



The relationship between trembling aspen phenology and larval development of the large aspen tortrix

D. Parry, W.J.A. Volney, and C.R. Currie

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Cover photo:

One of the phenological stages of developing trembling aspen buds and shoots. This photograph shows condition class 6, which is characterized by shedding bud scales, elongating and unrolling leaves.

**THE RELATIONSHIP BETWEEN TREMBLING
ASPEN PHENOLOGY AND LARVAL
DEVELOPMENT OF THE
LARGE ASPEN TORTRIX**

D. Parry, W.J.A. Volney, and C.R. Currie

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ABSTRACT

The large aspen tortrix, *Choristoneura conflictana* (Walker), is an occasional defoliator of trembling aspen, *Populus tremuloides* Michx. in western Canada. Although the essential details of its life cycle are well known, the development of the insect with respect to its host plant is poorly understood. Large aspen tortrix and trembling aspen bud and shoot development are described from observations at two sites in 1994. Degree-day models based on a common threshold temperature of 5°C were developed for both insect and bud and shoot development of its host. Parameter estimates for models of aspen development suggest that there is considerable variation in budbreak between sites, whereas *C. conflictana* exhibited less variation of this kind. Parameter estimates for *C. conflictana* development models were somewhat at odds with plots of the raw data for the onset of feeding. Clonal control of phenological development of aspen and microsite differences in temperature regimes are among the phenomena that must be considered if the models to predict phenological events accurately in the field are to be improved.

RÉSUMÉ

La tordeuse du tremble, *Choristoneura conflictana* (Walker), est un défoliateur occasionnel du peuplier faux-tremble, *Populus tremuloides* Michx., dans l'ouest du Canada. Si les différentes étapes du cycle évolutif du ravageur sont bien connues, de nombreux aspects liés au synchronisme qui existe entre le développement de l'insecte et celui de l'hôte demeurent nébuleux. Les chercheurs ont décrit le développement de la tordeuse du tremble et la croissance des bourgeons et des tiges du peuplier faux-tremble à partir d'observations effectuées dans deux sites en 1994. Ils ont élaboré des modèles degrés-jours utilisant un seuil thermique critique de 5 °C pour le développement du ravageur et la croissance des bourgeons et des tiges de l'hôte. Les estimations des paramètres pour les modèles du développement du peuplier faux-tremble laissent supposer l'existence de fluctuations considérables entre les sites pour ce qui est du débourrement. Les écarts étaient moins prononcés chez le ravageur. Les estimations des paramètres liées aux modèles de développement de *C. conflictana* présentaient un faible niveau de concordance avec les diagrammes des données brutes sur le début de la phase d'alimentation chez le ravageur. La régulation clonale du développement phénologique du peuplier faux-tremble et les différences de régimes de température entre les microsites figurent parmi les phénomènes qu'il convient de considérer pour améliorer les modèles permettant de prévoir avec précision les événements phénologiques sur le terrain.

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NOTE

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INTRODUCTION

The large aspen tortrix, *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae), is an occasional defoliator of trembling aspen, *Populus tremuloides* Michx., in western Canada. Periodic outbreaks can defoliate as much as 25 600 km² annually (Prentice 1955). The most recent large outbreak of *C. conflictana* in the prairie provinces, which began in Saskatchewan in 1991 and peaked in 1993, resulted in 359 434 ha of aspen being moderately to severely defoliated (Brandt 1994). Outbreaks of *C. conflictana* tend to last only 1–3 years, so the effects on host trees are limited to increment loss and some dieback of twigs (Cerezke and Volney 1995). Factors involved in the release of populations to outbreak levels are not understood, although the collapse of outbreaks is primarily due to starvation of late-instar larvae (Beckwith 1970).

The life cycle of *C. conflictana* has been described previously (Prentice 1955; Wickman 1963; Beckwith 1968; Wong 1979). Briefly, in the prairie provinces, eggs of *C. conflictana* hatch in early July and neonates feed gregariously on aspen leaves. In late August, first instars descend to the base of trees, where they spin a silk hibernaculum beneath loose bark, in bark crevices, or in moss on the lower bole. After molting to the second instar, larvae spend the winter within hibernacula. In late April and early May, larvae emerge and ascend trees to colonize suitable buds. If buds have not begun to swell, larvae can disperse on silk threads or spin a secondary hibernaculum and wait for buds to soften before penetrating bud scales to commence feeding. Second and third instars remain within buds as they develop and flush. As the shoot elongates, fourth and fifth instars tie leaves together to create

an enclosed feeding area where larvae complete their growth. Pupation occurs on the foliage in mid-June and adults emerge about two weeks later.

There is considerable variation in trembling aspen budbreak (Barnes 1969; Peterson and Peterson 1992). Clonal variation in the timing of aspen budbreak is thought to influence survival of *C. conflictana* (Witter and Waisenen 1978) because populations were significantly higher on aspen trees flushing in synchrony with the emergence of second instars from hibernacula than on trees that flushed later. This suggests that there might be a narrow phenological window available for successful colonization of aspen buds in the spring. Despite the ecological implications of phenological synchrony between trembling aspen and *C. conflictana*, quantitative studies directly linking the phenology of both species are lacking.

Stochastic models have been used to describe the relationship between other species of *Choristoneura* and their hosts (i.e., Dennis et al. 1986; Lysyk 1989; Volney and Cerezke 1992). The advantage of such models is that they describe the phenology of both the host and the defoliator simultaneously, allowing comparisons of variation in development between the two populations. In this paper, the model used is adapted to describe the temporal relationship between *C. conflictana* and trembling aspen phenologies. In addition, the first categorization of the phenological stages occurring during budbreak and leaf expansion of trembling aspen is provided, and how changes in the sequence of these temporal events can influence the success or failure of large aspen tortrix populations is discussed.

MATERIALS AND METHODS

Phenological Sampling

In 1994, plots were established in central Saskatchewan to study the relationship between *C. conflictana* development and trembling aspen phenology. Phenological observations were made in two trembling aspen stands 1 km apart, located about 25 km southeast of Waskesiu, Saskatchewan. In the previous year, moderate levels of defoliation

attributed to *C. conflictana* had occurred in these stands. Observations on *C. conflictana* and trembling aspen development were made every second day from May 1 to the end of the pupal period. Initially, samples were collected from four randomly selected aspen trees in each stand. As *C. conflictana* populations declined, trees adjacent to the original trees and in approximately the same phenological state were sampled. On each sampling date, pole

pruners were used to remove one upper and one lower crown branch from each tree. Branches were placed in paper bags, labeled, and returned to the laboratory for examination.

Aspen buds and shoots were classified into 10 phenological stages using an arbitrary scale similar to those used by Turgeon (1986) and Volney and Cerezke (1992) for the buds and shoots of white spruce (Table 1; Fig. 1). The final class was not used because observations on *C. conflictana* were discontinued before aspen shoots became lignified.

To describe *C. conflictana* development, all larvae from the terminal 75 cm of each branch were collected and counted. The distribution of instars on each sampling day was determined by comparing individual head-capsule widths against marks on measuring cards, corresponding to head-capsule dimensions for the different instars described by Prentice (1955) and Beckwith (1968). Each larva was measured against the card and assigned to the correct stage (instars 2–5 or pupa). Observations at the second sample site were discontinued prior to pupation after the *C. conflictana* population declined precipitously.

Choristoneura conflictana population densities were calculated as the number of larvae per 25 buds (Henson 1954), because the number of aspen buds varied considerably on each 75-cm branch section. The larvae were counted in the 25 terminal buds or shoots for four upper-crown and four lower-crown branches at each site on each sampling date. These counts were expressed as the mean number of larvae per bud. This density estimate was plotted against accumulated degree-days (DD) in order to facilitate comparison with the developmental

models for trembling aspen and the phenology of *C. conflictana*.

Calculation of Developmental Thresholds

Daily maximum and minimum temperatures, obtained from an Environment Canada weather station located at Waskesiu, were used to calculate degree-day accumulations using Allen's (1976) modified sine procedure. There were no significant orographic features between the weather station and the study sites.

In the absence of independent data about developmental thresholds for either species, degree-day accumulations were calculated for threshold temperatures between 1° and 8°C. A nonlinear regression procedure was used to estimate parameters for phenological models of the type described by Dennis et al. (1986). Parameters were estimated for both *C. conflictana* and trembling aspen using the same range of threshold temperatures. R^2 values were used to select the best developmental threshold temperature for *C. conflictana* and aspen bud and shoot development. Degree-day accumulations above this threshold temperature and the parameters obtained were used to plot generalized development curves for instars 2 to 5 for *C. conflictana* and the nine aspen shoot developmental stages. These curves were used to locate developmental milestones for each population corresponding to the peak of the intermediate stages and the date at which 50% of the first and last developmental stages left or entered that stage.

Table 1. Classification of aspen bud and shoot development

Condition class	Description
1	Firm, brown winter bud, scales tight, no apparent development
2	Buds swelling but still firm and brown
3	Green coloration visible along edges of bud scales, bud becoming soft
4	Bud soft, scales separating, leaf tips visible
5	Scales separated, leaf tips protruding and elongating
6	Scales shed, leaves elongating and unrolling
7	Leaves unrolled and expanding
8	Leaves expanding and shoot expanding, leaves still lime green
9	Leaves and determinate shoots fully expanded, leaves dark green
10	Determinate shoots lignified

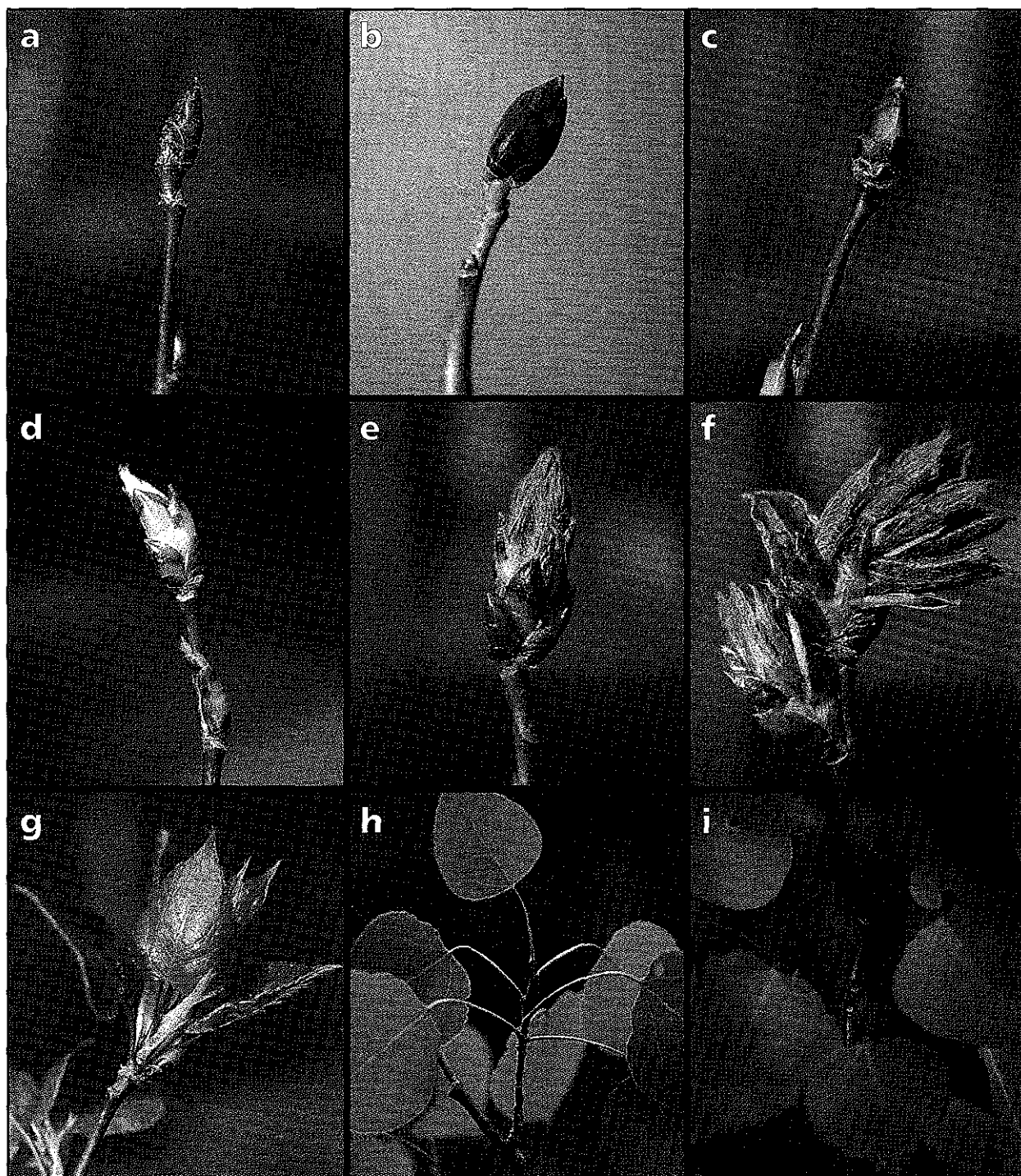


Figure 1. Phenological stages of developing trembling aspen buds and shoots. Condition class 1 (a) Firm, brown winter bud, scales tight, no apparent development. Condition class 2 (b) Buds swelling but still firm and brown. Condition class 3 (c) Green coloration visible along edges of bud scales, bud becoming soft. Condition class 4 (d) Bud soft, scales separating, leaf tips visible. Condition class 5 (e) Scales separated, leaf tips protruding and elongating. Condition class 6 (f) Scales shed, leaves elongating and unrolling. Condition class 7 (g) Leaves unrolled and expanding. Condition class 8 (h) Leaves expanding and shoot expanding, leaves still lime green. Condition class 9 (i) Leaves and determinate shoot fully expanded, leaves dark green.

RESULTS

The most-appropriate threshold temperature for models of *C. conflictana* and trembling aspen development was within the range of 3° to 5°C (Table 2). Above 5°C, no adequate solution to the nonlinear regression equation could be found for *C. conflictana* development at Site 1. Also, R^2 values declined significantly for threshold temperatures above 5°C at Site 2. Similarly, R^2 values declined above 5°C for the models of trembling aspen development at both sites. Based on these values of R^2 , 5°C was chosen as a compromise threshold temperature for modeling *C. conflictana* and trembling aspen development.

Trembling aspen shoot development at the two sites was modeled using the parameter estimates in Table 3. These models explained 63% and 44% of the variance at Sites 1 and 2, respectively. At Site 1, trembling aspen development began with the swelling of the buds in early May at 50 DD (Fig. 2). Development commenced earlier at the second site, at around 35 DD (Fig. 3). Buds were soft enough for *C. conflictana* larvae to start mining at 60 DD at Site 1 and 40 DD at Site 2. Budbreak began at 75 DD at Site 1 and at 50 DD at the second site. About 99% of leaves were fully expanded by 280 and 235 DD at Sites 1 and 2, respectively. Once growth began, trembling aspen proceeded rapidly through seven phenological states within 100 DD at both sites. As many as six states, each representing more than 5% of the population, occurred simultaneously at both sites during this time period.

In contrast to the intersite variation in the onset of trembling aspen development, the phenological models suggest that *C. conflictana* development was similar at both sites. Emergence from hibernacula began at both sites around 85 DD (Figs. 4 and 5; Table 4). Larvae were finished feeding by 310 DD at Site 1. At Site 2, the population crashed prior to pupation, so development was modeled only for instars 2 through 5. The peak of each instar was distinct and with little overlap. At both sites, instars 2, 3, and 4 were all represented by more than 5% of the population during a narrow time period extending from 130 DD to 180 DD. Intervals from 50% emergence of second instars, to peak of third, to peak of fourth, and to 50% final (fifth) instars were 15, 35, and 45 DD at Site 1, and 15, 45, and 15 DD for the corresponding developmental milestones at Site 2. The appearance of particular instars was not coincident with the same trembling aspen

developmental classes at the different sites. The slower development of aspen at Site 1 resulted in the presence of both second and third instars before budbreak. At Site 2, the scales were off the buds and leaf growth was underway before third instars were present in the population.

The phenological models did not capture the large differences observed in development of *C. conflictana* between the two sites (Figs. 6a and b). This is particularly evident for the second and third instars, when their peaks occurred 42 and 29 DD, respectively: later in Site 1 than in Site 2. At Site 1, the peak of second, third, fourth, and fifth instars occurred at 139, 160, 210, and 287 DD, respectively (Fig. 6a). The corresponding dates from the phenology model are 130, 145, 180, and 225 DD, respectively. At Site 2, these same peaks occurred earlier at 97, 131, 210, and 247 DD (Fig. 6b). The corresponding dates from the model were 130, 145, 190, and 205 DD. The discrepancy in predictions of phenological dates thus vary from 7 to 62 DD. The uncertainty of prediction in terms of calendar dates depends on temperature, but a 62-DD discrepancy is in the order of 5 days in early June. Although the models consistently underestimated the DDs required to reach a certain phenological milestone at Site 1, the opposite was true for dates at Site 2.

Population densities of *C. conflictana* varied between sites and crown levels (Figs. 7a and b). As emerging larvae colonized trees, branches in the lower crown initially had higher densities. This pattern was reversed after the larvae established feeding sites. Upper-crown branches had consistently higher population densities than branches from lower crowns, which is reflected in the models for aspen development. At Site 1, highest densities occurred between 130 and 160 DD, when the population was dominated by third instars. At Site 2, peak density occurred earlier, from 80 to 130 DD, when the majority of the larvae were second instars. This suggests that at Site 1, the emergence of second instars and the subsequent colonization of buds was more protracted than at Site 2. Population density declined dramatically after 125 DD at Site 2. This decline occurred synchronously with the unrolling and expansion of trembling aspen leaves. Although the decline was not as dramatic at Site 1, it was associated with the same aspen phenological states.

Table 2. Comparison of nonlinear regression R^2 s for different developmental thresholds for trembling aspen and large aspen tortrix at two sites near Waskesiu, Saskatchewan

Threshold temperature (°C)	Trembling aspen		Large aspen tortrix	
	Site 1	Site 2	Site 1	Site 2
1	0.6347	0.4663	— ^a	0.9627
2	0.6388	0.4103	—	0.9606
3	0.6352	0.4322	0.8478	0.9571
4	0.6347	0.4797	—	0.9337
5	0.6282	0.4352	0.8451	0.9623
6	0.6227	0.4319	—	0.8416
7	0.6132	0.3927	—	—
8	0.6103	0.3822	—	—

^a Dashes indicate no convergent solution to nonlinear regression equation obtained.

Table 3. Parameter estimates for trembling aspen development model at two sites near Waskesiu, Saskatchewan, in 1994^a

Site	Parameter	Estimate	Asymptotic standard error	Asymptotic 95% confidence interval	
				Lower	Upper
1	a ₁	80.646	0.476	79.708	81.584
	a ₂	91.748	0.582	90.600	92.895
	a ₃	117.592	0.580	116.448	118.736
	a ₄	130.247	0.518	129.226	131.269
	a ₅	134.962	0.513	133.949	135.975
	a ₆	143.000	0.537	141.940	144.061
	a ₇	170.059	0.772	168.536	171.581
	a ₈	210.269	1.000	208.296	212.243
	a ₉	211.013	1.072	208.897	213.128
	b ²	0.646	0.020	0.606	0.685
2	a ₁	58.540	0.518	57.515	59.565
	a ₂	68.765	0.472	67.831	69.699
	a ₃	79.170	0.515	78.151	80.189
	a ₄	90.913	0.577	89.771	92.054
	a ₅	106.400	0.594	105.226	107.575
	a ₆	118.594	0.352	117.898	119.290
	a ₇	151.458	0.617	150.238	152.678
	a ₈	167.057	1.013	165.053	169.061
	a ₉	181.835	1.166	179.529	184.142
	b ²	0.570	0.022	0.526	0.614

^a Development threshold temperature = 5°C.

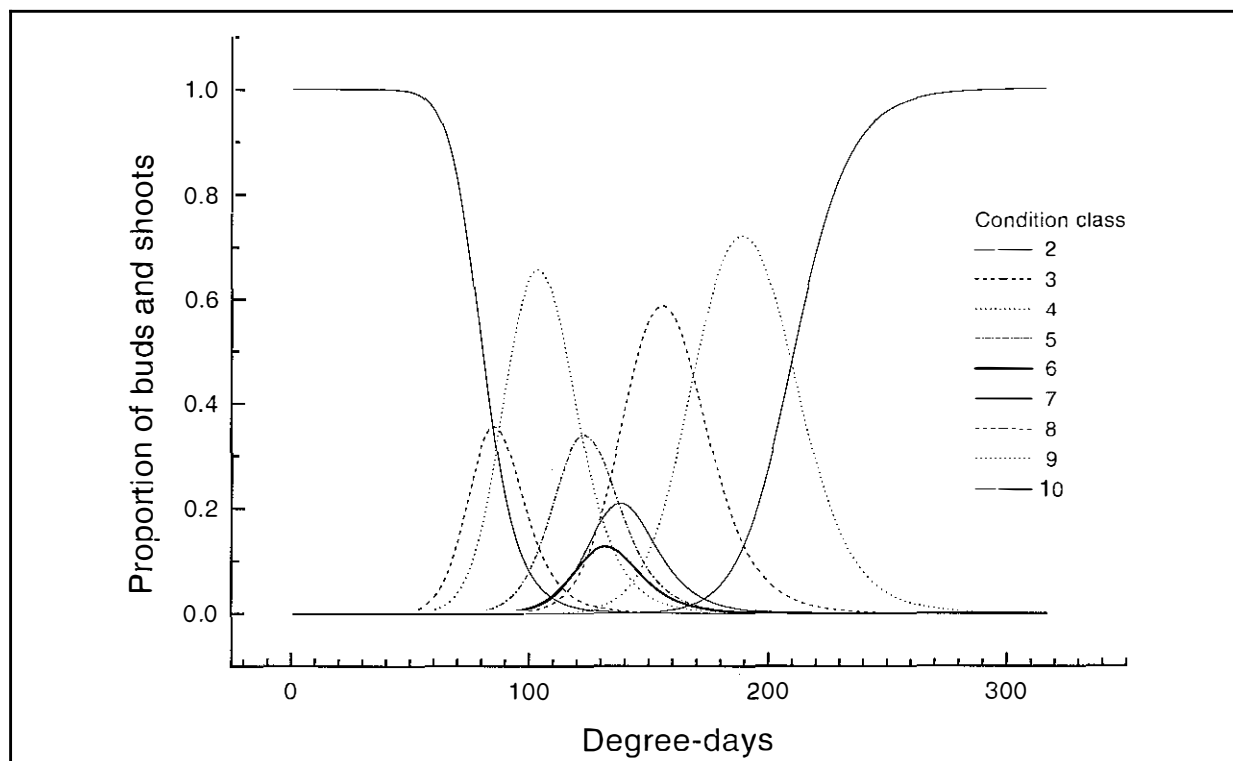


Figure 2. Development curves for aspen buds based on a 5°C threshold, at Site 1.

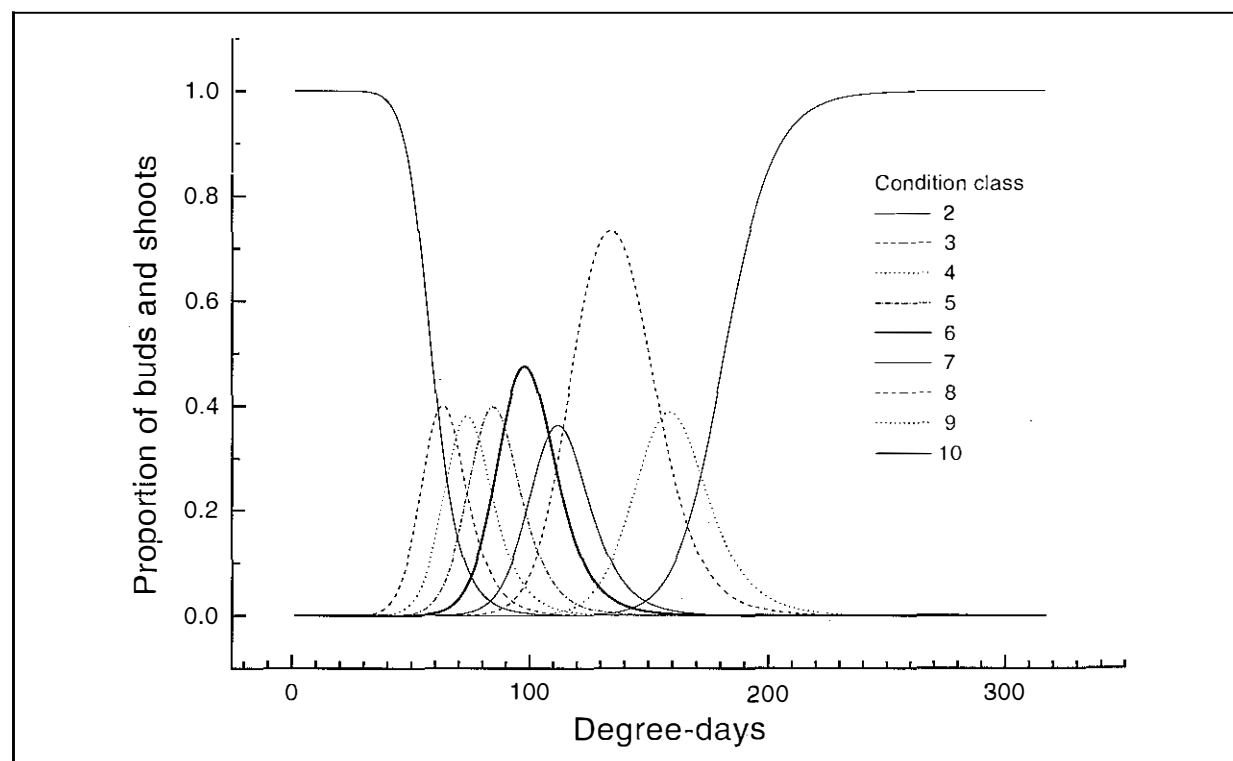


Figure 3. Development curves for aspen buds based on a 5°C threshold, at Site 2.

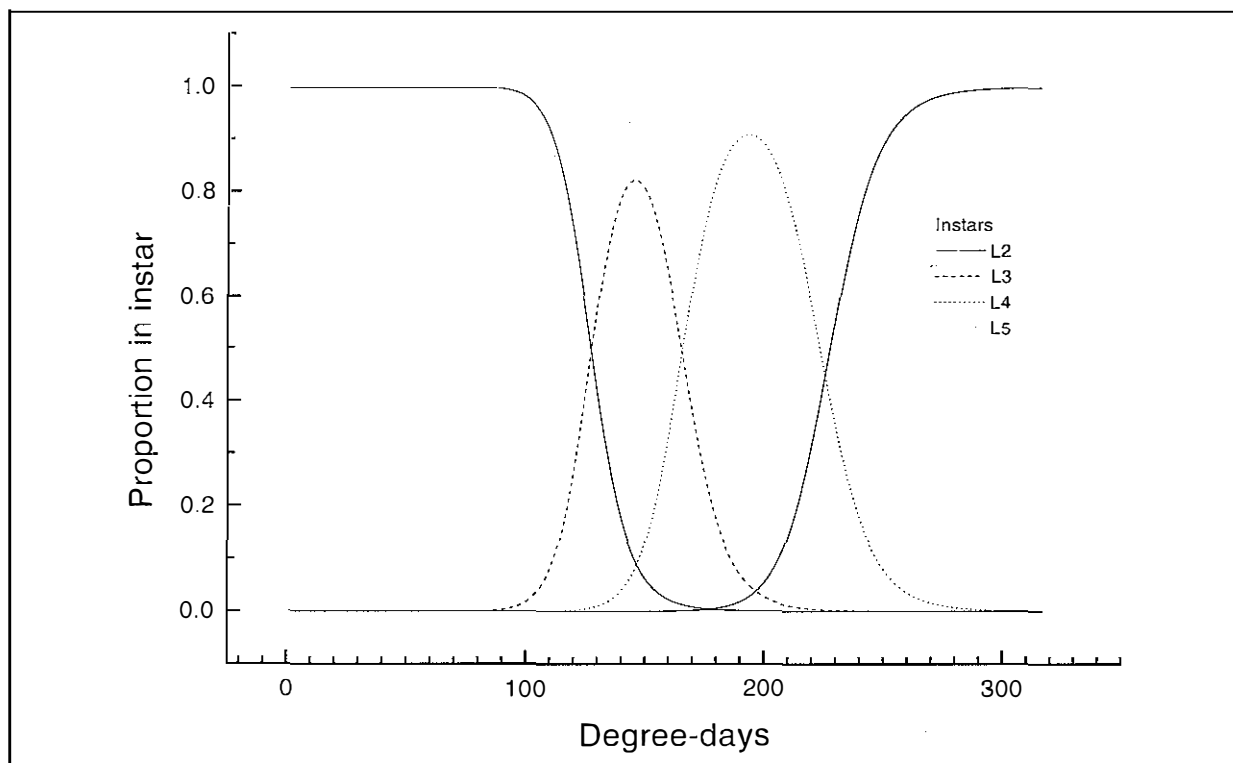


Figure 4. Development curves for large aspen tortrix based on a 5°C threshold, at Site 1.

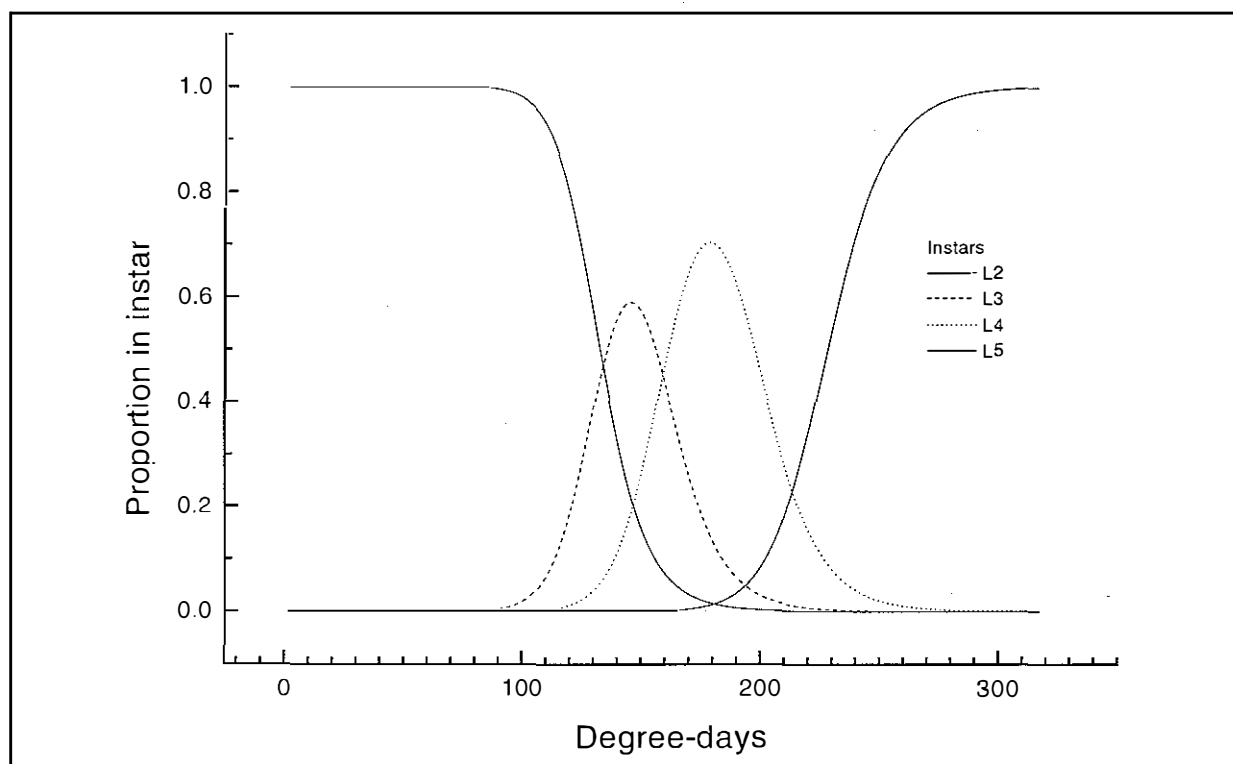


Figure 5. Development curves for large aspen tortrix based on a 5°C threshold, at Site 2.

Table 4. Parameter estimates for large aspen tortrix development model at two sites near Waskesiu, Saskatchewan, in 1994^a

Site	Parameter	Estimate	Asymptotic standard error	Asymptotic 95% confidence interval	
				Lower	Upper
1	a ₁	129.849	0.809	128.238	131.460
	a ₂	162.263	1.525	159.226	165.299
	a ₃	207.834	1.440	204.966	210.702
	a ₄	208.298	2.960	202.401	214.195
	b ²	0.440	0.041	0.358	0.522
2	a ₁	127.520	0.665	126.199	128.850
	a ₂	165.999	1.827	162.347	169.625
	a ₃	223.830	3.787	216.284	231.372
	a ₄	227.889	3.814	220.283	235.480
	b ²	0.464	0.046	0.373	0.555

^a Developmental threshold temperature = 5°C.

DISCUSSION

Emergence of *C. conflictana* preceded bud softening by about 1 week at Site 1, but was synchronous with the softening of the buds at Site 2. The early colonization of buds appeared to be tightly linked to the softening of buds, an observation made by previous researchers (Prentice 1955; Wickman 1963). At Site 1, lack of synchrony between emergence and bud softening forced larvae to spin secondary hibernacula on the outside of buds. This behavior has been reported in the past as a response to poor weather (Beckwith 1968), but its occurrence only at Site 1 precludes this explanation. Findings from the current study suggest that secondary dispersal is a response to poor synchrony between larval emergence and the presence of aspen buds in a suitable phenological state for colonization. This behavior was also described by Witter and Waisanen (1978), who found that for *C. conflictana*, colonized buds from late-flushing aspen clones at significantly lower rates than buds of clones flushing as little as 6 days earlier.

Prentice (1955) recorded emergence times for *C. conflictana* in the early 1950s at two sites within 150 km of the site of this study. At Glaslyn, Saskatchewan, larvae began emerging on May 1, May 5, and May 15 in 1952, 1953, and 1954, respectively. Emergence of *C. conflictana* began on May 10 and May 21 at Lac la Ronge, Saskatchewan, in 1953

and 1954, respectively. In the current study, the first larvae were observed on April 30. The large variation in emergence times at particular sites between years indicates that the initial emergence is determined more by temperature than by photoperiod.

The consequences to *C. conflictana* populations of emerging late relative to trembling aspen bud-softening are unknown. Reduced fecundity and survivorship stemming from decreased plant quality, or increased foliar chemical defences, are a possibility. Both nitrogen and water content decrease significantly in aspen foliage in the few weeks following budbreak (James and Smith 1978; Lindroth et al. 1987). The interaction between declining nitrogen content and foliar defensive chemicals has been shown to have deleterious effects on several folivorous aspen feeders (Lindroth and Bloomer 1991; Lindroth and Hemming 1990). Optimal growth of early instar gypsy moth (*Lymantria dispar* L.) and forest tent caterpillar (*Malacosoma disstria* Hübner) is linked to synchronous development with budbreak of trembling aspen (Hunter and Lechowicz 1992). For these species, there is a rather narrow phenological window in which they can initiate feeding before decreases occur in growth rate and survivorship. In Alaska, higher *C. conflictana* growth and survival rates occurred on trembling aspen receiving nitrogen fertilizer than

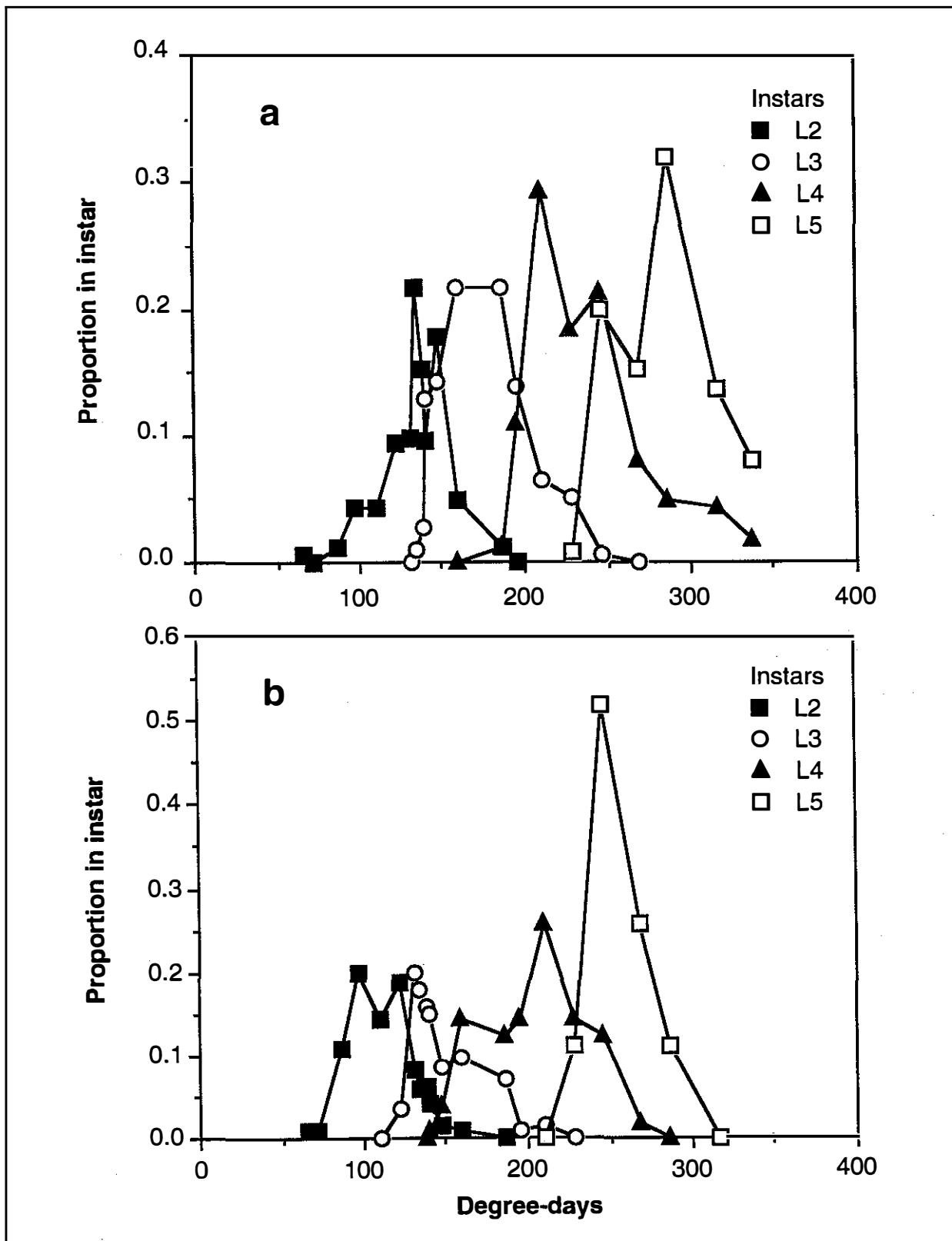


Figure 6. Proportion of total large aspen tortrix instar count present at each sampling date at Site 1 (a) and Site 2 (b).

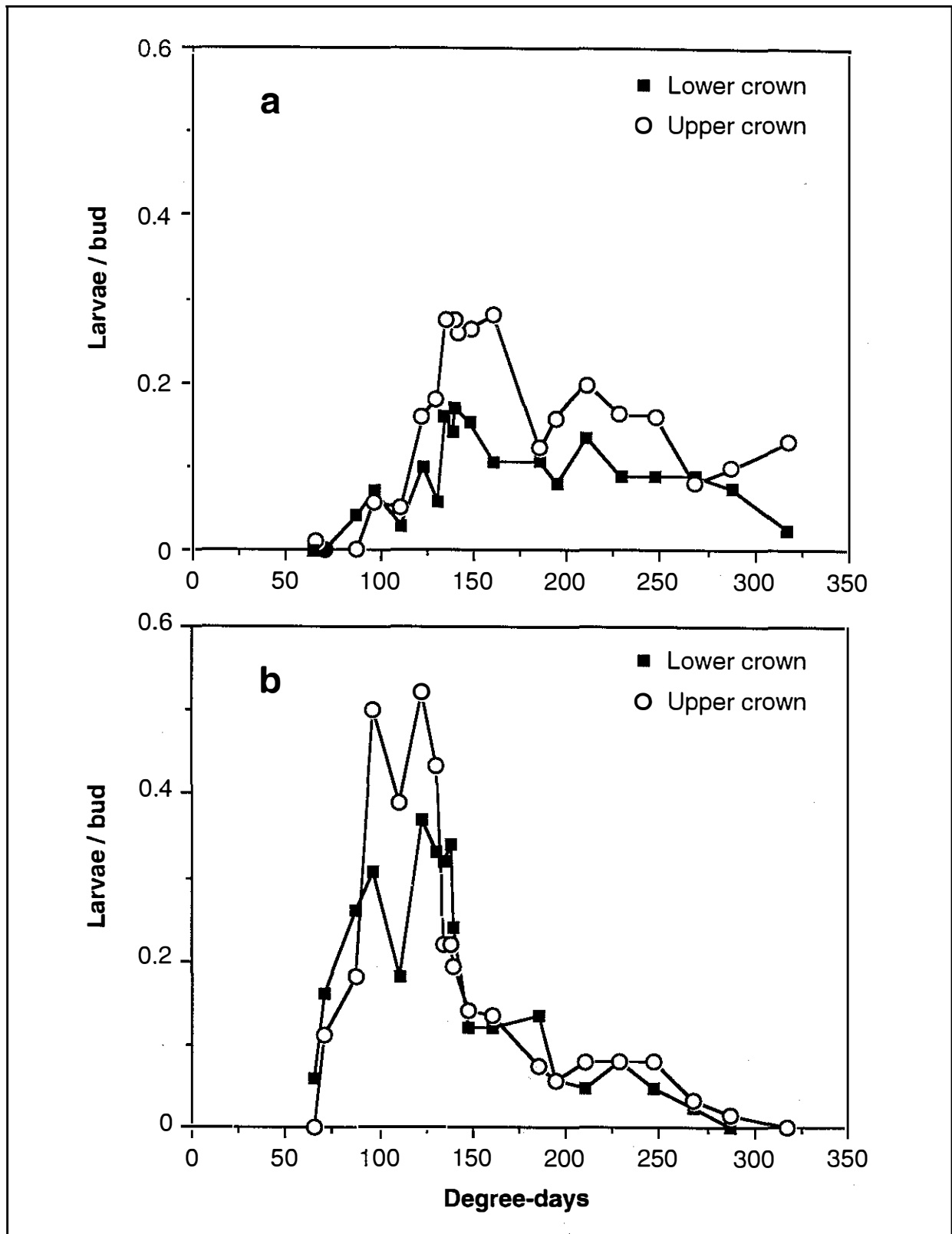


Figure 7. Mean number of large aspen tortrix larvae per bud or growing shoot at each sample date at Site 1 (a) and Site 2 (b).

on unfertilized trees (Bryant et al. 1987). This suggests that the same phenological constraints operating on other early season defoliators of trembling aspen can also affect growth and development of large aspen tortrix.

Indirectly, asynchrony can affect population dynamics through increased exposure to parasitoids and predators. In early stages of aspen development, the larvae are completely enclosed within the bud scales. The rapid decline in population densities observed in this study was associated with the unrolling and expansion of leaves. At this stage, *C. conflictana* larvae were constructing leaf rolls, which are open at both ends. The decline was primarily due to larval disappearance. We suspect that predation is an important factor at this stage because the disappearance of larvae was associated with aspen phenological states that increased their vulnerability to natural enemies. Further mortality of up to 50% was caused by tachinids (probably *Omotoma fumiferanae* [Tothill]) attacking final-instar larvae within the leaf rolls. Thus, larvae might be under strong selective pressure to develop quickly in the bud and young shoot so as to minimize the portion of their life cycle spent feeding on aspen shoots in later phenological states.

Stochastic models based on degree-day accumulations did not appear to fit the phenology of trembling aspen very well. The high degree of variability in flush times between different aspen

clones could account for the models' poor performances. Aspen phenology is influenced by air and soil temperatures as well as genetics; by contrast, models used in this study were based solely on degree-day accumulations derived from air temperatures alone. Some aspen development occurred at Site 2 prior to the initiation of sampling on May 1. This could also account for the lower R^2 relative to Site 1. Blocked experimental designs that account for clonal differences in aspen development are required to represent aspen shoot phenology more accurately using temperature driven models.

Variations in microclimate can account for the apparent discrepancy between the modeled phenology of *C. conflictana* and the curves generated from the raw data. Maximum and minimum temperatures obtained from a single weather station do not account for intersite differences in temperature. Further error can be introduced by using air temperatures to approximate the phenology of leaf-rolling or leaf-tying insects such as *C. conflictana*. Depending on orientation of leaves and intensity of solar radiation, temperatures within leaves rolled by *C. conflictana* can be as much as 15°C above ambient (Henson 1958). This would result in an underestimation of the degree-days required to complete larval development. These effects would be more apparent on larvae developing in areas receiving greater insolation such as south-facing slopes or at northerly latitudes with longer day lengths.

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