WHITE SPRUCE AND THE SPRUCE BUDWORM: DEFINING THE PHENOLOGICAL WINDOW OF SUSCEPTIBILITY

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Abstract

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Synchrony of insect and host tree phenologies has often been suggested as an important factor influencing the susceptibility of white spruce, *Picea glauca* (Moench) Voss, and other hosts to the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae). We evaluated this hypothesis by caging several cohorts of spruce budworm larvae on three white spruce populations at different phenological stages of the host trees, and then comparing budworm performance with host phenology and variation of 13 foliar traits. The beginning of the phenological window of susceptibility in white spruce occurs several weeks prior to budbreak, and the end of the window is sharply defined by the end of shoot growth. Performance was high for the earliest budworm cohorts that we tested. These larvae began feeding 3–4 weeks prior to budbreak and completed their larval development prior to the end of shoot elongation. Optimal synchrony occurred when emergence preceded budbreak by about 2 weeks. Larval survival was greater than 60% for individuals starting development 1–3 weeks prior to budbreak, but decreased to less than 10% for those starting development 2 or more weeks after budbreak and thus completing development after shoot elongation ceased. High performance by the budworm was most strongly correlated with high levels of foliar nitrogen, phosphorous, potassium, copper, sugars, and water and low levels of foliar calcium, phenolics, and toughness. These results suggest that advancing the usual phenological window of white spruce (i.e. advancing budbreak prior to larval emergence) or retarding budworm phenology can have a large negative effect on the spruce budworm's population dynamics.

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Résumé

Le synchronisme de la phénologie d'un insecte et de celle de son hôte est souvent invoqué pour expliquer la sensibilité de l'épinette blanche, *Picea glauca* (Moench) Voss, et d'autres arbres hôtes à la Tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae). Nous avons étudié la validité de cette hypothèse en encageant plusieurs cohortes de larves de la tordeuse sur trois populations d'épinettes blanches à divers stades phénologiques; nous avons ensuite observé la performance des tordeuses en fonction de la phénologie des hôtes et en fonction de 13 caractéristiques foliaires. Le début de la période de sensibilité de l'épinette se produit plusieurs semaines avant l'éclosion des bourgeons et la fin de la période arrive abruptement, à la fin de la croissance des rameaux. La performance s'est avérée très bonne chez les cohortes les plus hâtives de tordeuses que nous avons testées. Les larves ont commencé à se nourrir 3–4 semaines avant l'éclosion des bourgeons et avaient complété leur développement avant la fin de la croissance des rameaux. Le synchronisme était optimal lorsque l'émergence précédait l'éclosion des bourgeons d'environ 2 semaines. La survie des larves s'est avérée supérieure à 60% chez les individus qui ont commencé à se développer 1–3 semaines avant l'éclosion des bourgeons, mais a été estimée à moins de 10% chez les individus qui ont commencé à se développer 2 semaines ou plus après l'éclosion des bourgeons et qui ont donc complété leur développement après la période d'élongation des rameaux. La meilleure performance des tordeuses était en forte corrélation avec des concentrations foliaires élevées d'azote, de phosphore, de potassium, de cuivre, de sucres et d'eau, avec de faibles concentrations foliaires de

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calcium et de produits phénolés et avec une coriacité peu élevée. Ces résultats semblent indiquer que le déplacement de la fenêtre phénologique habituelle de l'épinette blanche pour qu'elle couvre une période plus précoce (par manipulation de la période d'éclosion des bourgeons de façon à ce qu'elle se produise avant l'émergence), ou le retard de la phénologie de la tordeuse pourraient avoir des effets négatifs importants sur la dynamique des populations de tordeuses.

[Traduit par la Rédaction]

Introduction

The spruce budworm, *Choristoneura fumiferana* (Clemens), is the most important forest defoliator in North America, causing 10–55 million ha of severe defoliation during outbreaks that last for several years (Blais 1983; Hardy et al. 1986) in boreal forests of white spruce [*Picea glauca* (Moench) Voss], red spruce (*P. rubens* Sarg.), black spruce [*P. mariana* (Mill.) B.S.P.], and balsam fir [*Abies balsamea* (L.) Mill.]. The reasons for vast, long-lasting outbreaks of spruce budworm are many (Royama 1984; Mattson et al. 1988). However, central to any explanation is the fact that the budworm is an early spring consumer of newly developing foliage. Emergence of overwintering second-stage larvae generally coincides with bud swelling and precedes budbreak of their principal host trees, balsam fir and white spruce (McGugan 1954; Greenbank 1963). Feeding while the leaves are actively growing in the spring confers certain crucial advantages to the budworm. For example, new foliage is usually nutrient rich, fiber poor, and succulent, thereby enhancing insect growth, survival, and fecundity. In fact, it appears that spring folivores, as a group, have evolved to exploit plant foliage when it is at its yearly optima for insect nutrition (Mattson and Scriber 1987).

Spring leaf exploitation is not, however, without risk. Leaf development can begin either too early or too late from the insect's perspective. Foliage quality is initially high, but it also declines quickly because of foliar expansion, causing a dilution of essential nutrients and water, and a simultaneous increase in fiber, tissue toughness, and some weakly essential nutrients (e.g. calcium) (Mattson and Scriber 1987; Clancy et al. 1988; Mattson et al. 1991). If leaf development is "too early," the speed at which foliage quality deteriorates may outpace an insect's capacity to adjust physiologically, thereby setting the stage for a race by the insect to complete its feeding before the plant reaches a point of marginal usability. If leaf development is "too late" (e.g. delayed budbreak), the insect may encounter a long initial period of no food or poor quality food. The stage of leaf development encountered by the folivore, i.e. the degree of insect–host synchrony, is dependent on variation in both insect and host tree phenologies. This logic has been the basis of the "windows of susceptibility hypothesis" (Feeny 1976; Mattson et al. 1982). The hypothesis presumes that there is a finite limit to such windows, outside which insect success is practically nil. If such a window exists, it can provide strong selective pressure for the insect population to synchronize both its emergence and development with the plant, so as to maximize its reproductive output. Recently, several studies provide convincing experimental evidence that supports the window hypothesis for several species of spring folivores (Leather 1986; Watt 1987, 1992; Du Merle 1988; Raupp et al. 1988; Hunter 1992; Hunter and Lechowicz 1992; Quiring 1992, 1994).

In the case of the spruce budworm, numerous studies have suggested there may be only a short window of opportunity (e.g. Blais 1957; Eidt and Cameron 1971; Thomas 1987; Volney and Cerezke 1992). Similar phenological dependence has been suggested for the western spruce budworm (*C. occidentalis* Freeman) in western North America (Cates et al. 1983b; Volney 1985; Shepherd 1992) and its European counterpart, the European fir budworm (*C. murinana* Hübner) (Schönherr 1980; Du Merle et al. 1992). Asynchrony results in reduced survival, growth, and fecundity in budworms (Greenbank 1956; Eidt and Little 1970; Eidt and Cameron 1971; Mattson et al. 1983; Thomas 1983, 1987; Blake and Wagner 1986). The causes of asynchrony may be related to inherent differences in the mechanisms

controlling larval emergence and initiation of vegetative growth (Volney 1985; Dewar and Watt 1992). For example, larval emergence is determined primarily by ambient air temperatures (Thomas 1976; Régnière 1990), whereas initiation of vegetative growth in several conifers is determined by both soil and air temperatures (Cleary and Waring 1969; Lavender et al. 1973; Beckwith and Burnell 1982; Lopushinsky and Max 1990).

The concept of phenological windows is important not only from a theoretical perspective but also from a practical one. If such a window can be verified and defined for a particular insect and host, then it has far-reaching implications for insect management. An understanding of the phenological window would permit more effective timing of management activities (Volney and Cerezke 1992) and possible development of new management tactics. For example, by delaying insect development, such as through application of a mild feeding deterrent, larval development could be eclipsed by the close of the window and hence cause insect populations to decline. Alternatively, the pattern of host phenological windows confronting a target insect could be manipulated through tree selection and planting programs (Shepherd 1994).

Our study evaluated the phenological window of the spruce budworm on white spruce by examining these phenological relationships over the insect's entire post-diapause larval development under field conditions. Several levels of insect–host asynchrony are used, and measurements are made of seasonal variation in several plant traits. Our objectives were to (1) test the hypothesis that a phenological window of susceptibility to spruce budworm exists in white spruce, (2) determine the exact timing and duration of such a window of susceptibility, and (3) describe phenological changes in key host traits that are related to host susceptibility.

Materials and Methods

We conducted experiments between 1985 and 1987 in a white spruce provenance plantation located in Wexford Co., Michigan, in the Huron-Manistee National Forest. The trees were 27 years old in 1985 and were part of the "White Spruce Seed Source Variation Study G-113," which was established by the USDA North Central Forest Experiment Station in 1962 (Nienstaedt 1969; Wright et al. 1977).

Phenological Window of Susceptibility. We evaluated the relationship between host phenology and budworm performance by using three white spruce populations that differed in their timing of bud flushing and by introducing eight cohorts of spruce budworm larvae to these trees at different phenological stages of the host trees. This gave a 3×8 factorial experiment. Seed sources 1665 from Stony Rapids, Saskatchewan (SASK), and 1677 from McLeod Lake, British Columbia (BC), were selected as the early- and late-flushing populations, respectively, and seed source 1663 from Beachburg, Ontario (ONT), was an intermediate- to late-flushing population (Department of Forestry, Michigan State University, unpublished data). Eight open-grown trees were randomly selected from each population.

Insects were obtained from a colony maintained by the Insect Production Service of the Forest Pest Management Institute, Canadian Forest Service, in Sault Ste. Marie, Ontario. They were received as overwintering second-instar larvae that had completed diapause requirements and remained enclosed in their silken hibernacula on gauze strips. We placed budworms on trees by enclosing a gauze patch containing a known number of larvae (ca. 30) within a small-mesh nylon sleeve cage (70 cm length) on a mid-crown branch of each tree; 24 branches (three spruce populations × eight trees/population) were caged for each of the eight budworm cohorts. Each tree eventually received a total of eight cages, one for each budworm cohort. Cages were located on all sides of each tree to prevent excessive destruction of foliage on one side when branches were later cut from the trees. Cage positions were uniformly distributed around the tree circumference within each spruce population and budworm cohort.
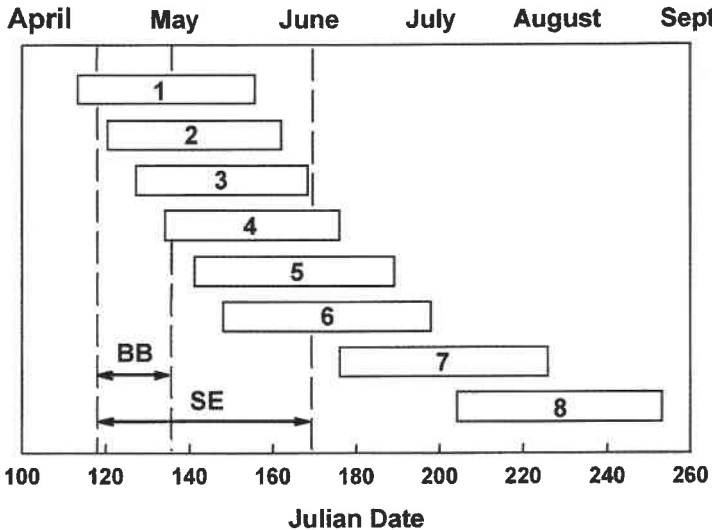
THE CANADIAN ENTOMOLOGIST

FIG. 1. Relative timing of larval development of eight spruce budworm cohorts and ranges of budbreak (BB) and shoot elongation (SE) periods of white spruce trees in 1985.

The timing of placement of the eight budworm cohorts ranged from 3 weeks prior to budbreak (i.e. bud scales separating and exposing green needles) to about 4 weeks after completion of shoot growth (Fig. 1). The first cohort started near the time of spring emergence of wild populations of second-instar budworms, which was estimated to peak at about 100 degree-days (dd) based on a threshold of 5.6°C and a starting date of 1 March (Miller et al. 1971; Shaw and Little 1973; Thomas 1976). Cohort 1 was placed on the trees on 23 April 1985 at ca. 170 accumulated dd (4 calendar days after the 100 dd target), or about 1–2 weeks prior to budbreak on early-flushing trees. The next five cohorts were started at weekly intervals. Cohort 2 (30 April, 230 dd) and cohort 3 (7 May, 290 dd) started during the budbreak period. Cohort 4 (14 May, 400 dd) started when new shoots were 50% elongated on early-flushing trees, and buds were breaking on late-flushing trees. Cohort 5 (21 May, 470 dd) and cohort 6 (28 May, 550 dd) started later in the shoot growth period. Cohort 7 (25 June, 900 dd) and cohort 8 (23 July, 1370 dd) were started 4 and 8 weeks, respectively, after cohort 6; both began after the cessation of shoot growth.

To provide fresh, vigorous insects for all cohorts, larvae were received in three batches from the Canadian stock colony (April batch = cohorts 1–3, May batch = cohorts 4–6, June batch = cohorts 7 and 8). Larvae used for cohorts 1–7 were stored at 5°C for no more than 3 weeks prior to use in the field; cohort 8 was stored for 5 weeks. Variation in budworm growth and survival among batches was minimal for insects reared in controlled conditions as part of laboratory feeding studies (Lawrence 1990).

Each cohort remained on the trees until larval development was completed, i.e. about 6 or 7 weeks. When most individuals of a cohort attained the pupal stage, all caged branches of that cohort were cut from the trees and examined in the laboratory. Pupae were held in individual plastic vials at ca. 23°C, and adults were frozen within 24 h after emergence, oven-dried at 60°C, sexed, and weighed. Budworms that were still in the final larval stage when collected were fed current-year foliage from the same spruce population and allowed to complete development in petri dishes. Larvae that did not pupate within 4 days after removal from the trees were not included in analyses of body mass; only 5% of adults were thus excluded.

We measured ambient air temperature each year using a recording hygrothermograph. From these records, we computed cumulative degree-days (threshold = 5.6°C) from 1 March using a sine-wave method (Allen 1976).

Survival of Early and Late Cohorts. In 1987, we assessed the effect of insect–host synchrony on the form of the spruce budworm survivorship curve by using an "early" cohort (started 10 April at 133 dd) and a "late" cohort (1 June at 760 dd) on 10 trees of the population from Ontario. We followed the techniques used in 1985, but we evaluated survival at several points during larval development of each cohort, rather than only at pupation. Budworms were caged on five mid-crown branches of each tree for each cohort. We then removed a caged branch from each tree at four 7- to 8-day intervals, examined them in the laboratory, and recorded budworm survival, developmental stage, and location on the branch. The fifth caged branch on each tree was removed when most budworms were pupae. We computed the average larval developmental stage for each sample date by measuring larval head capsule widths (McGugan 1954; Bean and Batzer 1957; Crummey and Otvos 1980).

Seasonal Variation in Host Traits. We monitored the phenological stage of buds and percentage shoot elongation on all study trees at weekly intervals from mid-April until growth ceased in 1985 and 1986. Measurements were made on four randomly selected terminal shoots of lateral branches (two on the north side and two on the south) at mid-crown level of each tree. The phenological stage of the terminal bud on each shoot was rated using a six-point system following Nienstaedt and King (1970): (1) bud in winter condition; (2) bud beginning to swell; (3) bud globose and swelling prominently; (4) bud green with bud scales expanding and thinning but still intact; (5) "budbreak," bud scales separating and exposing green needles; (6) shoot elongating.

Seasonal variation in levels of foliar nitrogen, minerals, total sugar, and total phenolics was measured in 1985; seasonal variation in leaf water content and leaf toughness was measured in 1986. In 1985, the first foliage collection was made on 1 May, immediately prior to budbreak on the earliest-flushing trees, and consisted of separate samples of the previous-year (1-year-old needles) and current-year (expanding vegetative buds) growth. Subsequent samples were collected at 1- to 3-week intervals and consisted of only current-year foliage. Each sample of shoots (ca. 5 g fresh weight/tree) was sealed in plastic bags, transported to the laboratory in ice-chilled containers, and stored at −10°C. Samples were next oven-dried at 60°C for 48 h, twigs and bud scales were removed, and the foliage was ground to a fine powder in a Wiley mill and stored in a dry condition at ca. 22°C until further processing.

Total nitrogen and total phosphorous were determined with standard micro-Kjeldahl techniques (Jones and Case 1990). Totals for elemental minerals (K, Ca, Mg, Mn, Cu, Fe, Zn) were obtained using plasma emission spectroscopy on a Beckman Spectrometrics Spectraspan Model III-A DCP emission spectrometer (DeBolt 1980).

We analyzed the soluble sugar content of samples with a high pressure liquid chromatography (HPLC) technique that efficiently extracted five-, six-, and 12-carbon sugars (R. Haack et al., unpublished data). Each sample was prepared by placing 200 mg of powdered foliage and 10 mL of 83:17 acetonitrile/water in a centrifuge tube and shaking the tube for 24 h in darkness. The sample was then centrifuged briefly; the supernatant passed through a Sep-pak C_{18} cartridge (Waters Assoc.) to remove particulate matter and unwanted compounds; and the sample was refrigerated in a glass vial until analyzed. Analysis was accomplished by injecting 75 µL of sample onto a Waters HPLC system with a Waters carbohydrate analysis column and differential refractometer, using a mobile phase of 83:17 acetonitrile/water and a flow rate of 2 mL/min. A Hewlett Packard integrator performed data integration. Peaks were identified by comparison with retention times of known standards and quantified by comparison with a calibration curve.

Analysis of total phenolics began with extraction of 100 mg of powdered foliage in 20 mL of 50% methanol, shaking in darkness for more than 8 h, and then filtering. The filtrate was analyzed on an Alpkem Rapid Flow Analyzer using the Folin-Denis reagent with a 50% tannic acid solution (50% v/v methanol) as the standard.

Measurements of the phenological changes in leaf water content and leaf toughness were made in 1986 on the same trees studied in 1985. Foliar samples for water content analysis were collected during 1100–1500 hours at 1- to 2-week intervals during April–May and at 3- to 4-week intervals during June–August. Each sample consisted of one shoot collected at mid-crown level on the south side of each tree. The needles were immediately cut from each shoot, placed in tightly sealed, pre-weighed plastic vials, and transported in cool, dark conditions to the laboratory. No samples were collected when moisture (dew or precipitation) was visible on the foliage. Fresh mass of the foliage was determined within 12 h after collection, and dry mass was determined after 48 h of drying at 60°C.

For leaf toughness, one shoot was collected per tree, placed in a tightly capped vial, transported in cool, dark conditions to the laboratory, and stored at ca. 5°C until further processing. Using 10 needles per shoot, toughness was determined by measuring the grams of force required to break a needle using a penetrometer similar to that developed by Feeny (1970). A cylindrical aluminum shaft (2.5 mm diameter) was used to break each needle as it was held in place spanning a 3.0-mm hole in an aluminum block. A Chatillon fruit puncture gauge measured the level of force at which the needle broke.

Statistical Methods. Budworm performance was measured by computing percentage larval survival (second-instar larva to pupation) and percentage pupal survival (pupation to adult emergence) within each caged branch, and adult dry mass (mg) and length of development period (second-instar larva to adult emergence measured in degree-days) for each insect. Accumulated degree-days, rather than number of days, were used for measuring development because temperature patterns varied among budworm cohorts developing at different time periods. All variables were examined for normality; arcsine transformation was performed on larval survival data prior to data analysis.

We used multivariate repeated measures analysis (Winer 1971; LaTour and Miniard 1983) with PROC GLM of SAS (SAS Institute Inc. 1988) to evaluate the effects of budworm cohort and spruce population on budworm performance and the effects of sample date and spruce population on host foliage quality. Individual tree values were used in all repeated measures analyses. For budworm development time and adult body mass, variables having multiple observations per tree at each repeated measure (cohort), a mean value was computed for each tree and cohort. Spruce population was the between-subjects effect. Budworm cohort or foliage sample date was the within-subject effect. Wilks' lambda criterion (Morrison 1976) was the multivariate test statistic used for the repeated measure effect (cohort or sample date) and for the repeated measure × spruce population interaction. F-values were computed from Wilks' lambda using Rao's (1973) procedure. The test for the between-subjects (population) effect is a univariate analysis of variance of tree sums (values for each tree are summed across all repeated measures).

We further examined the relationship between budworm performance and host phenology by comparing the patterns in performance data with the seasonal variation in foliar nutritional traits. The value of each foliar trait on each tree was estimated for a point in late larval development of each budworm cohort equivalent to 75% of the total degree-days required for larval development. The 75% point in larval development is roughly equivalent to the early sixth larval stadium (Régnière 1987) and the start of the period of the greatest food consumption and gain in body mass (Retnakaran 1983). Foliar values of each tree were determined individually for budworm cohorts 1–6 (i.e. the cohorts that were started at weekly intervals in the spring prior to and during shoot growth) by interpolation of the foliar data using appropriate degree-day values. Relationships between budworm performance and

foliar nutritional traits were then evaluated by examining bivariate plots of the data and using linear and polynomial regression techniques with analysis of homogeneity of variances (SAS Institute Inc. 1988).

Results

Phenological Window of Susceptibility. Budworm performance declines with advancing tree phenology. As expected, cohort timing significantly affected larval survival among the eight budworm cohorts (repeated measures analysis, $F = 334.8$, $P < 0.001$, df = 7,15). Survival was, on average, more than 60% for the first three cohorts, but then dropped to less than 35% in cohort 4, and further deteriorated to less than 10% in each of the last three cohorts (Fig. 2A). Because of the poor survival in later cohorts, analyses on other performance variables for budworms were possible only for cohorts 1−4, for which the necessary balanced data sets were available. Timing of cohorts 1−4 significantly affected ($P < 0.001$) all performance variables for spruce budworms (Table 1).

Pupal survival was generally high ($>75\%$) for all cohorts, although it was lowest in the first two (Fig. 2A). Reduced pupal survival in early cohorts was partially the result of parasitism by ichneumonid wasps, which were able to parasitize some budworms by inserting their ovipositors through the cloth surface of the branch cages. Parasitoids emerging from budworm pupae accounted for more than a third of total pupal mortality in cohorts 1−3, although they rarely emerged from pupae in later cohorts.

The pattern of adult mass among cohorts followed the pattern of larval survival: steadily decreasing from averages of 26.0 and 13.6 mg (females and males, respectively) in cohort 1 to 12.6 and 6.2 mg in cohort 8, with the largest decrease in mass occurring between cohorts 3 and 4 (Fig. 2B). The number of degree-days required for budworm development substantially increased in the later cohorts (Fig. 2C). For example, female development needed only 612 dd in cohort 2, but 957 dd in cohort 7. Male development needed only 585 dd in both cohorts 1 and 2, but 935 dd in cohort 7.

Adjusting differences in spruce phenology removes spruce population effect. Spruce population significantly ($P \leq 0.05$) affected all performance variables for budworms except pupal survival (Table 1). SASK trees were the least suitable hosts for budworms (Fig. 3), although there was a significant population × cohort interaction effect on adult mass and length of development.

One explanation for the reduced budworm performance on SASK trees is the more advanced phenology of those trees. To test this hypothesis, repeated measures analyses were performed using equivalent cohorts from phenologically similar hosts, i.e. budworm cohorts 1, 2, and 3 on SASK trees were reclassified as equivalent to cohorts 2, 3, and 4 on the ONT and BC trees (Fig. 3). The phenology of the SASK population was about 1 week ahead of the other two populations, and budworm cohorts 1−4 were started at 1-week intervals. This gave three levels of insect–host synchrony that were common to all three spruce populations, i.e. budworm cohorts starting 2 weeks prior to budbreak, 1 week prior, and the same time as budbreak. As a consequence, the spruce population effect disappeared ($P > 0.05$) for all performance variables for budworms except female adult mass (Table 1). Examination of the phenologically aligned cohorts in Figure 3 indicates that the highest larval survival, largest body mass, and shortest development time occurred among those insects that were placed on the trees at 1−3 weeks prior to budbreak.

Survival of Early and Late Cohorts. The general shape of the spruce budworm survivorship curves was a negative exponential for both early (April−June) and late (June−July) cohorts (Fig. 4). More than 85% of the total larval mortality occurred by the time larvae became third instars, thus demonstrating a typical "type A" survivorship curve (sensu Price 1984) as was reported by Morris and Miller (1954) for "wild" spruce budworm.
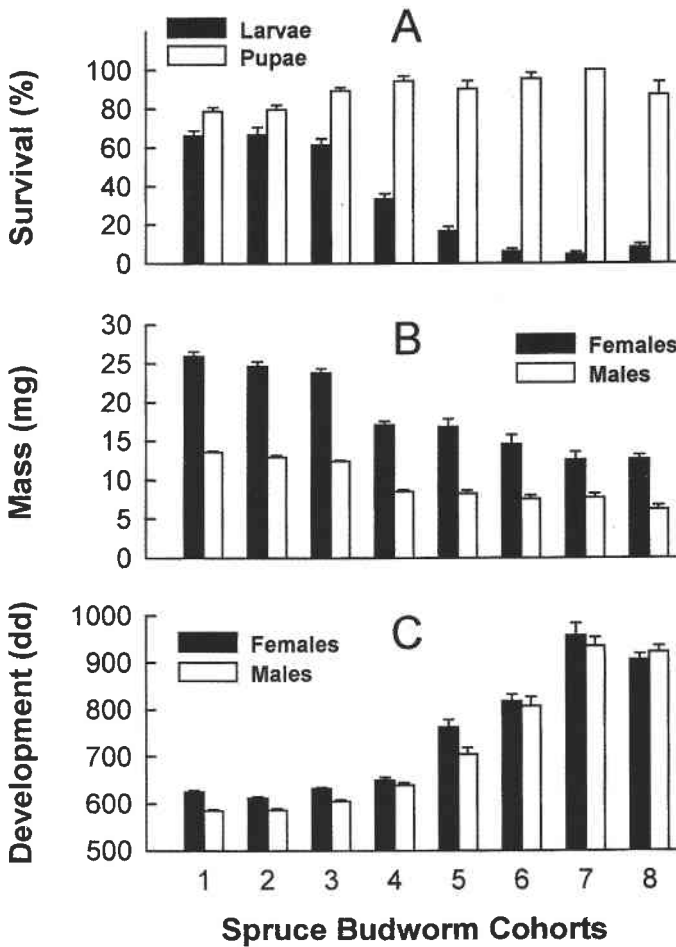
FIG. 2. Mean (+ SE) (A) percentage survival of larvae and pupae, (B) female and male adult dry mass, and (C) female and male length of development (degree-days, base 5.6°C) from second instar to adult for eight spruce budworm cohorts caged on white spruce in 1985.

Prior to budbreak, most second- and third-instar larvae of the early cohort were either mining the previous year's needles or were in silk webbing at the bases of those needles (Table 2). As the vegetative buds became swollen, more larvae were located adjacent to or within the buds. Larvae were clearly able to penetrate buds that had reached a phenology rating of 3 (buds globose and swelling) or greater. After budbreak, older larvae fed primarily on foliage of newly expanding shoots. In contrast, second and third instars of the late cohort were rarely found on or in the 1- and 2-year-old foliage (Table 2). Instead, almost all mining occurred in the new needles of expanding shoots. Thus, late cohort larvae fed almost exclusively on current-year foliage throughout their development.

The seasonal trends in budworm performance in 1987 closely matched results from 1985. Larval survival and adult mass were much higher and degree-days required for development were many fewer for the early cohort (started 4 weeks before budbreak) than for the late cohort (started 3 weeks post-budbreak) (Table 3). The early cohort in 1987 was

TABLE 1. Multivariate repeated measures analysis of spruce budworm performance on three white spruce populations (WS pop.) in 1985 using budworm cohorts (SBW coh.) 1–4, or three phenologically similar cohorts (cohorts 1–3 on SASK trees and cohorts 2–4 on ONT and BC trees), as repeated measures

Dependent variable	Source of variation	Cohorts 1–4*			Phenologically similar cohorts†		
		Wilks' lambda	F-value	Prob.	Wilks' lambda	F-value	Prob.
Larval	SBW coh.	0.1458	37.10	<0.001	0.3194	21.31	<0.001
survival (%)	WS pop.		5.39	0.013		0.97	0.397
	Coh. × pop.	0.7258	1.10	0.380	0.6643	2.27	0.079
Pupal	SBW coh.	0.3441	12.07	<0.001	0.2789	25.86	<0.001
survival (%)	WS pop.		1.27	0.300		0.75	0.487
	Coh. × pop.	0.8056	0.73	0.634	0.9485	0.27	0.897
Female	SBW coh.	0.1267	43.66	<0.001	0.2125	37.06	<0.001
adult dry	WS pop.		16.96	<0.001		8.23	0.002
mass (mg)	Coh. × pop.	0.4194	3.45	0.008	0.5485	3.50	0.015
Male	SBW coh.	0.0467	129.29	<0.001	0.1428	60.04	<0.001
adult dry	WS pop.		13.98	<0.001		2.67	0.093
mass (mg)	Coh. × pop.	0.5540	2.18	0.067	0.3452	7.02	<0.001
Female length	SBW coh.	0.3848	10.12	<0.001	0.4556	11.95	<0.001
of development	WS pop.		4.49	0.024		2.56	0.102
(degree-days)	Coh. × pop.	0.3821	3.91	0.004	0.6558	2.35	0.071
Male length	SBW coh.	0.2757	16.64	<0.001	0.2108	37.44	<0.001
of development	WS pop.		5.30	0.014		0.64	0.539
(degree-days)	Coh. × pop.	0.3032	5.17	0.001	0.7539	1.52	0.216

*Degrees of freedom for analyses of cohorts 1–4: SBW cohort = 3,19; WS population = 2,21; cohort × population = 6,38.
†Degrees of freedom for analyses of phenologically similar cohorts: SBW cohort = 2,20; WS population = 2,21; cohort × population = 4,40.

placed out 40 dd sooner (133 dd versus 173 dd) and 1–2 weeks earlier in terms of host phenology than cohort 1 in 1985. Nevertheless, both had peak pupation at ca. 85% shoot elongation. The timing of the late cohort in 1987 was slightly later than that of the sixth cohort in 1985 (starting at ca. 90% shoot elongation versus ca. 60% shoot elongation), but both had peak pupation at ca. 3 weeks after the cessation of shoot growth.

Seasonal Variation in Host Traits. Budbreak and shoot growth. Bud expansion and budbreak occurred first in the SASK population and followed about 1–2 weeks later in the ONT and BC populations in both 1985 and 1986 (Table 4). The relative timing of phenological events was nearly identical in both years. In the early-flushing SASK population, budbreak occurred between 28 April and 8 May (i.e. between 200 and 300 dd), and 50% shoot elongation occurred at ca. 13–14 May (400–410 dd) in both years. The same between-year similarities occurred for ONT and BC trees, although the timing of phenological events in these populations was 7–10 days and 100–125 dd later than that of the SASK population. The advanced phenology of the SASK population was also apparent in shoot growth (Fig. 5). The shoot growth period in BC trees coincided with ONT trees, although ONT trees had a slightly extended growth period. Budbreak timing and degree-day relationships are in complete accord with observations on early- and late-flushing white spruce clones studied by Nienstaedt and King (1970).
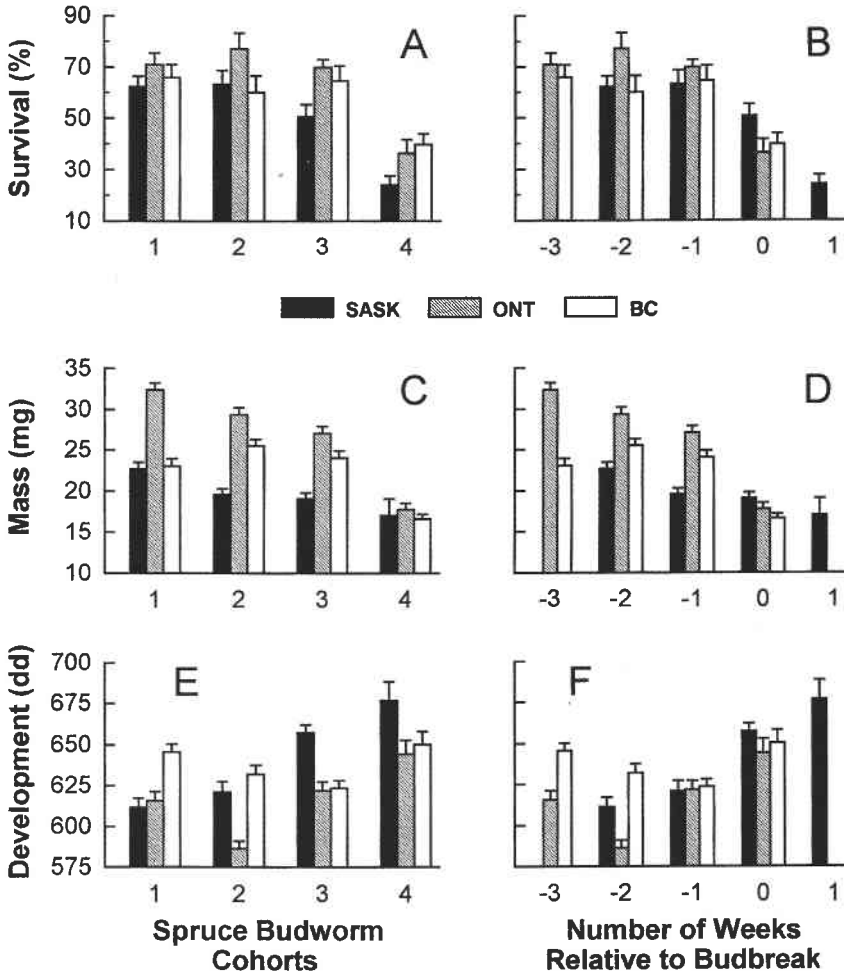
FIG. 3. Mean (+ SE) (A and B) percentage larval survival, (C and D) female adult dry mass, and (E and F) female length of development on three white spruce populations (SASK, ONT, and BC) for spruce budworm cohorts 1–4 (left column) and cohorts 1–4 grouped by phenologically similar host trees (right column). Number of weeks relative to budbreak represents the phenological timing of cohort placement on trees (budbreak = week 0).

Nutritional traits of current-year foliage. As expected, all measured nutritional traits in current-year foliage varied significantly among sample dates (repeated measures analysis; $P \leq 0.001$; df = 4,18 for water and toughness; df = 5,17 for all other traits). The greatest quantitative changes occurred during the periods of active shoot growth (Figs. 6–8). There was a significant spruce population effect for P, K, Mn, Cu, Fe, and water ($P \leq 0.05$; df = 2,21), and a population × sample date interaction effect for all nutritional traits except total sugar, Ca, and Cu ($P \leq 0.05$; df = 8,36 for water and toughness; df = 10,34 for all other traits).

Total N and P levels were highest in the swelling buds, declined rapidly during initial shoot elongation, and then remained uniformly low and stable through the summer (Fig. 6). Levels of K also declined during shoot elongation, but did not reach their lowest points until after cessation of shoot elongation (Fig. 6). Levels of Ca, Mg, Cu, and Zn in current-year foliage generally decreased during shoot elongation, but then increased thereafter (Fig. 7).
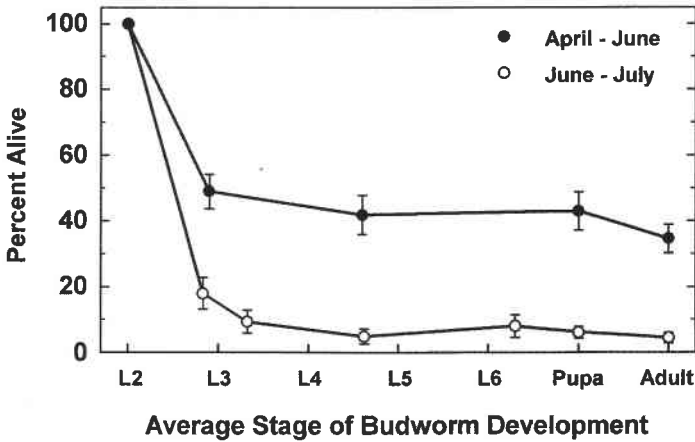
FIG. 4. Spruce budworm survivorship curves (mean percentage alive ± SE) for an early cohort (April–June) and a late cohort (June–July) on the ONT white spruce population in 1987.

The increase in Ca began in early June during the latter days of shoot elongation, whereas increases in Mg, Cu, and Zn commenced later in the summer after shoot elongation had ceased. Trends in the levels of Mn and Fe are less clear, although the levels of these nutrients generally increased during the summer (Fig. 7).

Total foliar sugar (fructose + glucose + sucrose) in new foliage peaked near the middle of the shoot elongation period and thereafter generally decreased (Fig. 8). For example, the highest total sugar levels observed on SASK (15.0%) and ONT (15.5%) trees occurred when shoot growth had reached 60% elongation, although the latter occurred 12 days later.

TABLE 2. Average larval stage and distribution of spruce budworm larvae on caged white spruce branches in relation to timing of budbreak during the 1987 survivorship experiment

| | April–June cohort | | | June–July cohort | | | |
| | Number of weeks prior to budbreak | | | Number of weeks after budbreak | | | |
Budworm parameters	2	1	0	4	5	6	7
No. larvae observed	89	102	93	50	24	13	16
Larval instar							
Average	2.8	2.9	4.6	2.8	3.3	4.6	6.0
Range	2–3	2–3	3–6	2–4	2–5	3–6	6
Percentage of total larvae by location on branch							
Old needles—Mines	49.4	14.7	1.1	2.0	0.0	0.0	0.0
Old needles—External	37.1	39.2	10.7	0.0	0.0	0.0	0.0
Vegetative buds*	6.7	40.2	64.5	—	—	—	—
New needles—Mines*	—	—	—	22.0	16.7	0.0	0.0
New needles—External*	—	—	—	54.0	50.0	76.9	81.2
Moving or not on branch	6.7	5.9	23.7	22.0	33.3	23.1	18.8

*Vegetative buds were present only during the April–June cohort. Expanded shoots with new needles were present only during the June–July cohort.

TABLE 3. Performance of the two spruce budworm cohorts in the 1987 survivorship experiment

	April–June cohort			June–July cohort		
Budworm performance	N	Mean	(± SE)	N	Mean	(± SE)
Larval survival (%)	10	43.0	(± 5.8)	10	6.2	(± 1.8)
Pupal survival (%)	10	84.2	(± 5.6)	7	81.0	(± 14.3)
Female adult dry mass (mg)	40	31.2	(± 1.0)	6	13.8	(± 1.7)
Male adult dry mass (mg)	37	14.3	(± 0.4)	4	6.5	(± 0.9)
	N	Median*		N	Median*	
Female length of development (degree-days)	40	780		6	912	
Male length of development (degree-days)	37	728		4	850	

*Median values are given for length of development because some insects in the April–June cohort had completed development prior to the time of final branch examination.

Levels of total phenolics in current-year foliage decreased during shoot elongation but increased thereafter (Fig. 8), following a pattern similar to that of foliar Ca. They fell to their lowest levels of 4–5% dw at ca. 80–90% shoot elongation in early June (ca. 600 dd). Additionally, analysis of total phenolics at the time of budbreak on a single SASK tree revealed a level (8.7%) in the newly emerging needles that was much higher than observed for other dates prior to the end of shoot growth. Mattson et al. (1988) similarly reported that total phenolic levels peaked at the time of budbreak in white spruce and declined consistently during shoot growth to a minimum occurring at ca. 600 dd.

TABLE 4. Bud phenology rating and percentage of buds burst for three white spruce populations (SASK, ONT, and BC) during April–May of 1985 and 1986 (N = 32 buds per population each year)

|			Mean bud phenology rating (± SE)			Percentage of buds burst*		
Year	Julian date	Cum. degree-days	SASK	ONT	BC	SASK	ONT	BC
1985	114	182	2.2 (± 0.1)	1.0 (± 0.0)	1.0 (± 0.0)	0	0	0
	120	234	4.3 (± 0.1)	3.0 (± 0.0)	1.9 (± 0.1)	34	0	0
	128	309	5.8 (± 0.1)	3.8 (± 0.1)	3.1 (± 0.1)	97	6	0
	135	421	6.0 (± 0.0)	5.9 (± 0.1)	5.3 (± 0.2)	100	97	75
	142	481	6.0 (± 0.0)	5.9 (± 0.1)	6.0 (± 0.0)	100	97	100
	149	570	6.0 (± 0.0)	6.0 (± 0.0)	6.0 (± 0.0)	100	100	100
1986	104	117	1.2 (± 0.1)	1.0 (± 0.0)	1.0 (± 0.0)	0	0	0
	111	149	1.5 (± 0.1)	1.3 (± 0.1)	1.0 (± 0.0)	0	0	0
	118	241	4.2 (± 0.1)	2.6 (± 0.2)	1.4 (± 0.1)	21	0	0
	125	305	5.2 (± 0.1)	3.8 (± 0.1)	2.4 (± 0.2)	100	6	0
	132	397	6.0 (± 0.0)	5.6 (± 0.1)	4.5 (± 0.1)	100	94	56
	146	556	6.0 (± 0.0)	5.9 (± 0.0)	5.7 (± 0.1)	100	100	100
	169	875	6.0 (± 0.0)	6.0 (± 0.0)	6.0 (± 0.0)	100	100	100

*Bud phenology rating ≥5, see text.
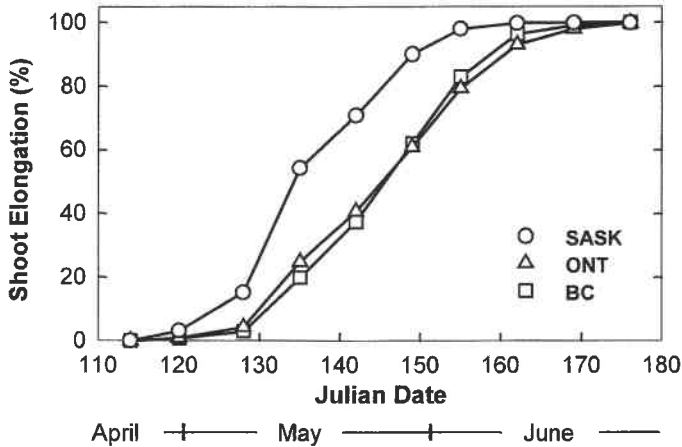
FIG. 5. Mean percentage shoot elongation of three white spruce populations (SASK, ONT, and BC) in 1985.

Water content of the current-year foliage (1986) peaked at ca. 80% for all spruce populations soon after budbreak in mid-May, and then steadily decreased during the shoot growth period to less than 60% by mid-July (Fig. 8). Toughness of the new needles (1986), however, increased rapidly during the period of shoot elongation (Fig. 8). An earlier increase in toughness accompanied the more advanced phenology of the SASK population, although population differences were not significant (repeated measures analysis; $P = 0.17$; df = 2,21).

Nutritional traits of 1-year-old foliage. One-year-old foliage was sampled from all three spruce populations (three to eight trees each) at less than 1 week prior to budbreak on the earliest-flushing trees. Not surprisingly, the levels of most foliar traits (Table 5) were similar to those in end-of-season current-year foliage (Figs. 6–8). However, a major exception to this trend was water content (46%) which was about 20% less than the mid-August level (57%) in new foliage.

Relationship of Budworm Performance to Host Foliar Traits. Better budworm performance (i.e. higher survival, larger body mass, and shorter development time) was associated with higher levels of foliar N, P, K, Mg, Cu, sugar, and water, and lower levels of foliar Ca, Mn, phenolics, and toughness during larval development (Table 6).

All performance variables for budworms were strongly associated with levels of N (Table 6). Larval survival and female adult mass steadily increased with increasing levels of N up to maxima occurring when N levels were ca. 1.5–1.9% during late larval development (Fig. 9). Similarly, length of female development was shortest with levels of N of ca. 1.5–1.9% during late larval development.

The general relationships of adult mass and length of development with levels of N were nearly identical for female and male budworms, except for typical sex differences (i.e. females weighed about twice as much and their length of development was slightly longer than that of males.) This pattern was consistent for all foliar traits.

Strong positive relationships were also present between budworm performance (particularly larval survival and length of development) and levels of P and K (Table 6; Fig. 10A, B). Relationships with P were nearly identical to that of relationships with N because of the very similar patterns of decline of foliar P and N concentrations during shoot elongation (Fig. 6). Levels of foliar K declined later in shoot phenology and more slowly than did levels of foliar P and N (Fig. 6).
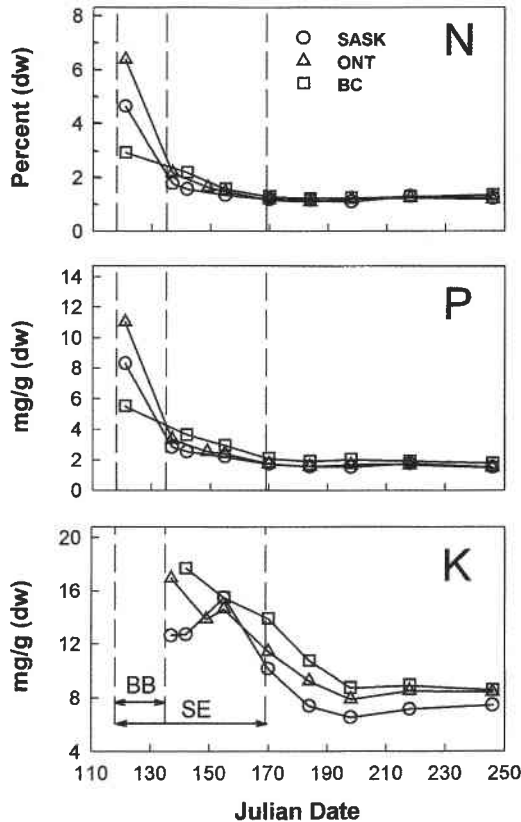
FIG. 6. Seasonal variation of N, P, and K in current-year foliage of three white spruce populations (SASK, ONT, and BC) in 1985. The ranges of budbreak (BB) and shoot elongation (SE) periods for all trees are indicated by arrows and broken lines.

Among the other measured foliar traits, budworm performance was positively related to levels of Cu, Mg, and total sugar, which also declined during shoot elongation (Figs. 7, 8A). Relatively strong negative relationships were present between budworm larval survival and levels of Ca and total phenolics (Table 6; Fig. 10C, D). These two traits were at their lowest levels during the later stages of shoot elongation and the later stages of larval development for the earliest budworm cohorts. Relationships between budworm performance and levels of foliar Fe and Zn were very poor (Table 6).

Levels of foliar water and toughness were unfortunately not measured during the 1985 experiments. These traits were measured in 1986 using the same trees studied in 1985, and the data were used to compute estimated levels of water and toughness for the appropriate host phenological stages present during each budworm cohort in 1985. Regression analyses revealed remarkably strong relationships between budworm performance and levels of water and toughness (Table 6): performance was positively associated with water content and negatively associated with toughness (Fig. 10E, F).

Budworm performance and foliar trait data were also extensively analyzed using multiple regression and canonical correlation techniques (SAS Institute Inc. 1988). Neither approach provided any additional insights into these relationships. Because of the high level of intercorrelation among foliar variables, it was possible to construct many significant
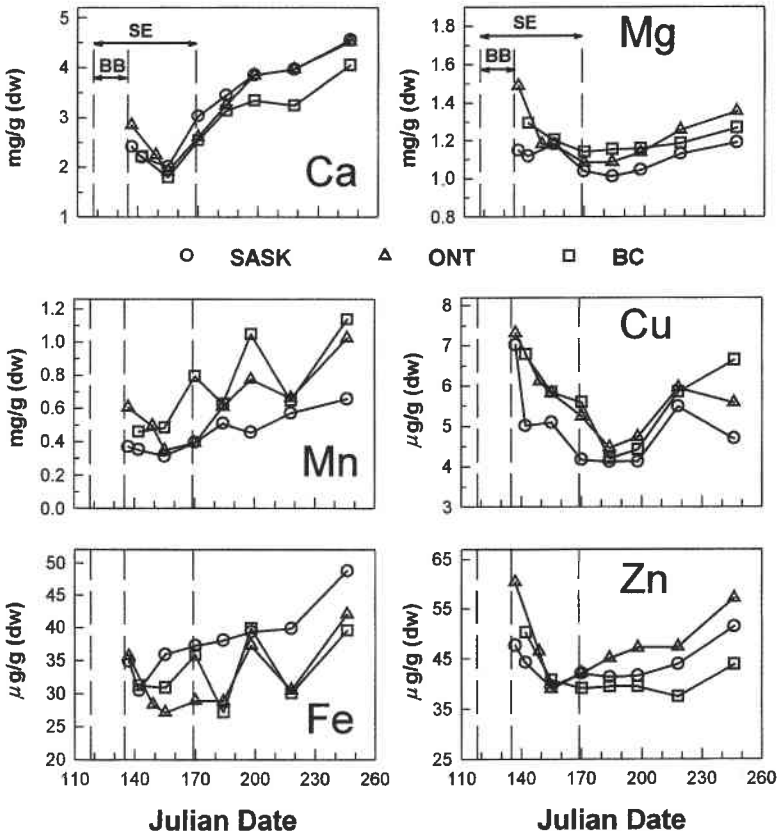
Fig. 7. Seasonal variation of Ca, Mg, Mn, Cu, Fe, and Zn in current-year foliage of three white spruce populations (SASK, ONT, and BC) in 1985. The ranges of budbreak (BB) and shoot elongation (SE) periods for all trees are indicated by arrows and broken lines.

multiple regression models that each explained a high proportion of variation ($r^2 > 0.7$) in budworm performance.

Discussion

Defining the Window of Susceptibility. The window of susceptibility in white spruce for the spruce budworm may begin as early as 4 or more weeks prior to budbreak. The earliest cohorts in 1985 and 1987 began 3 and 4 weeks, respectively, before budbreak and yet had good success as measured by all performance variables. In fact, the performance values for all cohorts that started feeding prior to budbreak were quite similar to those for budworms reared on nutrient-rich, artificial diets under controlled laboratory conditions (Lawrence 1990). Thus, to define clearly the beginning of the window of susceptibility, budworm cohorts need to be tested on white spruce at even earlier host phenological stages than were used in this study.

The end of the window of susceptibility, on the other hand, is clearly associated with the end of active shoot growth. Budworms starting at budbreak, in most cases, did not complete larval development until shortly after shoot elongation ended. These insects, which in 1985 included cohort 3 on SASK trees and cohort 4 on ONT and BC trees, developed at the later limits of the window. The largest decreases (38–53%) in larval survival occurred
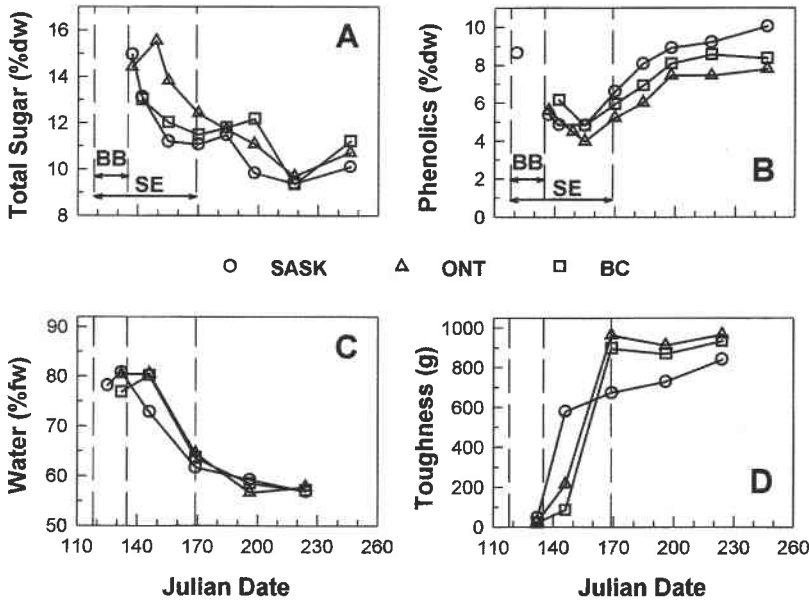
FIG. 8. Seasonal variation of (A) total sugar and (B) phenolics in 1985 and (C) water and (D) toughness in 1986 in current-year foliage of three white spruce populations (SASK, ONT, and BC). The ranges of budbreak (BB) and shoot elongation (SE) periods for all trees are indicated by arrows and broken lines.

between cohorts 3 and 4 on each spruce population (Fig. 3). Yet, only 7 days separated the starting dates of these two cohorts, thus indicating an abrupt end to the window. Using a very different approach, Thomas (1987) observed a similar rapid decline in host quality when budworm sixth instars were fed artificial diets containing powdered current-year white

TABLE 5. Mean values (± SE) of 12 nutritional traits of 1-year-old foliage on three white spruce populations (SASK, ONT, and BC) sampled prior to budbreak in 1985 or 1986

Foliar trait*	Units	N per mean	<1 week prior to budbreak	1–2 weeks prior to budbreak	
			SASK	ONT	BC
Nitrogen	% dw	3	1.12 (± 0.04)	1.21 (± 0.08)	1.22 (± 0.02)
Phosphorous	mg/g dw	3	1.46 (± 0.07)	1.45 (± 0.12)	1.49 (± 0.09)
Potassium	mg/g dw	3	6.97 (± 0.79)	6.80 (± 0.61)	6.70 (± 0.69)
Calcium	mg/g dw	3	5.24 (± 0.96)	5.77 (± 0.41)	4.61 (± 0.73)
Magnesium	mg/g dw	3	1.09 (± 0.06)	1.19 (± 0.03)	1.15 (± 0.01)
Manganese	mg/g dw	3	1.01 (± 0.29)	1.36 (± 0.22)	1.44 (± 0.21)
Copper	µg/g dw	3	3.51 (± 0.16)	4.53 (± 0.44)	4.11 (± 0.14)
Iron	µg/g dw	3	55.2 (± 11.2)	47.2 (± 11.6)	39.0 (± 0.7)
Zinc	µg/g dw	3	60.5 (± 10.0)	68.0 (± 7.6)	54.6 (± 5.2)
Phenolics	% dw	3	8.49 (± 0.99)	8.26 (± 0.64)	8.91 (± 0.49)
Water	% fw	8	46.0 (± 0.005)	46.5 (± 0.002)	45.7 (± 0.003)
Toughness	g	80	859.4 (± 12.2)	965.5 (± 6.2)	890.5 (± 9.6)

*Nitrogen, minerals, and phenolics sampled on 1 May 1985. Water content and toughness sampled on 28 April 1986.

TABLE 6. Results of regression analysis of budworm performance in 1985 on levels of foliar traits occurring during late larval development (i.e. foliar trait levels at 75% elapsed degree-days for each budworm cohort for cohorts 1–6)

Foliar trait	Larval survival (N = 144)		Female adult dry mass (N = 119)		Female length of development (N = 119)	
	Degree*	r^2	Degree*	r^2	Degree*	r^2
N	2	0.574	3	0.476	2	0.492
P	2	0.544	2	0.333	3	0.448
K	3	0.558	1	0.179	2	0.438
Ca	3	0.453	1	0.160	1	0.194
Mg	1	0.170	1	0.115	1	0.093
Mn	1	0.118	1	0.061	1	0.162
Cu	2	0.414	2	0.248	3	0.328
Fe	1	0.040	1	0.043	—	n.s.†
Zn	2	0.058	1	0.040	—	n.s.†
Sugars	1	0.218	1	0.352	1	0.136
Phenolics	2	0.385	1	0.176	1	0.271
Water‡	1	0.729	1	0.608	2	0.659
Toughness‡	3	0.551	1	0.464	2	0.479

*Degree of polynomial of the form: $Y = \beta_0 + \beta_1 X + \beta_2 X^2 + \beta_3 X^3$. Results are shown for models having significant values ($P \le 0.05$) for F and all β parameters other than β_0.
†Not significant ($P > 0.05$).
‡Estimated levels based on foliar measurements at phenologically similar stages in 1986.

spruce shoots of various ages. Budworm survival and adult weight dropped sharply when larvae were fed diets containing shoots of greater than 90% elongation.

The optimal timing of emergence for spruce budworms is probably 1–3 weeks prior to budbreak on white spruce. Larvae at this time are confined at first to feeding in old needles for only a brief period, or if fortunate, they may be able to enter expanding buds directly. Vegetative buds in this study were sufficiently swollen (phenology rating ≥ 3) to allow penetration by larvae at 1–2 weeks prior to budbreak. Additionally, this early start allows larvae to complete feeding prior to the end of shoot elongation. Larvae developing within this phenological window are able to minimize feeding on the less nutritious older foliage, take advantage of the maximum levels of N and water occurring in young foliage, and complete development before the current-year foliage reaches its maximum toughness and minimum water content. Historical records for the western spruce budworm (the ecologically similar relative of the spruce budworm) suggest a similar optimal phenology: all recorded outbreaks in British Columbia have been preceded by, or were contemporaneous with, years in which larvae emerged 17–18 days prior to budbreak of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] (Thomson et al. 1984).

The spruce budworm appears well adapted for emergence prior to host budbreak. Diapause ends in February, with larval sensitivity to heat gradually increasing as they remain in their hibernacula during the post-diapause period preceding warm spring temperatures (Régnière 1990). Increasing heat sensitivity may be the key mechanism that synchronizes their emergence with host phenology. Both the spruce budworm and the western spruce budworm have broad periods of larval emergence at the population level (Thomas 1976; Volney et al. 1983), and emergence is skewed over time such that most larvae emerge early in the emergence period (Reichenbach and Stairs 1984; Régnière 1990). Such a pattern would be especially advantageous to budworms when staminate flowers are abundant, because staminate flowers, an important larval food, are open a week or more prior to vegetative
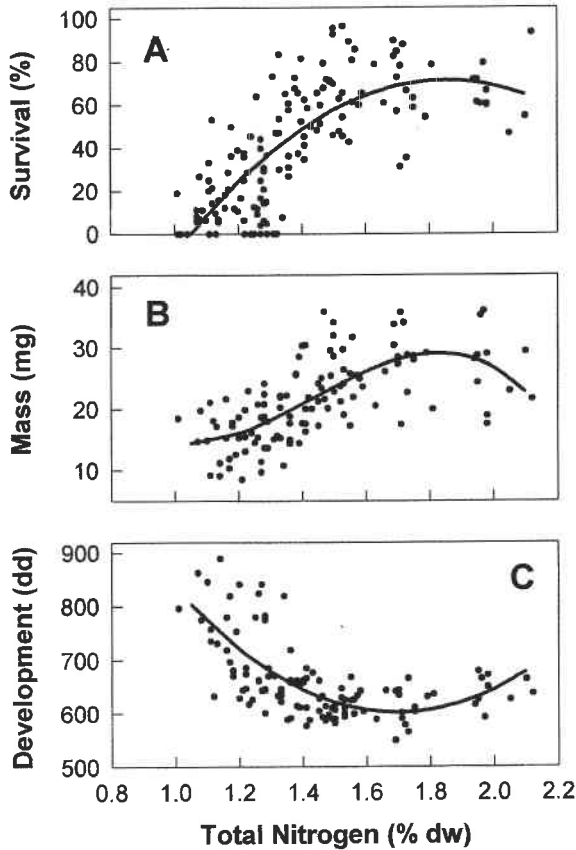
FIG. 9. Relationships of (A) percentage larval survival, (B) female adult dry mass, and (C) female length of development with total nitrogen levels occurring in current-year foliage during late larval development. Each data point represents one budworm cohort on one tree.

buds. The presence of staminate flowers can greatly enhance budworm survival (Mattson et al. 1996), and in effect expand the window of plant susceptibility to an earlier point (Blais 1957).

Delayed tree phenology. When host tree phenology is delayed relative to spruce budworm phenology (i.e. budbreak follows larval emergence by several weeks), budworm larvae encounter increased risks resulting from prolonged exposure to low quality diets and extended periods of larval dispersal. If staminate flowers are unavailable, larvae must mine 1- and 2-year-old needles for an extended period before vegetative buds swell enough to allow larval entry. Older foliage has substantially lower nutritional value and greater toughness (Table 5) comparable to that of current-year foliage at the end of summer (Figs. 6–8), and water content of older foliage is even lower. Budworm survival, development rate, and fecundity are reduced if larvae are forced to feed for long periods on older foliage (Blais 1952; Mattson et al. 1983). Furthermore, as larvae search for suitable feeding sites over an extended period, additional larval mortality occurs when dispersing larvae are lost from host trees (Miller 1958; Régnière and Fletcher 1983). In the current study, where larvae were caged on branches and protected from dispersal losses, the highest mortality rates occurred among young larvae. We hypothesize that extended feeding on low quality
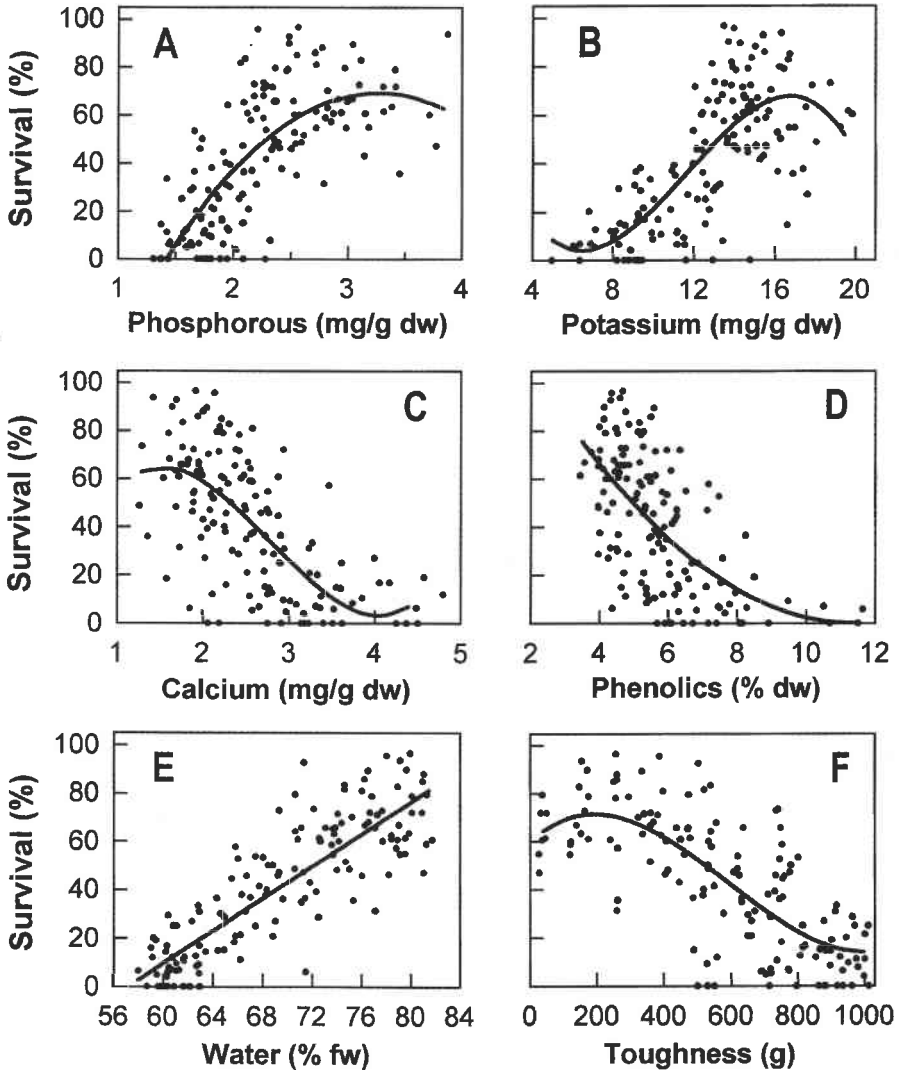
FIG. 10. Relationships of percentage larval survival with levels of (A) phosphorous, (B) potassium, (C) calcium, (D) phenolics, (E) water, and (F) toughness occurring in current-year foliage during late larval development. Each data point represents one budworm cohort on one tree.

diets increases early larval mortality, so that dispersal losses, starvation, and toxicity may be competing sources of budworm mortality in the early spring.

Advanced tree phenology. On the other hand, when host tree phenology is advanced relative to spruce budworm phenology (i.e. budbreak occurs prior to or during larval emergence), budworm survival and body mass are dramatically reduced, while development time is greatly increased. If the asynchrony is great enough, larvae may start feeding too late to take advantage of the high levels of foliar nitrogen which decay rapidly during and immediately after budbreak, and then larvae must feed for a longer period on tougher low-moisture foliage during the later instars when the greatest gains in body mass typically

occur. These conclusions are further supported by lowered nutritional indices (e.g. relative growth rates and efficiency of food utilization) for both spruce budworm and western spruce budworm larvae feeding on older current-year foliage (Blake and Wagner 1986; Thomas 1987, 1989). Fecundity is also much lower, because it is highly correlated with body mass (Miller 1957).

Larvae developing later relative to host tree phenology are also likely to undergo greater predation from at least two factors. First, protracted development allows more time for predation and parasitization. Second, a greater proportion of larval development occurs when larvae are physically more exposed to natural enemies, i.e. larvae spend more time feeding on expanding shoots than within closed buds. For example, Shepherd (1985, 1992) observed that densities of western spruce budworm larvae often rapidly declined after Douglas-fir budbreak, and the greatest reductions occurred where the length of time between budbreak and budworm pupation was the greatest. He concluded that predation was a major cause of this larval disappearance.

Pathogens may also play a role in budworm–host synchrony by delaying budworm larval development relative to host phenology. For example, sublethal infections by the microsporidian *Nosema fumiferanae* (Thomson) cause prolonged budworm larval developmental periods, as well as reductions in pupal weights, fecundity, and adult longevity (Bauer and Nordin 1988, 1989). If the delay in larval development is great enough, infected larvae are likely to encounter rapidly deteriorating host tree quality as the phenological window closes, thus further decreasing budworm growth rates and fecundity. Royama (1984) included microsporidia in his "fifth agent," a complex of diseases and other mortality agents that he considered a major mortality factor in the budworm's population dynamics. In fact, the incidence of *N. fumiferanae* infection within budworm populations often increases as a budworm outbreak continues over several years (e.g. Wilson 1977; Burke 1980), and thus, the potential for microsporidians to affect the budworm's population dynamics through phenological asynchrony or other means may increase during a budworm outbreak.

Advanced tree phenology has occurred during collapses of both spruce budworm and western spruce budworm outbreaks. For example, Douglas-fir budbreak followed larval emergence by a much shorter interval than normal during the collapse of three of five western spruce budworm outbreaks examined by Thomson et al. (1984). Asynchrony likewise occurred for 3 consecutive years (1981–1983) during the collapse of the last spruce budworm epidemic in Newfoundland, where larval activity commenced about 2 weeks after budbreak on balsam fir (Raske 1985). Although there is no evidence that asynchrony was the cause of outbreak collapse, it may play a role in population decline.

Potential production of foliage can also be affected by the direction and degree of insect–host asynchrony. For example, if large numbers of larvae mine vegetative buds, they can quickly and completely destroy the entire potential foliage yield of those buds. Early-flushing trees are less likely to have complete destruction of buds than are late-flushing trees (Thomson 1979; Hansen and Dimond 1982; Dimond 1985). The damage potential of each larva is reduced if it begins feeding after buds have flushed.

Relationship of Budworm Performance to Host Foliar Traits. Our study revealed strong correlations between budworm performance and levels of foliar N, P, K, Ca, Cu, sugars, phenolics, water, and toughness. Because of the intercorrelation among these foliar traits, it is impossible to isolate and identify the key factors affecting host susceptibility. Determination of which trait(s) are most important to budworms will be best done using experimental diets (e.g. Harvey 1974; Clancy 1991, 1992a, 1992b; Mattson et al. 1991; Clancy and King 1993). Nevertheless, the relationships between insect performance and foliar traits observed in this study clearly delineate the phenological window of susceptibility and highlight a suite of traits that could be evaluated further for their roles in host tree susceptibility.

Levels of N and minerals in current-year foliage were consistent with well-known patterns of seasonal variation in other conifers (Clancy et al. 1988) and most other plants (Mattson and Scriber 1987). The strong relationship between insect performance and N has been well documented for many phytophagous insects (e.g. Mattson 1980; Scriber 1984a; White 1984; Mattson and Scriber 1987) as well as the spruce budworm and western spruce budworm specifically (Harvey 1974; Mattson et al. 1983, 1991; Brewer et al. 1985, 1987; Cates et al. 1987; Clancy 1992b). Relationships between spruce budworm performance and levels of N, P, and K (Figs. 9, 10A, B) seem to agree with dome-shaped response curves observed for the western spruce budworm (e.g. Brewer et al. 1985, 1987; Clancy and King 1993), although few data are available in our study for nutrient levels greater than those associated with maximum budworm performance.

Little information exists on mineral levels in insect tissues and on insect dietary requirements for specific mineral elements. However, most studies indicate that P, K, and Mg are the dominant mineral elements in insect tissues (Mattson and Scriber 1987). Moreover, P, Cu, Zn, and Fe in spruce budworms (Mattson et al. 1983) and Cu and Zn in western spruce budworms (McLean et al. 1983) occur at levels that are at least twice that of host foliage, and thus may be the minerals most likely to be limiting. In tests of the western spruce budworm on artificial diets, Clancy (1992b) observed that the ratio of Zn to N was a good predictor of budworm fitness, and further, that budworms performed best at moderate P concentrations and low Mg concentrations, relative to concentrations in host foliage, but were relatively unaffected by Ca concentrations (Clancy and King 1993). The negative correlation between spruce budworm performance and Ca in our study may suggest that higher Ca levels are in some way deleterious, e.g. by interfering with the uptake of other foliar elements (Mattson et al. 1991), or, on the other hand, it may be indicative of the roles that Ca plays in plant cell wall structure and metabolic activity (Hanson 1984).

The levels of sugars in new foliage were highest near the middle of shoot elongation. This is consistent with earlier studies on white spruce (McLaughlin 1986; Mattson et al. 1988) in which levels of foliar sugars increased during early shoot elongation, peaked at about the time budworms reached the penultimate (fifth) instar, and declined during the latter half of shoot elongation. A moderate positive relationship exists between budworm performance and levels of total sugars in our study. Both the spruce budworm and western spruce budworm can develop and reproduce on diets of very low levels of sugar, thus suggesting that there are other sources of energy for these herbivores (Harvey 1974; Clancy 1992a). However, spruce budworms in artificial diet experiments have performed best at moderately high levels of sugar and N (12.8 and 4.9%, respectively) (McLaughlin 1986). Furthermore, the spruce budworm appears to be well adapted to developing synchronously with continuously changing levels of sugars and N (i.e. N levels peaking early and sugar levels peaking later as N declines). McLaughlin (1986) observed that the optimal ratio of sugar to N in terms of budworm performance generally increases when the level of N is low. Additionally, the feeding preference of fourth-instar larvae is correlated with levels of foliar N, whereas that of sixth instars is correlated with levels of foliar sucrose (Albert and Bauce 1994). Levels of sugars in our study were adequate for budworm development in all cohorts; hence, it is not likely that they were a major determinant of variation in budworm performance among cohorts.

Levels of total phenolics decreased during shoot elongation, a pattern consistent with previous reports for white spruce (Mattson et al. 1988), but then began increasing just prior to the end of shoot growth and continued increasing throughout the summer. This pattern, identical to that of Ca, reflects the generally deteriorating quality of host foliage as leaf tissue matures. The meager evidence available to date does not indicate a strong relationship between total phenolics or individual compounds and resistance to the spruce budworm (Mattson et al. 1991). For example, phenolic compounds seem to have little or no deleterious

effect on performance by the spruce budworm or western spruce budworm at the levels found in host foliage (Cates et al. 1983*a*, 1983*b*; Mattson et al. 1983; Wagner and Blake 1983), although they may reduce the spruce budworm's utilization of Fe and Zn (Mattson and Scriber 1987; Mattson et al. 1991). Pungenin, a phenolic glucoside feeding deterrent for late-instar spruce budworms (Heron 1965; Strunz et al. 1986), is present in mature spruce foliage, but absent or present only at very low levels in young white spruce foliage, and thus may contribute to the budworm's preference for young, current-year foliage.

The positive correlation of budworm performance with water and the negative correlation with toughness were among the strongest for all foliar traits measured. These strong correlations indicate how well the periods of rapid decline in water levels and dramatic increase in toughness define the phenological window of susceptibility for the spruce budworm. Furthermore, seasonal variation of these two traits more clearly illustrated the phenological differences among spruce populations in this study than did any other foliar trait. Thus, leaf water content and toughness may be important factors that affect larval survival and length of development, i.e. those performance variables for budworms that are closely associated with phenological differences among spruce populations.

Water content of current-year foliage peaked at more than 80% soon after budbreak and decreased to less than 60% by early July. Chrosciewicz (1986) observed a nearly identical pattern for white spruce and similar patterns but with slightly lower peaks for balsam fir and black spruce. A positive relationship between leaf water content and the performance of insect folivores has been demonstrated for many insect species (e.g. Scriber 1978; Scriber and Slansky 1981; Scriber 1984*b*). In contrast, Clancy (1991) observed a negative relationship between unusually high water content (>80%) of artificial diets and performance of western spruce budworms.

Leaf toughness is related to the levels of compounds that together comprise "fiber" (lignin, silica, pectin, cellulose, hemicellulose, etc.) and structural components such as sclerenchyma fibers (Huang and Führer 1979; Vincent 1982; Mattson and Scriber 1987). Leaf toughness has frequently been associated with reduced levels of herbivory or reduced insect performance (Huang 1975; Coley 1983; Raupp 1985; Hagen and Chabot 1986). Additionally, components of leaf toughness may increase following heavy herbivory. Bauce and Hardy (1988) reported that increased raw fiber content of current-year balsam fir foliage was related to spruce budworm defoliation during the 2 preceding years, and caused decreases in budworm pupal body mass, larval developmental rate, and survival. Burr and Clancy (1993) found epidermal thickness of current-year Douglas-fir foliage greater in susceptible trees defoliated by the western spruce budworm when compared with putative resistant trees.

Success of the spruce budworm in relation to host tree phenology is determined ultimately by a combination of several host tree traits and a variety of other biotic and abiotic factors. However, several combinations of foliar traits function as good predictors of herbivore performance. For example, the general trend of declining levels of water and N in maturing foliage occurs in most, if not all, plants (Scriber 1984*b*). Because of the consistency in phenological variation in water and N levels, and their crucial roles in governing the course of plant physiology (Ågren 1985; McIntyre 1987), these two traits are valuable as indicators of the entire chemical and physiological "gestalt" of a host plant (Mattson and Scriber 1987). Levels of foliar water and N are negatively correlated with toughness, and each of these traits exhibits its greatest variation during leaf maturation. These three traits were consistently the strongest predictors of all performance variables for budworms in our study.

One caveat for our study is the potential for induced host effects resulting from budworm feeding and foliage sampling. All eight budworm cohorts developed on and repeated foliar samples were collected from each white spruce tree in 1985. Although much evidence exists for inducible defenses in deciduous trees, there is little and inconsistent evidence for

inducible defenses in coniferous trees (Wagner 1988; Mattson et al. 1991; Neuvonen and Niemelä 1991). Severe defoliation levels may be required for significant induced effects to occur in conifers (Mattson et al. 1991). The quantity of foliage removed from our study trees was small in relation to the total foliar volume of the trees.

Conclusions. White spruce has a sharply defined phenological window of susceptibility to the spruce budworm. For budworm larvae to develop successfully on white spruce, they must emerge and begin feeding within a 3- to 4-week period preceding budbreak. This timing minimizes the period of mining in older, less nutritious foliage prior to significant bud expansion; it allows larvae to take advantage of high levels of nitrogen, water, and other nutrients in young foliage; and it allows completion of larval development prior to the end of shoot growth, when leaf toughness, phenolics, and other foliar components are increasing to potentially deleterious levels. Larvae whose development is not synchronized with this window not only encounter a less nutritious diet, but may also encounter increased mortality as a result of dispersal losses prior to budbreak or predation during shoot expansion.

Phenological variation of several foliar traits is highly correlated with budworm performance. It is not yet clear which host traits are key factors in determining performance, although it is likely that the phenological window is defined by the combined effects of variation in several traits. To evaluate the roles of individual foliar traits, we need to understand how budworms respond at each stage of larval development to changing levels of those traits. What effects does an increase or decrease in a foliar trait have when it occurs at various stages in larval development? How do these effects vary as simultaneous changes occur in other foliar traits?

Knowledge of the phenological window of susceptibility for a budworm – host tree association has important implications for forest management. Shepherd (1992, 1994) has suggested that planting early- or late-flushing Douglas-fir provenances in susceptible climatic areas within the mountainous terrain of western North America may be an effective management tool for reducing defoliation by the western spruce budworm. In eastern North America, breeding for delayed budbreak of white spruce has been suggested as a method of inducing budworm–tree asynchrony, and thereby increasing resistance to the spruce budworm (Blum 1988), as well as a method to reduce damage from spring frosts (Nienstaedt 1985). Although some limited gain in lateness of budbreak might be achieved, the effectiveness of such gain for either purpose is questionable (Nienstaedt 1985; Blum 1988). On the other hand, the results of our study suggest that advancing, rather than delaying, tree phenology in relation to spruce budworm phenology may have a greater deleterious effect on budworm performance and, thus, white spruce susceptibility. The end of the phenological window is abrupt, and reduction in budworm performance is dramatic when tree phenology is advanced. However, advancing the timing of budbreak would increase the problem of spring frost damage. Additionally, it is likely that budworms would be able to evolve to "track" a shift in the phenological window, either an advance or a delay. There is wide variability within and among populations of both the spruce budworm and western spruce budworm for many life history traits (Volney 1985), including rates of spring emergence in response to temperature (Thomas 1976; Volney et al. 1983).

Another potential management approach may be simply to retard budworm development relative to host phenology by employing low levels of antifeedants (e.g. Alford and Bentley 1986) or other growth-delaying compounds or pathogens that would allow budworm development to be eclipsed by the end of the phenological window. The duration of budworm larval development is extended, for example, by sublethal doses of *Bacillus thuringiensis* (Alford and Holmes 1986; Ramachandran et al. 1993). Nevertheless, much work is needed to elucidate further the relationships between insect and host phenologies, and how phenological asynchrony could be effectively employed as a management tool.

Acknowledgments

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