic mixed split-split-split-plot model using individual tree mortality that included distance to gap and position relative to gap center as effects in addition to gap size, with gap replicate as the random effect (SAS NLMIXED procedure). Position was investigated by transforming azimuth from gap center to a 0–2 range with a cosine function and doing separate analyses using a range of azimuths for the minimum and maximum (e.g., south–north, southwest–north-east, etc.) (Beers et al., 1966).

Growth analyses were based on individual trees because tree diameter growth rates varied with diameter; therefore diameter and a quadratic term (DBH^2) at the beginning of each time period were covariates in the models. The response variable was annual diameter increment based on DBH measurements for each time period. The gap-size analysis of growth used stand age, gap size, position, and crown group as fixed effects; stand(age), gap, and position(gap) as random effects; and time as a repeated effect. The position effect classified trees as north or south of gap center (or control center). Because of the diameter covariates in the model, the means shown in figures are least-square estimates of the fixed effects. Raw means were 13% and 15% higher than least-square means for overstory trees in mature and old-growth stands, respectively, but were 4% and 24% lower for understory trees in mature and old-growth stands, respectively.

2.4. Tree cores

Increment cores were mounted and sanded, and rings measured by year using a microscope and a Velmex "TA" tree-ring system (Velmex Inc., Bloomfield, NY). Measurement resolution was 0.001 mm. Annual radial increment rates were calculated for the nine growing seasons after gap formation (1991–1999) and the nine years prior to gap formation (1982–1990) for each core, and averaged for each tree. (Analyses of basal area change provided the same results, so only radial increment is reported.) Proportional change in ring increment was calculated as (post-gap growth rate – pre-gap growth rate)/pre-gap growth rate. There were no correlations between 1990 to 1997 basal area growth rates measured from DBH and the change in growth measured with increment cores, so all cores within a species group and gap size were

pooled. A generalized linear model was run on individual tree changes in growth rates using gap size and species-crown class group as fixed effects and gap replicate within stand as the random effect.

3. Results

3.1. Tree mortality

The gap-size analysis indicated no significant effect of gaps compared to controls or of gap size on mortality, either alone ($F_{4,28} = 0.2$, $P = 0.92$) or in any interactions ($P > 0.30$). The annualized mortality rate of trees in controls and within 8 m of gap edges was $1.19\% \pm 0.20$ across the eight replicates (437 of 2390 trees). Mortality was higher in the first two time periods than the last one ($F_{2,150} = 9.9$, $P < 0.0001$; Fig. 2). The crown group and stand age*crown group interaction were highly significant ($F_{1,150} = 38.9$, $P < 0.0001$ and $F_{1,150} = 7.3$, $P = 0.008$, respectively) for the full period, and mortality by crown group differed by time period as well ($F_{2,150} = 4.4$, $P = 0.014$). Separation of means indicated mortality of overstory trees was lower than for understory trees in both stand age classes, but mortality of understory trees was lower in old-growth stands than in mature stands (Table 1); and that mortality of understory trees in the second time period was higher than in the last time period.

A separate model that included species as a fixed effect across all time periods indicated that mortality differed by species and by crown group within species ($F_{5,86} = 6.5$, $P < 0.0001$ and $F_{3,86} = 5.8$, $P = 0.001$, respectively), but gaps or gap size were not a significant factor, solely or as part of an interaction. The mortality rate of *Pseudotsuga* was greater than *Tsuga* for understory trees in mature stands, and to a lesser extent for overstory trees in old-growth stands (Table 1). For comparison with rates from other studies, crown classes were combined; the annual mortality rates for *Pseudotsuga* and *Tsuga* in old-growth stands were 0.92 and 1.16%, respectively. *Cornus* mortality was very high, likely the result of the regional epidemic of the non-native fungus dogwood anthracnose (*Discula destructiva* Redlin). The mortality rate for understory *A. amabilis* in the old growth stands was quite low.

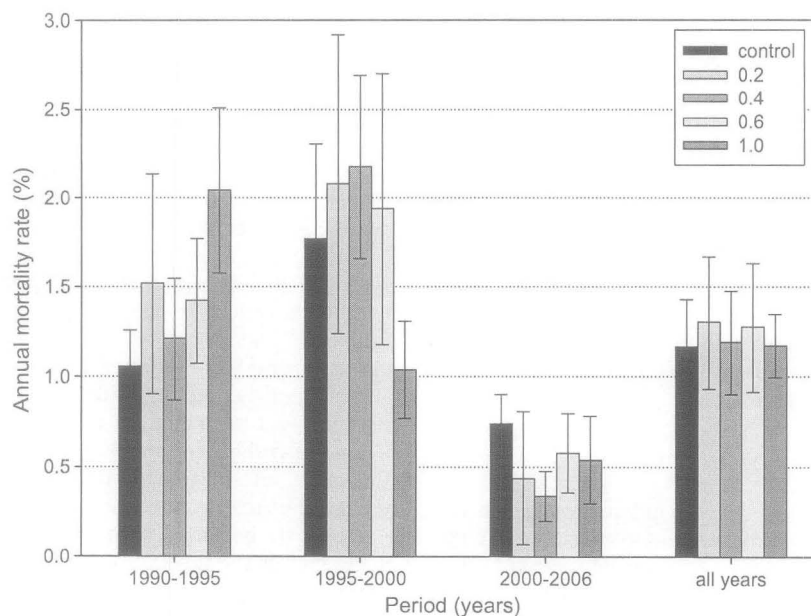


Fig. 2. Tree mortality (means and standard errors) did not differ by gap size for any time period, and mortality was higher in the second 5-year period than the first after gap creation. Gap sizes (ratio of gap diameter to overstory tree height) are indicated in the legend.

Table 1

Tree species annual mortality rates over 16-years by stand age class (mean and standard errors by stand replicate, $N = 2-4$). Total number of trees alive after gap formation shown, only species with more than 10 observations shown, but final row includes all species.

Species	Mature			Old growth			
	Overstory		Understory	Overstory		Understory	
<i>Abies amabilis</i>				0.69 (0.69)	11	0.70 (0.41)	249
<i>Abies procera</i>			6.63 (2.44)				
<i>Cornus nuttallii</i>							
<i>Pseudotsuga menziesii</i>	0.29 (0.11)	599	2.74 (0.62)	0.85 (0.26)	132		
<i>Taxus brevifolia</i>						0.78 (0.45)	42
<i>Thuja plicata</i>				0.13 (0.13)	31	1.05 (0.2)	105
<i>Tsuga heterophylla</i>			0.00 (0)	0.39 (0.23)	178	1.25 (0.63)	586
All species	0.29 (0.11)	604	2.69 (0.58)	0.58 (0.13)	360	1.38 (0.38)	989

The results of the gap-distance analysis of mortality also indicated no significant effect of gap size on mortality for either overstory or understory crown classes ($P > 0.20$). However, mortality of understory trees declined with increasing distance from gap edge ($t_{1,31} = 3.0$, $P = 0.006$); a squared term for distance was not significant. Models run with different minima of cosine-converted azimuths were significant for west and southwest azimuths, with the strongest effect indicating mortality of understory trees was greater on northeast sides than southwest sides ($t_{1,31} = -2.2$, $P = 0.03$; Fig. 3). Results suggested that the average annual mortality rate of understory trees was 0.8–1.1% higher on gap edges than 10 m from gap edges, depending on direction from gap center. Considering the mean annual mortality rate for understory trees in controls was 2.1% (and 2.3% around gaps), these suggest that higher mortality rates within the first few meters of a gap were compensated by reduced mortality further away, perhaps because of better growing conditions (e.g., more belowground resources but less exposure to wind or radiation) compared to controls.

The number of mortality trees (437) precluded the use of complex statistical models to evaluate interactions of multiple effects with mortality causes. However, single-effect models indicated that there were significant interactions between mortality cause and stand age ($F_{6,162} = 2.5$, $P = 0.025$), gap size ($F_{24,162} = 2.7$, $P = 0.0001$), time period ($F_{12,567} = 15.6$, $P < 0.0001$), crown class group

($F_{6,378} = 12.4$, $P < 0.0001$), and species ($F_{30,455} = 3.8$, $P < 0.0001$) (Table 2). Few trees experienced delayed mortality from logging damage. Mortality from bark beetle was important, particularly in the first period after gap creation (1990–1995), in overstory *Pseudotsuga* in the mature stands (this coincided with a regional outbreak triggered by beetle breeding in fresh dead wood created by an intense regional windstorm in the winter of 1989–1990). Mortality from wind-throw and tree strike was also important, mainly in the larger gaps in the 1995–2000 period. Suppression mortality (interpreted for heavily-shaded trees with low crown ratios prior to death) was important in the controls and 0.2 gap sizes, particularly in the 2000–2006 period and in mature stands.

3.2. Tree growth

There were 2,280 trees alive in 1990 and 2006 with tree measurements at all time periods, of which 1,932 were in controls and within 8 m of gap edges (new trees that grew into the plots were not included). The gap-size analysis with controls indicated a significant effect of gap size on DBH growth as a single factor ($F_{4,28} = 7.6$, $P < 0.001$); in interaction with stand age, crown class group, and direction from gap center ($F_{4,5612} = 8.0$, $P < 0.001$); and in interaction with time period ($F_{8,5612} = 2.4$, $P = 0.014$). The tree diameter covariate was highly significant and both DBH and

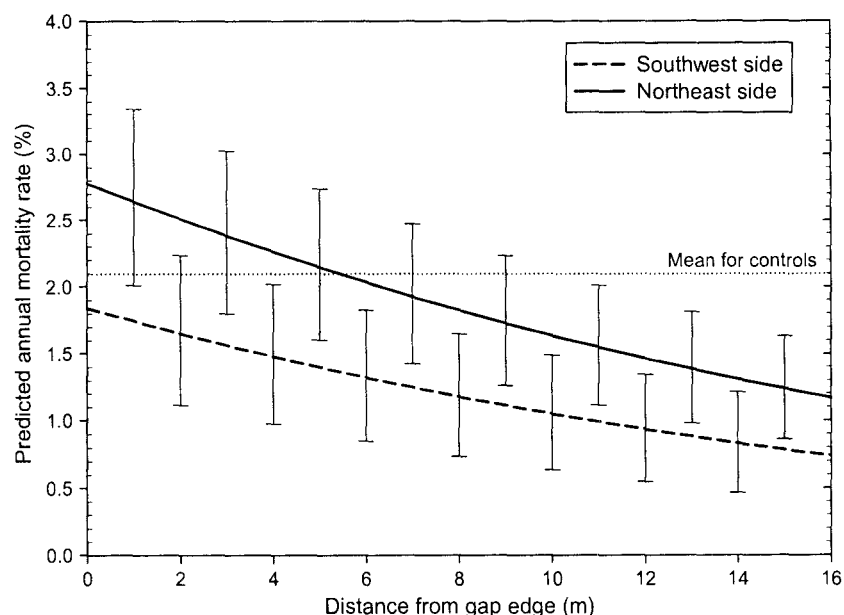


Fig. 3. Predicted mortality rate for understory crown class trees declined with distance from gap edge, with a higher rate on northeast sides than southwest sides of gaps. Predicted fixed effects across all gaps are shown, with reference to the mean for understory trees in controls. Standard error bars are shown at arbitrary distances for simplicity.

Table 2

Causes of tree mortality (mean and standard errors by replicate, $N = 8$) for various stand and tree attributes.

Variable	N	Logging		Bark beetle		Windthrow		Tree strike		Suppression		Other		Unknown		Total
All trees	437	2.3	(0.7)	12.1	(3)	22.7	(2.6)	10.1	(1.8)	26.5	(3.3)	3.9	(0.9)	22.4	(2.1)	100.0
<i>Gap size</i>																
Control	201	0.0	(0)	10.0	(3.4)	13.9	(3.4)	8.5	(3.1)	42.3	(5.4)	5.5	(1.9)	19.9	(3.8)	100.0
0.2	38	0.0	(0)	21.1	(12)	31.6	(10)	2.6	(2.1)	26.3	(5.3)	0.0	(0)	18.4	(3.7)	100.0
0.4	53	5.7	(2)	7.5	(6.3)	37.7	(5.2)	9.4	(3.7)	11.3	(4.3)	1.9	(1.4)	26.4	(6.1)	100.0
0.6	66	3.0	(1.9)	13.6	(7.2)	31.8	(6)	16.7	(6.3)	9.1	(3.6)	1.5	(0.9)	24.2	(3.8)	100.0
1.0	79	6.3	(2.2)	15.2	(10.4)	22.8	(4.8)	12.7	(4.2)	11.4	(4.8)	5.1	(3.3)	26.6	(6.4)	100.0
<i>Time period</i>																
1990–1995	166	6.0	(1.9)	25.9	(5)	6.0	(1.8)	3.6	(1.4)	17.5	(3.6)	5.4	(2.1)	35.5	(4.5)	100.0
1995–2000	196	0.0	(0)	4.6	(2.2)	39.3	(4.7)	12.2	(3)	25.0	(4.2)	4.1	(1)	14.8	(2.7)	100.0
2000–2006	75	0.0	(0)	1.3	(1)	16.0	(3.5)	18.7	(5.2)	50.7	(6.2)	0.0	(0)	13.3	(4.2)	100.0
<i>Crown class group</i>																
Overstory	58	0.0	(0)	44.8	(7.7)	27.6	(6.5)	0.0	(0)	1.7	(1.8)	3.4	(2.1)	22.4	(6.6)	100.0
Understory	379	2.6	(1)	7.1	(2.2)	21.9	(2.8)	11.6	(2.1)	30.3	(3.6)	4.0	(1)	22.4	(2.2)	100.0
<i>Stand age class</i>																
Mature	205	1.5	(1)	14.6	(5.5)	22.9	(4.3)	4.9	(1.6)	34.1	(5.1)	3.4	(0.8)	18.5	(2.9)	100.0
Old growth	232	3.0	(1.1)	9.9	(2.8)	22.4	(3.2)	14.7	(2.9)	19.8	(3.7)	4.3	(1.7)	25.9	(2.8)	100.0
<i>Species</i>																
ABAM	51	3.9	(3)	19.6	(6)	3.9	(3.5)	3.9	(3.6)	31.4	(7.6)	0.0	(0)	37.3	(6.9)	100.0
CONU	30	3.3	(4.4)	0.0	(0)	20.0	(9.6)	10.0	(6.6)	23.3	(6.2)	13.3	(5.1)	30.0	(8.5)	100.0
OTHR	7	28.6	(18.4)	0.0	(0)	14.3	(14.3)	0.0	(0)	14.3	(14.3)	14.3	(14.3)	28.6	(18.4)	100.0
PSME	194	0.5	(0.6)	21.6	(5.7)	24.2	(4)	3.6	(1)	32.5	(4.7)	1.5	(0.8)	16.0	(2.4)	100.0
THPL	18	5.6	(4.7)	0.0	(0)	27.8	(13.4)	27.8	(11.3)	5.6	(5.9)	11.1	(9.4)	22.2	(10.1)	100.0
TSHE	137	2.2	(1)	0.7	(1)	27.7	(3.6)	19.7	(3.7)	20.4	(4.4)	5.1	(1.9)	24.1	(4.3)	100.0

DBH² terms were included in the model. Separation of means indicated that growth was greater in gap sizes 0.4, 0.6, and 1.0 than in controls, with some fluctuation by time period (Fig. 4). Although growth rates declined over time in controls and 0.2 gaps, responses varied among the larger gaps and were most segregated in the last period. Tests of simple effects in significant interactions with contrasts indicated that gap size was a significant effect ($P < 0.05$) for all categories of overstory and understory trees in mature and old-growth stands. Growth of overstory trees in mature stands was similar across gap sizes, and higher than controls (Fig. 5). In contrast, growth of overstory trees in old-growth stands increased

with gap size, but dropped in 1.0 gaps to mean levels similar to the controls. The surprisingly low growth rates in old-growth 1.0 gaps were consistent across replicates, with no outlier trees driving the pattern, and reflected low growth on both north and south sides of gaps. The maximum mean increase in growth in gaps over controls ranged from 39% for overstory trees in mature stands to 111% for understory trees in mature stands. Tests of simple effects of location indicated that where significant differences occurred, growth of overstory trees was higher on the south sides of gaps, while growth of understory trees was greater on the north sides of gaps (Fig. 5). Although diameter growth differed by species, patterns by

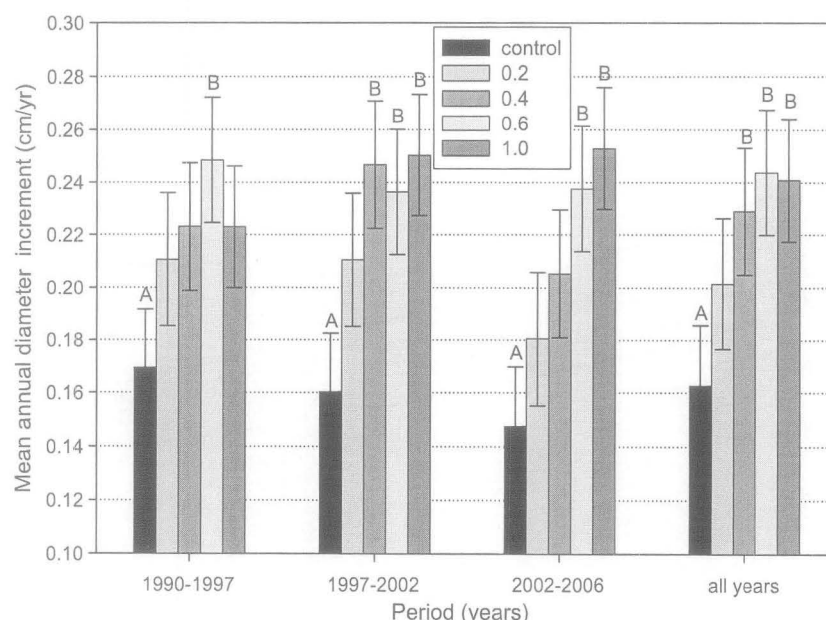


Fig. 4. Tree diameter growth (means and standard errors) varied by time period, but was usually greater in large gaps than in controls. The greatest separation among gap sizes was evident in the last time period. Letters indicate significant differences between gap size means within each time period; values are least-squared means for fixed effects.

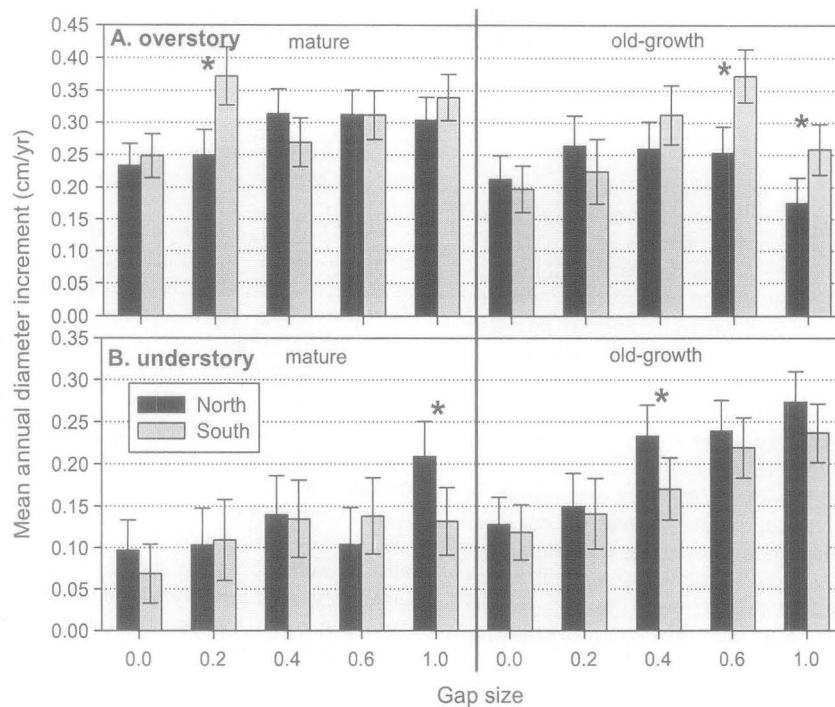


Fig. 5. Tree diameter growth (means and standard errors) differed by north or south sides of gaps for several combinations of stand age class, gap size, and crown class. Overstory tree growth was often greater on north sides of gaps than south sides, while the opposite was true for understory tree growth. Asterisks (*) indicate significant differences between position for each pair of means; values are least-squared means for fixed effects.

stand age, gap size, and crown group were similar to those reported for all species combined; analyses and a summary of results are presented in online Appendix_B.

DBH growth increment declined significantly with distance from gap for all trees ($F_{1,4006} = 38.7$, $P < 0.001$) and in interaction with gap size, position, and crown group ($F_{3,4006} = 3.3$, $P = 0.019$) and in interaction with time period ($F_{2,4006} = 3.2$, $P = 0.040$). Interactions were investigated through simpler, separate analyses by

crown group and time period. Interactions of distance with gap size and gap position were strongest in the third period when the effect was weak for overstory trees ($F_{3,599} = 2.2$, $P = 0.086$) but significant for understory trees ($F_{3,701} = 4.3$, $P = 0.005$). Predictions of growth rates in the third period were generated for understory trees of representative DBH (50 cm) for different distances from gaps of different sizes (Fig. 6). The magnitude of predicted slopes suggests that on north sides of gaps, growth declined more with

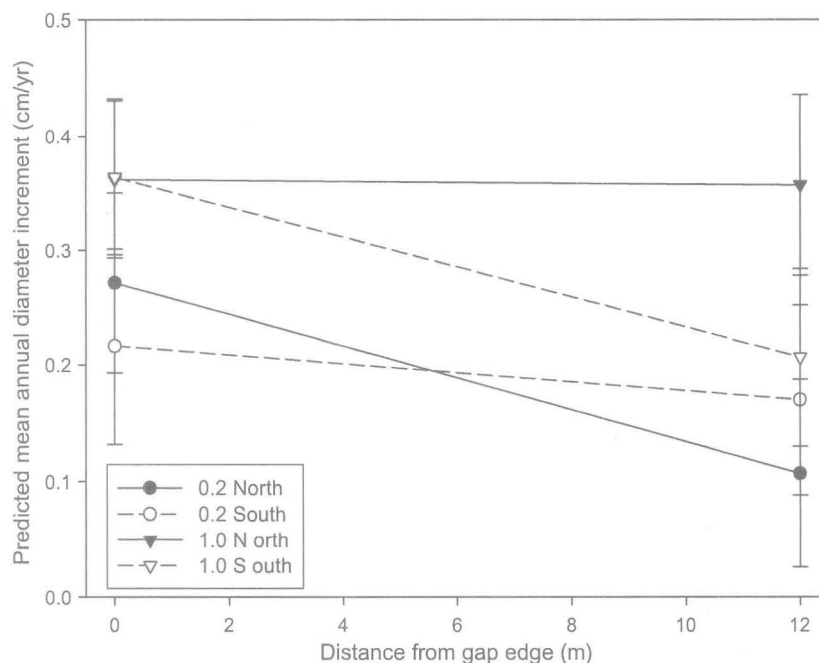


Fig. 6. The decline in predicted understory tree diameter growth rate with distance from gap edge was greater on north sides than south side of the smallest (0.2) gaps but the reverse was true for the largest (1.0) gaps. Patterns were similar for overstory trees and slopes changed predictably in intermediate gap sizes.

distance in smaller gaps than larger gaps for both crown classes. The opposite is suggested on south sides of gaps, with greater declines with distance in large gaps than small gaps.

3.3. Tree increment response to gap formation

Changes in diameter increment between the nine years before and after gap creation were positive and significantly greater for trees around the 1.0 gap size than in controls ($F_{2,18} = 6.2$, $P = 0.009$), with a difference among tree classes suggestive but not significant ($F_{3,112} = 2.2$, $P = 0.092$; Table 3). The proportional increases in increment around gaps aligned well with differences in post-gap DBH growth between gaps and controls for mature *Pseudotsuga* and understory *Tsuga*. For old-growth *Pseudotsuga* and overstory *Tsuga* in old-growth stands, however, the patterns were different. In the case of old-growth *Pseudotsuga*, post-gap increment was somewhat lower in 1.0 gaps than in controls, which matches the DBH results (Fig. 5), but pre-gap increment was even lower in 1.0 gaps, resulting in a positive proportional change. It's not clear whether the low pre-gap increment for these trees was anomalous or—given substantial annual variation observed in annual rings—whether nine years was an accurate reflection of pre-gap growing conditions. In the case of overstory *Tsuga*, post-gap increment increased with gap size, while DBH measurements did not, even for the same trees that were cored for increment (mean 1990–1997 DBH change was 2.03, 2.34, and 1.88 cm for cored trees in controls, 0.4, and 1.0 gaps, respectively). Although multiple cores were collected for each tree in part to account for the tendency of *Tsuga* to distribute ring increment unevenly around the bole (e.g., Kellogg and Barber, 1981), it's possible that two cores per tree were not adequate to characterize increment for the circumference of the bole. Results suggest that overstory trees in old-growth stands can have some positive responses to gaps in the 1.0 size range, but the generality and extent of those responses are not clear.

4. Discussion

This study indicates that canopy gaps can affect survival and growth of trees in surrounding forests and that these effects vary with successional stage and tree social and physiological status. Although diameter growth of trees next to gaps generally increased over a 16-year period in both successional stages, there were

exceptions that suggested inhibition of growth might operate in some larger gaps and differential response to above- and below-ground resources could be occurring. Gap creation generally had no effect on mortality of surrounding trees with the exception that mortality of understory trees declined with distance from gap. Our findings have implications for the role of tree age and physiology, competitive status, and natural vs. created gaps in forest succession.

We expected exposure to wind or sudden increase in insolation to result in greater mortality of trees around gaps than in controls. Increased mortality is often seen at edges of larger clearings (Sprugel and Bormann, 1981; Chen et al., 1992) and gaps appear to expand in size episodically (Runkle and Yetter, 1987; Van Pelt, 1995). However, as long as gap closure from lateral crown expansion is not rapid, even random mortality can only result in gaps increasing in size over time. By comparing mortality rates next to gaps with those in controls we were able to address the question of enhanced mortality around gaps. Although we found similar mortality rates in our study between gaps and controls (see also Davis et al., 2007), we did find that northeast sides of gaps had increased mortality of understory trees compared with southwest sides and that understory tree mortality was lower 10 m away from gaps than on edges of gaps or in controls. Greater mortality on gap edges could be caused by exposure to wind (wind-throw was an important mortality type in gaps), as well as by moisture stress from high temperatures and soil moisture depletion found on north sides of large gaps (Gray et al., 2002). Lower mortality at 10 m from gaps could be caused by increased light levels from nearby gaps. Annual mortality checks allowed more accurate reconstruction of key mortality events or chronic mortality causes than if checks had been done periodically (e.g., every five years). Because our gaps were experimentally created, we would not expect to see gap expansion from biotic agents like root disease, which spreads in circles from infected trees and may be an important gap-making mechanism in many stands (Rishbeth, 1957; Rizzo and Slaughter, 2001; Aukema et al., 2010). As expected from standard succession theory, mortality was greater for understory trees than for overstory trees, and understory mortality rates were greater in mature stands where most trees were the relatively shade-intolerant *Pseudotsuga* than in old-growth stands where most understory trees were shade-tolerant *Tsuga*. Annual mortality rates for trees in old-growth stands in this study were greater than those found by Franklin and DeBell (1988) for the period 1947–1983 (0.92 vs. 0.62 for *Pseudotsuga* and 1.22 vs. 0.59 for *Tsuga*), suggesting an increase over time but not to a doubling in mortality rates over a 17-year period as suggested for this region by van Mantgem et al. (2009).

Differences in tree growth among gap sizes increased over time, indicating a lag in the adjustment of mature trees to their new environment (e.g., Williamson, 1982; McDowell et al., 2003). Increased exposure from thinning or gaps can lead to negative or no growth response in mature and old-growth trees in the first decade after disturbance, or delays in positive response for up to 20 years (Latham and Tappeiner, 2002; Maguire et al., 2006; Garber et al., 2011). In our study, differences in growth of overstory trees between gaps and controls were greatest in mature stands, where growth was similar across gap sizes and varied little with position around gap. Similar results have been seen in other studies of trees in a vigorous condition, and suggest a primary response to additional soil moisture rather than light (McDonald et al., 1996; Pedersen and Howard, 2004; York and Battles, 2008).

In contrast, diameter growth of overstory old-growth trees did vary with gap size and position around gap, and suggested a positive effect from intermediate increases in solar radiation and a negative effect at higher light levels in the largest gaps. The causes of potential negative growth effects of the large gaps on overstory

Table 3

Comparison of radial diameter increment for 9-years prior to and 9-years following gap creation, by tree class and gap size, as measured from a subsample of trees with increment cores. Means and standard errors of growth rates and proportions from individual trees are shown ($n = 9–12$).

Gap size	Pre-gap growth (cm)	Post-gap growth (cm)	Proportional change
<i>Old-growth Pseudotsuga</i>			
0	1.244 (0.187)	1.137 (0.165)	−0.043 (0.08)
0.4	1.001 (0.225)	1.121 (0.24)	0.121 (0.087)
1	0.716 (0.09)	0.977 (0.172)	0.350 (0.165)
<i>Mature Pseudotsuga</i>			
0	2.515 (0.401)	2.122 (0.349)	−0.137 (0.058)
0.4	2.365 (0.33)	2.164 (0.318)	−0.041 (0.08)
1	2.412 (0.347)	2.390 (0.347)	−0.006 (0.066)
<i>Overstory Tsuga</i>			
0	2.380 (0.322)	2.543 (0.4)	0.090 (0.117)
0.4	2.203 (0.195)	2.680 (0.438)	0.222 (0.164)
1	2.413 (0.332)	2.953 (0.432)	0.228 (0.088)
<i>Understory Tsuga</i>			
0	0.733 (0.145)	0.643 (0.179)	−0.155 (0.069)
0.4	1.145 (0.155)	1.207 (0.269)	0.136 (0.17)
1	0.824 (0.203)	1.343 (0.457)	0.436 (0.233)

old-growth trees are not clear. Exposure of trees in gaps may be greater than in a heavy thinning, since the gaps were in an otherwise intact stand, with little increase in horizontal air movement and greater heat loads on foliage. Heat load would not be much of a factor on south sides of large gaps, but the high growth rates of understory trees may have increased competition with old-growth trees for belowground resources. Old-growth trees appear to transpire less than younger trees despite similar sapwood area (Moore et al., 2004; Winner et al., 2004), which might increase sensitivity to exposure or competition. Damage and loss of shade-adapted foliage may also play a role in growth declines and delayed response to openings (Harrington and Reukema, 1983; Garber et al., 2011). Differences in below-ground environment and resource allocation may also play a role in differences in growth between old-growth and mature stands. More of the carbon fixed by old trees may be allocated to roots, or simply lost, below-ground (Ryan et al., 2006). Loss of mycorrhizal mats, which tend to be more abundant in older stands but are absent in gaps (Griffiths et al., 2010), may reflect reduced mycorrhizal connections and ability for some trees to extract below-ground resources. Increasing dominance of older stands by *Tsuga*, which have greater fine root density and produce more acidic soils than *Pseudotsuga* (Alban, 1969; Meinzer et al., 2007) could change the way in which trees extract soil moisture and nutrients.

The diameter growth response of understory trees differed substantially from that of overstory trees. The gap effect on understory tree growth in mature stands was minimal across all gap sizes except the largest, while growth increased with gap size in old-growth stands. The shade-intolerant *Pseudotsuga* understory trees in mature stands likely have a higher light threshold to trigger a growth response than the *Tsuga* found in old-growth stands, reflecting differences in minimum light compensation points for photosynthesis (e.g., Winner et al., 2004). In addition, growth of understory trees was greater on north sides of gaps than south sides, the opposite of the overstory response. This suggests a positive response to increased exposure to light for understory trees, particularly for the shade-tolerant species found in old-growth stands. Similar responses of shade-tolerant understory trees have been found in northern hardwoods (Jones and Thomas, 2004) and Sierran mixed conifer stands (McDonald et al., 1996). Understory trees in old-growth stands exhibited the greatest growth rates in the locations that had the greatest mortality rates. Similar results in seedling establishment studies (e.g., Gray and Spies, 1996) suggest that if trees occur in favorable microsites they can survive and grow more rapidly under higher radiation and temperature levels.

Contrasting growth responses of overstory and understory trees in mature and old-growth stands suggest greater limitation of below-ground resources in mature stands and greater limitation of above-ground resources in old-growth stands. An upper threshold of tolerance to increased exposure is suggested for overstory trees in old-growth stands, although increment cores did indicate some growth response that simply may take more than 16 years to become apparent. It is not clear whether the weak response of old-growth trees to gaps is related to trees' physiological capability to respond to gap formation, or indicates some other mechanism by which overstory trees "lose their grip" on the proportional productivity in a stand as stands age (Binkley, 2004). In any case, this study reveals that canopy gaps can be an important driver of the dynamics of the surrounding forest matrix and that responses to gaps can be complex and variable depending on location, time, species, and canopy position.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2012.06.035>.

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