Linkages Between the Phenologies of Jack Pine *(Pinus Banksiana)* Foliage and Jack Pine Budworm (Lepidoptera: Tortricidae)

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LINKAGES BETWEEN THE PHENOLOGIES OF JACK PINE (*PINUS BANKSIANA*) FOLIAGE AND JACK PINE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

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ABSTRACT

A field study conducted in 2001 and 2002 in the Michigan Upper Peninsula investigated seasonal associations between the development of jack pine, *Pinus banksiana* Lamb., and larvae of the jack pine budworm *Choristoneura pinus* Freeman (Lepidoptera: Tortricidae). There was almost no active relationship between post-diapause emerging second instars and elongation of vegetative shoots. Early instars were not closely synchronized with the flushing of current-year needle fascicles, which is required to optimize larval feeding. However, there were close feeding and shelter relationships between early instars and year-2 pollen cone development. Associations with, and larval damage to, year-2 seed cones were dependent upon larval population size and posed only minimal and periodic threats to jack pine seed production. As a consequence, early instar jack pine budworm relied almost exclusively on pollen cones for survival. Third to fifth instars vacated pollen cones as soon as they became desiccated. Only then did these larvae start close associations with vegetative shoots. First, they excised partially emerged needles at their base, and when the needle-pairs completely escaped their fascicle sheath, the larvae fed routinely on the complete needle lamina. Late instars, pupae and adults were associated with previous years' and current-year foliage without any apparent bias. This study has shown that it might be more practical to time insecticide strategies, which are intended to manage jack pine budworm larvae, to the tree's phenology rather than jack pine budworm larval indices.

INTRODUCTION

Jack pine, *Pinus banksiana* Lamb., is an important commercial species of the boreal and cool temperate forests of North America east of the Rocky Mountains. Its geographic range extends from the Atlantic coast of Maine and Nova Scotia to the MacKenzie Valley in the Northwest Territories and from Central Wisconsin, with artificial extensions in Nebraska (Boldt 1969) to North Central Quebec (Critchfield and Little 1966). The species occupies a significant number of hectares in some of the United States Lake States (Heyd 1995), Ontario (Howse and Meating 1995) and the Canadian Prairie provinces (Moody 1986), but is of lesser importance in the maritime regions. Jack pine silvics have been reviewed (Fowells 1965, Rudolph and Laidly 1990), and the development of its reproductive structures is well described by Moore and Nozzolillo (1991). Vegetative jack pine foliage develops primarily as two or three distinct phases or flushes. Shoots, sometimes referred to as candles, can begin growing as early as April in some parts of Canada and the United States, but if favorable conditions prevail, jack pine frequently has a second period of shoot elongation in late autumn (Rudolph and Laidly 1990). In addition, and equally important, the

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needles develop much later than the initial shoot elongation, but as a separate flush. For the purpose of this study, post-winter development of jack pine trees is described as three distinct foliar developmental events: 1) The elongation of vegetative shoots (terminal and lateral buds) that start prior to, and as a separate event from needle development, 2) the production of reproductive structures (pollen cones [microstroboli] and seed cones [megastrobili]) that are initiated during the previous season (Moore and Nozzolillo 1991) and, 3) needle fascicles elongating and differentiating at the same time as shoots are growing.

Of the several insects that attack jack pine (Fowells 1965, Howse 1984), the jack pine budworm *Choristoneura pinus* Freeman (Lepidoptera: Tortricidae) is the most significant pest of jack pine forests in Canada and the Lake States region of the United States (Howse 1984). Like its principal host, jack pine budworm biology and development are influenced by temperature, photoperiod and food intake; thus it appears that the insect and the tree are inextricably linked. The biology and life cycle of *C. Pinus* are well documented (DeBoo and Hildahl 1968, Ives and Wong 1988, Nealis 1995). Briefly, the species lay egg masses on host trees in late July or early August and these hatch within 14d. Each year's population begins as first instars that hatched the previous year and overwintered as diapausing second instars in hibernacula. Those that survive respond the following spring to temperature and photoperiod (Lysyk and Nealis 1988), disperse in search of food and shelter, then molt four or five times before pupating. Population outbreaks *of C. pinus* occur periodically (Howse 1986, Volney 1988), often causing extensive and severe defoliation, top-kill and tree mortality in jack pine stands (Benjamin et al. 1961, Kulman et al. 1963, Gross 1992). As a consequence, the five major jack pine regions (Ontario, Manitoba, Michigan, Wisconsin and Minnesota) have at times implemented operational insecticide programs to manage jack pine budworm outbreaks.

It is now widely recognized that effective management of the jack pine / jack pine budworm complex requires decisions that are supported by in-depth understanding of the insect, its host tree and their interactions.

The objectives of this study were to examine and determine phenological associations between jack pine foliage and jack pine budworm larvae and how the interactions might influence management strategies.

MATERIALS AND METHODS

This study was conducted during 2001 and 2002 in a jack pine plantation (~ 100 ha) at the Raco Plains area in the Sault Ste. Marie District of the Michigan Upper Peninsula. The research area, located in the eastern section of the Hiawatha National Forest was previously illustrated and described by Heym et al. (1993), McCullough et al. (1995), and Conway et al.(1999). Four independent replicated plots (each ~500 × 300 m) separated by ~200 m- wide buffer zones, were prepared in even-aged stands of 95%, 25-year-old jack pine, interspersed with ~5% red pine (*P. resinosa* Ait.). Fifty dominant and co-dominant jack pine were randomly selected throughout each plot and marked as sample trees.

We placed meteorological equipment (Campbell Scientific Canada Corp., Edmonton, AB.) in the approximate center of the plantation and monitored temperature, rainfall and sunlight continuously from March to September each year. We chose these three variables primarily because they significantly influence both tree and insect phenology. A temperature probe (#204) within a radiation shield (#41301-5) was installed at the top of a 3m mast to measure the ambient air temperature. Rainfall was measured with a Texas Tipping Bucket rain gauge (TE525) and we used an UV light monitor (BW-20-T-10) to measure periods of sunlight. The sensors were controlled with a data logger (CR10x) fitted with a card storage module (Model CSM1) that recorded and stored large data sets accumulated over long continuous data- logging periods. The variables were sampled every 2 sec, with data output at hourly intervals. Rainfall and UV

were presented as daily totals whereas temperatures were determined as daily means with minima and maxima. In addition, using these data, we calculated accumulated heat units or growing degree days (GDD) with computer software (Allen 1976, Higley et al. 1986) using 4.5 °C and 32 °C, as lower and upper thresholds, respectively as these satisfied developmental requirements of the insect and its host.

Biological samplings were conducted every 2, 3, or 7d with the two shorter intervals corresponding with periods of most rapid tree and insect development. At each sampling, eight (16%) of the chosen trees in each plot were randomly chosen as that date's sample trees. A 60-cm branch tip was taken with pole pruners from the mid - to upper- crown of each of the chosen trees, placed in a cotton bag and secured to prevent larvae from escaping, then taken to the Canadian Forest Service (CFS) laboratory at Sault Ste. Marie, ON within 1h. The branches were examined immediately or stored in a cold room (4 °C) until they were processed within 48h. We determined the number and phenology of vegetative shoots (buds) and year-2 pollen-cone clusters (Batzer and Jennings 1980, Barnes and Wagner Jr. 1981, Moore and Nozzolillo 1991) on each branch. The latter reproductive structures, although not technically flowers (Barnes and Wagner Jr. 1981) are also referred to as staminate or male flowers (Lejeune 1950, Nealis 1990, Rose et al. 1999) or male cone clusters (Batzer and Jennings 1980). In addition we noted the presence or absence of year- 2 seed conelets. Jack pine budworm stages (egg to adults) found on each branch were removed and counted. Larval stadia were visually classified, then later confirmed by measuring head capsules (Lejeune 1950, Nealis 1987) with an electronic measuring device (Model MMS 235, Leica Canada Inc., Willowdale, ON) fitted to a binocular microscope. From these determinations, larval indices were compiled (Dorais and Kettela 1982) for each sample date.

STATISTICAL ANALYSIS

BMDP computer software (Dixon et al. 1990) was used for data analyses. Raw data with wide variability were log (x + 1.0) transformed before analysis to eliminate excessive skewness (Bartlett 1947). However, the data presented throughout the manuscript are non-transformed. Quantitative data relating to vegetative and reproductive jack pine structures as well as *C. pinus* larval populations and adult oviposition were analyzed with Analysis of Variance (ANOVA). Multiple comparison t-tests were used to separate significantly different means. We used Program 1R (Linear Regression of Groups) to examine relationships primarily because linear regressions describe relationships only between dependent and independent variables without introducing interactions with unknown nuisance factors. For all tests, probability values ≤ 0.05 were judged to be significant.

RESULTS AND DISCUSSION

Weather parameters during 2001 and 2002 are presented in Fig.1. Mean temperature profiles and overall temperatures during both years (Fig.1A) were similar. Thus it is unlikely that temperatures would have significantly influenced any phenological differences observed between 2001 and 2002; unless subtle temperature change significantly affect jack pine or *C. pinus*. Growing degree days (GDD) accumulated more slowly in 2001 than in 2002; but after approximately 55d the total GDD were similar (Fig.1A). Seasonal relationships between Julian days (JD) and GDD were almost constant in 2001 and 2002 (y = 0.295x, R^2 = 0.329 and y = 0.305x, R^2 = 0.2915, respectively, where x = JD and y = GDD; Fig.1A). These rates of heat-accumulation during the two years were not significantly different (Program 1R, Comparison of Slopes, df = 1,40; F = 0.255; P = 0.6164). It is also unlikely that differences in GDD would have contributed to significant differences in the jack pine or insect phenology between the years.
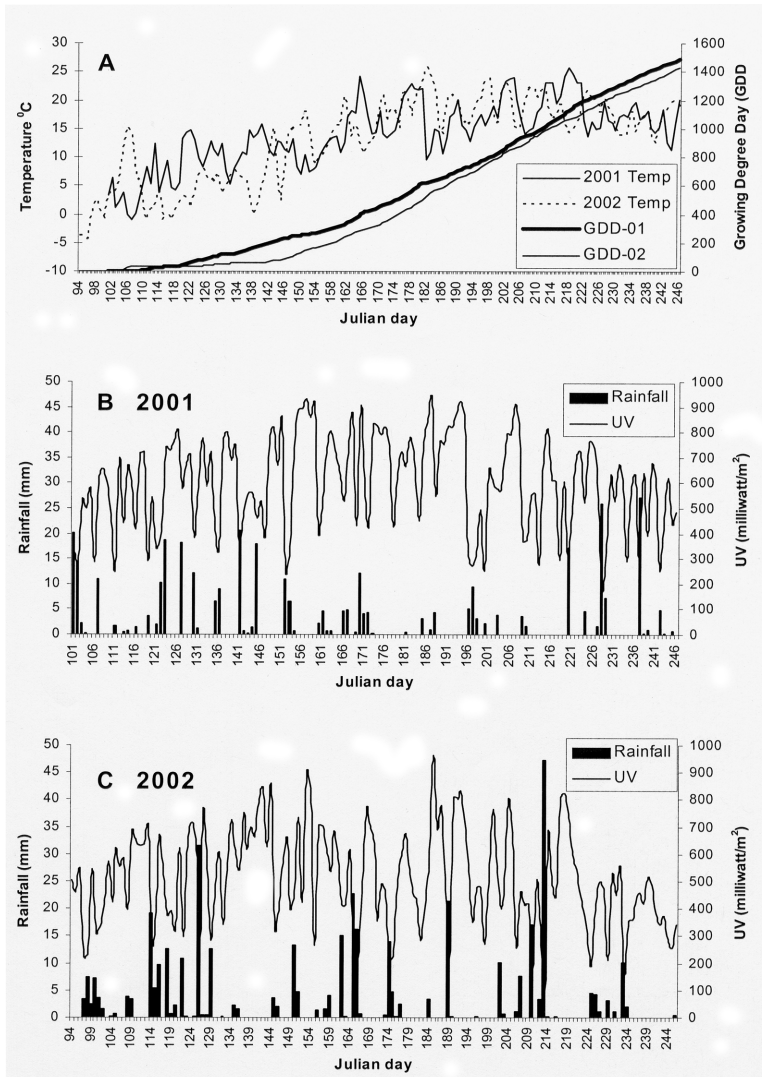
Fig. 1. Weather conditions that prevailed during 2001 and 2002 in a jack pine stand at Raco, Michigan. (A) Mean daily temperatures and relationships between (x) Julian days and (y) accumulated growing degree days (GDD), where $y = 0.295x$; $R^2 = 0.329$ and $y = 0.305x$; $R^2 = 0.2915$ in 2001 and 2002, respectively. The slopes were not significantly different (BMDP Comparison of Slopes, df = 1,40; $F = 0.255$; $P = 0.6164$). Patterns of rainfall (indicated by bars) and ultra-violet light (indicated with lines) in 2001 and 2002 are shown in B and C, respectively.

There were no significant lengthy periods of irregular sunlight (UV light) that might have negatively influenced the phenologies of the host tree or the insects. Less rain fell in 2001 (361.4 mm from 59 rainy sessions) than in 2002 (391.2 mm from 64 rainy sessions), but the overall seasonal distributions were similar in both years (Figs 1B and 1C).

In addition to rainfall, total snowfalls that were not measured in both years, might have contributed to soil moisture that was available to influence jack pine development. In 2001 and 2002, snow in the plots had completely receded by JD 143 (Calendar date, May 21) and JD153 (Calendar date, June 2), respectively. These dates should not infer different levels of snow precipitation, as rates of snow-melt could be differentially affected by respective spring temperatures.

While it is accepted that seasonal climate and daily weather conditions influence the phenologies of both jack pine and jack pine budworm, there was no evidence that drought or extreme temperatures would have made the tree and insect phenologies in 2001 significantly different from those in 2002.

Jack pine shoot phenology. As determined with red pine, *P. resinosa* Ait., shoot length is controlled by water supplied during the previous year's growing season, whereas needle elongation responds to current-year water supply (Garrett and Zahner 1973). Therefore, evaluating jack pine phenology, in relation to water supply, presented a challenge which was compounded in our study because we had no rainfall data for 2000. Nevertheless, although elongation of jack pine vegetative shoots started much earlier in 2001 than in 2002, the respective rates of growth were not significantly different, either on a JD or a GDD basis (ANOVA, df = 1, 34 ; $F = 0.307$; $P = 0.5828$; and df = 1, 33; $F = 2.498$; $P = 0.1234$, respectively) (Figs. 2 and 3).

However, it was not shoot growth per se but the development of the needle fascicles that provided the initial availability of new foliage as food for newly emerged post-diapause *C. pinus* larvae. During early development, the needle fascicles oriented approximately parallel to the shoot; but as the needles elongated, they escaped the fascicle sheath, exposing some of their green tissue at the tips only. It was only then that new leaf-tissue was assessed to be readily available as larval food. In addition, needle fascicles slowly flared and changed their orientation until they reached what Audus (1969) refers to as their preferred orientation; for jack pine the preferred orientation was at ~45° to the shoot.

The mean number of vegetative shoots per branch in 2001 was significantly lower (two sample *t*-test, $P < 0.05$) than in 2002 (Table 1). However, means were significantly different among plots in 2001 (ANOVA, $F_{3, 64} = 3.64$; $P = 0.017$) but not in 2002 (ANOVA, $F_{3, 76} = 2.69$; $P = 0.056$). This suggests that there was considerable variation in shoot production among plots in 2001 when insect populations were high but less variation in 2002 when larval populations were decreasing.

We found significantly more (two sample t test, $P = 0.05$) pollen cone clusters/branch in 2001 than in 2002 (Table 1). Similar to the vegetative shoots, the number of pollen cone clusters per branch among plots was significantly different in 2001 (ANOVA, $F_{3,64} = 7.73$; $P = 0.001$), but not in 2002 ($P = 0.056$). In 2001 the ratio of pollen cone clusters to vegetative shoots was high (1:24 ± 10) but dropped by ~ 30 × (1:722) in 2002. In 2001, ~ 99% of the branch samples had 1.0 pollen-cone cluster, but in 2002, 56% of the branches had no clusters at all. It is in reference to these host tree developments that *C. Pinus* interactions with its principle host were observed.

Jack pine budworm larval phenology - Figs. 3 and 4 show the larval development of *C. pinus* during 2001 and 2002 in relation to growing degree days (GDD) and Julian days (JD), respectively. Larval jack pine budworm populations in 2001 were moderately high (22.85 ± 9.4 per branch [seasonal $\bar{x} \pm SD$]).
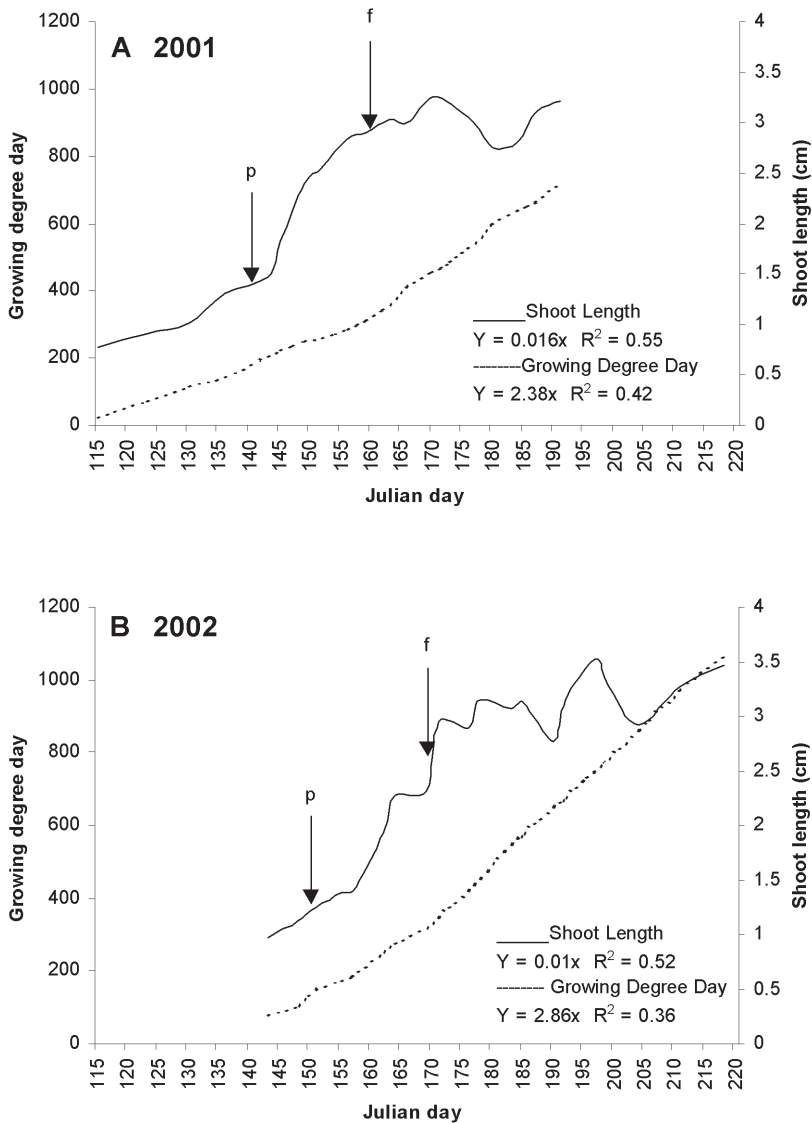
Fig.2. Elongation of jack pine vegetative shoots and growing degree days in relation to calendar days in (A) 2001 and (B) 2002. The rates of shoot elongation were not significantly different (BMDP Comparison of slopes, df = 1,34; F = 0.307; P = 0.5828). Time of pollen-shedding is denoted by 'p' and 'f' shows when jack pine needle-pairs escaped the fascicle sheath.
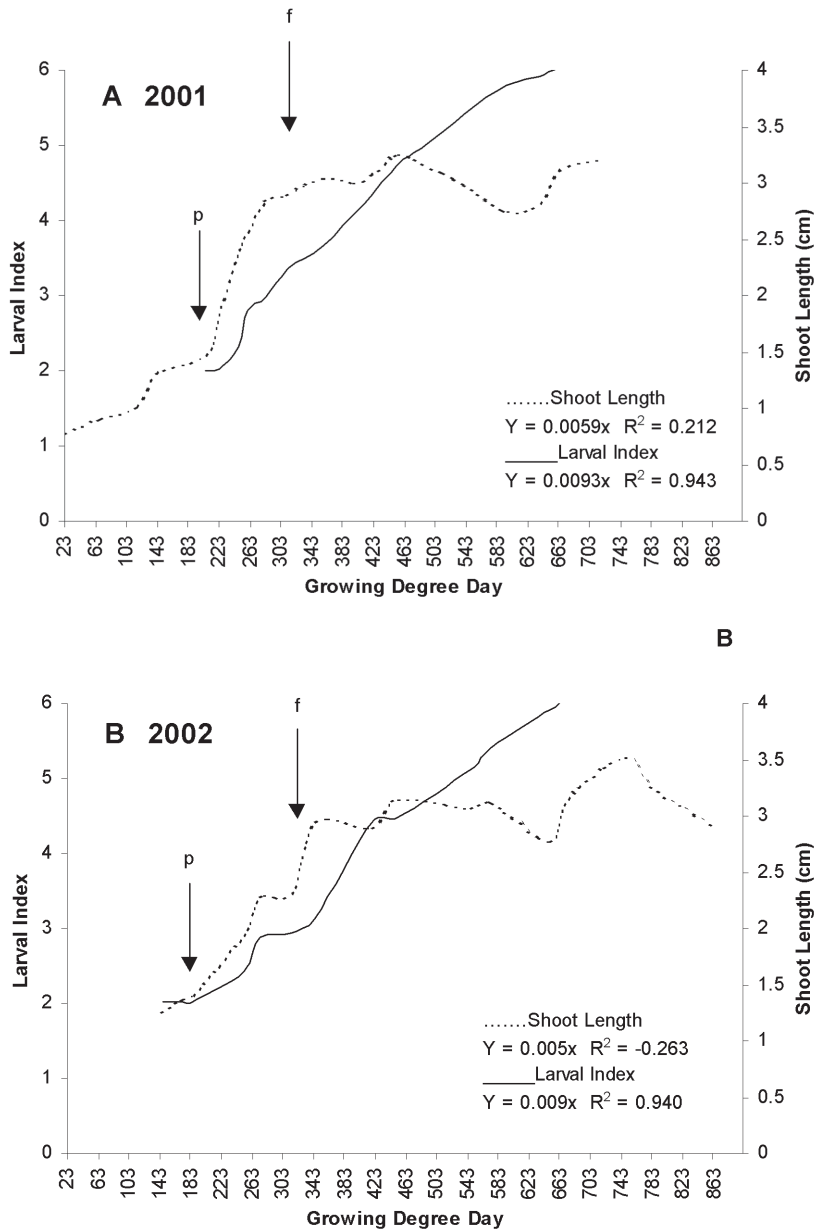
Fig.3. Development of larval jack pine budworm and elongation of jack pine vegetative shoots in (A) 2001 and (B) 2002 in relation to growing degree days. Rates of larval development during the two years were significantly different (BMDP Comparison of slopes, df = 1,23; F = 52.54; P = 0.001) but shoot elongation was not significantly different (df = 1,33; F = 2.498; P = 0.1234). Jack pine pollen shedding is indicated by 'p' whereas 'f' shows when the needle-pairs escaped the fascicle sheaths.

Fig.4. Relationships between calendar days, jack pine budworm larval development and growing degree days in a jack pine stand. Rates of larval development in (A) 2001 and (B) 2002 were not significantly different (BMDP Comparison of Slopes, df = 1,30; $F = 0.950$; $P = 0.3375$) Time of pollen shedding is denoted by 'p' and time when the needle tips escaped the fascicle sheaths is denoted by 'f'.
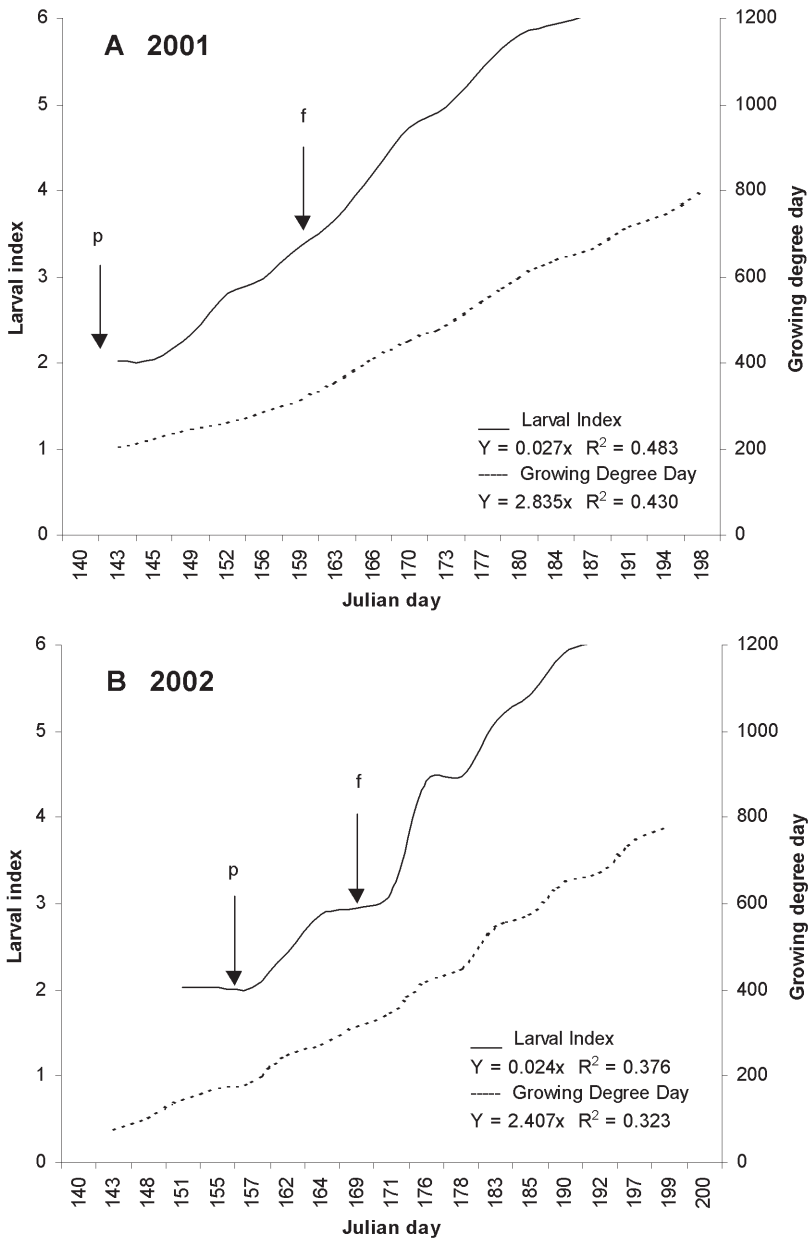
The following year the mean jack pine budworm population was approximately 4.5x smaller (Table 1) and these two populations were significantly different (two sample *t*-test, $P < 0.05$). When based on JD, there was no significant difference in larval development between the two years (Fig. 4, Program 1R, Comparison of slopes, df = 1, 30; $F = 0.950$; $P = 0.3375$), but when assessed on GDD (Fig.3), the development during the two years was significantly different (df = 1, 23; $F = 52.54$; $P < 0.001$). This suggests that GDD might be a more sensitive predictor of *C. pinus* development than JD.

Weber (1995) postulated that female *C. pinus* oviposit part of their egg complement (supposedly to lighten their payloads) before emigrating from heavily defoliated stands (i.e., by implication, from stands with high larval populations). In our study, the number of egg masses recovered in 2001 (when the populations were high) and in 2002 (with low populations) was not significantly different ($P < 0.05$). These findings do not support Weber's (1995) hypothesis, otherwise, we should have encountered, as would have been expected, a significantly higher number of small egg masses in 2001 than in 2002.

These data suggest that when *C. pinus* populations collapse, the reductions start with significantly less oviposition rather than with mortality of early instars as is now widely believed. This possibility, clearly identifies a need to further research and better understand inter-relationships between *C. pinus* larval numbers, the adults that subsequently develop and their reproductive capacity (sex ratio, oviposition and fertility). Information on how these factors influence population collapses could be important to better define the bionomics and management of the species.

Phenological linkages. In 2001 and 2002, overwintering jack pine budworm emerged from diapause on JD 143 and 151, respectively (Fig.4). These dates correspond to 205 and 146 GDD of accumulated heat units, respectively (Fig.3). It is accepted that inter-year emergence dates of *C. pinus* might be widely dissimilar; however, these results suggest that post diapause emergence of *C. pinus* might also occur at widely disparate accumulated heat units.

We found no published reports that compared inter-year julian days / calendar dates or accumulated heat units for jack pine shoot development. Nevertheless, in our study, measurable shoot elongation also started at different GDD and JD in 2001 and 2002 (Figs. 2 and 3). *C. pinus* emergence during both years occurred when the vegetative shoots (buds) were still very dormant. In 2001, larvae emerged when year-2 pollen cones were producing pollen (i.e. at the 'Mid-May' stage), but when they emerged in 2002, the cone clusters had only developed to the 'Early-May' stage (Moore and Nozzolillo 1991) (Figs. 3 and 4). This shows that when 2nd instar *C. pinus* emerge in the spring, it is almost certain that current-year needles would not be readily available as food; and furthermore, that occasionally, pollen cones might also not be suitable as food for short periods. This uncertainty of an available food source for newly emerged post-diapause *C. pinus* might also be a contributing factor to the instability of *C. pinus* populations.

Linkages between jack pine budworm and jack pine reproductive structures - Early- instar *C. pinus* associations with jack pine pollen cones are well documented (Graham 1935, Batzer and Jennings 1980, Nealis 1990, Weber 1995). In our study, even though current-year needles were unavailable as food for newly emerged post-diapause *C. pinus*, we observed that these larvae seldom mined needles from previous years' growth as spruce budworm *Choristoneura fumiferana* (Clem) do. In the absence of suitable food, early- instar jack pine budworm usually wander until the pollen cones reached the 'Mid-May' (see Moore and Nozzolillo 1991) stage of development and had begun to shed pollen. In our study, this occurred at JD 143 (205 GDD) and JD 157 (186 GDD) in 2001 and 2002, respectively (Figs.3 and 4). Only then did larvae occupy the pollen cones. It is evident that although pollen was shed approximately 16d later in

Table 1. Jack pine shoots, pollen-cone clusters, jack pine budworm larval populations and adult oviposition during two study years in Michigan Upper Peninsula .

| Study Year | Vegetative shoots* | Number per branch ($\bar{x} \pm$ SD) | | |
		Pollen cone clusters*	Jack pine budworm*	Egg masses**
2001	50.34 ± 14.7 a	2.7 ± 2.4 a	22.85 ± 9.4 a	0.62 ± 1.25 a
2002	129.90 ± 38.96 b	0.63 ± 1.96 b	4.99 ± 4.2 b	0.79 ± 0.57 a

* n = 270 - 383 branches from 14 - 24 samplings in 2001(May to August) and 2002 (April to August), respectively.
** n = 47 and 48 branches during August/September in 2001 and 2002, respectively.
Means in a column followed by different letters are significantly different (two sample t-test, $P = 0.05$).

2001 than in 2002, there was a surprising synchrony with respect to growing degree days. In 2002, when the jack pine trees produced very few pollen cone clusters (Table 1), groups of ~3 to 10 early- instar *C. pinus* were observed at the bases of old needles. Although no needle damage was evident, we hypothesized that the massing of larvae at these locations might be beneficial to them.

During both study years approximately 90% of the larvae taken from samples during the pollen-shedding periods were recorded from pollen cone clusters. Although it appears that green 'Early-May' cones did not attract early instars, as soon as pollen was produced, larvae readily fed on both pollen grains and internally on cone tissues. However, when pollen grains became desiccated and appeared to be no longer viable as larval food, some larvae continued feeding on cone tissue until the cone clusters were completely desiccated and were disintegrating.

Therefore, the abundance and availability of year-2 pollen cones play important roles in the population dynamics of *C. pinus*. Nevertheless, there is no consensus among researchers, whether pollen cones provide any developmental advantages to early instar jack pine budworm (Lejeune 1950, Clancy et al. 1980, Hansen 1988, Nealis and Lomic 1994). Our study shows that jack pine pollen cones are a timely, important, but relatively short-lived source of food and shelter for early- instar *C. pinus* and that this food source, provided at a time when current year vegetative foliage is largely unavailable, must somehow enhance larval survival and therefore influence jack pine budworm populations. However, in our study the presence in 2001, or the absence in 2002, of pollen-shedding cones when overwintering *C. pinus* emerged, did not significantly alter the overall rate of larval development between the two years (Figs. 3 and 4). Nor did the initial presence or absence of pollen, respectively accelerate or retard larval development during that brief period when pollen cones were available as food (Larval indices were 2.0 to 4.2 and 2.5 to 4.1 in 2001 and 2002, respectively).

Pollen cones reached the 'Early-June' (i.e., complete dessication) stage (Moore and Nozzolillo 1991) at JD 166 (409 GDD) and JD 171 (345 GDD) in 2001 and 2002, respectively and were no longer desirable as larval food. As a consequence ~95% of the resident larvae abandoned the clusters for the vegetative shoots. Nevertheless, weeks after disintegration of the cones, small numbers (0.001 larvae /cone cluster) of larvae continued to occupy tunnels within the central axis of what were formerly the pollen cone clusters. None of these tunnel larvae completed development although some persisted for weeks before dying. We found no shed larval head capsules within the tunnels, therefore it is likely that the axial stems might have been only adequate to maintain life but not sufficiently nutritious to promote larval molts. It seems therefore ironic that the same reproductive structures that sustained early instar jack pine budworm at a critical period in their life history, appeared to have also curtailed stadial development at a later period.

We found no strong linkages between *C. pinus* and the development of jack pine seed cones.

Pollinated year-2 seed cones (Moore and Nozzolillo 1991) were clearly evident on JD 151 (256 GDD) and JD 162 (251 GDD) in 2001 and 2002, respectively. Whereas these calendar dates were widely divergent, there was good synchrony between the growing degree days. This suggests that heat units, and not calendar dates, might be the primary variable, influential in their development. There was no evidence that *C. pinus* colonized pollinated year-2 seed cones in the same way as they did pollen cones or that seed cones are influential in the development of *C. pinus* larvae. In 2001 when larval populations were moderately high (Table 1), 70% to 80% of the red conelets of pollinated seed cones were damaged by C. *pinus* larvae, but in 2002, when larval populations were low, no conelets were attacked, which suggests that conelet damage might be insect-density dependent.

These findings suggest that high larval *C. pinus* populations, albeit periodic, do not pose a serious threat to jack pine seed production.

Relation between C. pinus and jack pine vegetative shoots. The primary relationships between a forest insect defoliator and its principle host focus on one or the other gaining or defending advantages. Most reported incidences of *C. pinus* relationships with jack pine foliage refer to quantitative assessments of insect damage to the host tree; thus concentrating on the insects' advantage over the tree. Only a few (e.g., Ives and Wong 1988, Hansen 1988) have examined wider interactions between jack pine budworm and jack pine vegetative shoots to provide both qualitative and quantitative accounts of these associations. As noted earlier, *C. pinus* overwinter as larvae and are essentially flush-feeders; (i.e., they feed primarily on newly flushed foliage) and that the vegetative shoots and the needle fascicles that are part of the flushing shoot, develop differently. Although jack pine shoot elongation indicates the potential long-term volume of foliage that would be available for larval food, needle development over the short term is probably more important to early instars of the species.

In our study, second instars emerged from diapause 14 - 17d before jack pine needles escaped their fascicle sheaths and exposed their green tissue. We found no evidence that the copious amounts of resin that were routinely produced by the growing vegetative shoots inhibited *C. pinus* larval movements on, or associations with its host. This implies that this material probably is not intended as a defence mechanism against the defoliator, but might be a physiological plant response, induced by climate. In 2001 and 2002, needle tips began to escape their sheaths (Fig. 5A) at JD 160 ± 1.7 and JD 170 ± 1.0 ($\pm$ SD), respectively, providing the first opportunities for larvae to freely feed on partially exposed current-year foliage. It was therefore evident that vegetative shoots were not a significant food source for 2nd and 3rd instar jack pine budworm during the critical period from the time larvae emerged in the spring to when needles escaped their fascicle sheaths.

Our study objectives did not require quantitative foliar measurements. However, during the periods when jack pine budworm were vacating the desiccated disintegrating pollen cones (JD 164-173), there were significant increases in damage to immature needle fascicles. At that time, the vegetative shoots had elongated substantially (Fig. 2), but the length of needle fascicles averaged 0.9 cm. In addition, the needle pairs were still bound by the sheath at the base (Figs. 5A,B) and only the tips of needles were readily accessible as larval food (Figs. 5A,B). With a relative shortage of current-year foliage on which to feed, *C. pinus* larvae (now primarily larval indices 3.8 to 4.9 and 2.9 to 3.5 in 2001 and 2002, respectively) attacked needle fascicles by boring into the fascicle sheaths (Fig. 5B) and feeding on the needle pairs. Our observations of fascicle mining agree with the observations made by Ives and Wong (1988). This mining almost always resulted in the immature needles being severed laterally, killing them. It is questionable if these lateral excisions (Ives and Wong 1988) are the jack pine budworm's innate feeding style or if they are opportunistic responses to circumstances. We suggest that it is the latter. Even after *C. pinus* larvae penetrate the fascicle sheath, gaining full access to the needle pairs and utilizing their full food potential would still be restricted. The remnant fascicle sheath (Fig.5B) apparently constrains longitudinal consumption of the needle; thereby limiting larval feeding to the diameter of the entry hole. In addition, because of the narrow width of needle blades, complete excisions seem inevitable.

It is likely that this type of restricted feeding requires multiple fascicle attacks in order to provide sufficient levels of food for developing larvae and this might be one reason why high larval *C. pinus* populations inflict such severe damage to developing vegetative shoots. In our study, dead immature needles remained generally within the fascicle sheath and were retained on the shoot by larval webbing for the summer. When large numbers (90%) of these needles were killed, the shoot usually died as well.
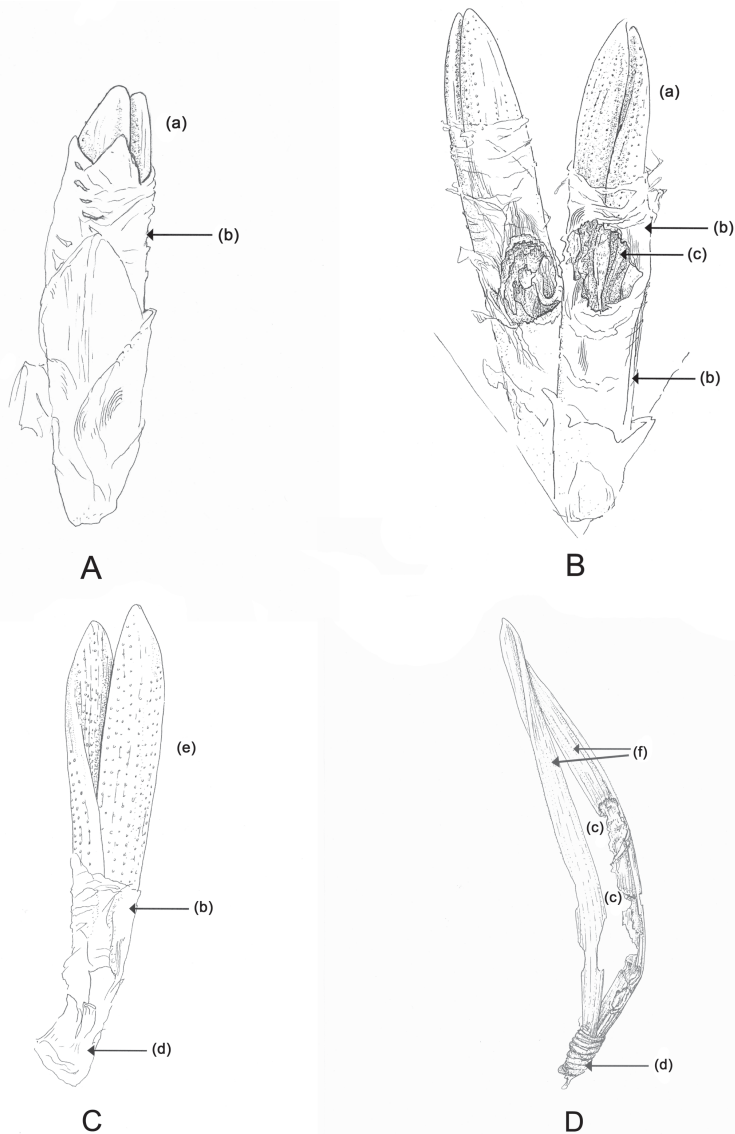
Fig.5. Jack pine needle fascicles (not to scale) showing a) needle tips as they escape the fascicle sheath, b) intact fascicle sheath, c) typical larval damage, d) the fascicle base, e) a needle pair that has largely escaped the fascicle sheath and f) mature needle pair without a fascicle sheath.
A. Undamaged needle tips as they escape a fascicle sheath. B. Fascicles showing typical mining damage by 3rd and 4th instar jack pine budworm that results in lateral excision of the encased needles. C. Undamaged needle pair that has largely escaped the fascicle sheath. D. Dislodged mature needle pair with typical feeding damage along the needle blade, and with an intact fascicle base; suggesting physiological abscission rather than larval lateral excision.

Jack pine budworm larvae are reported to be wasteful feeders because of this reputation for excising needles at their base and leaving them mostly un-eaten (Kulman et al. 1963, Ives and Wong 1988, Volney 1988, Nealis 1995). Our observations suggest that this reputed wastefulness might be overstated.

As discussed earlier, lateral needle excision, which implies wastefulness, appear to be largely a temporary feeding phase. We observed that when jack pine needle pairs had completely outgrown the fascicle sheath (Fig.5C) and had flared, *C. pinus* became semi cryptic (see Ives and Wong 1988) and fed and behaved similarly to spruce budworm. That is, they routinely fed on all sections of the needle blade (Fig.5D). This showed that *C. pinus* larvae were not re-stricted to one feeding style and that late instars do not obligately excise needles laterally. We collected dead needles in 2001 when larval populations were high (Table 1), and 64 % (n = 414 needle pairs) had been shed with their fascicle base intact (Fig. 5D) and not cut off laterally by larvae at the needle base. Almost all (92.5%) of those that were shed with the base intact had needle blades that were damaged by insects. In 2002, when larval populations were low, fewer needles were collected but the trend of the previous year continued on a small scale. These findings suggest that most fallen mature needles might not result from wasteful lateral excisions, but might be caused by the tree's physiological re-sponses to needle damage. Lateral excisions sever the leaf lamina above the fascicle base, whereas physiological abscissions result in needle pairs with fas-cicle bases intact (Fig. 5D). It is possible that when insect defoliators injure jack pine needles, the tree responds by prematurely abscising those needle fascicles instead of containing the injuries with wound healing. Additional studies are required to further explore this aspect.

Choristoneura pinus are reported to have either six or seven instars (Lejeune 1950, Nealis 1987) but for practical reasons, during this study we treated the two stages as 6th instars. The first of these late instars were found on JD170 (454 GDD) and JD176 (419 GDD) in 2001 and 2002, respectively, but this stage did not peak until ~18d later during both years (Figs. 3 and 4). In both years, this peaking coincided with shoot development (Figs. 2 and 3) that might be able to withstand larval feeding . Late instar *C. pinus,* like 6th instar spruce budworm (Talerico 1984), are responsible for most of the volume of foliage consumed; however, we speculate that jack pine budworm instars 3 - 5 might be equally destructive considering the high number of immature needle fascicles, and as a consequence entire shoots, they destroy.

Even in the presence of current-year foliage, late instar *C. pinus* fed and readily pupated on both current and previous-years' foliage. Pupae were first observed on JD 180 (586 GDD) and 190 (651 GDD) in 2001 and 2002, respec-tively. From year to year, the rate of larval development varied depending on how it was measured, but it is very unlikely that accumulated heat units (GDD) per se imposed thresholds on pupal emergence. We suspect that peri-ods of pupal development might be more influenced by larval food intake than by time (JD) and, or temperature (GDD). In 2001 we observed our first adults on JD 187 (664 GDD) and on JD 199 (782 GDD) in 2002. However, we found no relationships between jack pine phenology and adult emergence, nor were there any obvious associations between foliage development and jack pine budworm oviposition. We could not find any foliar developmental characteristic that consistently related to or coincided with moth emergence or oviposition.

Relationships between jack pine budworm and jack pine in general, appear as suggested (Wagner 1991), to be one of those patterns occurring in nature that result from a complex set of current and historical factors. These factors interact with one another and with the adaptive plasticity of plants and animals.

Insecticide applications to control jack pine infestations are traditionally timed to coincide with the larval phenology of the insect; that is, when, for example, *C. pinus* populations are peak 3rd or 4th instars. Findings from our study suggest that the timing of insecticide strategies to manage jack pine budworm might be better supported by closely observing and using the tree's phenological events than by calculating larval development. It is a relatively simple task and considerably less onerous to visually monitor tree phenology than to regularly sample insect populations and construct larval indices. We identified the following three distinct milestones in jackpine phenology that can be used successfully to time spray applications or other management strategies.

1) Sprays that are intended to target early post-diapause instars should be applied when year-2 pollen cone clusters have reached, or just before they reach the first pollen or 'Mid-May' stage.

2) Treatments prescribed for peak 3rd and 4th instar *C. pinus* could be applied when the majority of pollen cones have turned brown and started to dessicate ('Early-June' stage). The larvae will at the time be vacating them, and therefore be exposed, but before appreciable damage is inflicted to needle fascicles. This will usually coincide with the partial escape of current-year needle tips from their fascicle sheaths and should be easy to identify. We propose that this timing would significantly enhance effective pesticide/target pest interactions, potentially prevent extensive defoliation of the host tree, and, as a consequence improve the success of *C. pinus* control programs. In addition, it complies with environmental requirements of not spraying while plants are in bloom.

3) Our third option proposes spraying anytime after the current-year needle-pairs have completely escaped the fascicle sheaths but before *C. pinus* larvae have pupated. The primary objective of this timing would be larval population reduction. However, the goal of such a late application should not be to protect foliage

CONCLUSIONS

This study has shown that:

Choristoneura pinus larval development was not always closely synchronized with the growth and maturation of jack pine foliar structures. Overwintering larvae consistently emerged before jack pine needles flushed and there was little feeding on either previous-years foliage or dormant shoots. These initial plant / herbivore phenological associations favoured the tree but later ones favoured the insect.

Second and third instars fed almost exclusively on year-2 pollen cones and seemed dependent on these reproductive structures for survival over the short term.

Choristoneura pinus seriously attacks current-year jack pine needles only after pollen cones are unsuitable as food and during the period of pollen-cone abandonment, high larval populations can inflict heavy damage to shoots by laterally excising large numbers of immature needles.

Development of both jack pine and jack pine budworm are more closely related to growing degree days than to calendar dates.

Jack pine budworm's reputedly wasteful feeding by lateral excision of both immature and mature needles might be overstated, and it is likely that abscised needles are routinely mistaken as laterally excised.

Having closely examined relationships between jack pine budworm and its principle host, it would be preferable and more practical to time insect-targeted insecticide sprays on observed jack pine phenology rather than on the presently used method of sampling larvae to determine the prescribed insect development.

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