

Balancing risks of disturbance from mountain pine beetle and western spruce budworm

V.G. Nealis, M.K. Noseworthy, R. Turnquist, and V.R. Waring

Abstract: The effect of removing lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and retaining Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to reduce the risk of disturbance from mountain pine beetle (*Dendroctonus ponderosae* Hopk.) in mixed conifer stands in southern British Columbia, Canada, on population processes influencing outbreaks of western spruce budworm (*Choristoneura occidentalis* Free.) was evaluated in 10 paired (open vs. closed) field plots. Overall feeding damage to Douglas-fir was significantly, but only slightly, lower in open stands compared with closed stands. Although open plots tended to recruit more budworms, the losses resulting from the dispersal of spring-emerging budworms in search of feeding sites were significantly greater in open plots. The forest management benefits of these early season losses were mitigated, however, by more mortality of budworms from natural enemies, particularly diseases, in the closed plots during the budworm feeding period. These results are discussed in terms of compensating population processes and balancing objectives in forest pest management. In this case, selective harvesting of lodgepole pine as a mitigation strategy for the mountain pine beetle conserved the midterm timber supply potential represented by associated Douglas-fir even in the presence of an outbreak of the western spruce budworm.

Résumé : Dans les peuplements mélangés de conifères du sud de la Colombie-Britannique, au Canada, on élimine le pin tordu (*Pinus contorta* Dougl. ex Loud.) en conservant le douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) pour réduire les risques de perturbation par le dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopk.). L'effet de cette pratique sur les processus démographiques qui influencent les épidémies de tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Free.) a été évalué dans 10 paires (peuplements ouverts vs peuplements fermés) de parcelles sur le terrain. Globalement, les dommages subis par le douglas de Menzies à cause du broutement étaient, quoique légèrement, significativement plus faibles dans les peuplements ouverts que dans les peuplements fermés. Bien que les peuplements ouverts aient eu tendance à recruter plus de tordeuses, les pertes dues à la dispersion des tordeuses qui émergent au printemps à la recherche d'endroits pour se nourrir étaient plus élevées dans les peuplements ouverts. À la suite de ces pertes en début de saison, les bénéfices de l'aménagement forestier ont cependant été atténués par une plus forte mortalité des tordeuses causée par ses ennemis naturels, particulièrement les maladies, dans les peuplements fermés pendant la période de broutement de la tordeuse. La discussion porte sur la compensation des processus démographiques et l'équilibre entre les objectifs en lien avec le contrôle des ravageurs forestiers. Dans ce cas, la stratégie qui préconise la récolte sélective du pin tordu pour atténuer l'impact du dendroctone du pin ponderosa a permis de maintenir le potentiel d'approvisionnement en bois à mi-terme que constitue le douglas de Menzies associé au pin tordu, même en présence d'une épidémie de tordeuse occidentale de l'épinette.

[Traduit par la Rédaction]

Introduction

Outbreaks of the western spruce budworm (*Choristoneura occidentalis* Free. (Lepidoptera: Tortricidae)) are characteristic disturbances in conifer forests in western North America. The principal host of the budworm is Douglas-fir, *Pseudotsuga menziesii* (Mirb.), although species of true firs, spruce, and other conifers also may be defoliated throughout the extensive latitudinal range of the insect (Furniss and Carolin 1977). These outbreaks have become more extensive in the past century, apparently associated with human-

induced changes to forest structure at the stand and landscape levels (Swetnam and Lynch 1993). In Oregon (USA), for example, selective removal of pine and increased fire suppression have resulted in mixed-conifer forests with continuous canopies that have significantly increased forest susceptibility to western spruce budworm (Powell 1994).

Defoliation by western spruce budworm has been mapped in British Columbia (BC), Canada, since 1909. These records indicate a dramatic increase in the area of defoliation beginning in the late 1970s in the southern interior of the province (Parfett et al. 1994). The area of defoliation has exceeded 400 000 ha annually from 2002 to the present (Westfall 2006). Repeated defoliation results in mortality of early and advance regeneration and in significant reductions in growth and form of intermediate and dominant trees, affecting both current and future inventory (Alfaro et al. 1982). Long-term volume losses may exceed 50% of the potential stand volume (Alfaro and Maclauchlan 1992).

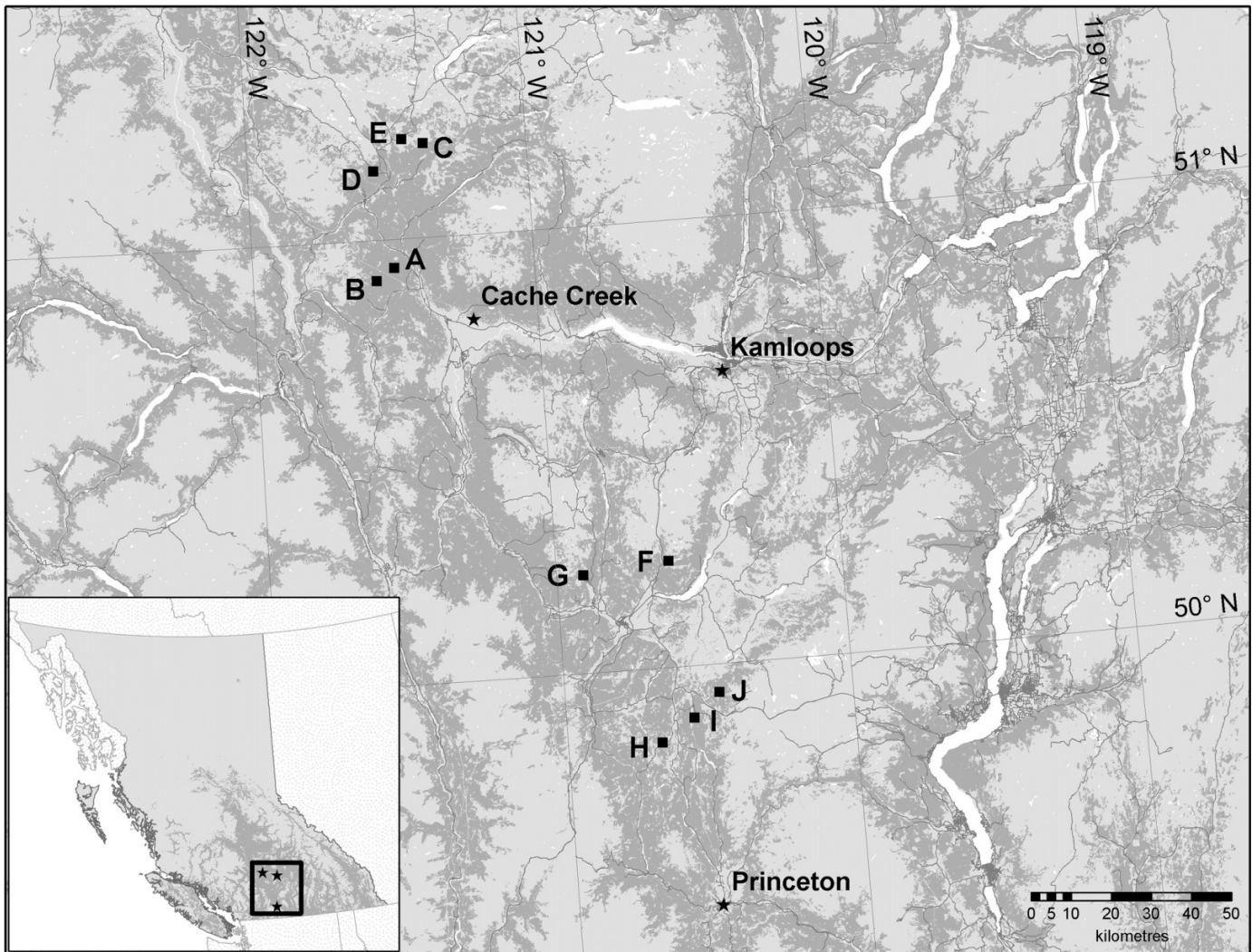
The impact of the western spruce budworm outbreak in

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Fig. 1. Location of paired-plot field sites in southern British Columbia, Canada. Dark grey shading indicates interior Douglas-fir zone. Note that most plots are at the edge of the zone, as they are in high-elevation transition zones where Douglas-fir is mixed with lodgepole pine.



BC has been eclipsed, however, by an even more extensive outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopk. (Coleoptera: Curculionidae: Scolytinae)). Forest managers have responded to this bark beetle outbreak with accelerated harvest of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) either to salvage damaged stands or to reduce future susceptibility to mountain pine beetle (Hall 2004). In areas where lodgepole pine grows in association with Douglas-fir, selective removal of pine and retention of Douglas-fir is a preferred management strategy and results in stands with significantly reduced stem density and more homogeneous species composition, often leading in mature Douglas-fir. This residual forest is the midterm inventory following the mountain pine beetle outbreak and so it represents a critical timber supply in the depleted forests (British Columbia Ministry of Forests and Range 2007).

This paper evaluates the response of western spruce budworm populations on Douglas-fir in mixed stands to selective removal of associated lodgepole pine. More precisely, we are interested in whether forest management practices aimed at one pest disturbance results in a change in risk to

another pest disturbance. We focused on the effects of partial clearing of lodgepole pine on damage suffered by Douglas-fir. Well-established methods of measuring spruce budworm populations and knowledge of key processes affecting their dynamics (Nealis and Régnière 2004a, 2009; Régnière and Nealis 2007) were applied to analyze the relationship between tree damage and population behaviour of the western spruce budworm and to provide greater confidence to inferences at the landscape level.

Materials and methods

Life cycle of the western spruce budworm

The western spruce budworm is univoltine. Eggs are laid in masses on the needles of host trees in midsummer. Hatching first instars disperse away from the egg mass and settle in sheltered niches throughout the tree where they establish hibernacula, molt to a second instar, and pass the winter. Larvae emerge the following spring and disperse back to the branch tips seeking feeding sites. Ballooning on silken threads is characteristic of dispersal within and between

trees, and many budworms are lost during this period (Nealis and Régnière 2009). As spring emergence is usually several days in advance of bud flush, budworms must first mine old needles and move several times (Shepherd 1992). Eventually, budworms are able to penetrate buds (Nealis and Nault 2005) and feed on the developing shoots. They complete a total of six larval instars before pupating among the needles. Moths emerge, mate, and lay eggs in the same season.

Field sites and defoliation

All field sites were located in the interior Douglas-fir zone in the southern interior of BC between 1070 and 1240 m a.s.l. where Douglas-fir is often associated with lodgepole pine (Fig. 1). Each site consisted of a pair of plots: one that had been cleared of lodgepole pine, leaving predominantly Douglas-fir; and an adjacent, intact plot (referred to hereafter as “open” and “closed”, respectively). Harvesting of lodgepole pine in the open sites had occurred within 6 years of this study. Six sites were established in 2006 (A, B, F, G, H, and I) and four more were added in 2007 (C, D, E, and J) for a total of 10 plot pairs for which to compare damage. Defoliation data but no budworm life stage information was collected at site E, leaving nine sites for measurements of budworm density and stage-specific survival.

In each plot, 10 sampling stations centered on a codominant Douglas-fir were located at a minimum of 25 m intervals along a semicircular or longitudinal transect. The central, codominant tree was the sample tree, and sticky traps (see below) were placed just outside the drip line of this tree. To obtain unbiased plot descriptions, a second set of 10, fixed-radius subplots were established at 25 m intervals along a bearing irrespective of the presence of a Douglas-fir. The radius of each subplot was constant within a plot but ranged from 4.0 to 9.8 m among plots with different tree densities to ensure at least three codominant Douglas-fir per fixed-radius plot. Within these subplots, all live conifer tree species >1 m in height were counted and recorded by species. Lodgepole pine was enumerated in two size classes, <10 cm or ≥10 cm diameter at breast height (DBH: 1.3 m above ground). The DBH of all live Douglas-fir trees ≥10 cm DBH were measured to the nearest centimetre. Trees with 2 < DBH < 10 cm were counted and combined in a single size class and assigned a DBH of 6 cm, the median value of the class interval. The density of all classes of trees was expressed as the number of trees per hectare. The total mass of live Douglas-fir foliage in metric tons per hectare in each plot was calculated from the relationship between DBH and mass of foliage (Nealis and Régnière 2009).

Defoliation of current-year foliage, F , was measured in late summer by removing one 45 cm branch from the mid-crown of each of the 10 sample trees, using extendable poles with a cutting head attached. Twenty-five randomly selected shoots from each of these 10 branches were assessed for defoliation by using the method of Fettes (1950). At the time sites were established, a history of defoliation up to 3 years previous was reconstructed by estimating defoliation classes on the appropriate years' shoot. Damage classes were converted to percentage defoliation by using the midpoint of

the Fettes damage categories (MacLean and MacKinnon 1997).

Sampling western spruce budworm

The density of budworms was estimated directly at the egg and the early- and late-stage feeding larval periods by removing two 45 cm foliated branch tips from the mid-crowns of the 10 sample trees. The fresh masses of branch tips were recorded and all budworms were removed and counted. Determination of each individual's instar was made by measuring head capsule size (Stein 1981). The density of budworms was expressed as the mean number of insects per kilogram of foliage. The distribution of life stages for the sample date, t , was summarized as an average instar, α_t (Hardy et al. 1976), in which the six larval instars were given values = 1–6, pupae = 7, and eclosed pupae (or moths) = 8.

Egg density, n_1 , was obtained from the same branch samples taken at the end of the season to estimate defoliation. The number of eggs per kilogram of foliage was estimated by multiplying the number of egg masses found by the mean number of eggs per mass, as estimated by counting individual eggs in a subset of empty egg masses from each site. Samples to estimate the density of early-stage feeding larvae, n_3 , were timed to coincide with the end of the spring dispersal period as indicated by a marked reduction in catches of dispersing budworms on sticky traps (see below). The average instar at the time of collection of early-stage larvae was in the interval $3.2 < \alpha_t < 4.3$. Thus, all samples were taken after feeding shelters were established but before there was significant mortality caused by major natural enemies (Nealis and Régnière 2004a). Samples to estimate the density of late-stage feeding larvae, n_4 , were timed to coincide with the end of the larval feeding period. The average instar in these samples was in the interval $5.2 < \alpha_t < 6.8$.

The number of budworms that successfully survived the winter, n_2 , could not be estimated directly from branch sampling without bias, and so was estimated as the sum of the number of early-stage budworms that successfully established feeding sites, n_3 , and the unsuccessful budworms lost to dispersal, as measured by sticky traps (Nealis and Régnière 2009). For this purpose, ten 45 cm square sticky traps were placed in each plot prior to spring emergence of budworms and checked weekly until the few larvae trapped were fourth instars. Budworms captured on these sticky traps were considered lost to the population, as they would unlikely regain the host tree (Beckwith and Burnell 1982). Budworm losses, measured as the number of insects lost per hectare, were converted to the number of insects lost per kilogram of foliage, l_2 , by dividing the observed number of insects lost per hectare by the estimate of foliage mass per hectare for each site (Table 1). We could then calculate $n_2 = n_3 + l_2$.

Moth density, n_5 , also could not be measured directly. It was estimated by multiplying the measured density of late-stage larvae, n_4 , by the rate of survival in rearing of the corresponding cohort (see below). While this overestimates actual moth density, as it does not account for mortality occurring after the late-stage larval sample date, we assume that this bias is approximately equal between plots within sites, as the average instar at sample date did not vary be-

Table 1. Number of live lodgepole pine and Douglas-fir per hectare in diameter breast height (DBH) classes, mean (SE) DBH of Douglas-fir, and total mass of Douglas-fir foliage in open and closed plots in each study site.

Site	Plot	Lodgepole pine		Douglas-fir		Mean (SE) trees \geq 10 cm DBH	Foliage (metric tons/ha)
		<10 cm	\geq 10 cm	<10 cm	\geq 10 cm		
A	Open	5	0	730	230	17.87 (1.31)	6.09
	Closed	80	80	840	420	20.76 (2.60)	12.05
B	Open	0	5	90	120	23.46 (3.00)	3.74
	Closed	140	20	2960	420	13.91 (0.85)	9.94
C	Open	0	0	33	87	19.42 (1.60)	2.35
	Closed	220	20	400	440	20.41 (1.74)	13.58
D	Open	10	0	545	235	16.53 (0.76)	4.97
	Closed	13	0	2763	239	32.58 (5.04)	14.14
F	Open	0	0	310	95	29.9 (4.73)	4.11
	Closed	220	60	2120	320	27.81 (4.70)	14.58
G	Open	5	5	370	145	23.24 (2.66)	5.23
	Closed	40	120	1500	260	32.08 (5.91)	13.37
H	Open	40	0	435	475	19.74 (0.72)	13.59
	Closed	0	20	1820	840	19.88 (1.24)	26.40
I	Open	0	0	1200	390	15.21 (1.19)	7.22
	Closed	100	20	980	560	20.21 (2.04)	15.98
J	Open	0	0	350	320	19.94 (1.37)	9.67
	Closed	800	60	1480	400	20.90 (2.22)	14.63

tween plots. Further, evidence presented here (Fig. 2B) and from related systems (Régnière and Nealis 2007) show that observed mortality in laboratory rearing of cohorts is correlated strongly with changes in density in the field.

Stage-specific survival (change in budworm density between successive life stages) was estimated by

$$[1] \quad h_i = n_i/n_{i-1}$$

where i is life stage (2, 3, 4, 5). Thus, h_2 is the survival between overwintered and early-stage feeding larvae, h_3 is the survival between early- and late-stage feeding larvae, and h_4 is the survival between late-stage larvae and adults. The egg/female moth ratio, h_5 , is a measure of per capita recruitment rate to the next generation. It was estimated as the ratio of egg density (n_1) to the density of female moths in the previous generation, $0.5 \times n_5$, assuming a 1:1 sex ratio (Nealis and Régnière 2004b).

Rearing western spruce budworm

A subsample of live budworm larvae and pupae from early- and late-stage samples at each plot was placed in individual glass vials; fed a preservative-free artificial diet (McMorran 1965); and reared at 20 °C, 70% relative humidity, and a 16 h light : 8 h dark photoperiod. All budworms from single branches were placed in rearing vials until a minimum of 200 insects per plot was obtained. When samples yielded fewer than 200 individuals, all insects were placed in rearing vials so that no subsampling was done at the branch level. Each rearing vial was examined every 1–3 days until either death of the budworm or adult emergence. The cause of death was determined by macroscopic and microscopic examination. Insects that died from obvious handling or failure to establish on the artificial diet were excluded from further analysis. Analysis of the impact of specific mortality agents recovered is beyond the scope of this

paper, but we do report estimates of mortality attributed to parasitoids, pathogens, and unknown causes. We calculated overall rearing survival, R_t , as the proportion of the budworm cohort from sample t in each sample plot that survived to adult (Régnière and Nealis 2007). The rate of parasitism, P_t , and the incidence of disease-caused mortality, D_t , were calculated similarly.

Statistical analysis

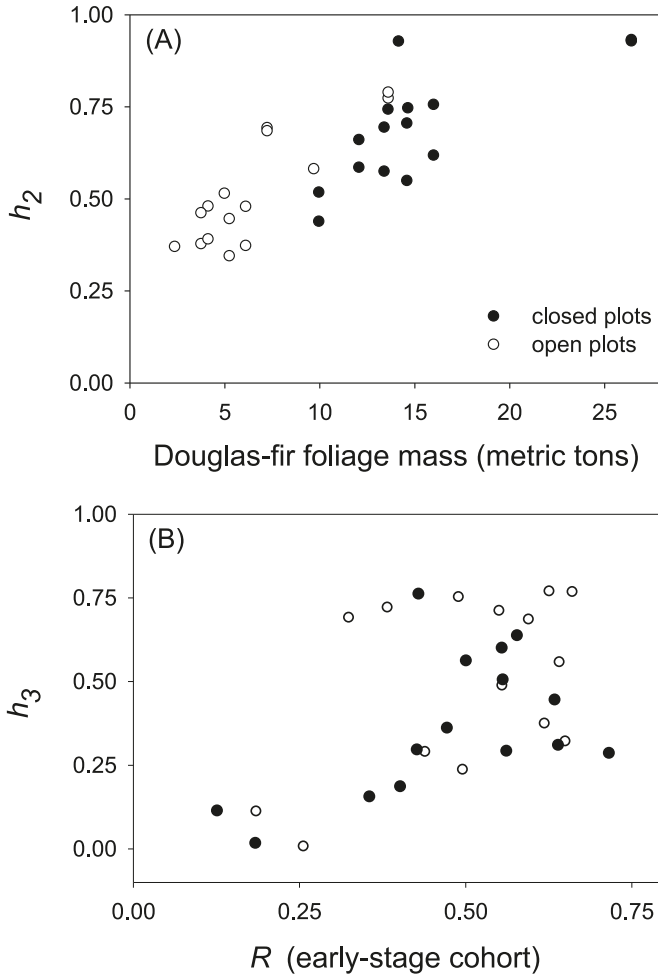
The paired-plot design allowed analysis as a randomized complete block with site (S) as block and open vs. closed plots as a two-level, within-block treatment (T). Annual measures (A) were made of most variables and so year was included in the model as a repeated measure. Because some variables were not measured in all plots in all years, the General Linear Models procedure of Minitab 15.1 was used:

$$[2] \quad Y = \text{constant} + A + S + T + ST + AT + \varepsilon$$

where Y is one of the following variables of interest: (i) F^* , current-year defoliation (a proportion after $\sin^{-1}(\sqrt{F})$ transformation); (ii) $\log_{10}(n_i)$, stage-specific density where $i = 1-5$; $\log_{10}(h_j)$, stage-specific survival in stages $j = 2, 3, \text{ or } 4$, and h_5 , ratio of eggs per female moth; (iii) α_t , average instar of cohorts in sample t ; or (iv) R_t^* , P_t^* , and D_t^* , overall rates of survival, parasitism, and disease, respectively, observed in rearing cohorts from sample t (as proportions after $\sin^{-1}(\sqrt{R})$, (\sqrt{P}) , or (\sqrt{D}) transformations, respectively); and ε , a normally distributed error term. All variables are reported as untransformed values.

The effects of site (S) and treatment (T , open vs. closed) were tested by comparing their respective mean squares with the experimental error mean square (ST), error (a). The effect of year was tested by comparing both its interaction with treatment mean square (AT) as well as the main effect (A), with the overall error mean square, error (b) (e.g., Table 2)

Fig. 2. (A) Relationship between survival of budworms from spring emergence to establishing feeding sites, h_2 , and mass of Douglas-fir foliage in plot. (B) Relationship between survival of budworms from early- to late-larval stages, h_3 , and observed survival of early-stage cohorts in rearing, R .



(Steel and Torrie 1980). Residuals of all models (ϵ) were tested for normality by the Anderson–Darling (A–D) test.

Results

Defoliation

Annual defoliation varied significantly at the site level but was at least moderate to severe (>50%) in many sites in most years (Fig. 3). Mean (SE) overall defoliation in all sites in all years was 60.9% (3.6) for open plots and 67.3% (3.9) for closed plots. This difference in defoliation between closed vs. open plots was statistically significant ($F_{[1,9]} = 10.9, P < 0.01$; A–D = 0.64, $P = 0.09$), although in practical terms, small. Temporal trends revealed some recent regional patterns (Fig. 1): in most southern sites, defoliation exceeded 50% in most years except for recent declines in a few sites (Figs. 3F–3J); in the northern sites, defoliation was recent and either increased steadily or fluctuated between moderate and severe (Figs. 3A–3E).

Stage-specific densities and survival

The relative densities of eggs and over-wintered, early-

Table 2. ANOVAs of rates of survival between overwintered and early-stage larvae (h_2), between early-stage and late-stage feeding larvae (h_3), between late-stage larvae and adult moths (h_4), and per capita recruitment of eggs (h_5) in open and closed sites in 2006 and 2007.

Source	h_2			h_3			h_4			h_5		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Site	8	0.0288	3.7	8	0.214	9.0	8	0.00670	13.4	8	0.213	3.1
Open/closed	1	0.143	18.2	1	0.0738	3.1	1	0.00953	19.1	1	0.0401	0.6
Error (a)	8	0.00784		8	0.0237		8	0.000500		8	0.0687	
Year	1	0.000695	0.2	1	1.653	8.4	1	0.00432	1.9	1	0.722	6.2
Interaction	1	0.00466	1.4	1	0.0035	0.02	1	0.00198	0.8	1	0.00520	0.04
Error (b)	10	0.00517		10	0.0237		10	0.0176		10		
A–D			0.26, $P = 0.7$			0.40, $P = 0.3$			0.25, $P = 0.7$			0.73, $P = 0.05$

Note: A–D is the Anderson–Darling test of normality. Shaded row focuses on inference pertaining to open/closed treatment.

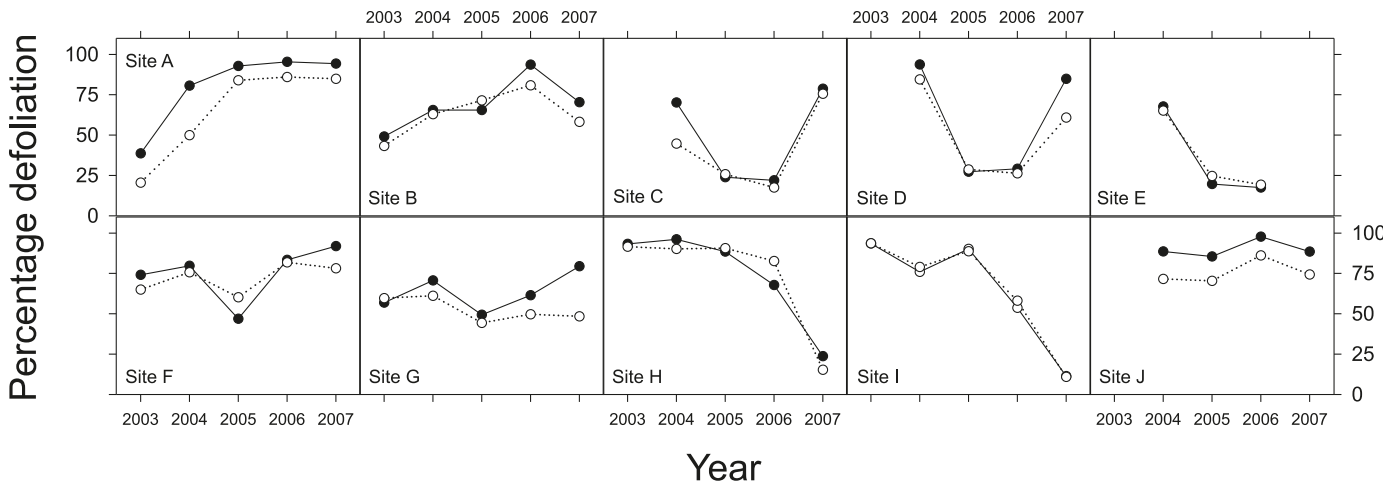
Table 3. Mean densities of larval stages (n_2 , n_3 , and n_4), moths (n_5), and eggs (n_1), and mean survival rates between overwintered and capita recruitment of eggs (h_5) in all open and closed paired plots in all sites in 2006 and 2007.

Site	Year	n_2 (overwintered larvae)		n_3 (early-stage larvae)		n_4 (late-stage larvae)		n_5 (moths)	
		Open	Closed	Open	Closed	Open	Closed	Open	Closed
A	2006	414.5	409.4	154.9	270.7	36.8	42.4	27.8	21.2
	2007	550.6	508.5	265.3	298.0	99.7	92.7	54.0	42.4
B	2006	565.7	448.4	214.1	197.0	62.3	36.9	34.2	18.8
	2007	331.3	282.1	155.7	146.2	87.1	42.9	58.6	25.8
C	2007	230.6	172.3	85.5	128.2	27.6	57.2	21.6	40.4
D	2007	163.0	199.6	83.9	185.4	64.6	53.2	49.0	28.2
F	2006	724.4	514.9	348.3	363.5	170.4	218.6	104.0	108.0
	2007	621.2	471.8	242.5	260.2	172.9	131.8	77.2	70.0
G	2006	308.1	182.8	106.5	127.0	80.3	37.8	55.2	22.4
	2007	251.5	226.2	112.5	130.8	86.5	83.5	49.6	46.0
H	2006	508.1	312.3	393.3	291.3	44.7	33.5	13.2	4.2
	2007	119.4	64.4	94.3	56.6	64.8	43.2	31.0	7.4
I	2006	1476.4	908.9	1023.8	562.4	8.9	10.2	1.6	0.0
	2007	95.6	92.1	65.5	69.7	47.3	39.3	22.0	20.0
J	2007	285.7	399.6	166.3	298.6	115.1	108.2	52.8	27.2
Mean (SE) ^a		96.8 (40.3)		8.4 (35.8)		9.2 (6.5)		11.3 (3.6)	

Note: NA, not available.

^aMean untransformed differences between open and closed paired plots. Mean values in bold are significantly different at $P < 0.05$. See text and Table 2 for ANOVAs.

Fig. 3. Percentage defoliation of Douglas-fir by western spruce budworm in open (○) and closed (●) plots in 10 field sites in British Columbia between 2003 and 2007.



stage, and late-stage feeding larvae (n_1 , n_2 , n_3 , and n_4) were not significantly different between open and closed plots, although on average, the densities of all stages were greater in the open plots, especially in the egg and overwintered larval stages (Table 3). Moth densities (n_5) were significantly greater in the open plots in both years ($F_{[1,8]} = 5.40$, $P = 0.05$; A–D = 0.33, $P = 0.5$) (Table 3).

The average instar at the time of branch sampling for early- and late-stage larvae, α , varied between years but was not significantly different between open and closed plots (early stage: $F_{[1,8]} = 0.02$, $P = 0.89$, A–D = 0.50, $P = 0.20$; late stage: $F_{[1,8]} = 2.08$, $P = 0.19$, A–D = 0.51, $P = 0.19$). Thus, we expected no bias in our analyses of survival based on large, between-plot differences in age distributions at the time of sampling. This result also suggests that there

were no large differences in the phenology of budworm development between open and closed plots within a site, which might have been suspected given changes in the microclimate associated with differences in stand structure.

Survival of larvae between the end of the winter and the early-stage feeding stage, h_2 , was significantly less in open vs. closed plots (Tables 2 and 3). Losses to the population determining h_2 are to a large extent the result of spring dispersal and are a function of previous defoliation and the amount of host-tree foliage at the plot level (Nealis and Régnière 2009). In this case, previous defoliation in the sites and years for which dispersal losses were measured was uniformly high in all plots in the immediate past (Fig. 3), and so the large difference in foliage mass between open and closed plots (Table 1) dominated the positive relationship

early-stage larvae (h_2), between the early- and late-stage larvae (h_3), between late-stage larvae and adults (h_4), and per

n_1 (eggs)		h_2		h_3		h_4		h_5	
Open	Closed	Open	Closed	Open	Closed	Open	Closed	Open	Closed
480.5	358.01	0.37	0.66	0.24	0.16	0.75	0.50	34.6	33.7
617.0	320.9	0.48	0.59	0.38	0.31	0.54	0.46	22.8	15.1
525.6	367.06	0.38	0.44	0.29	0.19	0.55	0.51	30.7	39.1
238.3	153.5	0.46	0.52	0.56	0.29	0.67	0.60	8.1	11.9
199.7	353.0	0.37	0.74	0.32	0.45	0.78	0.71	18.5	17.5
570.8	766.7	0.52	0.93	0.77	0.29	0.76	0.53	23.3	54.3
978.5	852.7	0.48	0.71	0.49	0.60	0.61	0.50	18.8	15.5
1045.0	1033.0	0.39	0.55	0.71	0.51	0.45	0.53	27.1	29.5
439.3	802.9	0.35	0.70	0.75	0.30	0.69	0.59	15.9	71.6
440.0	354.0	0.45	0.58	0.77	0.64	0.57	0.55	17.7	15.4
199.6	151.04	0.78	0.93	0.11	0.11	0.29	0.12	30.2	72.1
257.2	249.0	0.79	0.93	0.69	0.76	0.48	0.36	16.5	32.4
642.0	97.0	0.69	0.62	0.009	0.094	0.18	0.00	802.5	NA
399.5	368.0	0.69	0.76	0.72	0.56	0.46	0.51	36.3	36.8
262.0	390.0	0.58	0.75	0.69	0.36	0.46	0.25	9.9	28.6
45.2 (55.1)		-0.17 (0.03)		0.13 (0.05)		0.10 (0.02)		-11.64 (5.1)	

between survival of dispersing budworms and the amount of foliage in the plot (Fig. 2A). This accounts for the higher proportional losses of dispersing larvae in the open stands.

Survival between the subsequent early- and late-feeding stages, h_3 , and between the late-feeding larval and adult stage, h_4 , was greater in open vs. closed plots although this difference was statistically significant only for h_4 (Tables 2 and 3). These between-plot differences were consistent among sites in both years. Survival of feeding larvae between the early- and late-stage larval periods, h_3 , was positively correlated ($r = 0.50$, $P < 0.01$) with observed survival in rearing the early-stage cohorts (Fig. 2B). There was no difference in this relationship between open and closed plots ($t = 1.49$, $P = 0.15$). Thus, measured losses in field populations during the feeding stages were associated with the impact of natural enemies observed in rearing as noted in more extensive field data (Régnière and Nealis 2007). In fact, the significant difference in h_3 in all plots between years (Table 2) is associated with significantly greater overall mortality caused by natural enemies in the early-stage cohorts in 2006 compared with 2007 (Fig. 4: 0.63 vs. 0.44, respectively; $F_{[1,8]} = 23.5$, $P < 0.01$, A–D = 0.48, $P = 0.22$). Similarly, the significantly lower survival between the late-stage feeding larvae and the adults, h_4 , in closed plots in both years was associated with greater observed mortality by natural enemies in the late-stage cohorts in closed plots in both years (Fig. 4: $F_{[1,8]} = 20.7$, $P < 0.01$, A–D = 0.34, $P = 0.5$).

Mortality from natural enemies

The overwhelming majority of budworm mortality in rearing (0.92) was caused by parasitoids or diseases, with parasitism nearly three times as frequent as disease overall. Two ubiquitous budworm parasitoids *Apanteles fumiferanae* (Vier.) and *Glypta fumiferanae* Vier. (Hymenoptera: Ichneumonidae), which attack neonate budworms in the summer and kill the budworm the following spring, accounted for

90% of the observed parasitism. A nuclear polyhedrosis virus, characteristic of western spruce budworm (B. Morin, Atlantic Forestry Centre, Fredericton, New Brunswick, personal communication), accounted for 70% of all mortality attributed to disease.

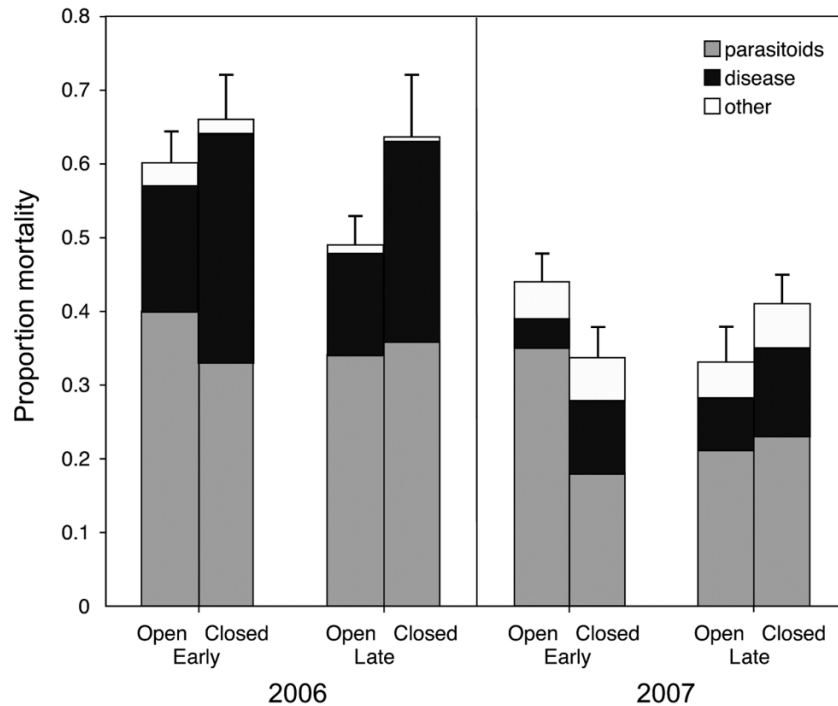
The combined impacts of these natural enemies on the larval feeding period was significantly greater in closed than in open plots ($F_{[1,8]} = 30.8$, $P < 0.01$; A–D = 0.46, $P = 0.26$). The rate of parasitism in the early-stage cohorts did not differ significantly between years ($F_{[1,10]} = 3.66$, $P = 0.08$, A–D = 0.51, $P = 0.2$) but was greater in open plots in both years ($F_{[1,8]} = 8.43$, $P = 0.02$). Disease was significantly more frequent in 2006 than in 2007 ($F_{[1,10]} = 31.3$, $P < 0.01$, A–D = 0.38, $P = 0.4$) and significantly greater in the closed plots in both years ($F_{[1,8]} = 25.2$, $P < 0.01$) (Fig. 4). As there was no difference in the rate of parasitism of late-stage larvae between open and closed plots, the greater mortality in closed sites was the result of significantly greater mortality caused by disease ($F_{[1,8]} = 5.95$, $P = 0.04$, A–D = 0.58, $P = 0.12$) (Fig. 4).

Per capita recruitment to the next generation, h_5 , was not significantly different between open and closed plots (Tables 2 and 3).

Discussion

The recent outbreak of the mountain pine beetle in western Canada has been unprecedented in both its severity and extent (Kurz et al. 2008). In the short term, few management options other than removal of infested trees are available. Where possible, selective removal of lodgepole pine and retention of Douglas-fir is preferred to recover current value and maintain future timber supply. However, Douglas-fir is susceptible to western spruce budworm, and outbreaks of this species also have been at record levels over this same period (Westfall 2006). The interaction of these two out-

Fig. 4. Proportions of overall budworm mortality (with standard error bar) caused by parasitoids, disease, and other mortality factors observed in rearing early- and late-stage larval cohorts from open and closed plots in 2006 and 2007.



break processes with pest management practices needs consideration in case active mitigation of one pest risk exacerbates the other. Selective removal of lodgepole pine and retention of Douglas-fir results in a significant change in forest structure that could affect the severity of damage at the stand level, as has been noted in several earlier studies of western spruce budworm (Fauss and Pierce 1969; Carlson et al. 1985; Swetnam and Lynch 1993) and in related insect defoliators (Nealis et al. 2004; Moreau et al. 2006).

In this study, annual defoliation by western spruce budworm was significantly, but only slightly, less in plots that had been partially cleared. Thus, if anything, selective removal of lodgepole pine resulted in reduced risk to Douglas-fir stands to western spruce budworm. This positive effect of partial clearing on damage has been noted before (Fauss and Pierce 1969; Carlson et al. 1985, 1988), but the reasons were unclear. Earlier measurements suggested that losses of dispersing early-stage larvae in the spring are greater in thinned than in fully stocked stands (Kemp and Simmons 1979; Beckwith and Burnell 1982; but see Carlson et al. 1985). However, no direct link between these dispersal losses, survival trends, and resulting densities of feeding budworm was made. Recent population studies show that spring dispersal losses of budworms are a key process of population dynamics and are related directly to foliage biomass in the stand (Régnière and Nealis 2007; Nealis and Régnière 2009). The results here, gained from direct measurement at several sites, confirm those conclusions and show how these dispersal losses are related to ultimate damage from the budworm.

The influence of stand structure on stage-specific survival, however, does not end with the dispersal period. During the feeding period, western spruce budworm densities are continually reduced by mortality caused by parasitoids and dis-

eases. In this study, net losses caused by natural enemies, particularly disease, were greater in closed vs. open plots and so tended to compensate for differential dispersal losses earlier in the life cycle. The result was that the density of the late-stage larvae, which cause the most damage, was similar in both open and closed stands; hence, the relatively small difference in defoliation associated with modification of stand structure.

The field data requirements for the analyses presented here were such that more extensive spatial and temporal representation of budworm populations was prohibitive. Nonetheless, we understand enough about factors influencing the key population processes measured here to suggest how robust these results are likely to be. For example, spring dispersal losses increase with severity of previous defoliation and may be greater in years in which weather prolongs the dispersal period (Nealis and Régnière 2009). While weather effects are expected to function at a large spatial scale and affect stands that differ in structure in a similar way, among-stand differences in defoliation resulting from differences in stand structure could feed back via the dispersal process to enhance differences between open and closed stands. Alternatively, changes in canopy structure over time could reduce differences between open and closed stands as foliage volumes increase more rapidly in open stands than closed stands.

The impacts of natural enemies vary temporally in spruce budworm populations (Régnière and Nealis 2007). The levels of parasitism were relatively stable in this study, but late-stage parasitoids associated with rapid rates of decline in budworm populations (Régnière and Nealis 2007) were notable for their absence. Their presence during the collapse of an outbreak could reveal additional relationships with forest structure (Cappuccino et al. 1998) and (or) budworm

density (Eveleigh et al. 2007). The impact of disease was more variable and its incidence less predictable. While overall increases in any source of mortality will reduce damage everywhere, local responses of these natural enemies in relation to stand structure will accentuate differences in damage among stands that differ in their structure (Moreau et al. 2006). More analysis and study of the role of these natural enemies in western spruce budworm dynamics are warranted to fully integrate forest management practices with insect population dynamics.

Differences in population processes between open and closed stands could be even more pronounced during other phases of the outbreak cycle. When spruce budworm outbreaks are extensive and severe, as was the case during this study, the large-scale increase in survival of larvae and mobility of moths tends to obscure more fine-scale differences among stands. The fact that we have revealed effects of structural differences between proximate stands on key population processes during this outbreak indicates that the ecological relationship between stand structure and budworm is a real and fundamental aspect of budworm dynamics and, hence, of disturbance ecology in these forests.

These results also inform more general aspects of western spruce budworm dynamics and forest management. Firstly, it is clear that a much greater portion of the interior Douglas-fir forests of BC is at risk of damage from the western spruce budworm than was apparent from historical surveys (Parfett et al. 1994). Not only is defoliation extending farther north in recent years but also, as this study shows, to the highest elevations of the interior Douglas-fir forest ecozone. Whether these new patterns are the result of changing climate (Thomson and Benton 2007) or more susceptible trees on the landscape (Swetnam and Lynch 1993; Powell 1994) is not clear. Secondly, our estimates of damage provide ground proof of repeated, severe defoliation in these stands reported from recent aerial surveys (Westfall 2006). Finally, these results confirm the significance of stand structure, in particular foliage volumes of host trees, on budworm dynamics and confirm how stand-level characteristics interact with population processes to reveal ecological relationships between the insect and the forest that have predictive value and can be incorporated into forestry practices.

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