Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia

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Abstract: Saplings of canopy tree species frequently undergo alternating periods of suppression and release before reaching canopy size. In this study, we document the effects of periods of suppression and release on current responses to variation in light by saplings of the 11 major tree species of northwestern, interior British Columbia. We were specifically interested in the degree to which increasing length of suppression had long-term effects on subsequent response to release in gaps or following partial cutting, and the degree to which the effects of suppression were ameliorated with time following release. At least some saplings of all 11 species had undergone alternating periods of suppression and release. The most shade-tolerant species generally did not show either a decline in growth over time during suppression or a gradual increase in growth at a given light level over time during release. The least shade-tolerant species exhibited significant declines in growth rate during suppression; however, in all of the species except trembling aspen (*Populus tremuloides* Michx.), the effects of suppression disappeared over time during release. Failure to account for the effects of past suppression and release leads to significant overestimates of the initial responses of shade-intolerant species to release. Our results suggest that competitive balances between species shift substantially over time as a result of growth history and that these shifts have significant effects on successional patterns.

Résumé : Les gaules des essences qui forment le couvert subissent fréquemment une alternance de périodes de suppression et de dégagement avant d'atteindre leur dimension finale. Dans cette étude, nous avons observé les effets de périodes de suppression et de dégagement sur la réaction courante à une variation de la lumière chez les gaules des 11 principales espèces d'arbres du nord-ouest de la zone intérieure de la Colombie-Britannique. Nous étions plus particulièrement intéressés à déterminer dans quelle mesure l'augmentation de la durée de la période de suppression a des effets à long terme sur la réaction subséquente à un dégagement dans les trouées ou suite à une coupe partielle et dans quelle mesure les effets d'une période de suppression sont compensés avec le temps suite à un dégagement. Au moins quelques gaules de toutes les espèces avaient subi une alternance de périodes de suppression et de dégagement. Les espèces les plus tolérantes n'ont généralement subi ni de diminution de croissance en fonction du temps en période de suppression, ni une augmentation graduelle de croissance en fonction du temps à un niveau donné de lumière en prériode de dégagement. Les espèces les moins tolérantes ont connu une diminution significative de leur taux de croissance en période de suppression; cependant, chez toutes les espèces à l'exception du peuplier faux-tremble (*Populus tremuloides* Michx.), les effets de la suppression ont disparu avec le temps suite au dégagement. Le fait de ne pas tenir compte des effets de périodes passées de suppression et de dégagement entraîne une surestimation importante de la réaction initiale à un dégagement chez les espèces intolérantes. Nos résultats suggèrent que l'équilibre compétitif entre les espèces change de façon importante avec le temps selon l'historique de croissance et que ces changements ont des effets majeurs sur les patrons successionnels.

[Traduit par la Rédaction]

Introduction

An understanding of patterns of sapling growth and mortality is fundamental to predicting forest successional dynamics (Pacala et al. 1994; Kobe 1996; Kobe and Coates 1997; Wright et al. 1998) and for prediction of forest regeneration in managed stands after partial or complete release of advance regeneration (e.g., Crossley 1976; Herring 1977; Herring and McMinn 1980; McCaughey and Ferguson 1986). There has been a great deal of study of the role of advance regeneration in gap-phase dynamics of temperate and tropical forests (e.g., Runkle 1981; Hibbs 1982; Canham 1988; Lertzman 1992; Kneeshaw and Bergeron 1998). There has also been a long-term debate in forestry over the management of advance regeneration following cutting (Pogue 1946; Gordon 1973; Crossley 1976; Herring 1977; Ferguson and Adams 1980; Herring and McMinn 1980; Graham 1982; Oliver 1985; Seidel 1985; Laackie and Fiddler 1986; McCaughey and Ferguson 1986; Carlson and Schmidt 1989; Bassman et al. 1992; Tesch and Korpela 1993). Saplings of different tree species clearly have different abilities to sur-

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Table 1. Characteristics of the data set: sample size (*n*), shade-tolerance ranking (low, medium, high), the range of latitude and elevation, the mean and range (in parentheses) of DBH, sapling height, and average light level from which saplings were collected for each of the 11 study species.

Tree species	*n*	Tolerance ranking*	Latitude (N)	Elevation (m)	DBH (cm)	Height (m)	Light level (% full sun)
Western redcedar	57	High	54°40′–55°30′	320–480	4.2 (0.4–10.3)	3.45 (1.00–7.50)	32.8
Western hemlock	278	High	54°40′–57°08′	290–1255	3.9 (0.2–10.6)	3.49 (1.00–7.80)	38.3
Mountain hemlock	103	High	54°40′–55°25′	520–1255	4.2 (0.3–11.6)	3.07 (0.80–7.90)	45.0
Amabilis fir	128	High	54°40′–55°30′	100–1200	4.2 (0.4–11.8)	2.8 (0.03–8.40)	44.5
Subalpine fir	679	High	54°01′–59°03′	320–1380	3.9 (0.3–16.5)	2.87 (0.60–10.50)	42.3
Black spruce	58	Medium	59°39′–59°37′	700–925	3.6 (0.6–6.9)	3.62 (1.10–7.60)	47.5
Hybrid spruce	674	Medium	54°01′–59°57′	130–1370	3.9 (0.1–13.3)	3.07 (0.50–9.20)	42.2
Lodgepole pine	434	Low	54°01′–59°57′	130–1450	4.2 (0.5–14.6)	3.33 (0.40–9.70)	50.8
Trembling aspen	68	Low	54°40′–55°30′	260–700	4.7 (0.0–10.3)	6.4 (2.30–10.70)	42.0
Cottonwood	52	Low	54°40′–55°30′	600–850	5.0 (0.5–12.1)	5.78 (1.10–12.00)	48.8
Paper birch	73	Low	54°40′–55°30′	260–700	4.3 (0.8–11.7)	5.66 (2.10–9.00)	44.3

*Estimates are from Krajina et al. (1982), Burns and Honkala (1990), and Kobe and Coates (1997).

vive periods of suppression (Kobe 1996; Kobe and Coates 1997) and different magnitudes of response to release (McCaughey and Ferguson 1986). In forests where gap-phase dynamics represent the dominant mode of canopy recruitment, individuals of shade-tolerant species typically undergo multiple episodes of suppression and release before reaching canopy size (Canham 1985, 1990; Merrens and Peart 1992; Rebertus and Veblen 1993; Orwig and Abrams 1994; Cho and Boerner 1995). Attributes such as sapling age, size, crown area and geometry, presence of injuries, and pathogens have been used to help predict sapling growth after release (e.g., Herring 1977; Ferguson and Adams 1980; Seidel 1980, Graham 1982; McCaughey and Schmidt 1982; Oliver 1985; Laackie and Fiddler 1986; McCaughey and Ferguson 1986; Canham 1988, Tesch and Korpela 1993). However, there have been no systematic studies of whether, and to what extent, previous periods of suppression or release have long-term effects on the growth of advance regeneration.

In this study, we examined the effects of the lengths of previous periods of suppression and release on the growth responses of eight conifers and three broadleaved tree species of northwestern, interior British Columbia. The 11 species ranged from very shade tolerant to shade intolerant and represent the dominant species of early to late-successional stands throughout the region. We were specifically interested in the degree to which increasing length of suppression had long-term effects on subsequent response to release in gaps or following partial cutting, and the degree to which the effects of previous periods of suppression were ameliorated with time following release.

Materials and methods

Study area and tree species

Data were collected for 11 tree species in study sites throughout the Prince Rupert Forest Region, located in central to northwestern British Columbia, Canada (Table 1). The 11 species include all the dominant and codominant species found in early to late-successional stands in this region (Banner et al. 1993). The species span a range of shade tolerance (Krajina et al. 1982; Burns and Honkala 1990; Carter and Klinka 1992; Klinka et al. 1992; Wang et al. 1994; Kayahara et al. 1996; Kobe and Coates 1997). Amabilis fir (*Abies amabilis* Dougl. ex Forbes), western redcedar (*Thuja plicata* (Dougl. ex D Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are considered shade tolerant. Black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) are intermediate in shade tolerance. Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray) are considered shade intolerant.

The forests of British Columbia have been classified into a system of biogeoclimatic zones, subzones, and variants (Pojar et al. 1987, Meidinger and Pojar 1991, Banner et al. 1993). We sampled within the five major forest zones of interior, northern British Columbia, and from one to three subzones within each zone, with from two to eight species sampled within a subzone (Table 1). Within each subzone, we sampled on sites with average soil moisture and nutrients in mature stands, canopy gaps, regenerating burns and associated mature remnants, road and trail cuts greater than 30 years old, and in partially cut and clear-cut areas. Areas with disturbance within the last 5 years (e.g., blowdown, insect related dieback, and new road cuts) were carefully avoided. A detailed analysis of geographic variation in sapling growth (without consideration of the effects of suppression and release) is presented elsewhere (Wright et al. 1998). For this paper, we present results from all subzones pooled (to increase sample size and statistical power, accepting that response as a function of light will be more variable for pooled data versus that of the representative subzone) and from one representative subzone, the moist, cool variant of the interior cedar–hemlock forests (ICHmc2), for which we have the largest number of species represented (nine). For our pooled data set we break the spruces into two groups: (*i*) black spruce from our boreal sampling and (*ii*) hybrid spruce, which includes any of the various mixtures of white, Sitka, and Engelmann spruce from within our sampling ar-

Table 2. Radial growth thresholds (mm radial growth/year) and corresponding light levels used to define periods of suppression versus release.

Tree species	Radial growth threshold (mm/year)	Light level (% of full sun)
Western redcedar	0.25	6
Western hemlock	0.3	5
Mountain hemlock	0.3	5
Amabilis fir	0.3	8
Subalpine fir	0.3	8
Black spruce	0.45	15
Hybrid spruce	0.6	12
Lodgepole pine	0.9	28
Trembling aspen	1.25	20
Cottonwood	1.6	27
Paper birch	1.8	37

Note: Periods of suppression were defined as periods with at least four or more consecutive years of growth below the threshold, without three or more consecutive years of growth exceeding the threshold. The growth rate associated with a sapling mortality of 10% over a 3-year period (Kobe and Coates 1997) was used as the threshold for each species. Also reported are the approximate light levels associated with that growth rate, from relationships in Wright et al. (1998).

eas. The complex nature of spruce hybridization in northwestern British Columbia is described in Coates et al. (1994). In our representative ICHmc2 subzone, white and Sitka spruce hybridize commonly.

Sampling design and measurements

Naturally regenerated saplings were obtained from a range of height classes (0.5–12.0 m) across the full range of light levels found within forests in this region (<5 to >90%). Sample sizes for a given species ranged from 52 to 679 saplings, depending on the number of forest types within which saplings were collected (Table 1). Sapling sizes were uniformly distributed across light levels for each species and climatic region. Where saplings occurred in clusters, the dominant individuals were selected to provide us with an estimate of optimum growth for that light level. Sampling took place at the end of the summer in 1995 and throughout the field season in 1996. For each sapling, total height and diameter at 1.3 m (diameter at breast height, DBH) were recorded, and a section of the stem was removed at 10 cm above the root collar for measurement of radial growth. Except for trembling aspen, a species that regenerates primarily by root suckers in our study area (Haeussler et al. 1990), all sample trees were of seed origin.

Annual ring widths were measured along a representative radius (the radius bisecting the angle formed by the longest and shortest radii of the cross section). Ring widths were measured with a digital ring analyzer to 0.025 mm resolution using a high-resolution colour video camera connected to a 40× stereoscope. The most recent growth ring was discarded for saplings obtained in 1996 because of incomplete radial growth.

Light

Hemispherical canopy photos were taken at 1–1.5 m above the stump of each cut sapling to quantify light available for growth over the growing season. Saplings were selected so that overstory canopy trees, rather than adjacent saplings, provided shading. In addition, sample trees were only obtained from areas where coniferous species dominated the canopy trees. GLI, an index of growing season light availability, was computed from each photograph (using GLI version 2.0 software) following Canham (1988). This index combines the seasonal distribution of sky brightness with the distribution of canopy openness to calculate a single index of available light in units in percentage of full sun for a specified growing season (mid-April through mid-September) (Canham et al. 1990).

Characterization of patterns of suppression and release

We considered suppression to be periods with at least four or more consecutive years of growth below a species-specific threshold, without three or more consecutive years exceeding the threshold (Canham 1985, 1990). The thresholds for each species were determined on the basis of functional relationships between growth and mortality, using the results of a recent study of 9 of the 11 tree species sampled in the same geographic location (Kobe and Coates 1997). Specifically, the growth rate associated with a sapling mortality rate of 10% over a 3-year period (Table 2) was chosen as the threshold, because it coincided with a steep inflection in the probability of mortality as a function of recent growth (Kobe and Coates 1997). Growth rates below the threshold resulted in sharply increasing mortality rates. Black spruce is considered intermediate in tolerance between subalpine fir and hybrid spruce (Krajina et al. 1982), and a threshold for black spruce using the difference between these two species was used in lieu of direct mortality data. The threshold for amabilis fir was set at the threshold for subalpine fir. Because of differences in the shade tolerance of the 11 species, the estimated light levels associated with the threshold between suppression and release ranged from 5 to 37% of full sun. In effect, the shade-intolerant species become suppressed at much higher light levels than the shade-tolerant species (Table 2).

On the basis of this definition, we calculated the total number of years of suppression and release, the number of distinct periods of suppression and release, and the length of the most recent (or current) period of suppression and release for each sapling. The individual patterns of suppression and release varied enormously among saplings and species. In a preliminary analysis, all independent variables were evaluated for use as predictive variables. The best fits were obtained using length of the most recent (or current) period of suppression and release. While it is possible that the entire sequence of past suppression and release events may affect current growth, we have concentrated our analysis on the effects of the most recent periods of suppression and release because of the very large number of permutations required to incorporate the entire growth history in the models outlined below.

Data analysis

The basic analysis of variation in growth as a function of light is presented elsewhere (Wright et al. 1998). That analysis examined a number of different functional relationships between light and growth (including Michaelis–Menten, Chapman–Richards, and Weibull functions, with and without

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Table 3. Radial growth patterns of suppression and release (mean and range), by species, across all sites.

Tree species	Age (years)	No. of periods of suppression	No. of years of suppression	No. of periods of release	No. of years of release	Length of last suppression (years)	Length of last release (years)
Western redcedar	31.08 (7–57)	0.34 (0–2)	3.81 (0–23)	1.10 (1–2)	27.27 (7–45)	3.56 (0–22)	26.46 (5–45)
Western hemlock	36.38 (5–155)	0.68 (0–5)	10.95 (0–88)	1.28 (1–5)	25.43 (3–89)	7.29 (0–70)	22.20 (3–82)
Mountain hemlock	53.39 (9–179)	1.07 (0–4)	20.20 (0–120)	1.44 (1–4)	33.18 (3–104)	10.14 (0–69)	26.83 (3–104)
Amabilis fir	49.72 (6–151)	0.99 (0–3)	32.27 (0–123)	1.19 (0–4)	17.45 (0–74)	26.98 (0–103)	14.81 (0–69)
Subalpine fir	47.00 (6–225)	0.89 (0–6)	19.24 (0–160)	1.36 (0–6)	27.75 (0–99)	12.84 (0–146)	23.79 (0–95)
Black spruce	41.84 (15–93)	0.95 (0–2)	25.29 (0–78)	1.02 (0–2)	16.55 (0–36)	23.12 (0–78)	15.83 (0–36)
Hybrid spruce	34.86 (8–161)	0.85 (0–5)	21.65 (0–141)	0.94 (0–5)	13.20 (0–58)	18.83 (0–141)	12.09 (0–58)
Lodgepole pine	22.78 (6–77)	0.72 (0–2)	15.00 (0–77)	0.68 (0–2)	7.78 (0–27)	14.48 (0–77)	7.63 (0–27)
Trembling aspen	12.07 (5–24)	0.37 (0–2)	2.88 (0–15)	0.96 (0–2)	9.19 (0–17)	2.81 (0–15)	9.04 (0–17)
Cottonwood	12.29 (5–26)	0.42 (0–1)	4.21 (0–24)	0.79 (0–2)	8.08 (0–23)	4.21 (0–24)	8.02 (0–23)
Paper birch	15.25 (6–32)	0.64 (0–2)	9.86 (0–32)	0.56 (0–2)	5.38 (0–16)	9.59 (0–32)	5.32 (0–16)

Note: Included in the table are the numbers of periods of suppression and release, the total years of suppression and release, and the lengths of the last periods of suppression and release prior to sampling.

non-zero intercepts). Based on the results of that analysis, we have used Michaelis–Menton functions (with a zero intercept) for the basic functional relationship between growth and light:

$$[1] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] + \varepsilon$$

where $Y = \log_{10}(\text{radial growth} + 1)$, a is the asymptote of the function at high light, s is the slope of the function at zero light, L is GLI (in units of percent full light received over the growing season), and ε is the error term of the equation. Since we avoided sampling in areas that had evidence of canopy disturbance in the past 5 years, radial growth was measured as the mean of the past 5 years to reduce measurement error. We analyzed absolute rather than relative growth (i.e., growth relative to size), because our data indicate that saplings of most of our species did not show a strong size dependency within the range of sizes sampled for this study (Wright et al. 1998). Radial growth was log transformed to stabilize the variance.

We used eight variants of eq. 1 to examine how the basic relationship between growth and light was altered by the lengths of the most recent periods of suppression and release for each sapling:

(1) The basic growth model (eq. 1, above)

(2–4) The basic model, plus a term (d) for length of the last (or current) period of suppression (YLS), a shape factor (f), and a term for the role of light (h) (allowing for the effects of past suppression to vary as a function of current light levels):

$$[2] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] \mathrm{e}^{-d\mathrm{YLS}}$$

$$[3] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] \mathrm{e}^{-(d\mathrm{YLS})^{f}}$$

$$[4] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] \mathrm{e}^{-(d\mathrm{YLS}+hL)}$$

(5–7) The basic model, plus a term (g) for the length of the last (or current) period of release (YLR), a shape factor (f), and a term for the role of light (h) (as above):

$$[5] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] \mathrm{e}^{g\mathrm{YLR}}$$

$$[6] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] \mathrm{e}^{(g\mathrm{YLR})^{f}}$$

$$[7] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] \mathrm{e}^{g\mathrm{YLR}+hL}$$

(8) The basic model, plus terms (d and g) for the length of the last suppression (YLS) and release periods (YLR):

$$[8] \qquad Y = \left[\frac{aL}{(a/s)+L}\right] \mathrm{e}^{g\mathrm{YLR}-d\mathrm{YLS}}$$

Parameters for all models were estimated for each species using the NONLIN procedure in SYSTAT 6.0 (Systat, Inc. 1996) and the simplex estimation method to minimize the loss function.

We fit models to saplings of each species for all subzones combined (Table 1), as well as separate models for saplings collected within the moist–cool subzone of the interior cedar–hemlock forests. The significance of the improvement in fit of the model due to the inclusion of additional parameters (d, g, f, h) in the basic model (eq. 1) was assessed using the extra sums of squares principle: $\mathrm{ESS} = [(\mathrm{SSRE}_1 - \mathrm{SSRE}_2)/(\mathrm{df}_1 - \mathrm{df}_2)/(\mathrm{SSRE}_2)/(n - p)]$, where SSRE_1 and df_1 are the residual sums of squares and degrees of freedom for the full model and SSRE_2 and df_2 are the residual sums of squares and degrees of freedom for the reduced model, n is the number of observations, and p is the number of parameters in the larger model. ESS is distributed as an F statistic with $\mathrm{df}_1 - \mathrm{df}_2$, $n - p$ degrees of freedom (Bergerud 1991).

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Table 4. Parameter estimates of the regression models for growth as a function of current light level and the lengths of the most recent periods of suppression and release for saplings from all sites combined.

Tree species	n	a	s	d	g	R^2, basic	R^2, full
Western redcedar	55	0.799	0.019			0.48	
Western hemlock	278	0.61	0.038	0.006		0.45	0.47
Mountain hemlock	103	0.532	0.015		0.006	0.51	0.54
Subalpine fir	679	0.824	0.012			0.42	
Amabilis fir	119	1.019	0.010		0.013	0.54	0.57
Black spruce	58	0.349	0.013		0.018	0.38	0.62
Hybrid spruce	674	0.548	0.022	0.008	0.012	0.36	0.53
Lodgepole pine	434	0.789	0.016	0.015	0.017	0.55	0.72
Trembling aspen	68	0.907	0.034	0.024		0.68	0.71
Cottonwood	52	0.753	0.035	0.011	0.012	0.39	0.48
Paper birch	73	0.688	0.044	0.016	0.015	0.59	0.72

Note: Parameters a and s control the basic shape of the response to light (eq. 1), while d and g control the magnitude of the effects of suppression and release, respectively (eqs. 2, 5, and 8). Also reported are the R^2 values for both the basic model (eq. 1) and the full model (eqs. 2, 5, or 8, incorporating either or both of the growth history parameters). Where no values are reported for d or g, inclusion of those parameters did not produce a significant improvement in the fit of the regression model.

Table 5. Parameter estimates of the regression models for growth as a function of current light level and the lengths of the most recent periods of suppression and release for saplings from ICH forests only.

Tree species	n	a	s	d	g	R^2, basic	R^2, full
Western hemlock	77	0.858	0.027			0.73	
Western redcedar	55	0.799	0.019			0.48	
Amabilis fir	79	0.911	0.010		0.016	0.47	0.51
Subalpine fir	78	1.044	0.015			0.71	
Hybrid spruce	74	0.623	0.017		0.026	0.61	0.72
Trembling aspen	68	0.907	0.034	0.024		0.68	0.71
Cottonwood	52	0.753	0.035	0.011	0.012	0.39	0.48
Paper birch	73	0.688	0.044	0.016	0.015	0.59	0.72
Lodgepole pine	68	3.496	0.009	0.005	0.020	0.81	0.85

Note: Parameters a and s control the basic shape of the response to light (eq. 1), while d and g control the magnitude of the effects of suppression and release, respectively (eqs. 2, 5, and 8). Also reported are the R^2 values for both the basic model (eq. 1) and the full model (eqs. 2, 5, or 8, incorporating either or both of the growth history parameters). Where no values are reported for d or g, inclusion of those parameters did not produce a significant improvement in the fit of the regression model.

Results and discussion

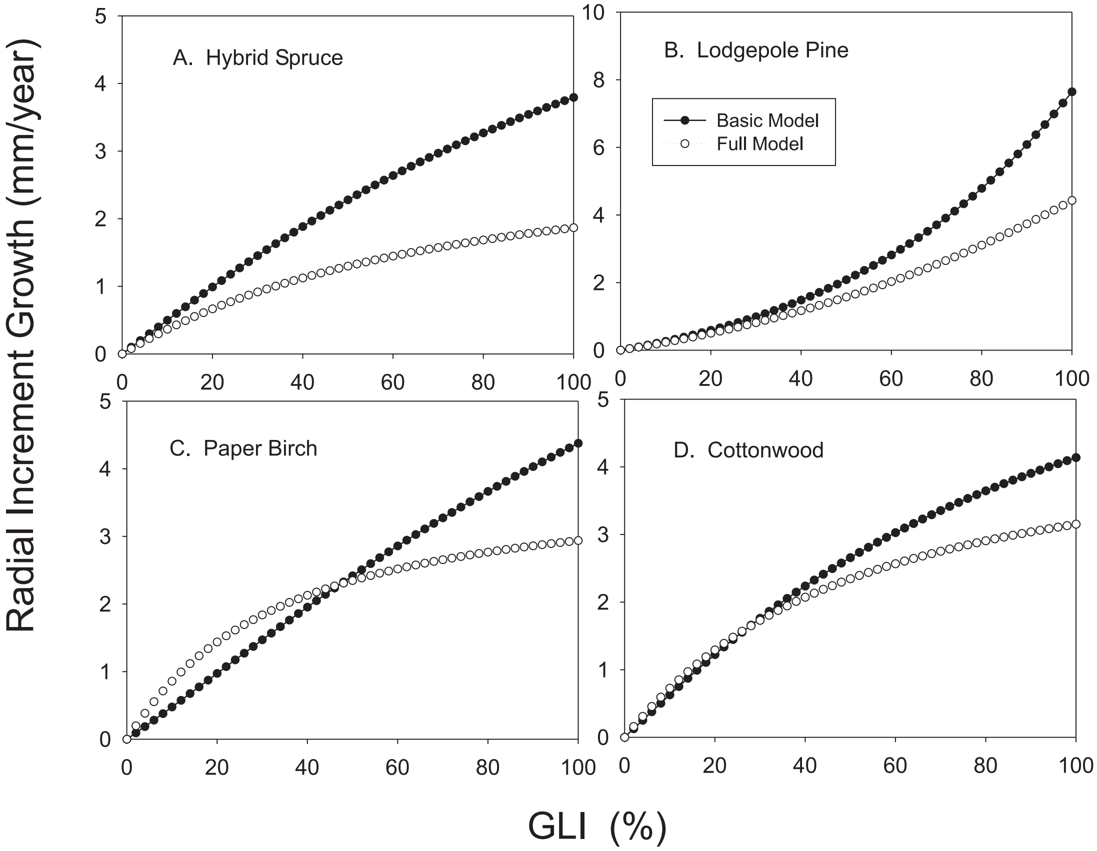
Interspecific variation in patterns of suppression and release

Average stem diameters of the samples were relatively uniform across species (ranging from 3.6 cm for black spruce to 5.0 cm in cottonwood), as were the average light levels in which we sampled (ranging from a mean of 32.8% of full sun for western redcedar to a mean of 50.8% for lodgepole pine) (Table 1). The mean ages showed much greater variation among species, ranging from 12.1 years for aspen saplings to 53.4 years in mountain hemlock. Mean age, by species, was closely correlated with the mean number of periods of suppression for a species (n = 11, r = 0.848, p = 0.015), which ranged from 0.34 periods in western redcedar to a mean of 1.1 periods of suppression per individual in mountain hemlock (Table 3). For all species except aspen and cottonwood, sapling age within species was also positively correlated with the percentage of the sapling's life-span spent in periods of suppression (n = 52–679, p < 0.05). Despite this, sapling age has not been reported to be an important factor in determining growth response following release for subalpine fir (Crossley 1976; Herring 1977), white or black spruce (Crossley 1976; Johnstone 1978), true fir, and mountain hemlock (Seidel 1985). Across all species, individual saplings had undergone as many as six distinct cycles of suppression and release, with the most recent periods of suppression lasting as long as 146 years (Table 3).

Interspecific variation in the effects of suppression and release on growth for all sites

None of the models incorporating either a shape parameter (f) or a parameter for the effect of current light level on the effect of growth history (h) (eqs. 3, 4, 6, and 7) showed a significant improvement in fit over models that incorporated simple terms for the length of the most recent periods of suppression or release (d and g), (eqs. 2, 5, and 8). Two of the 11 species (western redcedar and subalpine fir) showed no effects of previous periods of suppression and release on current response to light (Table 4). Both species are considered shade tolerant, and redcedar is generally considered among the most shade tolerant of the 11 species included in our study (Krajina et al. 1982; Burns and Honkala 1990;

Fig. 1. Predicted radial increment growth (mm/year) for saplings of four species in interior cedar–hemlock (ICH) forests as a function of light (GLI, in units of percentage of full sun) from the basic model (Wright et al. 1998), which does not incorporate historical effects of the most recent periods of suppression and release, versus the full model (Table 5 of this study), incorporating the effects of suppression and release. For the full models, the length of the most recent periods of both suppression and release were set to 0 to allow comparison of the predictions of the two models of the growth of saplings in the first year of release for saplings with no previous period of suppression.



Carter and Klinka 1992; Klinka et al. 1992; Kobe and Coates 1997). This contrasts the work by Johnstone (1978) who found the number of years since release to be useful for predicting growth response to release in subalpine fir.

Four species (hybrid spruce, lodgepole pine, cottonwood, and birch) showed significant responses to the lengths of the most recent periods of both suppression and release (Table 4). The latter three species are generally considered among the least shade-tolerant species in the region (Kobe and Coates 1997). For these species the cumulative effects of the most recent periods of suppression are ameliorated by current periods of release (i.e., significant *g* coefficients in Table 4). The remaining five species had significant responses to either suppression or release (but not both) and ranged from shade tolerant (western and mountain hemlock) to intolerant (aspen) (Table 4). This agrees with the work of Johnstone (1978) who also reported the number of years since release to be an important predictive variable for determining growth response of both white and black spruce following release, whereas length of suppression was not.

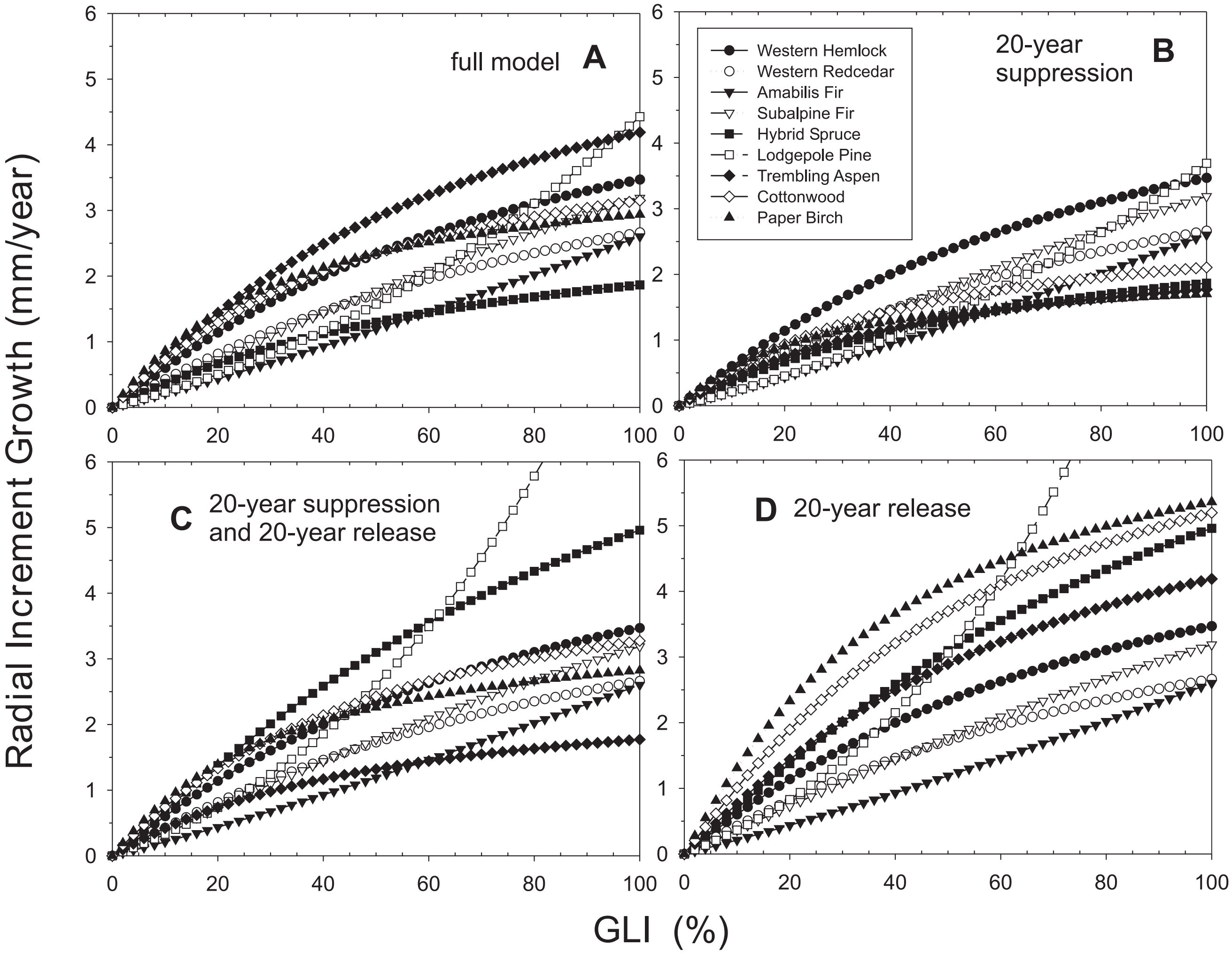
Of the six species for which there was a significant negative effect of the length of suppression, the magnitude of the effect (*d*) was positively correlated with the shade intolerance of the species, ranging from 0.006 in western hemlock to 0.024 in trembling aspen. The magnitude of the positive effect of release (*g*) was also roughly correlated with shade intolerance, ranging from 0.006 in mountain hemlock to 0.018 in black spruce (Table 4).

Effects of suppression and release on sapling growth in interior cedar–hemlock forests

Analysis of the subset of species and samples collected from the moist-cool subzone of the interior cedar–hemlock forests (ICHmc2 subzone) revealed similar relationships between shade tolerance and response to suppression and release (Table 5). The five most shade-tolerant species (western hemlock, western redcedar, amabilis fir, subalpine fir, and hybrid spruce) showed no response to the length of previous periods of suppression, and three of the five species showed no response to the length of release (Table 5). The three least shade-tolerant species (lodgepole pine, cottonwood, and birch; Wright et al. 1998) responded to the length of periods of both suppression and release (Table 5). Trembling aspen had the greatest reduction in growth as a function of the length of suppression and did not recover during release (i.e., no *g* coefficient in Table 5), while lodgepole pine had the smallest reduction in growth (Table 5).

Comparisons between the basic model (eq. 1, with no effects of growth history) and full models (eqs. 2, 5, or 8, with varying effects of suppression and (or) release) demonstrate

Fig. 2. Predicted radial increment growth (mm/year) for saplings of the nine major tree species of interior cedar–hemlock forests as a function of light (GLI, in units of percentage of full sun), under four different histories of suppression and release: (A) no suppression or release, (B) 20 years of suppression, (C) 20 years of suppression followed by 20 years of release, and (D) 20 years of release with no preceding period of suppression.



that ignoring the effects of suppression and release produces overestimates of initial growth response to release, particularly at high light levels (Fig. 1). In particular, the extremely rapid growth rate predicted by the basic model for lodgepole pine under high light appears to only develop over a period of time following release. (Table 5, Fig. 1). In effect, the data for saplings in high light represent individuals that had spent varying lengths of time in release. By ignoring growth history, we overestimated the potential initial response to release for the less shade-tolerant species (Wright et al. 1998).

Figures 2A–2D show the expected current growth rate at all light levels as a function of past growth history. Note that at light levels below the thresholds given in Table 2, current growth rates would represent suppression, while light levels above the species-specific thresholds represent saplings that are currently released. When the full model is used (but with history factored out by setting suppression and release to zero), aspen is dominant at all light levels <95% of full sun, whereas spruce and amabilis fir have the lowest growth (Fig. 2A). The high diameter growth rates of aspen, birch, and cottonwood at <60% full sun confirm our previous conclusion that interspecific variation in low-light growth rates is not predicted by shade tolerance (Wright et al. 1998) (Fig 2A). In fact, during the first year of growth for saplings with no history of suppression, the three broadleaved species have the highest growth rates of all species across the range from 0 to 50% of full sun (Fig. 2A). However, growth rates of all three of those species decline rapidly over time when suppressed (i.e., at light levels less than 20–40% of full sun; Table 2). Moreover, mortality rates of all three species rise sharply with declining light levels in this range (Kobe and Coates 1997). After 20 years of suppression, western hemlock is predicted to have the fastest growth rate at essentially all light levels when released (Fig. 2B). In contrast, growth of aspen saplings drops off dramatically after 20 years of suppression, and all three of the broadleaved species initially have relatively low growth rates when released, even at high light levels (Fig. 2B). In contrast to previous work (e.g., Canham 1985, 1990; Orwig and Abrams 1994) suppression here is defined on the basis of survival; much greater decreases in light are required to see a reduction in growth and an increase in mortality. As a result, suppression occurs at different light levels for different species (Table 2). By our definition, approximately 50% of saplings would survive 20 years at light levels where these species become functionally suppressed. Twenty years of suppression at the threshold for suppression in aspen (i.e., 20% of full sun) would reduce growth rates of aspen saplings well below the growth rate of western hemlock saplings that spent 20 years in much darker light levels required to induce suppression in that shade-tolerant species (i.e., 6% of full sun; Table 2).

After 20 years of suppression followed by 20 years of release, lodgepole pine growth rates exceed all other species at light levels greater than 60% of full sun, while hybrid spruce dominates at intermediate light levels (Fig. 2C). Because of the lack of response to release in aspen, saplings that had been suppressed for 20 years still have extremely low growth rates even after 20 years of release (Fig. 2C).

Delays in response to release have been reported previously for a number of tree species, including black spruce (Crossley 1976), subalpine fir (Herring 1977), Engelmann spruce, (McCaughey and Schmidt 1982; Carlson and Schmidt 1989), and true fir and mountain hemlock (Seidel 1985). The delay may reflect physiological and morphological adjustments of saplings following overstory removal (Tucker and Emmingham 1977; Ferguson and Adams 1980; Tucker et al. 1987). Seidel (1985) found that growth response in true fir and mountain hemlock reflected the degree of shading provided by the overstory and hence the degree of suppression, as did Sundkvist (1994) for Scots pine (*Pinus sylvestris* L.) seedlings. This is supported by the work of Bassman et al. (1992) who found that growth of regeneration following release was poor when the density of other vegetation was high, indicating that partial canopy removal may not result in an increase in light for smaller saplings because of shading by competing vegetation.

Performance of regeneration after 20 years of release for saplings that had undergone no previous periods of suppression (i.e., light levels over the past 20 years were above the species specific thresholds for suppression given in Table 2) are illustrated in Fig. 2D. There is a clear separation between shade-tolerant and -intolerant species, with amabilis fir having the poorest growth over all light levels and paper birch the highest growth at light levels <60% of full sun. Lodgepole pine growth is greater than the three broadleaved species at light levels exceeding 60%.

Summary and conclusions

Our results indicate that saplings of all of the major tree species of northern, interior British Columbia frequently experience multiple episodes of both suppression and release prior to reaching even subcanopy size. As silvicultural practices in the region shift from clear-cutting to various forms of partial harvesting, alternating periods of suppression and release are likely to become even more characteristic of the process of canopy recruitment in these forests. Our results show a clear relationship between shade tolerance and the magnitude of the effects of past periods of suppression and release on sapling growth. In general, there was no effect of previous suppression on the current response of shade-tolerant species to light. Similarly, the most shade-tolerant species did not show a gradual increase in growth rate at a given light level during the course of release. The less shade-tolerant species showed varying degrees of response to both suppression and release, with the strongest responses in the least shade-tolerant species. Our results clearly indicate that periods of suppression do not cause shade-tolerant species to lose their ability to respond to release following partial cutting. The less shade-tolerant species show a lag in response to release, particularly if they have been suppressed, but the effects of prior suppression in all of the species except trembling aspen disappear during the course of release.

Failure to incorporate these effects of growth history can result in misleading conclusions about patterns of interspecific variation in response to light environments. This is particularly true in the least shade-tolerant species, where failure to incorporate the effects of history are likely to significantly overestimate initial response to release (Fig. 1). More generally, competitive balances among species at a given light level shift strikingly as a function of history (see Fig. 2). SORTIE, a spatially explicit model of forest dynamics (Pacala et al. 1993) has been recently parameterized for the interior cedar–hemlock forests of British Columbia. Initial tests of the model show that runs that do not incorporate suppression–release dynamics do a poor job at predicting succession in these forests (unpublished data).

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