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Temporal size-dependent growth responses within density-stressed black spruce stands: Competition processes and budworm effects

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Abstract

This study assessed temporal size-dependent growth response patterns within 18 density-stressed black spruce (*Picea mariana* (Mill.) B.S.P.) stands situated on medium quality sites in central insular Newfoundland. The assessment employed a power function to analyze the relationship between mean annual stem volume increment and cumulative size. Parameters of the power functions were interpreted in terms of: (1) their expression of alternative modes of competitive interaction, according to potential interactions by either resource depletion or resource pre-emption; and (2) temporal size-dependent responses relating to an epidemic spruce budworm (*Choristoneura fumiferana* Clem.) infestation that occurred within the study area during the late 1970s. The results derived from the relationships did not allow alternative modes of competitive interaction to be distinguished due to the low levels of statistical power associated with parameter estimates. However, the analysis did reveal the effects of budworm defoliation on competitive dynamics within the sampled stands. Five distinct phases of response to budworm were revealed as follows: (1) competition-induced, size-proportional, growth rate declines among all-sized individuals during the pre-defoliation period (<1976); (2) budworm-induced, size-proportional, rapid growth rate declines among all-sized individuals during the period of severe defoliation (1976–1979); (3) delayed recovery among smaller-sized individuals during the post-defoliation period (1980–1982); (4) a recovery period (1983–1985) involving increasing competitive asymmetry, during which time the growth rate of larger-sized individuals increased at a greater relative rate than those of smaller-sized individuals; and (5) a period in which competitive asymmetry remained relatively stable (>1985). These patterns suggest that the principal effect of budworm defoliation was to increase competitive asymmetry within the sampled stands, thereby increasing the likelihood of episodic competition-induced mortality events. © 1998 Elsevier Science B.V.

Keywords: Competition processes; Statistical power analysis; Eastern spruce budworm

1. Introduction

Conceptually, intraspecific competition within even-aged, monospecific, plant populations has been characterized as either a resource depletion or pre-emption process (e.g., Koyama and Kira, 1956; Ford,

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1975; Mohler et al., 1978; West and Borough, 1983; Cannell et al., 1984; Brand and Magnussen, 1988; Thomas and Weiner, 1989; Newton, 1990; Weiner, 1990; Newton and Jolliffe, 1993; Schwinning and Fox, 1995; Newton and Jolliffe, 1998). The resource depletion process involves a symmetrical relationship in which individuals share limited environmental resources in direct proportion to their relative sizes. Conversely, the resource pre-emption process involves an asymmetrical relationship in which larger-sized individuals obtain a disproportionate share of resources at the expense of smaller-sized individuals. Recognition of these modes of competition, with their resultant effects on the size-dependent nature of growth responses, has led to a more complete description of size-distribution development within mono-specific plant populations (e.g., Koyama and Kira, 1956; Westoby, 1982; Hara, 1984a, b; Magnussen and Brand, 1989; Thomas and Weiner, 1989; Pacala and Weiner, 1991; Kohyama, 1991; Hara, 1992; Hara and Wyszomirski, 1994).

Analytically, size-dependent growth responses have been used to delineate between the resource depletion and pre-emption modes of competition within a number of density-stressed populations (e.g., Ford, 1975; Westoby, 1982; Magnussen and Brand, 1989; Weiner, 1990; Hara, 1992; Stoll et al., 1994). The resource depletion process is characterized by a linear size-dependent response in which absolute growth rates increase in proportion to size, whereas the resource pre-emption process is characterized by a convex size-dependent response in which absolute growth rates increase non-linearly with increasing size (Weiner, 1990; Hara, 1992). Quantitatively, these relationships may be distinguished using a simple power function: $VI = \beta_0 V^{\beta_1}$ where VI represents mean annual stem volume increment, V the cumulative size (stem volume), and β_0 and β_1 are the parameters of the relationship. The expected test consequences, under the resource depletion and pre-emption competition hypotheses, are $\beta_1 = 1$ and $\beta_1 > 1$, respectively.

The first objective of this study was to use this approach to explore size-dependent growth responses within density-stressed black spruce (*Picea mariana* (Mill.) B.S.P.) stands situated on medium quality sites throughout central insular Newfoundland. The second objective was to interpret the temporal response patterns of both parameters within the context of a

regional spruce budworm (*Choristoneura fumiferana* Clem.) outbreak which occurred within the study area during the late 1970s (Hudak and Raske, 1981).

2. Method

2.1. Sources of data

The data utilized in this analysis were derived from a larger study investigating competition processes within density-stressed black spruce stands (Newton and Jolliffe, 1998). Specifically, stem analysis data derived from 401 previously sampled subject trees situated within 18 sample stands were employed. The stands were situated within central insular Newfoundland (Forest Section B28a-Grand Falls of the Canadian Boreal Forest Region (Rowe, 1972)) and belonged to one of five discrete forest age-classes (year): 15 (number of stands (n) =3), 30 (n=3), 45 (n=5), 60 (n=4) and 75 (n=3). The stands were approximately equivalent in terms of species composition (monospecific black spruce stands with similar shrub, herb, moss and lichen species distributed throughout), site characteristics (upland black spruce–moss forest types situated on medium quality sites), disturbance history (naturally regenerated following wildfire or harvesting), edaphic factors (ferro-humic and humo-ferric podzolic soils), and age structure (even-aged). Collectively, the stands exhibited similar structural developmental patterns as those predicted under self-thinning conditions (Newton and Jolliffe, 1998).

Stem analysis procedures included the following steps: (1) establishing a minimum of three to a maximum of six variable-size circular temporary sample plots within each stand yielding a total of 68 plots within the 18 sample stands (n., plot size was conditional on ≈100 trees per plot and ranged from a minimum of 50.27 m^2 to a maximum of 706.86 m^2); (2) delineating a concentric circular sub-plot within each plot in order to reduce edge-effects (n., sub-plot radii were 1 m less in radius than that of the full plot within plots belonging to stands in the 15-year-old forest age-class; 2 m less in radius for plots belonging to stands in forest age-classes >15); (3) selecting 1 tree per diameter class for stem increment analysis employing a stratified random sampling procedure within each concentric sub-plot (n., 1 cm basal

diameter class width was used within plots belonging to stands in the 15-year-old forest age-class; 2 cm breast-height diameter class width was used within plots belonging to stands in forest age-classes >15); (4) sectioning the stem at 10% height intervals and at breast-height (1.30 m) yielding a total of 12 cross-sections per tree; (5) measuring annual ring widths (±0.01 mm) along three 120° separated radii per cross-section for varying temporal periods (Table 1); and (6) calculating *V*, *VI* and lateral stem surface area (LSA) estimates for each sample tree by year based on the following assumptions (i) stump, tip, and sections in between were treated as geometric solids of revolution resembling a cylinder, cone and frustum of a cone, respectively, (ii) for sections in which increments were not continuous throughout, computations were based on a geometric solid resembling a cone, (iii) vertical section lengths were based on Pythagorean's theorem, and (iv) total height estimates for a given age were obtained using Carmean's (1972) linear interpolation procedure, as modified by Newberry (1991). Note, indicative of budworm defoliation during the 1976–1979 period, virtually all of the sectioned sample trees within stands >15 years exhibited previous terminal leader damage.

2.2. Regression analysis

As detailed below, regression analysis involved (1) obtaining parameter estimates employing ordinary least squares (OLS) regression analysis on logarithmically transformed *VI–V* data by year and stand, (2) evaluating the resultant relationships on the basis of their significance, proportion of variation explained, compliance with the principal regression assumptions underlying OLS estimation, and predictive ability, and (3) interpreting the resultant power exponents in relation to their theoretical expectation with respect to the postulated competition processes.

(1) Transforming the simple power function (Eq. (1)) into a linear function (Eq. (2)) employing a double-logarithmic transformation and subsequently obtaining parameter estimates employing OLS regression analysis.

$$VI_{(ijk)} = \beta_{0(ik)} V_{(ijk)}^{\beta_{1(ik)}} \varepsilon_{(ijk)} \qquad (1)$$

where $VI_{(ijk)}$ is the mean annual stem volume increment specific to the *i*th growth year of the *j*th sample tree within the *k*th stand, $V_{(ijk)}$ is the stem volume at the beginning the *i*th growth year specific to the *j*th sample tree within the *k*th stand, $\beta_{0(ik)}$ and $\beta_{1(ik)}$ are a constant of proportionality and power exponent specific to the *i*th growth year and *k*th stand, respectively, and $\varepsilon_{(ijk)}$ is an error term specific to the *i*th growth year of the *j*th sample tree within the *k*th stand.

$$\log_e(VI_{(ijk)}) = \beta'_{0(ik)} + \beta_{1(ik)}\log_e(V_{(ijk)}) + \varepsilon'_{(ijk)} \quad (2)$$

where $\beta'_{0(ik)}(\log_e(\beta_0)_{(ik)})$ and $\beta_{1(ik)}$ are intercept and slope parameters specific to the *i*th growth year and *k*th stand, respectively, and $\varepsilon'_{(ijk)}(\log_e(\varepsilon)_{(ijk)})$ is the error term specific to the *i*th growth year of the *j*th sample tree within the *k*th stand.

(2) Evaluating the resultant relationships on the basis of their significance, proportion of variation explained, compliance with regression assumptions underlying OLS estimation and predictive ability. Specifically, the *F*-test for regression was used to determine the significance of the relationships (Draper and Smith, 1981): testing the null hypothesis that the slope coefficient is equal to zero. The index of fit statistic squared (I^2; Ezekiel and Fox, 1941) was used to measure the proportion of variation in the untransformed dependent variable explained by the retransformed regression relationship. The I^2 statistic ranges from zero to unity in value and is analogous to the coefficient of determination (r^2). Graphical analysis employing raw residual plots was used to assess the applicability of the correct model specification and constant error variance assumptions underlying OLS regression analysis (Draper and Smith, 1981). The normality assumption was evaluated employing (Shapiro and Wilks', 1965, 1968) *W*-statistic (Judge et al., 1985): testing the null hypothesis that the residuals derived from the $\log_e$-transformed regression relationship were normally distributed. Predictive ability was assessed employing Ek and Monserud's (1979) regression procedure: (i) applying OLS regression analysis to obtain intercept and slope parameter estimates for the model $Y_{(ijk)} = \delta_{0(ik)} + \delta_{1(ik)}\hat{Y}_{(ijk)} + \varepsilon_{(ijk)}$ where $Y_{(ijk)}$ and $\hat{Y}_{(ijk)}$ are the observed and predicted $\log_e(VI)$ values specific to the *i*th growth year of the *j*th sample tree within the *k*th stand, respectively, $\delta_{0(ik)}$ and $\delta_{1(ik)}$ are the intercept and slope parameters specific to the *i*th growth year and the *k*th stand, respectively, and $\varepsilon_{(ijk)}$ is an error term specific to the *i*th growth year of the *j*th sample tree within the *k*th stand; and (ii) given (i),

Table 1
Summary of regression results: sample sizes, fit-statistics, compliance with regression assumptions and predictive ability

Forest age-class (year)	Stand no.	Sample sizes				Relationship																	
		n	Years assessed	Sample trees		$\log_e(V/)-\log_e(V)$ regressions [a]								$\log_e(V/)-\log_e(LSA)$ regressions [f]								
			Range	Min	Max	F^2-statistic [b]			Normal distribution of errors [c] (W-statistic)		Predictive ability				F^2-statistic [g]			Normal distribution of errors [c] (W-statistic)		Predictive ability			
											Intercept [d] H_0: $\delta_0=0$ vs. H_1: $\delta_0\neq0$		Slope [e] H_0: $\delta_1=1$ vs. H_1: $\delta_1\neq1$							Intercept [d] H_0: $\delta_0=0$ vs. H_1: $\delta_0\neq0$		Slope [e] H_0: $\delta_1=1$ vs. H_1: $\delta_1\neq1$	
						Mean	Min	Max	H_0 (%)	H_1 (%)	H_0 (%)	H_1 (%)	H_0 (%)	H_1 (%)	Mean	Min	Max	H_0 (%)	H_1 (%)	H_0 (%)	H_1 (%)	H_0 (%)	H_1 (%)
15	151	9	1976–1984	23	25	0.938	0.882	0.979	100	—	100	—	67	33	0.922	0.813	0.978	100	—	100	—	78	22
	152	9	1976–1984	9	31	0.873	0.492	0.973	89	11	100	—	78	22	0.869	0.445	0.974	100	—	100	—	67	33
	153	9	1976–1984	9	15	0.876	0.787	0.915	100	—	89	11	55	45	0.875	0.789	0.938	100	—	100	—	55	45
30	301	16	1969–1984	9	24	0.828	0.349	0.983	88	12	100	—	69	31	0.865	0.470	0.988	75	25	100	—	88	12
	302	16	1969–1984	25	28	0.709	0.349	0.861	100	—	100	—	100	—	0.704	0.391	0.850	100	—	100	—	100	—
	303	16	1969–1984	34	37	0.858	0.747	0.907	100	—	88	12	81	19	0.846	0.747	0.907	94	6	100	—	88	12
45	451	10	1975–1984	3	15	0.751	0.203	0.998	100	—	100	—	100	—	0.832	0.464	0.990	100	—	100	—	100	—
	452	16	1969–1984	7	16	0.836	0.555	0.914	100	—	100	—	100	—	0.844	0.583	0.948	100	—	100	—	100	—
	453	17	1969–1985	18	18	0.719	0.195	0.955	100	—	100	—	100	—	0.725	0.222	0.957	94	6	100	—	100	—
	454	26	1962–1987	18	19	0.692	0.090	0.965	96	4	100	—	92	8	0.709	0.124	0.969	96	4	100	—	88	12
	455	26	1962–1987	20	21	0.763	0.474	0.957	96	4	100	—	92	8	0.749	0.468	0.961	88	12	100	—	88	12
60	601	26	1962–1987	15	29	0.729	0.281	0.936	100	—	88	12	85	15	0.722	0.299	0.950	92	8	88	12	85	15
	602	17	1969–1985	11	22	0.761	0.540	0.902	82	18	100	—	88	12	0.762	0.523	0.916	82	18	100	—	88	12
	603	17	1969–1985	6	18	0.800	0.358	0.993	92	8	100	—	100	—	0.795	0.351	0.989	100	—	100	—	100	—
	604	26	1962–1987	23	23	0.743	0.408	0.866	100	—	100	—	100	—	0.735	0.407	0.849	96	4	100	—	100	—
75	751	27	1964–1990	11	17	0.756	0.664	0.850	78	22	100	—	100	—	0.729	0.635	0.824	77	23	100	—	100	—
	752	26	1964–1989	24	24	0.848	0.718	0.891	92	8	100	—	58	42	0.840	0.741	0.881	100	—	100	—	46	54
	753	26	1964–1989	11	19	0.791	0.577	0.892	88	12	100	—	81	19	0.821	0.705	0.886	69	31	100	—	92	8

[a] All regression relationships were significant at the 0.05 probability level as determined by a F-test. Specifically, testing the null hypothesis, H_0: $\beta_j=0$, vs. the alternative hypothesis, H_1: $\beta_j\neq0$, at a probability level of 0.05, employing the following test criterion: reject H_0 if $F_0>F_{(0.95,1,J-2)}$, where F_0 is the F-statistic calculated under H_0 and subscript J denotes the total number of sample trees specific to the ith growth year and kth stand; otherwise do not reject H_0.

[b] $F_{(ik)}^2 = \left(\sum_{j=1}^J (Y_{(ijk)} - \bar{Y}_{(i,k)})^2 - \sum_{j=1}^J (Y_{(ijk)} - \hat{Y}_{(i,k)})^2\right) \big/ \sum_{j=1}^J (Y_{(ijk)} - \bar{Y}_{(ijk)})^2$ where $Y_{(ijk)} = VI_{(ijk)}$ and $\hat{Y}_{(ijk)} = \text{EXP}(\hat{\beta}_{0(ik)} + \text{CF}_{(ik)})V^{\hat{\beta}_{1(ik)}}$ (CF$_{(ik)}$ = SEE$_{(ik)}^2/2$ where SEE$_{(ik)}$ is the standard error of the estimate specific to the ith year and jth stand (Baskerville, 1972)).

[c] Testing the relationship-specific null hypothesis, H_0: ε^j are normally distributed, vs. the alternative hypothesis, H_1: ε^j are not normally distributed, at a probability level of 0.05, employing the following test criterion: reject H_0 if $W_0>W_{(0.95,1,J-2)}$ where W_0 is the W-statistic calculated under H_0, otherwise do not reject H_0. Note, regression assumptions of correct model specification and constant error variance were not rejected given that the residual plots exhibited a horizontal band of randomly scattered points (Draper and Smith, 1981).

[d] Testing the relationship-specific null hypothesis, H_0: $\delta_0=0$, vs. the alternative hypothesis, H_1: $\delta_0\neq0$, at a probability level of 0.05, employing the following test criterion: reject H_0 if $t_0>t_{(0.975,J-2)}$ where t_0 is the Student-t statistic calculated under H_0, otherwise do not reject H_0.

[e] Testing the relationship-specific null hypothesis, H_0: $\delta_1=1$, vs. the alternative hypothesis, H_1: $\delta_1\neq1$, at a probability level of 0.05, employing the following test criterion: reject H_0 if $t_0>t_{(0.975,J-2)}$ where t_0 is the Student-t statistic calculated under H_0, otherwise do not reject H_0.

[f] See text for explanation (Section 3). Note, all regression relationships were significant at the 0.05 probability level as determined by a F-test.

[g] Similar to calculation given in footnote b above with the exception: $\hat{Y}_{(ijk)} = \text{EXP}(\hat{\beta}_{0(ik)} + \text{CF}_{(ik)})\text{LSA}^{\hat{\beta}_{1(ik)}}$.

[h] Regression assumptions of correct model specification and constant error variance were not rejected given that the residual plots exhibited a horizontal band of randomly scattered points (Draper and Smith, 1981).

employing Student-t tests to evaluate the null hypotheses that the intercept and slope values were not significantly ($p \leq 0.05$) different from zero and unity, respectively. Relationships were considered unbiased predictors if the null hypotheses were not rejected.

(3) Employing 95% confidence intervals (Judge et al., 1985) to determine if β_1 was significantly different from unity. Furthermore, in cases where the null hypothesis ($\beta_1 = 1$) was not rejected, 95% power confidence intervals were constructed for β_1 employing a reverse statistical power analysis: determining the confidence limits which would be required to attain a desired power of 0.95, assuming the null hypothesis is true (Peterman, 1989, 1990).

3. Results and discussion

3.1. Regression statistics

Table 1 summarizes the regression results obtained. Significant regressions were attained for all regressions (i.e., slope coefficient was significantly ($p \leq 0.05$) different from zero). Overall, the index of fit statistics for both relationships indicated that on average $\approx 79\%$ of the variation in *VI* was explained by the retransformed regressions. Residual analysis indicated that there was insufficient evidence to reject the correct model specification and constant error variance regression assumptions given the concentrated horizontal band of randomly scattered residuals. Furthermore, the Shapiro and Wilks' (1965, 1968) *W*-statistic indicated that 95% of the regressions had normally distributed errors and, hence, the normality assumption was not rejected. The normality assumption was not accepted for 5% of the regressions and, thus, the stated probability levels associated with these regressions may be negatively biased (Gunst and Mason, 1980). Results derived from the predictive ability assessment indicated that the regression equations were adequate predictors overall given that (1) 98% of the intercept (δ_0) values were not significantly different from zero, and (2) 88% of the slope (δ_1) values were not significantly different from unity.
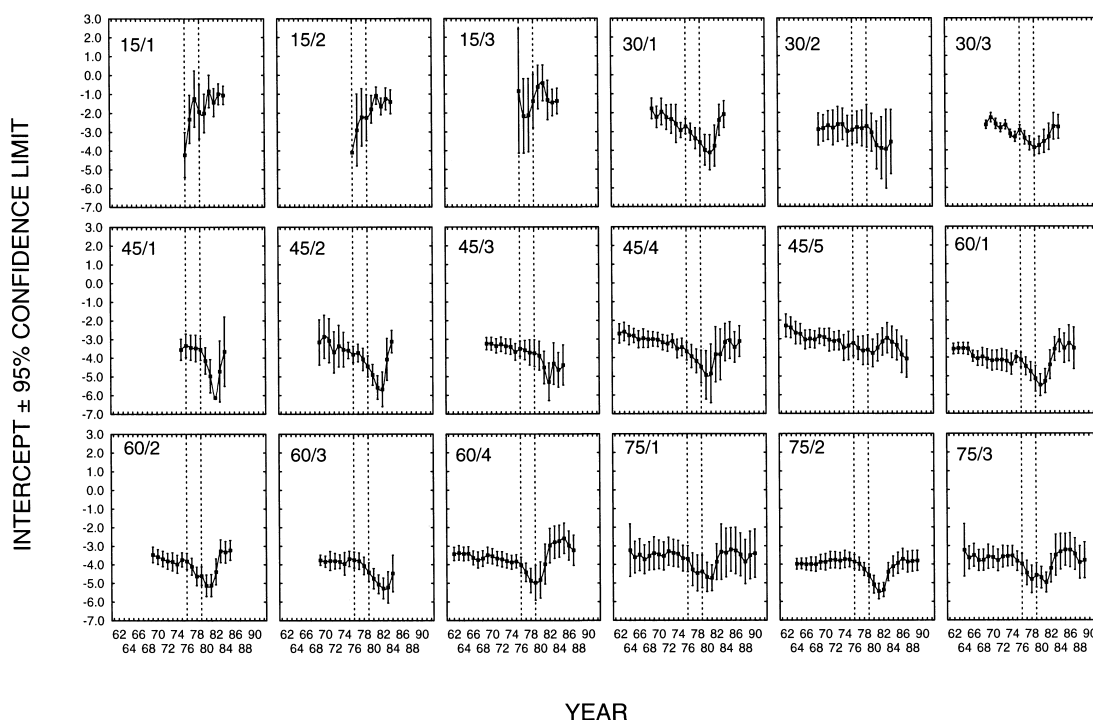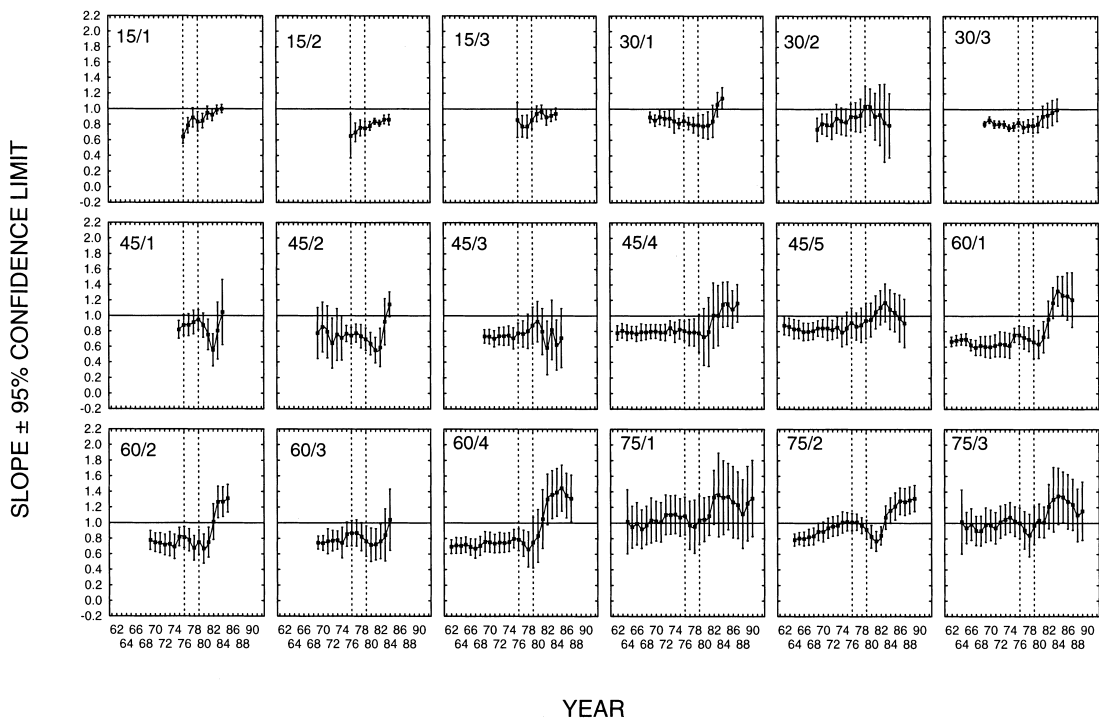

Fig. 1. Temporal trends in the $\log_e(VI)$–$\log_e(V)$ intercept value and associated 95% confidence intervals by stand. Notation: (1) forest age-class/stand number within each sub-graph; and (2) the period of severe defoliation enclosed by the vertical dashed lines.

Analysis of the regression relationships characterized by low I^2 values, non-normal residual distributions and poor predictive ability, indicated an association to sample size; these characteristics were observed in those years in which the number of sample trees was at a minimum. Given the significance of the regressions, levels of variation explained, compliance with regression assumptions and predictive ability, the regressions were considered to be adequate representations of the $\log_e(VI)$–$\log_e(V)$ relationship within the sample stands.

3.2. Competition processes

Intercept and slope parameter estimates for the $\log_e$-transformed VI–V power function (Eq. (2)) and associated 95% confidence intervals are graphically illustrated in Figs. 1 and 2, respectively. Similarly, slope values with associated 95% power confidence intervals are illustrated in Fig. 3. Examination of individual stand trajectories indicates that both parameters exhibited similar temporal variations, partly due to the intrinsic correlation between OLS parameter estimates (c.f., Figs. 1 and 2; Gujarati, 1988). Furthermore, parameter estimates for stands within the 30-, 45-, 60- and 75-year-old age-classes revealed 5 distinct periodic phases (Figs. 1 and 2): (1) linear declines in intercept values with slope values remaining relatively constant until 1976; (2) rapid declines in intercept values, but without a corresponding decline in slope values during the 1976–1979 period; (3) continued declines in intercept values with increasing slope values during the 1980–1981 period; (4) rapid increases in both parameters during the 1983–1985 period; and (5) relative constancy in both parameters after 1985. However, the low statistical power associated with those values not significantly ($p \leq 0.05$) different from unity rendered inconclusive any interpretation of the competition processes occurring (e.g., the probability of accepting the null hypothesis ($\beta_1 = 1$) when the null hypothesis was false ranged from 49 to 98% for the 15 year-old forest age-class).
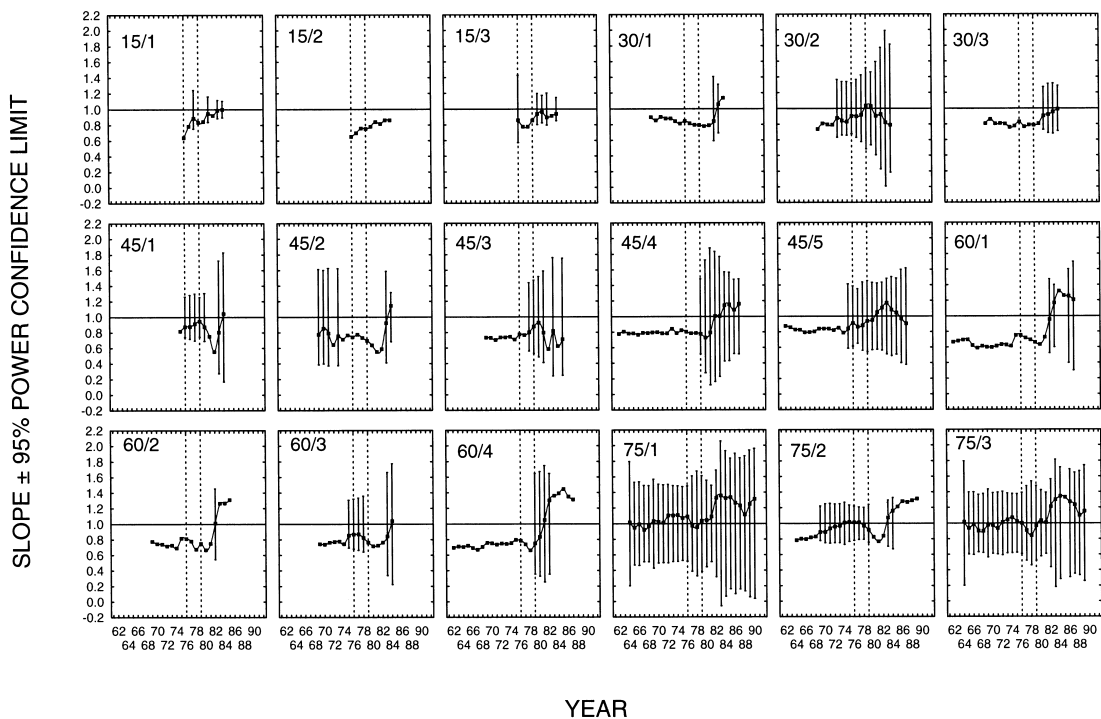

Fig. 2. Temporal trends in the $\log_e(VI)$–$\log_e(V)$ slope value and associated 95% confidence intervals by stand. Notation: (1) forest age-class/ stand number within each sub-graph; and (2) the period of severe defoliation enclosed by the vertical dashed lines.

Furthermore, contrary to expectation under the postulated competition hypotheses, the majority of the slope values were less than unity for the period preceding defoliation ($\beta_1 < 1$; Fig. 2). These results suggest two possibilities: (1) the test consequences associated with the competition hypotheses under consideration were incomplete in that a third mode of interaction may have been operating within the sampled stands; and (2) absolute stem growth rate may become less responsive with size due to the increased proportion of non-productive tissue within the main stem of excurrent forest tree species (i.e., absolute growth rate may intrinsically decline with increasing stem size (Brand et al., 1987)).

In reference to the former possibility, one plausible additional mode of competition may be a reverse asymmetric pre-emption relationship in which smaller-sized individuals obtain a disproportionate share of the below-ground resources at the expense of larger-sized individuals. Consistent with this plausibility would be an expected increase in intercept values with associated decline in slope values. Conversely, however, intercept values actually declined and associated slope values remaining relatively constant during the pre-defoliation period (Figs. 1 and 2), thereby negating the applicability of this mode of interaction.

In reference to the latter possibility, a supplementary analysis was conducted in which the regression analysis was repeated using lateral stem surface area (LSA) as the independent variable: LSA represents the active biotic surface at which both respiration and growth occur. The regression results were similar to those obtained for the $\log_e(VI)$–$\log_e(V)$ relationships (Table 1): significant regressions, high levels of variation explained, compliance with correct model specification, constant error variance and normality

Fig. 3. Temporal trends in the $\log_e(VI)$–$\log_e(V)$ slope value and associated 95% power confidence intervals by stand. Notation: (1) forest age-class/stand number within each sub-graph; and (2) the period of severe defoliation enclosed by the vertical dashed lines. Note, statistical power increases as the differential between the estimated parameter and the confidence limit decreases. Specifically, the probability of a Type II error decreases to 0.05 as the parameter estimate approaches the power confidence limit (i.e., the probability of not rejecting the null hypothesis when the null hypothesis is actually false declines as the differential decreases).

assumptions, and acceptable predictive ability. Furthermore, temporal trends in parameter estimates were similar to those exhibited by the parameter estimates obtained from the $\log_e(VI)$–$\log_e(V)$ relationships for stands >15 years of age (Figs. 4 and 5): (1) linear declines in intercept values with slope values remaining relatively constant until 1976; (2) declines in intercept values, but without a corresponding decline in slope values during the 1976–1979 period; (3) continued declines in intercept values with slopes remaining relatively constant during the 1980–1981 period; (4) continued declines in intercept values with increasing slope values during the 1983–1985 period; and (5) relative constancy in both parameters after 1985. Furthermore, the majority of the slope values were greater than unity ($\beta_1 > 1$), suggesting the existence of a resource pre-emption competition process. However, although slope values for the $\log_e(VI)$–$\log_e(LSA)$ relationships were within the range of expectation according to the postulated processes of competition ($\beta_1 \geq 1$), low levels of statistical power were also associated with those values not signifi-

cantly ($p \leq 0.05$) different from unity (Fig. 6). Consequently negating a conclusive interpretation of the mode of competition within the sampled stands.

Differential effects due to spruce budworm defoliation and variation in local competition levels among subject trees may have contributed to the low levels of statistical power attained, irrespective of the relationship assessed (Bonan, 1988, 1991; Miller and Weiner, 1989; Hara and Wyszomirski, 1994). Assessing competition hypotheses employing local measures of competition, exclusive of budworm infestation years, may be more applicable than the size-dependent approach within spatially heterogeneous populations (e.g., see Newton and Jolliffe (1998) for an alternative analytical approach).

3.3. Spruce budworm effects

Within the context of the spruce budworm outbreak in the study area, the five periodic phases
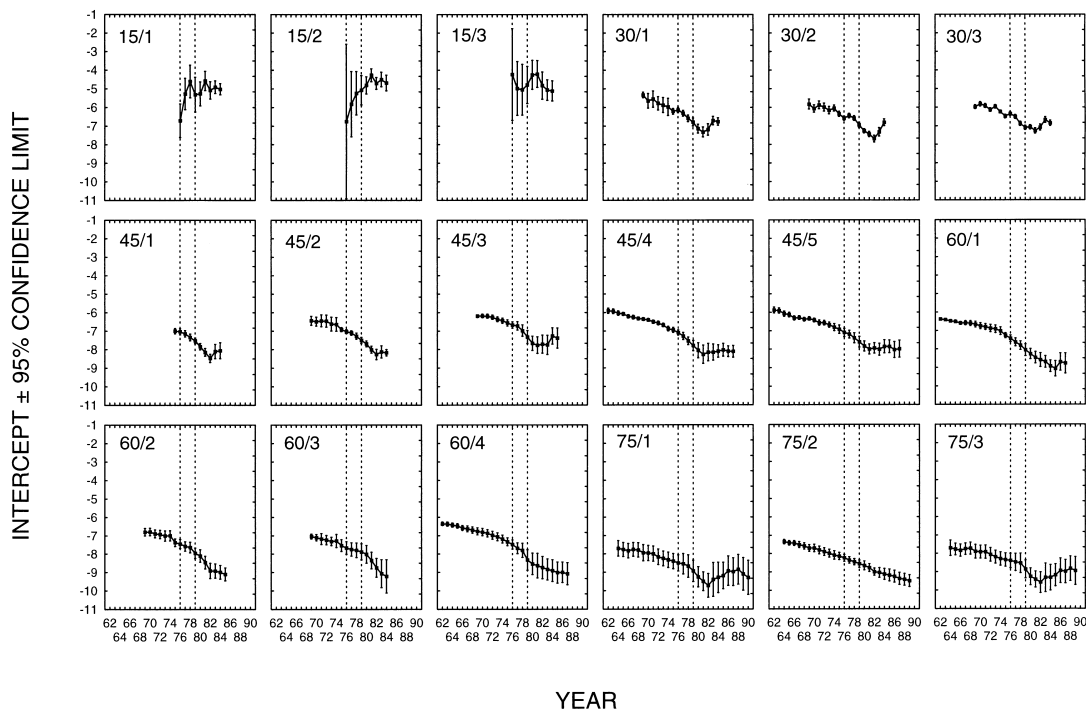

Fig. 4. Temporal trends in the $\log_e(VI)$–$\log_e(LSA)$ intercept value and associated 95% confidence intervals by stand. Notation: (1) forest age-class/stand number within each sub-graph; and (2) the period of severe defoliation enclosed by the vertical dashed lines.
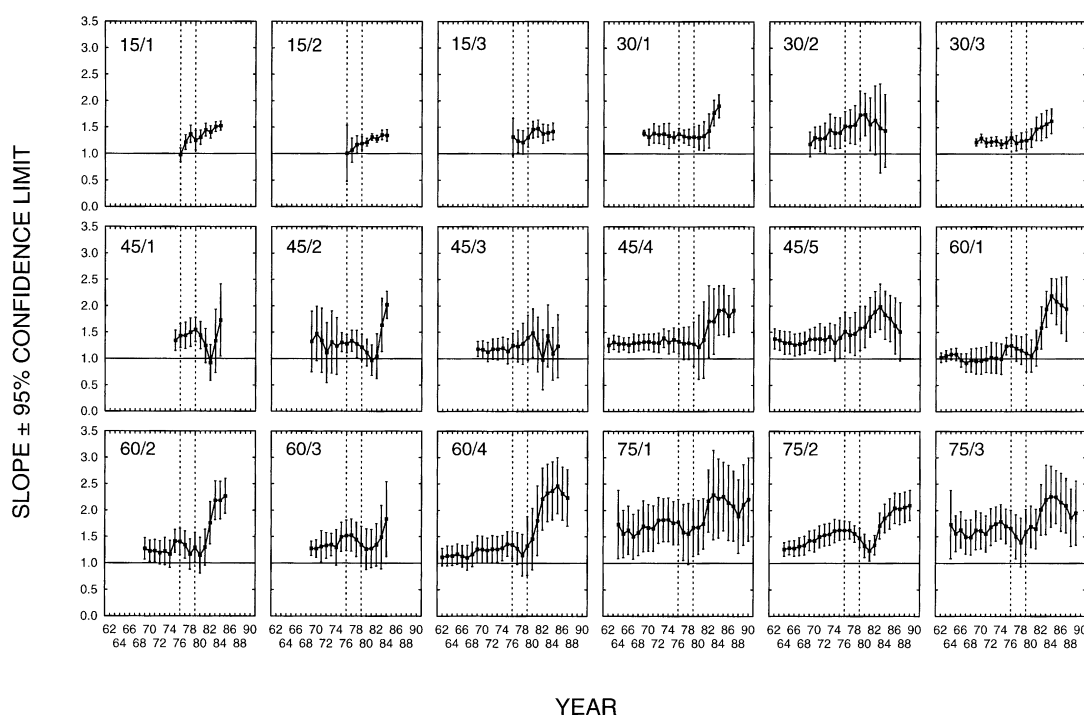
Fig. 5. Temporal trends in the $\log_e(VI)$–$\log_e(LSA)$ slope value and associated 95% confidence intervals by stand. Notation: (1) forest age-class/stand number within each sub-graph; and (2) the period of severe defoliation enclosed by the vertical dashed lines.

described above, were delineated as follows (Figs. 1, 2, 4, 5).

1. Pre-defoliation period (<1976) in which all-sized individuals incurred size-proportional growth rate declines due to increasing density-stress. Specifically, the linear decline in intercept values without a corresponding change in slope values, suggests that individuals were incurring relatively equivalent size-proportional growth rate declines, irrespective of their position in the size-hierarchy. Furthermore, the lack of variation in the slope parameter indicates a period of relative stability in terms of competitive interactions among different sized-individuals: size-dependent responses were temporally invariant during this period suggesting that individuals were moving along a common growth response curve.
2. Severe defoliation period (1976–1979) in which all-sized individuals experienced rapid size-proportional growth declines. Specifically, the rapid linear decline in intercept values without a corresponding change in slope values suggest a budworm-induced size-proportional absolute growth rate decline throughout the entire size-hierarchy.
3. Post-defoliation period (1980–1981) in which absolute growth rates of larger-sized individuals increased at a greater relative rate than those of smaller-sized individuals, suggestive of a recovery delay among the smaller-sized individuals.
4. Recovery period (1982–1985) which was characterized by growth rate increases for all-sized individuals with rates of larger-sized individuals increasing at a greater relative rate than those of smaller-sized individuals.
5. Period of relative stability (>1985) characterized by an asymmetrical competition relationship, indicative of a resource pre-emption competition process.

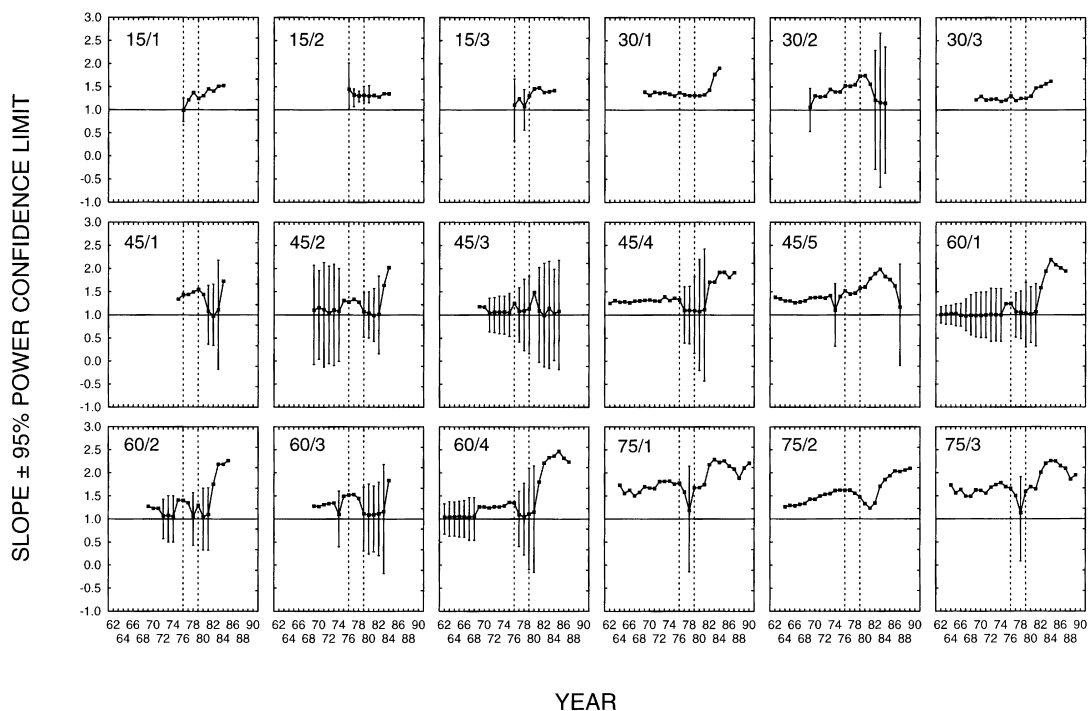Although the eastern spruce budworm has been considered a relatively minor pest with regards to

Fig. 6. Temporal trends in the $\log_e(VI)$–$\log_e(LSA)$ slope value and associated 95% power confidence intervals by stand. Notation: (1) forest age-class/stand number within each sub-graph; and (2) the period of severe defoliation enclosed by the vertical dashed lines. Note, statistical power increases as the differential between the estimated parameter and the confidence limit decreases. Specifically, the probability of a Type II error decreases to 0.05 as the parameter estimate approaches the power confidence limit (i.e., the probability of not rejecting the null hypothesis when the null hypothesis is actually false declines as the differential decreases).

black spruce (Blais, 1957), these results suggest that budworm defoliation resulted in a growth reduction among all-sized individuals followed by an increase in competition asymmetry (Fig. 7). Specifically, larger-sized individuals enhanced their competitive dominance over smaller-sized individuals during the post-infestation and recovery periods and subsequently maintained that advantage. This increase in competitive asymmetry may have resulted in increased density-dependent mortality rates as reported in subsequent years (e.g., Raske and Sutton, 1986).

4. Conclusions

The variability in the resultant parameter estimates and low statistical power associated with slope values not significantly different from unity negated the utility of the size-dependent approach in distinguishing between alternative modes of competition, resource pre-emption and depletion. Possible sources of variability include differential spruce budworm defoliation effects and local competition levels among the subject trees. Consequently, assessing these competition hypotheses employing local measures of competition, exclusive of budworm infestation years, may be more applicable than the size-dependent approach within spatially heterogeneous populations. Furthermore, the temporal patterns revealed by this analysis suggest that the principal effect of defoliation was to increase the degree of competitive asymmetry within the sampled stands, possibly resulting in episodic competition-induced mortality events, as observed in subsequent years.
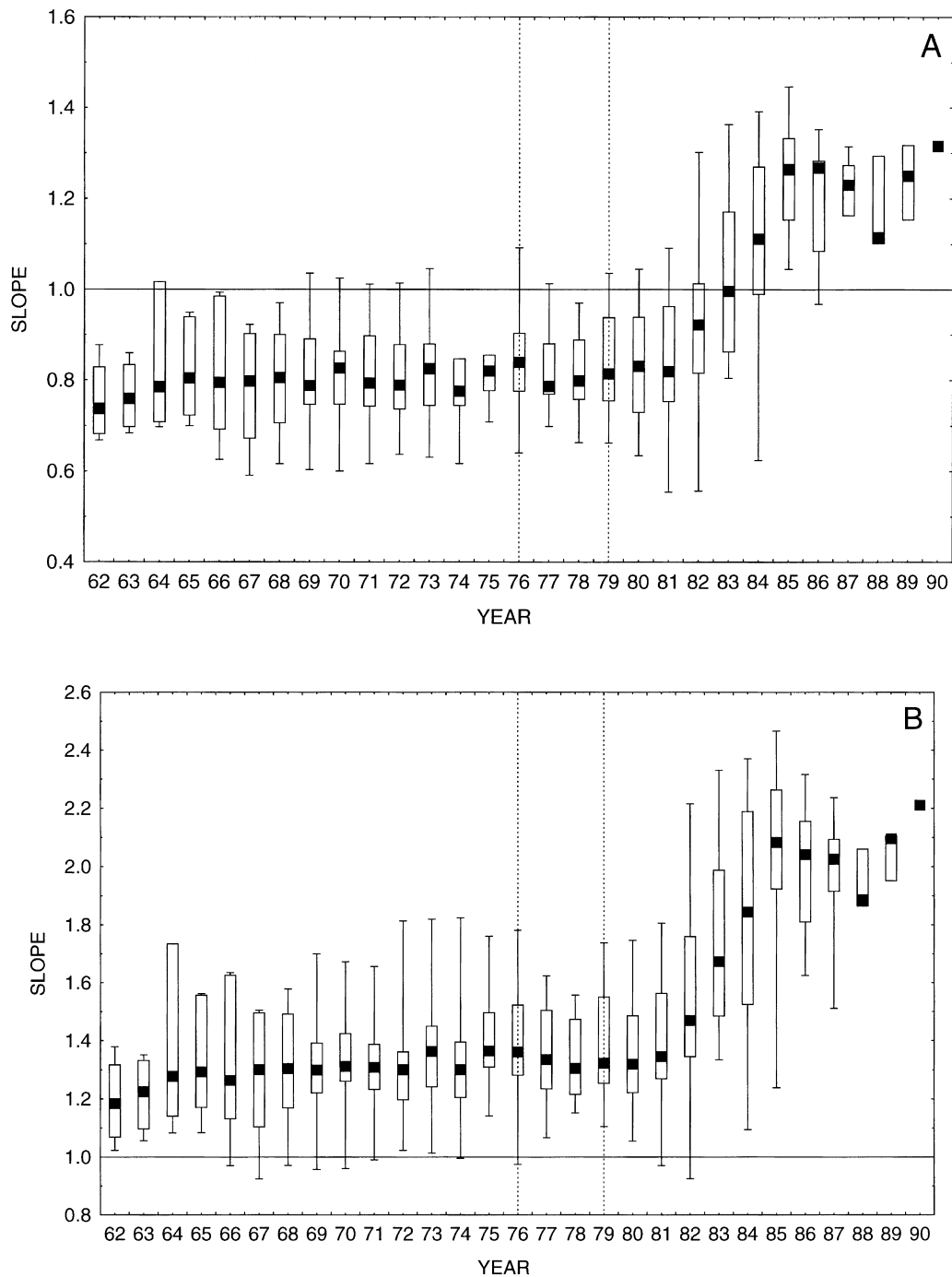
Fig. 7. Box and whisker plots summarizing the distributional characteristics of the slope values for the (A) $\log_e(VI)$–$\log_e(V)$ and (B) $\log_e(VI)$–$\log_e(LSA)$ relationships by year for stands within 30-, 45-, 60- and 75-year-old forest age-classes. Notation: (1) median value is denoted by the solid square within the open rectangle, first and third quartiles are denoted by the lower and upper horizontal sides of the open rectangle, respectively, and minimum and maximum values are denoted by the end points of the lower and upper whiskers, respectively; and (2) period of severe defoliation enclosed by the vertical dashed lines.

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