Growth releases of three shade-tolerant species following canopy gap formation in old-growth forests

Amanda B. Stan & Lori D. Daniels

Abstract

Questions: Do the number, duration and magnitude of growth releases following formation of natural, fine-scale canopy gaps differ among shade-tolerant *Thuja plicata*, *Tsuga heterophylla* and *Abies amabilis*? What is the relative importance of tree-level and gap-level variables in predicting the magnitude and duration of releases? What does this tell us about mechanisms of tree species coexistence in such old-growth forests?
Location: Coastal British Columbia, Canada.
Methods: We estimated the timing of formation of 20 gaps using dendroecological techniques and extracted increment cores from all three species growing around or within gaps. Using a species- and ecosystem-specific release-detection method, we determined the number of trees experiencing a release following gap formation. We quantified the duration and magnitude of individual releases and estimated the influence of tree-level and gap-level variables on these release attributes.
Results: Eighty-seven per cent (304 of 348) of all trees experienced a release following gap formation. *T. heterophylla* and *A. amabilis* experienced higher magnitude and longer duration releases than *T. plicata*. The effect of diameter on the duration of releases varied among species, with *T. heterophylla* and *A. amabilis* experiencing decreasing, and *T. plicata* experiencing increasing, duration of releases with increasing diameter. The effect of growth rate prior to a release on the magnitude of releases varied among trees of different diameters, with the slowest growing and smallest individuals of all species experiencing the most intensive releases.
Conclusions: Our results provide detailed information on the number, duration and magnitude of growth releases of the above three species following gap formation. Differences in response to canopy gaps suggest differences in how these species ascend to the canopy strata. *T. plicata* may be less dependent on gaps to reach the canopy. Differing strategies for

ascending to the canopy strata may be important in facilitating coexistence of these three species in old-growth forests of coastal British Columbia.

Introduction

Canopy disturbance is a primary process in forests that influences the growth of new and established trees. In forests where stand-destroying disturbances are infrequent, canopies are opened periodically by the death of single trees or small groups of trees (Wells et al. 1998; Frelich 2002). Changes in growth brought about by fine-scale canopy disturbances are often assessed by inspecting the radial-growth patterns of trees that survive the disturbances, as they can provide insight into the compositional and structural development of forest stands (Lorimer & Frelich 1989; Frelich 2002).

Radial-growth releases have been used to reconstruct the frequency and intensity of past canopy disturbances in temperate forests worldwide that are dominated by fine-scale processes of gap dynamics (e.g. Frelich & Lorimer 1991 (US Midwest); Orwig & Abrams 1994 (northeastern US); Lusk & Smith 1998 (New Zealand); Ishikawa et al. 1999 (Russia); Rozas 2003 (Spain); Gutiérrez et al. 2004 (Chile); Taylor et al. 2006 (China)). In general, releases resulting from canopy disturbances are defined according to three attributes: abruptness, duration and magnitude (Henry & Swan 1974; Lorimer & Frelich 1989; Nowacki & Abrams 1997; Frelich 2002). Various criteria for these three attributes have been used to identify releases and estimate past canopy disturbances in different forest types (Rubino & McCarthy 2004).

Over the years, research aimed at improving release-detection methods to better estimate past canopy disturbances has provided us with a better understanding of the factors that influence tree responses following canopy disturbances. In particular, prior

Stan, A.B. (corresponding author, astan@geog.ubc.ca) & **Daniels, L. D.** (daniels@geog.ubc.ca): Department of Geography, University of British Columbia, 1984 West Mail, Vancouver, BC, Canada V6T 1Z2.
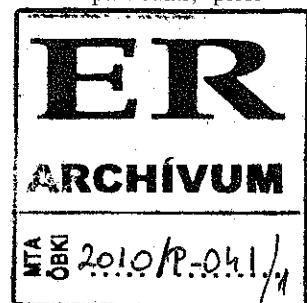
growth (i.e. growth rate prior to a release) and species, both known to influence the magnitude of releases, have received considerable attention. Researchers applying the widely used radial-growth averaging method (Henry & Swan 1974; Lorimer & Frelich 1989; Nowacki & Abrams 1997) to estimate past canopy disturbances have accounted for prior growth by applying various criteria to individual sections of growth series (Lorimer 1980; Glitzenstein et al. 1986; Dahir & Lorimer 1996) or individual trees in different canopy classes (Ruffner & Abrams 1998). More recent approaches that build on the radial-growth averaging method explicitly account for the effects of prior growth and species (Black & Abrams 2003, 2004; Fraver & White 2005). However, much less attention has been given to the possible influence of additional tree-level and gap-level variables on the magnitude or duration of releases. While potentially useful for further improving release-detection methods, this information may also help improve our understanding of tree species coexistence in old-growth forests that are dominated by fine-scale processes of gap dynamics.

In this study, we examined growth releases of three shade-tolerant tree species in old-growth, *Thuja plicata-Tsuga heterophylla* forests of coastal British Columbia, Canada. Our study used dendroecological analyses to assess the number of *T. plicata*, *T. heterophylla* and *Abies amabilis* that experienced a release following the formation of natural, fine-scale canopy gaps, along with the duration and magnitude of individual releases. We addressed two specific objectives: (1) to determine if the number, duration and magnitude of releases differ among species and (2) to assess the relative importance of tree-level variables (i.e. species, diameter, prior growth, distance from the gap centre and tree position around or within the gap) and gap-level variables (i.e. area, aspect, canopy openness and slope) in predicting the magnitude and duration of releases. Our results provide information for assessing mechanisms of tree species coexistence in old-growth, *T. plicata-T. heterophylla* forests.

Methods

Study area

The study area includes the Capilano, Seymour and Coquitlam River watersheds in the Coast Mountains of southwestern British Columbia (Fig. 1). Here, we sampled mid-elevation (300-700 m a.s.l.), old-growth forests (age >250 years) dominated by shade-tolerant *T. plicata*, *T. heterophylla* and *A. amabilis*, and a small number of

shade-intolerant *Pseudotsuga menziesii* (Acres International Limited 1999). These forests are in the Very Wet Maritime subzone of the Coastal Western Hemlock zone (Biogeoclimatic Ecosystem Classification system of British Columbia; Meidinger & Pojar 1991). Mean annual temperature ranges from 6°C to 7.5°C, with a mean of 15°C to 16°C in August and −1°C to 1°C in December. Mean annual precipitation ranges from 3000 to 4000 mm; mean growing season (May to September) precipitation ranges from 600 to 800 mm. Values for temperature and precipitation are based on spatially interpolated monthly climate normals for the period 1961-1990 (Wang et al. 2006). Soils are largely Humo-Ferric podzols derived from colluvium and glacial till (Valentine et al. 1978).

Stand developmental processes contribute greatly to the overall openness of mid-elevation, old-growth forests in the study area. Approximately 74% of the area of old-growth, *T. plicata-T. heterophylla* stands (A.B. Stan and L.D. Daniels, unpubl. data) is in canopy and expanded gaps (*sensu* Runkle 1982) of developmental origin (i.e. those created by the mortality of canopy dominants; Lertzman et al. 1996). Another 13% is in canopy and expanded gaps of edaphic origin (i.e. those associated with physiographic features, such as streams or rock outcrops; Lertzman et al. 1996). Only 13% of the area of these stands is in closed canopy (A.B. Stan and L.D. Daniels, unpubl. data).

Selecting canopy gaps

We used a combination of ecological inventory data and field reconnaissance to select canopy gaps. First, using forest cover maps of the study area (Acres International Limited 1999), we identified all remnant stands of mid-elevation, old-growth forest composed of ≥ 20% *T. plicata* and ≤ 20% *P. menziesii* by volume and situated on slopes ≤ 30°. Approximately 3000 ha of forest stands met these criteria. Second, we randomly selected a subset and inspected them to verify old-growth structural and compositional characteristics and assess site features and accessibility. Stands that were poorly drained, difficult to access because of streams or gullies or too small to contain canopy gaps not influenced by edge effects from roads or major streams were omitted. Third, we searched the suitable stands for canopy gaps that (1) were created by one or two uprooted canopy dominant(s) and (2) included gap-makers in decay classes I, II or III (Maser et al. 1979) that most likely died within the last 50 years (Daniels et al. 1997). In total, we located 45 gaps.
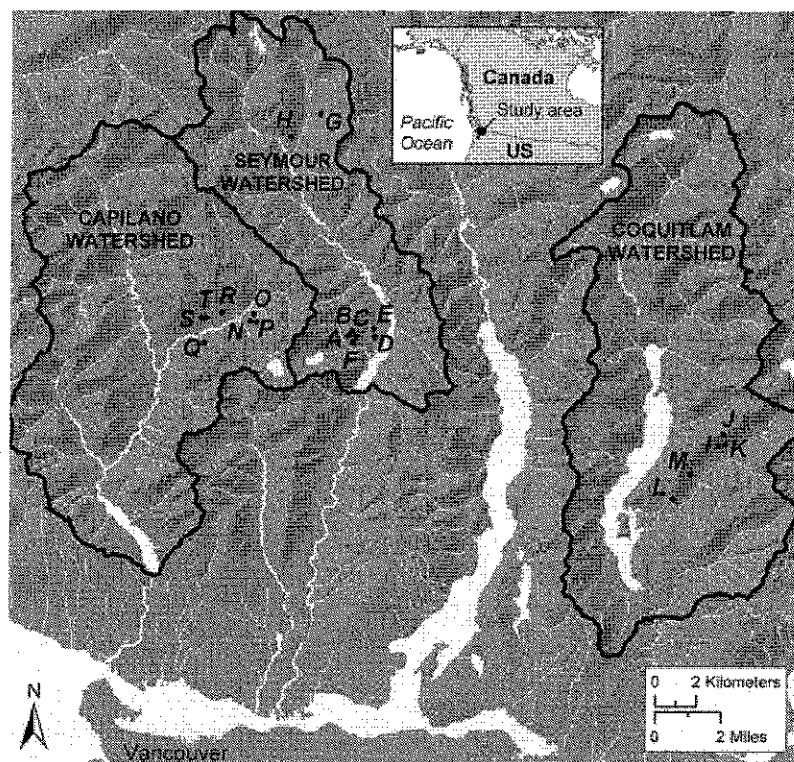
Fig. 1. Location of the 20 study gaps (A through T) within the Capilano, Seymour and Coquitlam River watersheds, southwestern British Columbia, Canada.

In an effort to determine the approximate timing of formation of each of the 45 gaps, we attempted to estimate the year of death and/or the year of fall of individual gapmakers from each gap using dendroecological techniques (Dynesius & Jonsson 1991; Daniels et al. 1997; Storaunet & Rolstad 2002). We used the outer-ring dates of increment cores to estimate the year of death. This technique, while common, may produce biased results. Specifically, rings may erode in areas where bark is absent or ring growth may cease prior to tree death, both resulting in dates that are lower than the actual year of tree death (Mast & Veblen 1994; Cherubini et al. 2002). We attempted to minimize the bias by (1) assessing multiple increment cores from the least decayed sections of the gapmakers and (2) verifying our results by estimating the year of fall using scar or reaction wood dates in trees injured by the gapmakers and establishment dates of seedling or saplings growing on the gapmakers. In total, we estimated the year of death and/or the year of fall of gapmakers from 20 gaps (Table 1; Fig. 1), which we used in all subsequent sampling.

Sampling and crossdating trees

To assess growth releases of *T. plicata*, *T. heterophylla* and *A. amabilis* following gap formation, we extracted two increment cores from all canopy and subcanopy trees [diameter at breast height (dbh) $\geq$ 10 cm] that defined the boundary of, or occurred within, the 20 gaps (Appendix S1). The boundary of a gap was delineated using the crown of canopy and subcanopy trees nearest to the gapmaker(s). All trees were cored on the side facing the centre of the gap at a height of approximately 30 cm above the ground. Cores were prepared using standard procedures (Stokes & Smiley 1968).

We applied a rigorous approach to crossdating because modest to severe suppressions were common for *T. heterophylla* and *A. amabilis*, which made crossdating difficult. First, we visually crossdated (Yamaguchi 1991) the two cores from each tree to identify locally absent tree rings (Fritts 1976). Then, we measured ring widths of all cores to the nearest 0.001 mm and used the program COFECHA (Holmes 1983; Grissino-Mayer 2001) to statistically verify our crossdating, both within individual trees

Table 1. Summary of data collected to estimate the timing of formation of the 20 study gaps using dendroecological techniques. Timing of formation was estimated using the year of death and/or the year of fall of gapmakers. [†]Number of crossdated ring-width series; values are underlined to indicate ring-width series that were successfully sampled but not successfully crossdated. [§]Mean Pearson's correlation coefficient between the crossdated ring-width series and the species-specific chronology (see Stan 2008) calculated using COFECHA. [‡]Most recent estimate as determined from outer-ring dates of the crossdated ring-width series. [+]Determined using scar or reaction wood dates in trees injured by the gapmakers. Italics are used to indicate the maximum year of fall (i.e. minimum time since fall) as determined from pith dates of seedlings or saplings that had established on the gapmaker. The number of injured trees, seedlings, and saplings that were sampled and visually crossdated is given in previous columns. [*]Gapmakers were on the same root plate. [‖]Dated using data from gap T, which was 30 m away and likely formed during the same storm. [++]Two scars were located on the same radii. Gapmaker likely fell in 1993 and shifted its position in 1998. Additional notes: Gaps were sampled during 2003 and 2004. na indicates that either no data were available to sample, no samples were successfully collected or no information could be obtained from the sample(s) to determine mean correlation, year of death or year of fall. Empty cells occur for gaps with two gapmakers to avoid any redundancy in values of year of death and/or fall.

Gap ID	Species of gapmaker	dbh (cm)	Cores from gapmaker[†]	Mean corr.[§]	Scars or reaction wood	Seedlings or saplings	Year of death[‡]	Year of fall[+]
A	*Thuja plicata*	110	7	0.64	0	1	1973	*1979*
B	*Thuja plicata*	180	2	0.65	2	1	1991	1992
C	*Thuja plicata*	132	5	0.61	0	0	1998	na
D	*Thuja plicata*	140	5	0.49	1	0	1998	na
E	*Thuja plicata*	108	9	0.42	1	1	1956	*1966*
F	*Thuja plicata*[*]	74	3	0.53	3	0	1974	1981
	Tsuga heterophylla	53	2	na	0	0		
G	*Abies amabilis*	93	2	0.39	2	1	1995	1993/1998[++]
H	*Thuja plicata*	99	6	0.52	1	0	1967	1978
I	*Thuja plicata*	106	4	0.51	0	0	1973	na
J	*Tsuga heterophylla*	66	3	na	1	0	na	1985
K	*Tsuga heterophylla*	99	2	na	1	0	na	1985
L	*Thuja plicata*	172	5	0.40	1	0	na	1963
M	*Thuja plicata*	160	3	0.56	1	0	1959	1976
N	*Thuja plicata*[*]	106	7	0.51	1	0	1995	1996
	Tsuga heterophylla	30	0	na	0	0		
O	*Abies amabilis*[*]	53	3	0.33	1	0	2000	1999
	Tsuga heterophylla	21	3	0.39	0	0		
P	*Thuja plicata*	200	3	0.70	0	0	1989	na
Q	*Thuja plicata*	165	2	0.55	1	0	1977	1978
R	*Thuja plicata*	312	3	0.44	1	0	1977	1999
S	*Tsuga heterophylla*[‖]	99	0	na	0	0	2000	na
T	*Thuja plicata*	147	3	0.59	0	0	2000	na
	Tsuga heterophylla	84	0	na	0	0		

and among all trees of a single species. In general, cores with the greatest number of suppressions and/or releases were difficult to statistically crossdate, and at best, could only be visually crossdated using narrow and wide marker rings.

Identifying growth releases of trees

We assessed growth series from all trees ($n = 348$) growing around or within the 20 gaps to determine the number of individuals of different species that experienced a release following the death or fall of the gapmaker(s). We converted ring widths into basal area increments, averaged the two series from each tree, and used a species- and ecosystem-specific version of the radial-growth averaging method (see Stan 2008 for more detail) to

determine if individual trees experienced a release. Releases were detected using the formula (Nowacki & Abrams 1997):

$$\%GC = (M_2 - M_1)/M_1 \times 100$$

where %GC is percentage growth change for a single year, M_1 is the mean basal area increment for the 5 years preceding that year, and M_2 is the mean basal area increment for the 5 years following that year. We identified a release as the highest peak growth change value $\geq 25\%$, within a ± 10-year window that surrounded the year of death of the gapmaker(s) (Fig. 2). The peak percentage growth change value represented the year prior to the onset of a release (Nowacki & Abrams 1997). If a peak $\geq 25\%$ did not occur, we assessed whether the last calculated growth change value within the window

was $\geq 25\%$. This secondary assessment was primarily useful for identifying growth releases of trees from the most recently-formed gaps in which too little time had passed for the percentage growth change curves to each form a peak with a descending limb. For three gaps, we determined only the year of fall of the gapmakers (Table 1). We assessed growth releases of trees from these gaps using a $-10/+5$-year window that surrounded the year of fall (Fig. 2). Examining several years before and after the year of death and fall reduces the potential for errors when estimating releases. For example, slow opening of the canopy from cambial and crown dieback of the gapmaker(s) may cause a tree to experience a release prior to the estimated year of death. Furthermore, trees may show a lag in response after the year of death or fall because new resources are allocated to other vital functions and structures before radial growth. Finally, examining several years before and after the year of death and fall helps account for any minor errors in these dates. We used all the detected releases in later analyses of duration and magnitude.

We assessed growth series from a subset of trees ($n = 94$) growing around or within six gaps (A, E, F, H, M and Q; Table 1) to determine the number of individuals of different species and canopy classes (canopy or subcanopy) that experienced a release following both the death and fall of the gapmakers. Light availability in and around gaps will increase as gapmakers die and may increase further when they fall, particularly if the gapmakers are large in size, as is the case in this study. A small increase in light availability when a gapmaker falls may allow for a secondary release (i.e. a secondary peak in the percentage growth change curve). For this analysis, we applied the same techniques used to detect a release relative to the year of death or fall but instead used a $+5$-year window for the year of fall. We used a subset of trees from six gaps because objectively identifying releases in this analysis required at least 15 years of growth before and after the year of death and at least 10 years of growth after the year of fall. The 15 years resulted from the $\pm$ 10-year window, coupled with the 5-year moving average (i.e. M_1 and M_2); while the 10 years resulted from the $+5$-year window, coupled with the 5-year moving average. Trees of different species and canopy classes were placed into one of four categories that described whether individuals experienced a release following the year of death only, the year of fall only, both the year of death and fall or if no release was detected. In the instance that the same release was detected for both the year of death and fall it was counted as being associated with the year of death.

Duration of releases

The duration of a release is the number of years from the onset to the end of a release. To determine
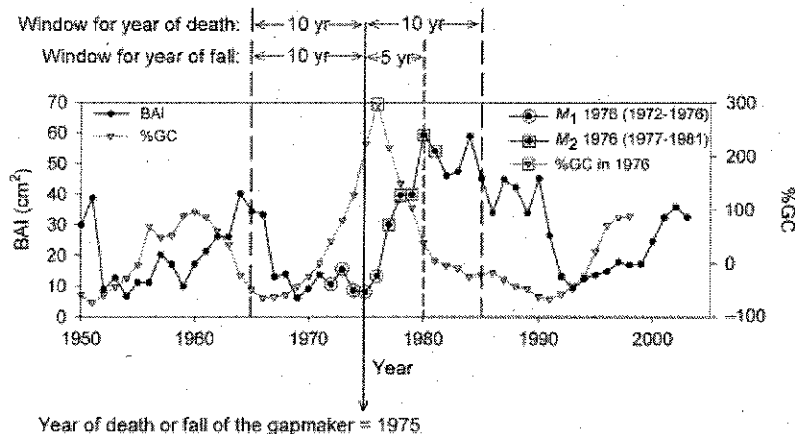
Fig. 2. Schematic of how we detected growth releases of trees that were growing around or within natural canopy gaps using the radial-growth averaging method. In this example, we identified a peak growth change value $\geq 25\%$ (our minimum threshold for a release), within a $\pm$ 10-year window surrounding 1975, the year of death of the gapmaker. The peak percentage growth change value, which occurred in 1976, represented the year prior to the onset of a release. We assumed the gap caused the release because of its proximity to the year of death of the gapmaker. For three gaps, we assessed releases of trees using a $-10/+5$-year window surrounding the year of fall of the gapmakers. See text for more detail. Additional notes: percentage growth change (%GC) in 1976 is equal to $(M_2-M_1)/M_1 \times 100$, where M_1 is the mean basal area increment (BAI) for the 5 years preceding 1976 (1972-1976), and M_2 is the mean BAI for the 5 years following 1976 (1977-1981) (Nowacki and Abrams 1997).

the duration of a release, we held M_1 for the year of the peak percentage growth change constant and shifted M_2 successively 1 year at a time (Fig. 2). We considered a release to have ended when percentage growth change decreased below the 25% threshold. Thus, the end of a release was defined as the last calendar year in M_2 when percentage growth change was still $\geq$ 25% (Fig. 2). Some releases were sustained, i.e. percentage growth change was $\geq$ 25% at the time of sampling and the end of the release was not observed.

We assessed the duration of releases using nonparametric and parametric survival functions (Kalbfleisch & Prentice 1980; Klein & Moeschberger 1997; Fox 2001). The survival function $S(t)$ is the probability that a release continues beyond time t, i.e. $\Pr(T > t)$, where T is a continuous random variable that represents the number of years from the onset to the end of a release (i.e. duration).

We estimated nonparametric survival functions (proc LIFETEST, SAS version 9.1.3) to determine the median duration of releases of individual species. We used the product-limit (Kaplan-Meier) estimate of the survival function (Kaplan & Meier 1958), which accounted for censored observations that resulted when a release continued beyond the date of sampling. This method estimates the survival function $S(t)$ as a product of t conditional observed survival probabilities:

$$S(t) = p_1 \times p_2 \times \ldots \times p_t$$

where $1, 2, \ldots, t$ are distinct times at which releases end and $p_i = (n_i - d_i)/n_i$ is the proportion of releases continuing through the ith year after they have continued for $i - 1$ years, where n_i is the number of releases at risk of ending at t_i (i.e. number of uncensored releases just prior to t_i) and d_i is the number of releases ending at t_i.

We used a parametric survival model (proc LIFEREG, SAS version 9.1.3) to assess the relative importance of tree-level and gap-level variables in predicting the duration of releases. The model was an accelerated failure time model in which the explanatory variables multiplicatively affected the failure time of a release or linearly affected the natural logarithm of a failure time, $\ln(T)$ (Kalbfleisch & Prentice 1980; Klein & Moeschberger 1997; Fox 2001). The model is of the form:

$$\ln(T) = X\beta + \sigma\varepsilon$$

where X is an $n \times p$ matrix of explanatory variables for n observations and p variables, β is a $p \times 1$ vector of unknown parameters, σ is a scale parameter and ε is a $n \times 1$ vector of random errors from a specified

survival distribution that is independent of X. In this study, we used a model in which T was defined as a Weibull distribution. This distribution is commonly used in survival analysis because it is flexible and appropriate for a range of monotonic survival functions (Kalbfleisch & Prentice 1980; Klein & Moeschberger 1997; Fox 2001).

In the model, we tested explanatory variables reported to be important in previous studies of tree growth relative to canopy gaps (e.g. Canham 1988a; Canham et al. 1990). Tree-level variables included species as a dummy variable, diameter in the year of a release (cm), prior growth (cm^2), distance from the centre of the gap (m) and an index of north-south tree position around or within the gap. Tree diameter in the year of a release was calculated by subtracting rings formed after a release to better represent diameter at coring height (inside bark) at the time of the event. Prior growth was mean basal area increment for the 5 years prior to the year of the peak percentage growth change value associated with the onset of the release. This variable was included because, in other studies, percentage growth change declined exponentially as prior growth increased (Black & Abrams 2003, 2004; Fraver & White 2005). The gap centre was the location of the root mound of the gapmaker. The north-south index was determined by calculating the cosine of the tree bearing relative to the gap centre. Gap-level variables included area of the expanded gap (m^2), an index of north-south hillslope aspect (i.e. cosine of aspect), percentage canopy openness and percentage hillslope gradient (Appendix S1). The expanded gap was defined by the boles of trees whose crowns delineated the opening in the canopy (Runkle 1982). Canopy openness was determined from hemispherical photographs taken with a Nikon F 35-mm camera equipped with a Nikkor 8-mm f/2.8 fisheye lens. At each gap, photos were taken 1 m above the forest floor within quadrats established relative to the gap centre and analysed using Gap Light Analyzer version 2.0 (Frazer et al. 1999). Results of the four photos were averaged to obtain a single value for canopy openness at each gap.

To determine which variables most influenced the duration of releases, we started with a model containing species, added additional tree-level variables then gap-level variables one at time, and tested for their significance. We tested the interaction of each continuous variable and species, along with the interaction of diameter and prior growth. Diameter and prior growth were transformed using the natural logarithm to improve model fit. All significant ($P < 0.05$) terms were kept in the model, where the

dummy variables for species or species by continuous variables were considered a single term.

Magnitude of releases

The magnitude of a release is the peak percentage growth change value associated with the onset of a release. We determined the mean magnitude of releases of individual species in different canopy classes. To assess the relative importance of tree-level and gap-level variables in predicting the magnitude of releases, we used a general linear model (proc GLM, SAS version 9.1.3), fitting in the same manner those variables used to assess the duration of releases. In addition to diameter and prior growth, percentage growth change was also transformed using the natural logarithm to improve model fit and normality of residuals.

Results

Number of trees and releases

There were 87 *T. plicata*, 180 *T. heterophylla* and 81 *A. amabilis* growing around or within the 20 gaps. *T. plicata* and *T. heterophylla* occurred in the greatest numbers in the canopy, while the sub-canopy was composed mostly of *T. heterophylla* and *A. amabilis*. Dbh (mean ± SE) was 141 ± 4.98, 62 ± 2.55 and 58 ± 3.52 cm for canopy *T. plicata*, *T. heterophylla* and *A. amabilis*, respectively. Dbh was 41 ± 1.45, 23 ± 0.85 and 18 ± 0.79 cm for subcanopy *T. plicata*, *T. heterophylla* and *A. amabilis*, respectively.

A total of 87% (304 of 348) of all trees from the 20 gaps experienced a release following the death or fall of the gapmakers. In addition, 39% (37 of 94) of all trees from the subset of six gaps experienced a release following both the death and fall of the gapmakers. For *T. heterophylla*, 53% (9 of 17) of

canopy trees and 38% (13 of 34) of subcanopy trees experienced a release following both the death and fall of the gapmakers (Table 2). For the other two species, 45% (13 of 29) of canopy *T. plicata* and 22% (2 of 9) of subcanopy *A. amabilis* experienced a release following both the death and fall of the gapmakers (Table 2).

Duration of releases

For *T. heterophylla*, *A. amabilis* and *T. plicata*, the median duration of releases ($S(t) = 0.5$) was approximately 37, 26 and 23 years, respectively (Fig. 3). There was a significant species×*log*diameter interaction (deviance = 6.11, $df = 2$, $P = 0.045$), indicating that the effect of diameter on the duration of releases varied among species. For *T. heterophylla*, increasing diameter resulted in decreasing duration of releases (slope = -0.664). *A. amabilis* also showed a pattern of decreasing duration of releases with increasing diameter (slope = -0.397). For *T. plicata*, the pattern was opposite, as increasing diameter resulted in increasing duration of releases (slope = 0.156). None of the other tree-level variables, gap-level variables or interactions tested were significant and were not retained in the model. Parameter estimates for the model of duration of releases are given in Appendix S2.

Magnitude of releases

All three species had variable growth rates both before and after releases (Fig. 4). *T. plicata* grew at an overall faster rate compared to *T. heterophylla* and *A. amabilis*. The magnitude of releases, when expressed as a percentage, was greatest for *T. heterophylla* and *A. amabilis* (Fig. 4). For canopy trees, mean growth change was 136% for *T. heterophylla* and 191% for *A. amabilis*. For subcanopy trees, mean growth change was 191% for *T. heterophylla* and 199% for *A. amabilis*. Maximum growth change

Table 2. Number of trees, by species and canopy class, from six gaps that experienced a release following the year of death only, the year of fall only or both the year of death and fall. The number of trees that did not experience a release is also given.

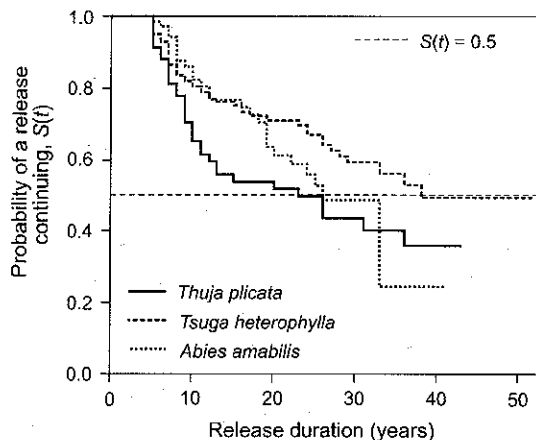| Species	Canopy class	n	Experienced a release following:			No release
			Year of death only	Year of fall only	Both year of death and fall	
Thuja plicata	Canopy	29	14	1	13	1
	Subcanopy	2	2	0	0	0
Tsuga heterophylla	Canopy	17	8	0	9	0
	Subcanopy	34	20	1	13	0
Abies amabilis	Canopy	3	3	0	0	0
	Subcanopy	9	5	1	2	1

Fig. 3. Duration of releases of *Thuja plicata*, *Tsuga heterophylla* and *Abies amabilis*. $S(t)$ is the probability that a release will continue beyond time t, having continued to time t. These survival functions are nonparametric product-limit (Kaplan-Meier) estimates.

was $>1000\%$ for *T. heterophylla* and $>800\%$ for *A. amabilis*. These findings differed from those of *T. plicata*, for which mean growth change was 83% and 98% for canopy and subcanopy trees, respectively, and maximum growth change was $>500\%$.

Based on the general linear model, the species×*log*diameter $(F = 3.42,$ $df = 2,$ $P = 0.034)$, species×*log*prior growth $(F = 3.16,$ $df = 2,$ $P = 0.044)$ and *log*diameter×*log*prior growth $(F = 10.81,$ $df = 1,$ $P = 0.001)$ interactions explained a significant amount of variation in the magnitude of releases. None of the other tree-level variables, gap-level variables or interactions tested were significant and were not retained in the model.

There was a pattern of decreasing percentage growth change with increasing diameter and increasing prior growth (Fig. 5). As shown by the *log*diameter×*log*prior growth interaction, the effect of prior growth varied significantly among trees of different diameters. The derived general linear model indicated that for the largest diameter *T. heterophylla* trees, prior growth had a minimal effect on percentage growth change. However, for the largest diameter *A. amabilis* and *T. plicata* trees, prior growth had a moderate effect, with higher values of prior growth resulting in lower values of percentage growth change. For the smallest diameter trees of all species, prior growth had a more substantial effect, with higher values of prior growth resulting in lower values of percentage growth change, particularly for *A. amabilis*. Parameter estimates for the model of magnitude of releases are given in Appendix S3.

Discussion

Number, duration and magnitude of releases

Thuja plicata, *T. heterophylla* and *A. amabilis* are responsive to gap formation. A high number of individuals of all three species experienced a release following the death or fall of the gapmakers. These findings are consistent with those of Daniels & Klinka (1996) who reported similar, positive responses of canopy and subcanopy *T. plicata*, *T. heterophylla* and *A. amabilis* following gap formation in old-growth stands within our study area. Moreover, canopy and subcanopy individuals of several other species have been found to exhibit positive growth responses following gap formation (Poage & Peart 1993; Pedersen & Howard 2004), with the most shade-tolerant species experiencing the most intensive responses (Jones et al. 2009). In the present study, secondary growth releases of *T. plicata*, *T. heterophylla* and *A. amabilis* after the fall of gapmakers further demonstrate the strong responses of highly shade-tolerant species following gap formation. We suspect these releases are the result of an increase in light. In gaps of similar size, at similar latitude, Battles & Fahey (2000) estimated that standing dead trees blocked as much as 10% of the transmitted radiation in gaps during the growing season.

The median duration of releases and the effect of diameter on the duration of releases differed among *T. plicata*, *T. heterophylla* and *A. amabilis*. These differences imply that the composition and structure of trees growing around and within a gap at the time of its formation have an important influence on its closure rate. For example, our findings suggest that a fine-scale gap with several large *T. plicata* boundary trees and many small *T. heterophylla* and *A. amabilis* within-gap trees at the time of formation may close more quickly than a similar size gap with several large *T. heterophylla* and *A. amabilis* boundary trees and many small *T. plicata* within-gap trees at the time of formation. Of course, this scenario simplifies the complex interactions among release durations, release magnitudes and a suite of other species life-history traits that influence rates of gap closure. Also, the expansion of gaps following the death of boundary trees and local topographic and edaphic conditions influence rates of gap closure. Furthermore, our data do not address lateral branch extension of boundary trees or height growth of within-gap trees, both of which are primary mechanisms by which gaps close (Runkle 1985).

While the mean magnitude of releases varied among canopy and subcanopy *T. plicata*, *T. heterophylla* and *A. amabilis*, for all three species, the
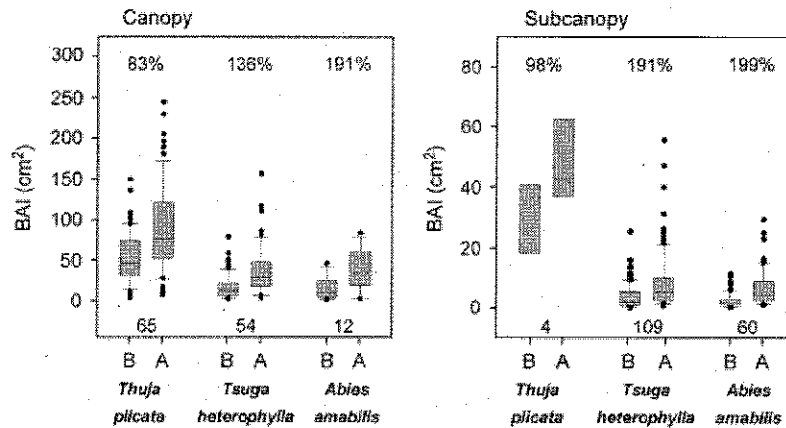
Fig. 4. Box plots of the mean basal area increment (BAI) 5 years before (B) and after (A) a release for canopy and subcanopy *Thuja plicata*, *Tsuga heterophylla* and *Abies amabilis*. Values at the top and bottom of the plots are mean percentage growth change and sample size, respectively. The horizontal line in each box is the median, the lower and upper limits of each box are the 25th and 75th percentiles, respectively, the lower and upper lines are the 5th and 95th percentiles, respectively, and the circles are outliers.
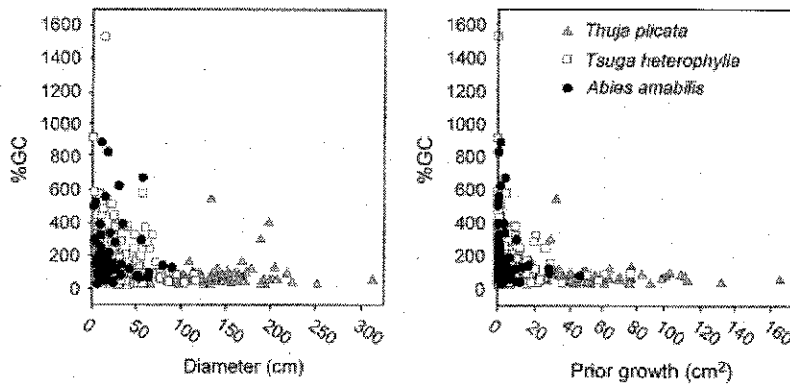

Fig. 5. Plots of percentage growth change (%GC) with respect to diameter and prior growth for *Thuja plicata*, *Tsuga heterophylla* and *Abies amabilis*.

slowest growing and smallest individuals had the most intensive releases following gap formation. Prior growth has been shown to have a strong effect on the magnitude of releases of several species, with the slowest growing individuals experiencing the most intensive releases (Black & Abrams 2003, 2004; Fraver & White 2005). Small trees, particularly those that are highly shade tolerant, tend to undergo slow growth because of shading or competition for belowground resources. Consequently, many of these individuals possess a strong capacity to increase their growth following canopy disturbances. Similar to the present study, greater magnitude growth responses of slower-growing, smaller-diameter trees versus faster-growing, larger-diameter trees have been directly observed for several other species following gap

formation (Jones et al. 2009). Furthermore, other studies have reported greater magnitude growth responses of smaller- versus larger-diameter trees following gap formation (Pedersen & Howard 2004) or a reduction of competition in general (Canham et al. 2004). In these studies, prior growth was not assessed, but may have been a factor influencing the growth responses of trees.

The lack of a statistically significant influence of many of our tree-level and gap-level variables on the magnitude and duration of releases merits discussion. This finding may reflect low variability among the characteristics of the study trees and gaps (see Appendix S1). For example, our data showed a trend of decreasing duration and magnitude of releases with increasing tree distance from the gap centre.

Ongoing research on growth releases of trees grow-ing along north-south transects that pass through the study gaps and into the adjacent forest has addressed this trend in more detail (Stan 2008). However, to further address gap-level characteristics, future re-search that incorporates gaps of a broader range of sizes, shapes and orientations is needed.

Gap dynamics and species coexistence

Various mechanisms, including differences in life-history traits, environmental heterogeneity fa-cilitated by recent and ancient disturbances and competition between neighbours, can act alone or together to promote the coexistence of tree species (Chesson 2000; Loehle 2000; Nakashizuka 2001; Nishimura et al. 2005). Chance events and neutral processes can also play a role in structuring patterns of tree diversity (Brokaw & Busing 2000; Hubbell 2001), but might be more important in species-rich communities (Nakashizuka 2001; Gravel et al. 2006).

In forests where fine-scale tree mortality and canopy gaps dominate the disturbance regime, dif-fering strategies among tree species for ascending to the canopy strata may be an important coexistence mechanism. For shade-tolerant trees, Canham (1988b, 1989, 1990) described two extremes in stra-tegies for reaching the canopy strata. At one end of the continuum, trees reach the canopy strata through continuous slow growth in more shaded conditions. These trees can be considered gap in-dependent because, by definition, they likely do not rely on gaps to reach the canopy. At the other end of the continuum, trees reach the canopy strata through multiple periods of suppressions and re-leases as a result of canopy gaps. These trees can be considered gap dependent because they likely re-quire gaps to reach the canopy.

In previous work on the influences of dis-turbance in old-growth stands within our study area, Daniels (2003) concluded that *T. plicata* was gap independent and *T. heterophylla* and *A. amabilis* were gap dependent. Our results do not support *T. plicata* as entirely gap independent because a si-milar number of *T. plicata*, *T. heterophylla* and *A. amabilis* experienced a release following gap for-mation. However, variation in the duration and magnitude of releases among *T. plicata*, *T. hetero-phylla* and *A. amabilis* does indicate subtle, but biologically relevant, differences in how these spe-cies respond to gaps, suggesting possible differences in how they grow into the canopy strata.

Tsuga heterophylla and *A. amabilis* were often extremely suppressed both in the canopy and sub-canopy, which gave them a tremendous capacity to experience a release following gap formation (Black & Abrams 2003, 2004; Fraver & White 2005). For both species, releases were intensive, with magnitudes > 1000% for *T. heterophylla* and > 800% for *A. am-abilis*. Releases were also persistent, with durations slightly longer for *T. heterophylla* than for *A. am-abilis*. These observations are consistent with independent research on population size structures and growth histories of the study species in the un-derstoreys of old-growth stands. Specifically, *T. heterophylla* and *A. amabilis* maintain a seedling and sapling bank of individuals available to experi-ence a release if or when a gap forms (Lertzman 1992; Antos et al. 2005; Parish & Antos 2006), and both species are able to undergo multiple suppressions and releases before reaching the canopy (Daniels & Klin-ka 1996; Wright et al. 2000; Passmore 2007). Taken together, these characteristics distinguish *T. hetero-phylla* and *A. amabilis* as gap-dependent species.

In contrast, *T. plicata* had high absolute growth rates both in the canopy and subcanopy, and there-fore, had less capacity to experience releases as intensive as those of *T. heterophylla* and *A. amabilis*. Releases of low magnitude and short duration were most common for *T. plicata*, which partly reflected its large size in the study stands. Low-intensity growth releases of *T. plicata* also indicate physiolo-gical differences in growth rates and responses to gaps compared to *T. heterophylla* and *A. amabilis*. High growth rates of subcanopy *T. plicata* prior to gap formation suggest that gaps are less important for this species to reach the canopy strata. Yet, a high number of *T. plicata* experienced a release following gap formation, even large canopy domi-nants. This finding implies complex tree interactions mediated by gaps, including competition for light and other limiting resources. To better understand the role of gaps for canopy ascendancy and growth of *T. plicata* will require additional research that specifically focuses on subcanopy individuals, which are lacking because of the population size structures in the study stands. Until more information is col-lected, it is difficult to place *T. plicata* along the continuum of gap-independent to gap-dependent species.

Differing strategy for ascending to the canopy strata among *T. plicata*, *T. heterophylla* and *A. am-abilis* is one of several mechanisms that may facilitate the coexistence of these species in old-growth forests of coastal British Columbia. Given the large dis-crepancy in potential lifespan among the study species, hypotheses related to longevity and canopy residence time also need to be considered. Specifically,

T. plicata lives much longer than *T. heterophylla* or *A. amabilis*, and this life-history trait might play a crucial role in maintaining a seed source for when conditions are most favourable for *T. plicata* to grow into the canopy strata (Lertzman 1992; Lusk & Smith 1998; Parish & Antos 2006; Mori et al. 2007). Competitive interactions among tree species might also be important. For mature and old-growth forests of northern, interior British Columbia, Canham et al. (2004) reported that crowding by *T. heterophylla* had a strong effect on the radial growth of *T. plicata*, but crowding by *T. plicata* had a weak effect on the radial growth of *T. heterophylla*. Lack of equivalence of interspecific effects of competition, and any possible impacts on coexistence, is worth exploring in forests of coastal British Columbia.

Conclusions

Our research provides detailed information on the number, duration and magnitude of growth releases of *T. plicata*, *T. heterophylla* and *A. amabilis* following the formation of fine-scale canopy gaps in old-growth forests of coastal British Columbia. In addition to a better understanding of the tree-level and gap-level variables that influence the duration and magnitude of releases, our research offers insight into mechanisms of tree species coexistence in these forests. Results indicate differences in how *T. plicata*, *T. heterophylla* and *A. amabilis* grow and respond to canopy gaps, suggesting differences in how these species ascend to the canopy strata. Specifically, gaps may be more important for *T. heterophylla* and *A. amabilis* to reach the canopy and less important for *T. plicata* to reach the canopy. Different strategies for ascending to the canopy strata among *T. plicata*, *T. heterophylla* and *A. amabilis* may facilitate the coexistence of these species in old-growth forests of coastal British Columbia. Additional research on growth responses to gaps over the lifespan of individual trees, as well as research on other life-history traits, is needed to further improve our understanding of the coexistence of these species through time.

References

Anon. (Acres International Limited) 1999. Annex to the Analysis Report, Watershed Management Plan #5, Volumes I-III. Greater Vancouver Regional District Watershed Ecological Inventory Program, Burnaby, BC, CA.

Antos, J.A., Guest, H.J. & Parish, R. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *Journal of Ecology* 93: 536–543.

Battles, J.J. & Fahey, T.J. 2000. Gap dynamics following forest decline: a case study of red spruce forests. *Ecological Applications* 10: 760–774.

Black, B.A. & Abrams, M.D. 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications* 13: 1733–1749.

Black, B.A. & Abrams, M.D. 2004. Development and application of boundary-line release criteria. *Dendrochronologia* 22: 31–42.

Brokaw, N. & Busing, R.T. 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15: 183–188.

Canham, C.D. 1988a. An index for understory light levels in and around canopy gaps. *Ecology* 69: 1634–1638.

Canham, C.D. 1988b. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69: 786–795.

Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70: 548–550.

Canham, C.D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club* 117: 1–7.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20: 620–631.

Canham, C.D., LePage, P.T. & Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34: 778–787.

Cherubini, P., Fontana, G., Rigling, D., Dobbertin, M., Brang, P. & Innes, J.L. 2002. Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently. *Journal of Ecology* 90: 839–850.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.

Dahir, S.E. & Lorimer, C.G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research* 26: 1875–1892.

Daniels, L.D. 2003. Western redcedar population dynamics in old-growth forests: contrasting ecological paradigms using tree rings. *Forestry Chronicle* 79: 517–530.

Daniels, L.D. & Klinka, K. 1996. The dynamics of old-growth *Thuja–Tsuga* forests near Vancouver, British Columbia. In: Dean, J.S., Meko, D.M. & Swetnam, T.W. (eds.) *Tree rings, environment, and humanity*. pp. 379–393. Radiocarbon, Tucson, AZ, US.

Daniels, L.D., Dobry, J., Klinka, K. & Feller, M.C. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. *Canadian Journal of Forest Research* 27: 1132–1141.

Dynesius, M. & Jonsson, B.G. 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. *Canadian Journal of Forest Research* 21: 655–665.

Fox, G.A. 2001. Failure-time analysis: studying times to events and rates at which events occur. In: Scheiner, S.M. & Gurevitch, J. (eds.) *Design and analysis of ecological experiments*. pp. 235–266. Oxford University Press, New York, NY, US.

Fraver, S. & White, A.S. 2005. Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research* 35: 1648–1656.

Frazer, G.W., Canham, C.D. & Lertzman, K.P. 1999. Gap light analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Simon Fraser University, Burnaby, BC, CA and Institute of Ecosystem Studies, Millbrook, New York, US.

Frelich, L.E. 2002. *Forest dynamics and disturbance regimes: studies from temperate evergreen–deciduous forests*. Cambridge University Press, Cambridge, UK.

Frelich, L.E. & Lorimer, C.G. 1991. Natural disturbance regimes in hemlock–hardwood forests of the upper Great Lakes region. *Ecological Monographs* 61: 145–164.

Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, New York, NY, US.

Glitzenstein, J.S., Harcombe, P.A. & Streng, D.R. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecological Monographs* 56: 243–258.

Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9: 399–409.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57: 205–221.

Gutiérrez, A.G., Armesto, J.J. & Aravena, J. 2004. Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *Journal of Ecology* 92: 598–608.

Henry, J.D. & Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772–783.

Hitchcock, C.L. & Cronquist, A. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA, US.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43: 69–78.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, US.

Ishikawa, Y., Krestov, P.V. & Namikawa, K. 1999. Disturbance history and tree establishment in old-growth *Pinus koraiensis*–hardwood forests in the Russian Far East. *Journal of Vegetation Science* 10: 439–448.

Jones, T.A., Domke, G.M. & Thomas, S.C. 2009. Canopy tree growth responses following selection harvest in seven species varying in shade tolerance. *Canadian Journal of Forest Research* 39: 430–440.

Kalbfleisch, J.D. & Prentice, R.L. 1980. *The statistical analysis of failure time data*. John Wiley and Sons, New York, NY, US.

Kaplan, E.L. & Meier, P. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53: 457–481.

Klein, J.P. & Moeschberger, M.L. 1997. *Survival analysis: techniques for censored and truncated data*. Springer-Verlag, New York, NY, US.

Lertzman, K.P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology* 73: 657–669.

Lertzman, K.P., Sutherland, G.D., Inselberg, A. & Saunders, S.C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77: 1254–1270.

Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *The American Naturalist* 156: 14–33.

Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61: 1169–1184.

Lorimer, C.G. & Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19: 651–663.

Lusk, C.H. & Smith, B. 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* 79: 795–806.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T. & Martin, R.E. 1979. Dead and down woody material. In: Thomas, J.W. (ed.) *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*. pp. 78–95. Agriculture Handbook 553, USDA Forest Service, Washington, DC, US.

Mast, J.N. & Veblen, T.T. 1994. A dendrochronological method of studying tree mortality patterns. *Physical Geography* 15: 529–542.

Meidinger, D.V. & Pojar, J. (eds.) 1991. *Ecosystems of British Columbia.* Special Report Series 6. British Columbia Ministry of Forests, Victoria, BC, CA.

Mori, A.S., Mizumachi, E. & Komiyama, A. 2007. Roles of disturbance and demographic non-equilibrium in species coexistence, inferred from 25-year dynamics of a late-successional old-growth subalpine forest. *Forest Ecology and Management* 241: 74–83.

Nakashizuka, T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology and Evolution* 16: 205–210.

Nishimura, N., Hara, T., Kawatani, M., Hoshino, D. & Yamamoto, S. 2005. Promotion of species co-existence in old-growth coniferous forest through interplay of life-history strategy and tree competition. *Journal of Vegetation Science* 16: 549–558.

Nowacki, G.J. & Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67: 225–249.

Orwig, D.A. & Abrams, M.D. 1994. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap-obligate versus gap-facultative tree species. *Canadian Journal of forest Research* 24: 2141–2149.

Parish, R. & Antos, J.A. 2006. Slow growth, long-lived trees, and minimal disturbance characterize the dynamics of an ancient, montane forest in coastal British Columbia. *Canadian Journal of Forest Research* 36: 2826–2838.

Passmore, J.A. 2007. Response of seedlings and saplings to canopy gaps in coastal old-growth forests. M.R.M. Thesis, Simon Fraser University, Burnaby, BC, CA.

Pedersen, B.S. & Howard, J.L. 2004. The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. *Forest Ecology and Management* 196: 351–366.

Poage, N.J. & Peart, D.R. 1993. The radial growth response of American beech (*Fagus grandifolia*) to small canopy gaps in a northern hardwood forest. *Bulletin of the Torrey Botanical Club* 120: 45–48.

Rozas, V. 2003. Regeneration patterns, dendroecology, and forest-use history in an old-growth beech–oak lowland forest in Northern Spain. *Forest Ecology and Management* 182: 175–194.

Rubino, D.L. & McCarthy, B.C. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21: 97–115.

Ruffner, C.M. & Abrams, M.D. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Canadian Journal of Forest Research* 28: 347–358.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533–1546.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics.* pp. 17–33. Academic Press, New York, NY, US.

Stan, A.B. 2008. Growth release of trees following fine-scale canopy disturbances in old-growth forests of coastal British Columbia, Canada. Ph.D. Thesis, University of British Columbia, Vancouver, BC, CA.

Stokes, M.A. & Smiley, T.L. 1968. *An introduction to tree-ring dating.* University of Chicago Press, Chicago, IL, US.

Storaunet, K.O. & Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. *Canadian Journal of Forest Research* 32: 1801–1812.

Taylor, A.H., Jang, S.W., Zhao, L.J., Liang, C.P., Miao, C.J. & Huang, J. 2006. Regeneration patterns and tree species coexistence in old-growth *Abies–Picea* forests in southwestern China. *Forest Ecology and Management* 223: 303–317.

Valentine, K.W.G., Sprout, P.N., Baker, T.E. & Lavkulich, L.M. (eds.) 1978. *The soil landscapes of British Columbia.* British Columbia Ministry of the Environment, Victoria, BC, CA.

Wang, T., Hamann, A., Spittlehouse, D.L. & Aitken, S.N. 2006. Development of scale-free climate data for western Canada for use in resource management. *International Journal of Climatology* 26: 383–397.

Wells, R.W., Lertzman, K.P. & Saunders, S.C. 1998. Old-growth definitions for the forests of British Columbia, Canada. *Natural Areas Journal* 18: 279–292.

Wright, E.F., Canham, C.D. & Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Canadian Journal of Forest Research* 30: 1571–1580.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21: 414–416.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Characteristics of the 20 study gaps and the number of *Thuja plicata, Tsuga heterophylla* and *Abies amabilis* growing around or within the gaps ($n = 348$).

Appendix S2. Parameter estimates for the Weibull survival model of duration of releases. Estimates are for levels of a given variable included in the model. Note: *P*-values for species or for spe-

cies by continuous variable interactions should be interpreted for all species combined and were given in the text.

Appendix S3. Parameter estimates for the general linear model of magnitude of releases. Estimates are for levels of a given variable included in the model. Note: *P*-values for species or for species by continuous variable interactions should be interpreted for all species combined and were given in the text.

Figure S1. A natural, fine-scale canopy gap formed by an uprooted *Thuja plicata* in an old-growth, *Thuja plicata–Tsuga heterophylla* stand, coastal British Columbia, Canada (photo by A.B. Stan).

Figure S2. A structurally complex, old-growth *Thuja plicata–Tsuga heterophylla* stand commonly found in unmanaged, mid-elevation forests of coastal British Columbia, Canada (photo by A.B. Stan).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.