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The phenological window for western spruce budworm: seasonal decline in resource quality

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Abstract

1 Western spruce budworm *Choristoneura occidentalis* Free. (Lepidoptera: Tortricidae) emerge in the spring before budburst and then face a rapidly deteriorating host quality each season.
2 Measures of fitness, survival and fecundity, were made on cohorts of final-instar spruce budworms deployed on host trees at several times during the season in four field locations in coastal and interior British Columbia, Canada.
3 Survival and fecundity were strongly correlated throughout the season and varied as much as four-fold from maxima at mid-season to minima at the end of the season.
4 Fitness values overall were greatest in the coastal compared with interior locations. Among interior locations, fitness was greatest at the highest elevation and least at the lowest elevation. Both cohort and sample-based estimates of survival of wild, final-instar budworms were relatively high in these outbreak populations.
5 The influence of the phenological window and degree of synchrony with the host plant on herbivore abundance often depends on other processes affecting population rates of change.

Keywords Budworms, fitness, host-plant interactions, phenology, synchrony.

Introduction

Outbreaks of forest defoliating insects are associated commonly with species that feed early in the spring during the period of rapid growth of host foliage (Hunter, 1991). Early-season feeding is interpreted as an adaptation aiming to utilize the ephemeral availability of nitrogen provided by the resource (Mattson, 1980; White, 1993) and to avoid the inevitable decline in host quality as the season progresses (Feeny, 1970; Hunter & Elkinton, 1999). Thus, the seasonal period of host suitability defines a phenological window and there is strong selective pressure for an herbivore to be well synchronized within this window (Hunter & Lechowicz, 1992; van Asch & Visser, 2007).

Synchrony with the host at the time of budburst when early-stage larvae are foraging is considered especially critical (Hunter, 1990; Zehnder *et al*., 2009) because high mortality and changes in abundance in these early stages characterize the life-history of most herbivores (White, 1993), especially Lepidoptera (Zalucki *et al*., 2002). Variation in synchrony is assumed to cause fluctuations in the abundance of herbivores (Hunter, 1992) and therefore account for the propensity in the outbreak behaviour of early-season herbivores (Hunter, 1990; Watt & McFarlane, 1991). Fitness, however, changes over the entire period of the seasonal relationship between the herbivore and its resource. Ideally, we would like to assess how this entire window varies in space and time to allow an examination of how variation in synchrony affects the distribution and abundance of herbivore populations (Visser & Both, 2005; van Asch & Visser, 2007).

Conifer-feeding budworms in the genus *Choristoneura* (Lepidoptera: Tortricidae) are among the most well-studied forest insects in North America and outbreak periodically over large areas. Budworms are early-season feeders in the extreme, overwintering as second-stage larvae and emerging in the spring several days to weeks in advance of budburst (Sanders, 1991; Nealis & Nault, 2005). During this emergence period, they disperse extensively throughout the host canopy, not only mining old needles, feeding on pollen cones when available, and foraging continuously for the first suitable buds of the season (Blais, 1952; Shepherd, 1992; Trier & Mattson, 1997), but also incurring substantial losses to the population in the process (Nealis & Lomic, 1994; Régnière & Nealis, 2007; Nealis & Régnière, 2009).

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Thomson *et al*. (1987) estimated the optimal strategy for western spruce budworm *Choristoneura occidentalis* Free, occurred when they emerged more than 2 weeks before current-year foliage was even available. Nealis and Régnière (2009) found the degree of synchrony, the period between median date of budworm emergence and median date of foliage suitability, was in the range 8–43 days in populations of budworms along a 600-m elevation gradient over five seasons and yet variation during that period had little effect on rates of change in population density. The cost of very early emergence might be offset by other factors, including the avoidance of more dire costs later in the season.

In a comprehensive series of experiments, Lawrence *et al*. (1997) showed that the fitness of spruce budworm *C. fumiferana* Clem., reared at different times of the season, on various host provenances that differed in their local phenology, declined rapidly once current-year foliage had flushed. Seasonal decreases in water content and nitrogen, and increases in fibre toughness were significantly associated with these declines. Interestingly, when budworms were placed on hosts 2–3 weeks in advance of bud-flush, which is the normal, observed phenology in the field, budworms had the best survival and reached their largest size. Apparently, budworms start the season early to avoid being late (W. Mattson, personal communication). There is a phenological window of resource availability for budworms and its significance to the ecology of these insects is defined by the extent to which the feeding stages of their life cycles coincide with the seasonal adequacy of their resource (i.e. the current-year growth of host conifers).

The present study reports a series of fitness measurements for western spruce budworm made over several years in different locations along an elevation gradient in forests of British Columbia, Canada, dominated by Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]. Western spruce budworm populations have caused visible defoliation in the southern interior of British Columbia subsequent to the late 1990s, continuing throughout the period reported in the present study (Maclauchlan *et al*., 2004; Nealis & Régnière, 2009; Nealis *et al*., 2009). By manipulating the seasonal timing of budworm cohorts and using locations that differed in elevation, the phenological window for western spruce budworm and its host could be examined over a broad-range of ecological conditions. The results are discussed with reference to measured, stage-specific rates of change in western spruce budworm populations in the field, as well as the importance of developing adequate models aiming to explore the relationship between phenological windows and population dynamics.

Materials and methods

Measuring fitness in field cohorts

Cohorts of western spruce budworm were first-generation progeny of parents collected from the study sites the previous season. Larvae were overwintered in the laboratory and reared during their early stadia on an artificial diet under an LD 16 : 8 h photocycle at 20 °C. When deployed to the field, most were recently-moulted final instars (L6), although some (<10%) were fifth instars (L5) approaching the end of that stage. These larvae were stored 24–48 h in groups of five in small, plastic cups without food at 15 °C before being taken to the field. In the field, five to 10 budworms were placed on a branch tip bearing several current-year shoots from which resident budworms had been removed. The branch tip with budworms was caged with stainless steel window screen folded into a bag and fastened with staples to contain the budworms and exclude predators. Temperature recorders placed inside and outside these cages for 1 week showed no significant diurnal temperature effect of these cages.

Cohorts were deployed at mid-crown from a 7-m orchard ladder and left until the majority of budworms had pupated. The branch tip with the caged cohorts was then cut and brought to the laboratory where it was searched and all budworm removed and counted. Survival (i.e. the first measure of fitness) was the ratio of live spruce budworm recovered to the number deployed for each cohort in each location.

Recovered pupae were weighed, their sex determined, and they were then placed in plastic cups. Budworm that were still in the final larval stage at the time of collection were placed in a ventilated plastic rearing box (16 × 8 × 3 cm) with a shoot from the same branch on which they had been caged in the field. The box was designed so that the cut end of the shoot could be placed in water to maintain hydration. The whole assembly was placed at 20 °C and checked daily. In most cases, budworms required no more than an additional 2 days to pupate. They were then removed from the rearing box and held for an additional 2 days before weighing to ensure that that their stage of development at weighing was comparable with that of cohort members that had pupated in the field.

The fresh weight of pupae is a surrogate measure of fecundity in spruce budworms (Miller, 1957; Wagner *et al*., 1987). To confirm this relationship, freshly-enclosed female moths of known pupal weight were placed separately with two male moths and a fresh shoot of Douglas-fir foliage in 500-mL glass jars covered with a screened lid. These cages were placed at 20 °C, moths were misted with water daily and egg masses were extracted weekly, until the females were dead. Egg masses from each female were held until at least some eggs had hatched to ensure fertility. The total number of eggs laid by each fertile female moth was considered to represent her lifetime fecundity. Fecundity of survivors is the second measure of fitness for each cohort in each location.

Field measures

A common garden experiment evaluated the effects of among-tree differences in host shoot development, time of season, and budworm sex on cohort survival and mean pupal weight. Ten Douglas-fir trees, approximately 10 m apart, were selected at the British Columbia, Forests, Saanich Seed Orchard in Saanichton (Table 1). Five of the trees had produced prolific cone crops that year and five had not. Cone production retards the seasonal growth of vegetative shoots in conifers and so these two categories of trees differed markedly in their shoot phenology. At the time of the experiment, current-year shoots of the five trees that had produced cones were visibly less developed relative to those on trees that had not produced

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Table 1 Location, elevation, and years for western spruce budworm cohort measurements on Douglas-fir

Location	Latitude (N)	Longitude	Elevation (m)	Years
Saanich Seed Orchard	48 °35′	−123 °23′	50	2000–2003
Clapperton Creek	50 °11′	−120 °40′	750	2000–2003
Kirby Creek	50 °11′	−120 °40′	1050	2000, 2003
Pentangle Ranch	50 °14′	−120 °39′	1350	2001–2003

Saanich Seed Orchard is in coastal British Columbia; all others are in the Nicola Valley in the southern interior of the province.

cones when compared using the bud development indices of Shepherd (1983). Differences among mean weights of pupae were analyzed by two-way analysis of variance, including all interactions among three categorical factors; day out (day 162 versus day 171), bud development (retarded versus advanced) and budworm sex (male versus female).

The Saanich Seed Orchard was one of four locations used as sites to examine seasonal changes in fitness correlates of western spruce budworm (Table 1). It is the only study site in the coastal zone; the other three are along an elevation gradient in the southern interior of British Columbia and have served as field sites for other studies of seasonal changes in the relationship between western spruce budworm and Douglas-fir (Nealis & Nault, 2005). At Saanich Seed Orchard, four to 10 cohorts were deployed between late May and the middle of July 2000–2003. This spans the potential feeding season for budworms on the coast. However, natural populations of budworm at this orchard during the present study were too low to allow observation of the actual phenology of resident budworms.

At the three interior locations, the temporal relationship between the period that experimental cohorts were feeding and the phenology of natural populations was estimated using the age distribution of resident budworms observed from periodic branch samples and by interpolating the approximate age distributions between samples with a degree-day model. A description of branch sampling and associated measures is provided by Nealis *et al*. (2009). Briefly, branch samples consisted of one or two branch tips removed from the mid-crowns of at least 10 trees per location using extendable poles equipped with a cutting head. Branches were weighed and all budworms were removed and counted, and the resulting estimate of budworm density was expressed as the number of insects per kg fresh weight of foliage. Each budworm was assigned an age category based upon size of the head capsule (Stein, 1981). This provided an empirical measure of the relative frequency of each age class at the location at that time.

The first sample of the season at each location was obtained when budworms were mainly in the second to fourth larval stages (L2–L4) and thus in advance of the stage used for cohorts (L6). A degree-day model using a threshold of 5.5 °C (Thomson *et al*., 1984) and hourly, site-specific temperature readings (Nealis & Nault, 2005) were used to advance the age distribution of the budworms between sampling events. Thermal requirements were estimated for each larval stage separately from stage-specific rates of development measured at a range of constant temperatures (V.G. Nealis, J.R. Régnière, M.K. Noseworthy, V.R. Waring and R. Turnquist, unpublished data). Because these simulations were initialized by observed age distributions of feeding budworms, the biases associated with use of degree-day models early in the season when ambient temperatures fluctuate near the threshold were reduced. Resident budworm larvae observed in branch samples were all assumed to be mid-way through the developmental period of their stage at the time of observation. The degree-day model advanced the development of each individual according to the number of degree-days measured at each site between any two dates. In this way, the age distribution of resident budworms during the period of deployment of each experimental cohort could be estimated. Branch samples taken during and after the periods when cohorts were feeding provided a check and adjustment to these estimates. The periods of cohort exposure relative to the age distribution of the resident population were categorized as: (i) 'early', when they coincided with more than 75% of the resident population in instars <L6; (ii) 'late', when they coincided with more than 75% >L6 and had completed feeding; or (iii) 'concurrent', the feeding period of cohorts coincided with that of resident final instars.

The sharp reduction in survival of budworms toward the end of the season affected sample sizes available for estimation of the mean weight of pupae in later cohorts and so a correction factor was used to enable the use of male budworm pupae in the calculation because both sexes respond equally to the seasonal changes. Female spruce budworm pupae are larger, on average, than male pupae (Table 2). For pupae recovered in all cohorts combined, female pupae weigh 1.08 times that of a male, so that the weights of male pupae were multiplied by this factor to obtain an adjusted weight independent of sex. A mean weight and its standard error were calculated for each cohort (date × location).

To compare survival of cohorts with that of concurrent, resident populations of budworms, an overall rate of survival for cohorts deployed during the late-feeding stages of resident budworms was calculated as the difference between the $\log_{10}$ total number of budworms retrieved and the $\log_{10}$ total number deployed using data from the experimental cohorts concurrent with resident, final-stage budworms. An independent measure of rate of survival of resident populations was calculated similarly as the difference between the $\log_{10}$ density of pupae (post-L6) and the $\log_{10}$ density of early-stage larvae (pre-L6) using measurements obtained from branch samples and rearing data described by (Nealis *et al*., 2009). Log survival of resident budworms was regressed on the log survival of cohorts in each year × location aiming to identify evidence of a relationship between these two independent measures of survival in the field.

Results

Relationship between weight of pupae and fecundity

There was a significant, positive relationship between lifetime fecundity of individual female western spruce budworms and their fresh weight as pupae [Fecundity (eggs) = 2088.2 (± 78.5) × Weight (g); $r = 0.61$, $P < 0.001$, $n = 87$]. The

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Table 2 Cohort survival (proportion) and mean ± SE fresh weight (g) of male and female western spruce budworm pupae on advanced and retarded shoots of Douglas-fir trees at British Columbia, Forests, Saanich Seed Orchard

Date out	Phenology of shoots	Number of insects deployed	Number of insects recovered	Survival	Pupal weight (g)	
Day 162 (11 June)	Retarded	200	97	0.48	Male	0.0861 (0.0034)[a]
					Female	0.116 (0.0041)[b]
	Advanced	200	99	0.49	Male	0.0952 (0.0028)[a]
					Female	0.121 (0.0051)[b]
Day 171 (20 June)	Retarded	75	21	0.28	Male	0.0678 (0.0072)[c]
					Female	0.0867 (0.0086)[d]
	Advanced	75	24	0.32	Male	0.0822 (0.0096)[c]
					Female	0.0935 (0.0082)[d]

Mean weights with different superscript letters are significantly different at $P < 0.001$.

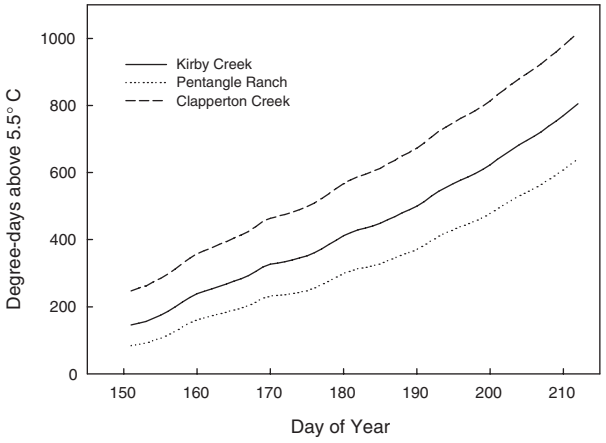

Figure 1 Cumulative degree-days above 5.5 °C during the feeding period of western spruce budworm in 2003 at three study locations that vary in elevation in the interior of British Columbia (for coordinates of locations, see Table 1).

fresh weight of pupae is therefore an adequate proxy measure of fecundity.

Thermal characteristics of field sites

Cumulative degree-days above a threshold of 5.5 °C during the period that cohorts were deployed (June and July) in 2003 for each of the three interior sites are shown in Fig. 1. The pattern of near parallel relationships between degree-days and day of year among the three sites with elevation was consistent over all years of the present study: Clapperton Creek at 750 m was warmest on average; Pentangle Ranch at 1350 m was coolest; and Kirby Creek at 1050 m was intermediate. There was no interaction between rate of accumulation of degree-days and location, so the degree-day model has no location-specific bias.

Common garden experiment

None of the three- or two-way interactions among factors in the common garden experiment were statistically significant. Among main effects, female pupae were significantly larger than males ($F_{1,233} = 20.0$, $P < 0.001$) and both male and female pupae were significantly larger in the early cohort (11 June) compared with the later cohort (20 June) ($F_{1,233} = 20.9$, $P < 0.001$). Interestingly, there was no significant difference in pupal weights between budworms reared on retarded versus advanced flushing trees in any combination ($F_{1,233} = 3.28$, $P = 0.071$). Survival rates of cohorts reinforced the effects of these factors on fitness, with early cohorts surviving equally well on both late and early flushing trees and better overall than cohorts on these same trees later in the season (Table 2).

Seasonal changes in fitness at all sites

Either one or both fitness correlates declined sharply toward the end of the season in all locations and years (Figs 2 and 3). Survival was especially reduced in the latest cohorts. Overall, the fitness of experimental populations at the Saanich Seed Orchard in coastal British Columbia (Fig. 2) was as good or better than that measured in any interior site (Fig. 3). The rate of survival for cohorts in the coastal site was >0.5 at some point in every year except 2003 and maximum mean pupal weight >0.10 g every year except 2000 (Fig. 2). By

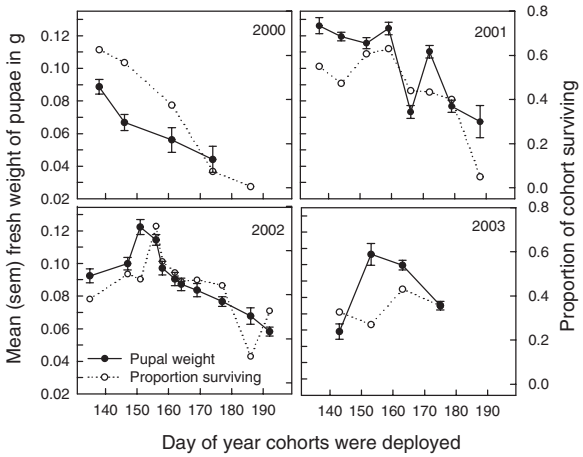

Figure 2 Mean ± SE fresh weight of pupae (g) (●) and proportion surviving (○) of cohorts of western spruce budworm deployed throughout the season at Saanich Seed Orchard in coastal British Columbia 2000–2003.

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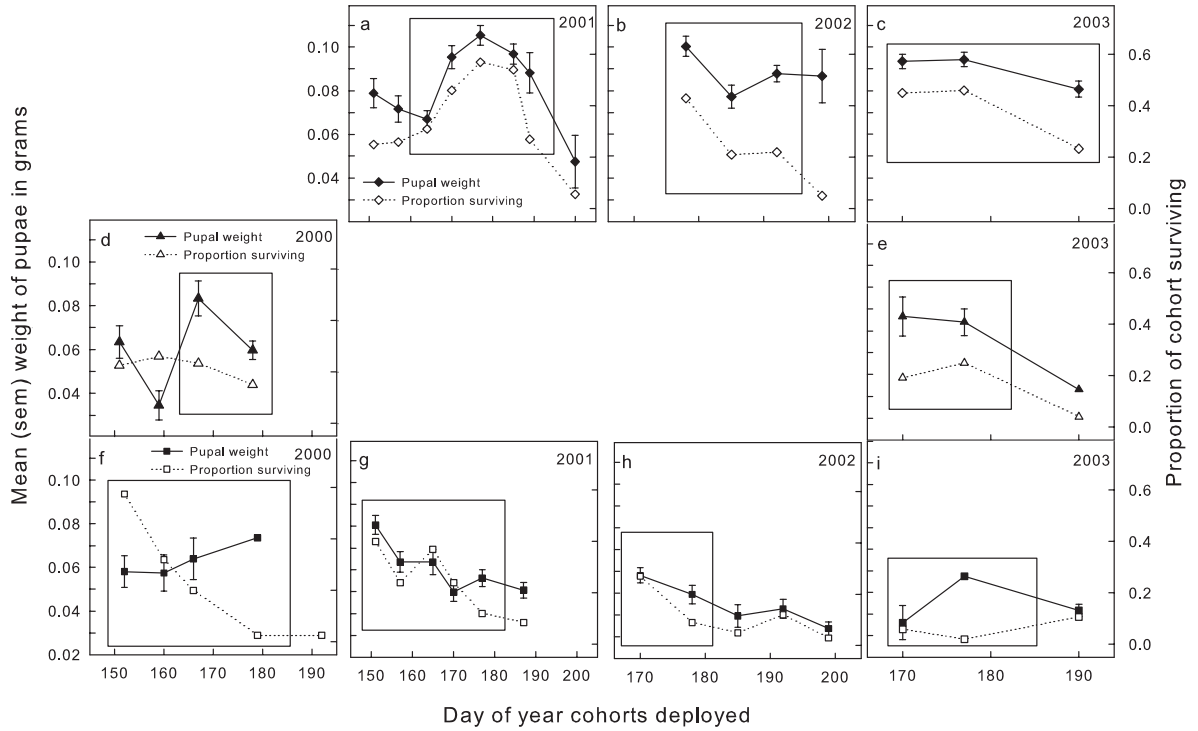

Figure 3 Mean ± SE fresh weight of pupae (g) (solid symbols) and proportion surviving (open symbols) of cohorts of western spruce budworm deployed throughout the season at three locations in the Nicola Valley, interior British Columbia 2000–2003: (a–c) Pentangle Ranch; (d, e) Kirby Creek; and (f–i) Clapperton Creek. For coordinates of locations, see Table 1. Data points in box inserts represent cohorts concurrent with late-instar stages of resident budworm populations.

comparison, rates of survival >0.5 were observed in only three cohorts at interior sites; twice at Pentangle Ranch in 2001 (Fig. 3a) and once at Clapperton Creek in 2000 (Fig. 3f). A mean pupal weight >0.10 g was measured only once in all interior sites in any year (Fig. 3a, Pentangle Ranch). Among interior sites, fitness was associated with elevation. Rates of survival were usually <0.30 (22 of 26 cohorts) at Clapperton Creek and Kirby Creek, which are the lower and middle elevation sites, but >0.30 in almost half the cohorts (seven of 15) at Pentangle Ranch, the highest elevation. Similarly, mean pupal weight of cohorts was <0.08 g for 23 out of 25 times at the lower and middle elevation sites but >0.08 g for 10 out of 15 times at the highest elevation (Fig. 3). The exceptions to these patterns were the locations and years with few data points (Fig. 3f, i) and so probably represent insufficient evidence rather than firm inference.

In the few cases where cohorts were placed early relative to the late feeding stages of resident budworms, survival and mean pupal weight were lower than later in the season when cohorts and resident late-instars were concurrent (Fig. 3a, d). The same pattern can be seen at the coastal location for survival in 2001 and for survival and pupal weight in 2002 and 2003 (Fig. 2), although the actual phenology of residents in those years is not known. The estimated phenology of resident budworms in the interior sites mostly coincided with the seasonal period when experimental cohorts indicated that budworm fitness should be at their seasonal optimum for that site (Fig. 3; box inserts indicate the estimated period of feeding for final instars). For the years of observation in the present study, western spruce budworm end-of-season phenology in the area was as good (in terms of fitness) as it could possibly be.

The limited data available provided no evidence of a statistically significant relationship between the field survival of western spruce budworm measured by cohorts and that measured independently by sampling populations directly ($F_{1,7} = 2.19$, $P = 0.18$) (Fig. 4).

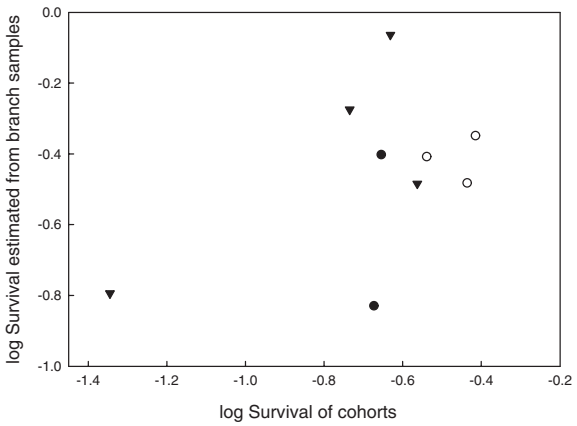

Figure 4 Relationship between $\log_{10}$ survival of western spruce budworm as estimated from branch samples and from experimental cohorts feeding at the same time at Kirby Creek (●), Pentangle Ranch (○) and Clapperton Creek (▼).

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Discussion

The cost of asynchrony between western spruce budworm and its host tree at the end of the season may be more formidable than early in the season, with consistent, annual reductions in survival of final-stage larvae, size of pupae and fecundity of adult moths over all sites in several years. The effects of seasonal change in survival were especially dramatic in the present study and provide an adaptive explanation as to why emerging in the spring more than 2 weeks before foliage is even available can still be an optimal strategy for spruce budworms (Thomson *et al*., 1984; Lawrence *et al*., 1997).

White (1993) describes the resource environment of animals as mostly inadequate. Life cycles are adapted to making the most of ephemeral, favourable periods and their dynamics reflect the extent to which they exploit successfully this temporal variability in resource quality. Each year, spruce budworms face a rapidly deteriorating resource as the season advances. The effects of this change for *C. fumiferana* are commensurate reductions in survival (Blake & Wagner, 1986), size and fecundity (Blais, 1952; Miller, 1957), and the rate of development associated with a seasonal decrease in nitrogen (Thomas, 1987) and an increase in fibre content (Lawrence *et al*., 1997) of the foliage. These same seasonal changes in survival and fecundity are reported in the present study for *C. occidentalis* and the patterns appear consistent over a broad, representative range of forest conditions and several seasons. As in other systems (Feeny, 1970; Hunter & Elkinton, 1999), a difference of even 1 week during a feeding period that may last several weeks has a significant impact on fitness correlates (Figs 2 and 3; Table 2).

The phenological window is a useful scaling concept for the investigation of interactions between an organism and its resource occurring over a wide spatial area and therefore varying weather and climate (Visser & Both, 2005). The opening of the phenological window for conifer-feeding budworms occurs when current-year buds become suitable for penetration (Blais, 1952; Sanders, 1991; Nealis & Nault, 2005). Early-stage larvae emerge several days to weeks in advance of bud suitability and forage extensively throughout the host canopy at demonstrable risk (Nealis & Lomic, 1994; Nealis & Régnière, 2009). However, in general, a prolonged period of spring emergence appears to spread this risk (Volney *et al*., 1983) and, under most conditions, budworms can utilize temporarily other resources such as the previous years' needles and pollen cones (Blais, 1952; Shepherd, 1992; Trier & Mattson, 1997). Despite wide variation in this needle-mining period among locations and years, variation in losses to populations of western spruce budworm is related to previous, density-associated damage to the host and to weather rather than to the degree of synchrony of emergence with host suitability (Nealis & Régnière, 2009).

Shifting the focus from early-season synchrony with bud-flush to declining food quality later in the phenological window and the final feeding stages of budworms relates directly to discussion of population dynamics because current evidence suggests that variation in survival at the end of the feeding stages is critical to intergeneration rates of change in budworms (Royama, 1984; Régnière & Nealis, 2007). Campbell (1993) noted a steady decline in generation survival of western spruce budworm during outbreaks in the U.S.A. and suggested that this pattern was the result of damage-related changes in host quality. His conclusion, however, was based on early-season feeding stages because density estimates for later feeding stages were not available. Host suitability during this early-season stage does matter, although for physical, not nutritional, reasons (Nealis & Nault, 2005; Nealis & Régnière, 2009). Experimental studies found little evidence for constitutive or induced plant defenses in the western spruce budworm system (Clancy, 2002) as had already been concluded for eastern spruce budworm (Mattson *et al*., 1991). Measured variation in tree susceptibility to western spruce budworm was related more to relative differences in tree phenology (Chen *et al*., 2003), as confirmed by the field results reported in the present study. Also noteworthy was that phenology-based differences between trees were only apparent early in the season. Once buds of trees that varied in early-season phenology had flushed and were suitable for budworms, differences among putative resistant and susceptible trees disappeared (Chen *et al*., 2003). As shown by the results in Table 2, even relatively small seasonal differences (9 days) can lead to greater effects on fitness of late-season cohorts than evident differences in phenology between host trees at the same location. Thus, significant inter-tree variation in host phenology is expressed early in the season. By the end of the season, the quality of all tree foliage as a resource for budworms deteriorates at the same time (Figs 2 and 3) given the among-site differences in ambient temperature (Fig. 1). Hence, there is a beneficial fitness value in emerging early, foraging extensively to find the earliest buds, and getting the greatest value from a rapidly deteriorating resource.

Both survival and fecundity of late-season cohorts in coastal British Columbia were superior to those measured in the interior (Figs 2 and 3), yet recent outbreaks have occurred exclusively in the interior. Constraints on both sides of the phenological window may be at play. Increasing early-season asynchrony associated with climate change has been suggested to explain the poor performance of western spruce budworm in coastal British Columbia and the recent disappearance of outbreaks there (Thomson & Benton, 2007), although other possible factors cannot be ruled out. Within a region, the severity of outbreaks is stratified commonly by elevation (Thomson *et al*., 1984; Shepherd, 1985) and the results of the present study show that this could be associated with variation in fitness along a gradient associated with resource conditions late in the phenological window (Fig. 3). During the period of the present study, western spruce budworm populations were defoliating the highest elevation Douglas-fir forests in the region for the first time in recent records (Nealis *et al*., 2009), which is consistent with this elevation gradient in late-stage fitness (Fig. 3).

If western spruce budworm is in an annual race to complete maturation before limited by the quality of the resource, does variation in that phenological window of suitability explain rates of change in populations? The results obtained in the present study are equivocal. Very low rates of survival measured in resident populations at Kirby Creek in 2000 and Clapperton Creek in 2005 contrasted with relatively high survival in all other plot-years (Fig. 4). These two measures of low survival are affected by the imprecision associated with

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estimating low densities in the field, whereas the cluster of points showing relatively good survival would be expected for sites within a region experiencing high population densities and good survival during these particular years (Maclauchlan *et al*., 2004; Nealis & Régnière, 2009; Nealis *et al*., 2009). Thus, the absence of a statistically significant relationship may be more the result of insufficient variation in the observed survival rates for this particular period and place than no actual effect. Evidence of a dominant effect of phenology may be more evident either where populations are sparse or at the margins of their geographical range of climatic suitability where asynchrony would further reduce rates of survival that are already relatively poor.

Rates of change in population density of western spruce budworm during the period of the present study were more closely related to losses associated with natural enemies (Nealis *et al*., 2009) and previous defoliation (Nealis & Régnière, 2009). In the few other studies where phenology and insect abundance were compared directly, other factors similarly affected the hypothesized relationship between synchrony and population performance (Watt & McFarlane, 1991; Hunter, 1992; Hunter & Elkinton, 2000; Zehnder *et al*., 2009). It is likely that spatial and temporal variation in the phenological window is one of many factors contributing to population dynamics of a species, and empirical studies such as these may be limited in identifying fully the population consequences of this variability. Greater integration of process-based phenology models with sufficient population data is required to incorporate estimated phenological windows into the analysis of population behaviour over a range of densities, landscapes and timeframes.

The concept of a phenological window offers a powerful approach to explaining the geographical and host range distributions of both native and invasive forest insects and the potential implications of climate change (Du Merle *et al*., 1992; Logan *et al*., 2003; Visser & Both, 2005; van Asch & Visser, 2007; Safranyik *et al*., 2010). Under different climate regimes, phenological relationships may be different and our notions of susceptibility and risk of disturbance from these insects in need of critical re-evaluation.

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