# Climate and outbreaks of the forest tent caterpillar

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Some have suggested that the periodic outbreaks of the forest tent caterpillar, *Malacosoma disstria* are triggered by weather the temperature at the time of early larval feeding, and overwintering temperatures To assess the role of these factors, defoliation maps, compiled annually from flight surveys for the province of Ontario, were compared to similarly scaled temperature records An analysis of the year to year variation shows no relationship between the pattern of increases or declines in defoliation and either temperatures during early larval development, or overwintering temperatures Four periods of defoliation by forest tent caterpillars were observed in Ontario over 41 yr, but at individual sites extensive defoliation did not occur for each of the outbreak periods Defoliation was less severe in regions with low overwintering temperatures, but was not related to the average number of degree days in the early spring Outbreaks were most common in areas where deciduous forests were extensive, and the mean overwintering temperatures were above –40°C While these weather variables do not apparently explain the details of population dynamics of forest tent caterpillars, extreme weather conditions might synchronize populations

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## Introduction

Weather conditions are popular among the explanations of fluctuations in population density of forest Lepidoptera Recent reviews suggest that studies of the forest tent caterpillar, *Malacosoma disstria* Hbn, provide evidence of weather triggering forest insect outbreaks (Martinat 1987, Wallner 1987) In particular, both the temperature through the early larval feeding period, and the minimum temperature through the winter have been implicated as determinants of when and where outbreaks occur

Several studies have provided evidence linking the rises and falls of populations to the temperature to which the early instar larvae are exposed (Table 1) These studies suggest that the temperature during the early larval feeding period is an important factor in determining lar-

val survival, with warm temperatures being favourable to population increases

A second climatic factor which might influence changes in forest tent caterpillar abundance is the overwintering temperature Hanec (1966) showed that a seasonal variation in glycerol content allows forest tent caterpillar eggs to be supercooled to temperatures as low as –41°C, below which they will freeze. A subsequent 9-yr study of forest tent caterpillar population dynamics in northern Minnesota (Witter et al 1975) found a sharp rise in egg mortality, due to factors other than parasitism and infertility, for those years in which the coldest temperature through the previous winter dropped below –40°C Egg mortality for the 5 yr for which the temperature did not drop below –40°C ranged from 0–10%, while in the 4 yr where temperatures dropped below this threshold, mortality ranged from 10–65% This suggests that the mini-

Table 1 Studies providing evidence of the relationship between forest tent caterpillar outbreaks and the temperature through the early larval feeding period

| Reference | Location | Extent of observations | Findings |
|---|---|---|---|
| Hodson (1941) | Northern Minnesota | 2 locations, 1 outbreak | Cold, wet weather for 3 weeks after hatch, high larval mortality |
| Blais et al (1955) | Manitoba and N-W Ontario | 2 locations, 1 outbreak | Prolonged cold and wet following hatch, outbreak collapsed |
| Ives (1973) | Ontario and Prairies | several locations and outbreaks | Years prior to start of outbreaks warmer than years prior to collapses |
| Hodson (1977) | Minnesota | 2 locations, 2 outbreaks | Warm in years prior to start of outbreaks, cool in years prior to collapses |

mum overwintering temperature may influence the rate of increase of forest tent caterpillar (Witter 1979)

The studies providing evidence that these two climatic factors determine when and where outbreaks occur have all been correlative, relating patterns of outbreaks to temperature records Results of such climatic studies are often difficult to interpret (Martinat 1987, Myers 1988), particularly when the number of associations considered are high, or the number of outbreaks considered are few The nature of this work makes it difficult to assess the significance of such a factor over a larger spatial and temporal extent While unfavourable climate may increase larval mortality in a particular location or year, it is not clear whether it has determined the pattern of changes in abundance over the course of several outbreaks or over a larger geographical area

In this study, 41 yr of information on defoliation by the forest tent caterpillar in Ontario, Canada are used in conjunction with macroclimatic and forest composition information to explore some previously developed hypotheses regarding the role of climate in outbreaks Data from sites across the province also allow comparisons of associations between forest composition and the severity of winter temperatures with the distributions of populations of forest tent caterpillars which undergo periodic outbreaks We begin by examining the relationship between the interannual changes in defoliation and both the temperature during larval feeding, and the minimum overwintering temperature The spatial pattern of outbreaks is then compared to patterns of climate and forest composition to understand limits to forest tent caterpillar distribution

## History of outbreaks

From 1948 to 1988, rangers from Forestry Canada's Forest Insect and Disease Survey recorded the extent of defoliation by the forest tent caterpillar in the province of Ontario This was done at the end of the larval feeding period each year (usually mid- to late-June) by flying over areas that may have been defoliated and sketching the noticeably defoliated areas The resulting maps pro-

vide a coarse measure of the interannual change in abundance of late instar larvae across the province

These maps show that there have been four province-wide outbreaks from 1948 to 1988 (Fig 1) At this scale the forest tent caterpillar appears to be a periodic defoliator, with peak years of defoliation occurring at 13 yr intervals However, many areas have had only one or two outbreaks sufficient to cause defoliation through this 41
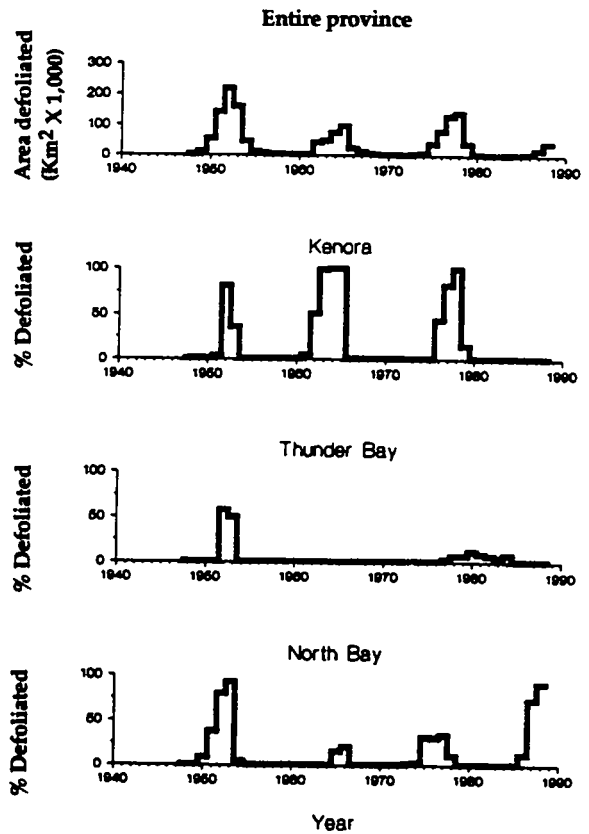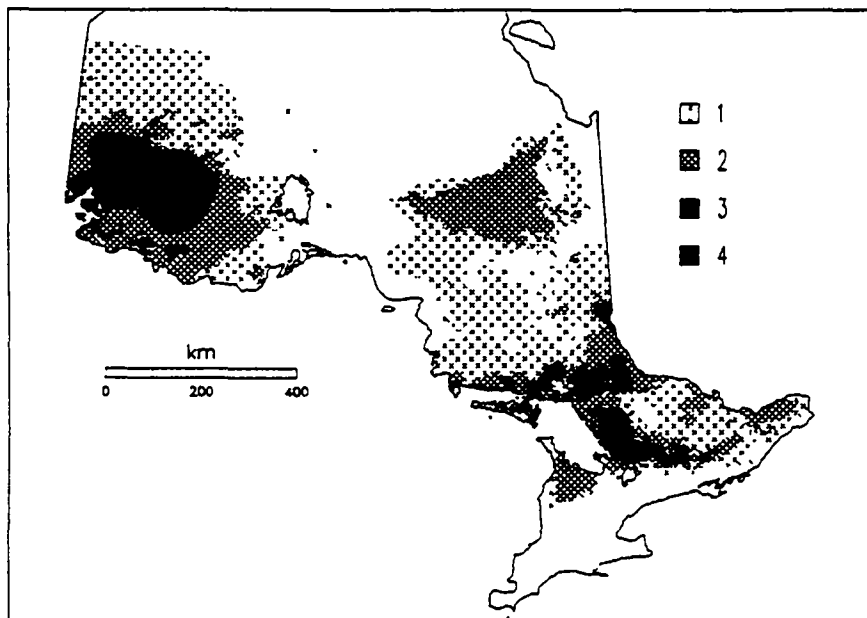


Fig 1 Total area within which defoliation has occurred each year in Ontario from 1948–88, and the percent area defoliated each year in three areas of Ontario demonstrating the variation in the extent of defoliation among outbreaks and locations

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Fig 2 The number of outbreaks that have occurred throughout Ontario from 1948–1988



yr period (Fig 2) although caterpillar populations could have increased but not have been sufficient to cause noticeable defoliation

## Methods

To investigate the relationship between the larval feeding temperature and interannual changes in abundance we used two sources of information the annual maps of defoliation from 1948 to 1988, and daily maximum and minimum temperature data, from the Atmospheric Environment Service of Environment Canada, for a network

of 20 stations across the province over this same period The temperature records were used to calculate an index of how favourable the larval feeding temperatures were for each station and year (or "station-year") This index was then compared to changes in defoliation, to see if warm springs corresponded with increases in abundance, and cool springs with decreases

## Larval feeding temperature index

As the hatch date of eggs varies from location to location, and from year to year, the first step in calculating a

Table 2 Actual hatch dates and those predicted by the Minnesota model for various times and locations in Ontario

| Location | Year | Source of actual hatch date | Actual date[1] | Model date | Difference (model-actual) |
|---|---|---|---|---|---|
| Fort Frances[2] | 1967 | Witter et al (1972) | 22 May | 18 May | −4 |
| | 1968 | | 1 May | 2 May | +1 |
| | 1969 | | 2 May | 30 Apr | −2 |
| Fort Frances[2] | 1970 | Mattson and Erickson (1978) | 13 May | 18 May | +5 |
| | 1971 | | 7 May | 6 May | −1 |
| | 1972 | | 12 May | 10 May | −2 |
| | 1973 | | 7 May | 6 May | −1 |
| | 1974 | | 17 May | 18 May | +1 |
| Cedar Lake | 1953 | Blais et al (1955) | 8 May | 7 May | −1 |
| Nagagami | 1966 | Hall (1967) | 24 May | 24 May | 0 |
| Bancroft | 1967 | Livesey (1968) | 1 May | 12 May | +11 |
| Earlton | 1974 | MacLeod et al (1975) | 18 May | 22 May | +4 |
| Muskoka | 1978 | Anonymous (1978) | 8 May | 13 May | +5 |
| Muskoka | 1988 | Howse (pers comm) | 3 May | 6 May | +3 |

[1] Actual date represents estimated date of 50% hatch As the average time between start and 90% hatch is 2 days (Raske 1974), 1 day was added to the date of those sources reporting only the hatch start  [2] Actual hatch dates were recorded near International Falls, Minnesota (about 10 km from Fort Frances, Ontario)

climatic index involved using a simple model to predict the hatch date each spring Two models predicting the hatch date of eggs from daily maximum and minimum temperature data have been developed for the forest tent caterpillar (Ives 1973, Hodson 1977), both use a heat unit (or degree-day) concept, a widely used method for predicting insect development (Wagner et al 1984)

The parameters for the model developed by Hodson (1977) are based upon recorded hatch dates in Minnesota, just across the border to the south of Fort Frances, Ontario, while that of Ives (1973) is based upon records from the province of Alberta As neither model had been tested in Ontario, recorded and predicted hatch dates, for both models, were compared at 14 locations and times across the province A triangular approximation (Ives 1973) was used to calculate the degree-days from daily maximum and minimum temperature data based on the following relationships

$$\text{degree days} = \begin{cases} ((h+m)/2 - t & m > t, \\ = (h-t)^2/(2(h-m)) & m \le t < h, \\ = 0 & h \le t \end{cases}$$

Where h = maximum temperature, m = minimum temperature and t = threshold temperature

For those test locations > 50 km from a climate station, hatch dates were estimated using a distance weighted average of the predicted dates for the two nearest stations

Table 2 compares the actual hatch dates to those predicted by the Minnesota model The predicted hatch dates are within a few days of the actual dates, the one exception being the Bancroft prediction in 1967 The Alberta model, which does not begin accumulating degree-days until 27 April, consistently predicted hatch dates well after the recorded ones This model's late starting date for heat unit accumulation probably explains its poor performance, as hatch dates before 1 May are quite common in Ontario 'The Minnesota model was therefore used to predict the hatch dates at each of the 20 climate stations from 1948 to 1988

To determine how favourable the temperature was for feeding in the early part of the larval stage for each station-year, we used an index similar to that previously developed by Ives (1973) which calculates the number of degree-days that accumulate above 15°C each year during the first 3 wk following hatch The threshold of 15°C is based upon past lab and field observations suggesting that larvae do not feed at temperatures below this (Hodson 1941) Only 3 wk after hatch are considered as this is how long newly hatched larvae are thought to be able to survive without food (Smith and Raske 1968) Finally Wellington (1950), in a study of the relationship between air temperatures and the surface temperatures of foliage, found that at temperatures between 15°C and 26°C, the leaves of trembling aspen (the primary host of forest tent caterpillar in Ontario) were no more than 1 6°C above the air temperature This suggests that, for forest tent caterpillar, macroclimatic temperature observations are a rela-

tively good measure of the temperature to which larvae are exposed while feeding

## Comparing climate and defoliation

Given an index of how favourable the feeding period was each spring at each of the 20 stations, the last step in this analysis was to calculate a measure of the change in abundance for each station-year As defoliation is mapped at the end of the larval stage each year, it provides an indication of each year's late instar larval abundance By comparing the proportion of a fixed-sized area that is defoliated in one year to the proportion of the same area defoliated in the following year, one can determine whether or not the late larval densities increased or decreased between years The relationship between changes in abundance and the larval feeding temperature can then be examined by comparing the change in defoliated area from, say, year t-1 to year t, to the feeding degree-days in year t for that same area

To do this for the 20 climate stations, we centered cells that were 100 km by 100 km in size at each of the 20 stations and calculated the proportion of the land area in each cell that was defoliated each year The difference, or change in defoliated area, was then compared to the feeding degree-days for that same station and year If temperatures at the time of larval feeding determine population change, one would expect to see decreases in defoliation associated with low degree-day years and/or increases associated with high degree-day years

## Feeding degree-days in years prior to increases

As the larval densities required to bring about noticeable defoliation are quite high, it is possible that the most important climatic influence occurs several years before any change in defoliation is recorded Ives (1973) used records of outbreaks and temperature for 10 stations in the Prairie provinces and Ontario, from 1930 to 1970, to show that outbreaks were preceded by a single year (2 to 4 yr earlier) with a high number of feeding degree-days

Checking this for the 20 stations in this study required distinguishing between those years in which defoliation first began to increase (or decrease) and subsequent increasing (or decreasing) years "Initial increase" years were used to define the beginning of outbreaks, and were said to occur for a station in year t when there was an increase in defoliation from year t-1 to year t, with no increase in defoliation in the previous three years (years t-3 to t-1) For defoliation to appear on an aerial sketch-map, we calculated that on the order of 1 000 late instar larvae per tree must be present (Daniel 1990) Therefore, any observed increase in defoliation indicated that an outbreak was already well underway Similarly, "initial decrease" years were defined as those years showing a decrease in defoliation in the current year and no de-
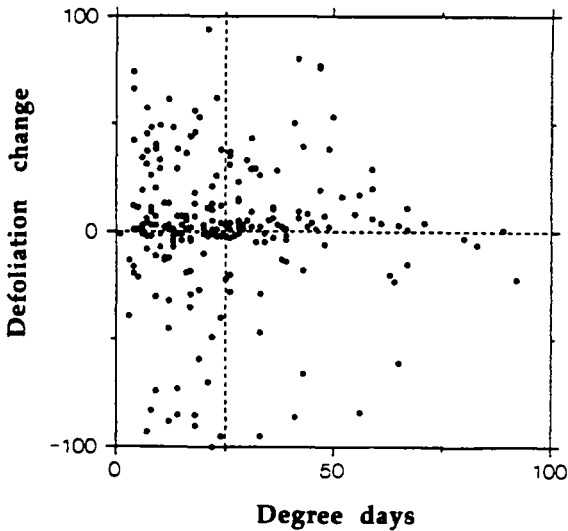
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**Degree days**

Fig 3 Relationship between the change in percentage of defoliated area and the feeding degree-days, for all stations and years with a non-zero change in defoliation Vertical line shows the mean number of feeding degree-days for all stations and years
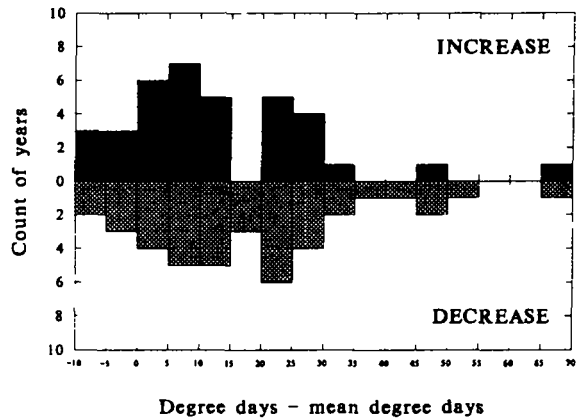


**Degree days – mean degree days**

Fig 4 The distribution of maximum feeding degree-day values in a period 2–4 yr prior to initial increase years and initial decrease years Degree-days are displayed relative to 25°C-days which is the mean number of feeding degree-days for all stations and years

creases in the previous 3 yr For every initial increase and decrease year (year t), the highest annual degree-day value in the previous 2–4 yr (years t-2, t-3 and t-4) was then determined This allowed us to compare the highest value of the feeding degree-days in the 2–4 yr prior to both the beginning and end of outbreaks

## Results

### Feeding temperatures and outbreaks

The expectation was that decreases in defoliation would be associated with low degree-day years and increases with high degree-day years Figure 3 shows no sign of such a relationship There were several station-years with very few degree-days and increases in defoliation, and others with high degree-day totals and defoliation decreases

The distribution of values for the highest annual feeding degree-day value in the 2–4 yr prior to initial increase and decrease years, for all 20 stations, is shown in Fig 4 Thirty of the 36 initial increase years (83%) were preceded by at least one year of above average degree-days This would appear to be consistent with the Ives hypothesis that there be a single year of favourable feeding temperatures prior to the beginning of outbreaks However, the distribution of maximum feeding degree-days prior to initial decrease years shows the same pattern Here 35 of the 40 initial decrease years (or 88%) were preceded by one or more above average degree-day years Years with above average feeding degree-days occur just as often prior to the end of outbreaks as they do prior to start

This suggests that over 3 successive years, the chance of having at least one warm year is quite high To examine this more closely, we estimated how the probability of having an above average feeding degree-day year might vary as a function of the period of successive years by taking the highest annual feeding degree-day value through all possible periods of 1 to 4 consecutive years for all stations and years (Daniel 1990) This analysis showed that for any given year, a single warm year is expected to occur in the preceding 2–4 yr 80% of the time by chance alone This explains the difference in conclusions regarding the effect of the larval feeding temperature of this study and that of Ives (1973)

An alternative way of examining the effect of temperature prior to outbreaks is to use an average of the feeding degree days over a fixed number of years prior to the start
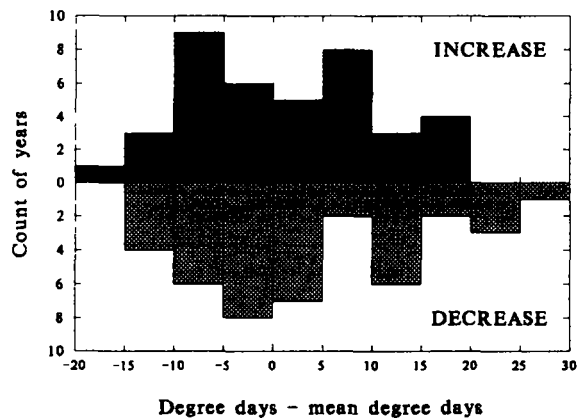


**Degree days – mean degree days**

Fig 5 The distribution of 4-yr averages of feeding degree-days prior to initial increase years and initial decrease years Degree-days are displayed relative to 25°C-days which is the mean number of feeding degree-days for all stations and years
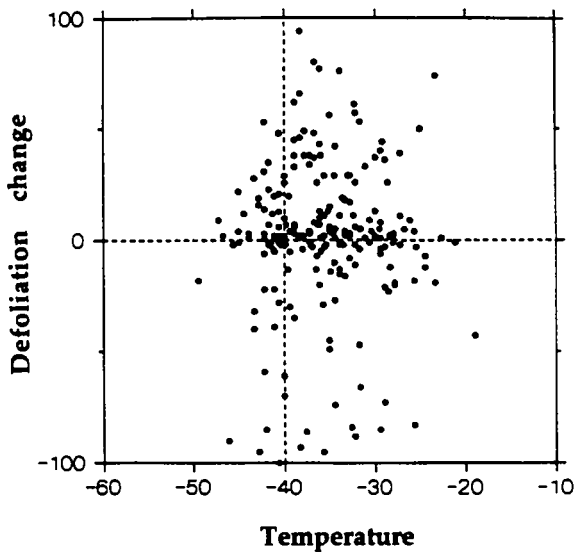
Fig 6 Relationship between the change in percentage of defo-liated area and the minimum overwintering temperature, for all stations and years with a non-zero change in defoliation Vertical line shows the -40°C threshold

The daily minimum temperature each winter, from 1947/1948 to 1987/1988, was recorded for each of the 20 climate stations across the province As with the analysis of larval feeding temperature, the defoliation for each station was calculated as the proportion of land area defoliated each year over a 100 km by 100 km station-centered cell If the overwintering temperature contributes to collapses of outbreaks, we expect decreases in defoliation for those years with lower overwintering temperatures, in particular those below −40°C In addition, increases in defoliation are not expected for those stations and years where the temperature dropped below this threshold

No apparent relationship between the minimum overwintering temperature and decreases in defoliation occurred in this study (Fig 6) There are several years with minimum temperatures well below −40°C and increases in defoliation There are also several years in which temperatures were well above −40°C and yet the defoliation still decreased substantially These results show no relationship between the interannual changes in defoliation and the minimum overwintering temperature

of defoliation (as in Wellington 1952). If the feeding degree-days are above average in one or more of the years prior to the start of an outbreak, the multi-year average should also be above average Unlike the previous measure, however, such an average is not biased by the length of the period over which it is measured To explore this possibility we used a 4 yr average (years t-3 to t inclusive) of feeding degree-days at each station as the climatic index for year t The new index values for those station-years showing initial increases were then compared to those showing initial decreases (Fig 5) These results show no difference between the 4 yr average of feeding degree-days prior to rises and those prior to collapses of outbreaks Twenty of the 39 initial increase years (51%) were preceded by a 4 yr average that was above the mean for all stations and years Similarly, 21 of 39 initial decrease years (54%) were preceded by a 4 yr average above the mean

## Overwintering temperature

To examine the relationship between the minimum over-wintering temperature and interannual changes in forest tent caterpillar abundance in Ontario, we compared the change in defoliation from one year to the next to the minimum overwintering temperature in the intervening winter, for each station from 1948 to 1988 As Wellington (1950) has shown that the daily minimum temperature of forest tent caterpillar egg masses is generally within 1°C of the air temperature, macroclimatic temperature observations should provide a good measure of the minimum temperatures experienced by the eggs

## Forest composition and long-term climate

To this point we have examined the relationship between two climatic factors and interannual changes in forest tent caterpillar abundance The last stage of our analysis explores the relationship between these same two factors and the long-term susceptibility of different parts of the province to forest tent caterpillar outbreaks

That some parts of the province are more susceptible to forest tent caterpillar outbreaks than others is shown in Fig 2 In particular, there have been no outbreaks reported in the southern and north-central parts of the province since 1948 (Fig 2) To explore this spatial variation in outbreak susceptibility further, we began by assessing the distribution of forested areas across the province This was accomplished using a forest inventory provided by Forestry Canada's Forest Resource Data Program (Anonymous 1988) The inventory was derived by aggregating stand level maps to a grid system with cells that were c 10 × 10 km in size From this inventory we determined where in the province continuous tracts of forested area existed

For most of the province, < 20% of the area within each inventory cell is not forested (Fig 7) In the southern part of the province, however, there is a sharp drop in the forested area as one enters a region where the land use is primarily urban and agricultural, and the forested areas that do exist are generally small, isolated woodlots This lack of forested area matches the southern boundary of the defoliation in past outbreaks, as shown in Fig 2, and could account for the low susceptibility to tent caterpillar defoliation of the southern part of the province

In an effort to explain the remaining variation in susceptibility across the province, the long-term record of

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Fig 7 Proportion of each inventory cell's area classified as non-forested

| | |
|---|---|
| ■ | > 08 |
| ■ | 06–08 |
| ■ | 04–06 |
| ⊠ | 02–04 |
| ◻ | < 02 |

km

0    200    400
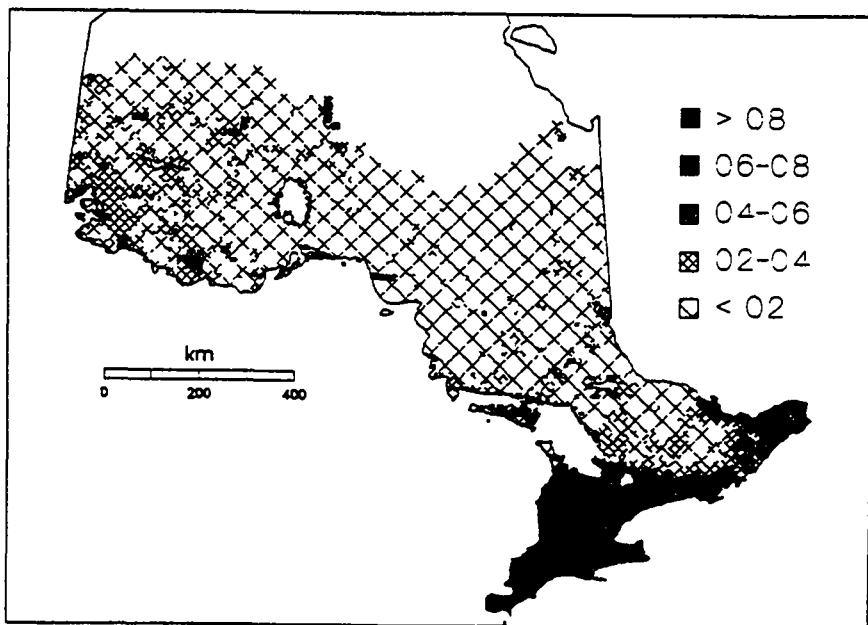
defoliation at each station was compared to that of the two climatic factors the larval feeding temperature and the minimum overwintering temperature The measure selected was the total number of years of defoliation from 1948 to 1988 This was calculated as the number of years in which some defoliation was reported within a 100 × 100 km cell centered upon each of the 20 stations Long-term means were also determined, using annual values from 1948 to 1988, for both the number of feeding degree days and the minimum overwintering temperature at each station

No apparent relationship exists between the feeding degree-days at a station and its long-term susceptibility to forest tent caterpillar outbreaks (Fig 8) For the over-wintering temperature, however, if one excludes those stations whose susceptibility has been reduced due to a lack of forest cover, one finds that areas with low over-wintering temperatures appear to be less susceptible to outbreaks Note that one should treat the results of this long-term comparison of overwintering temperatures and outbreak severity with caution As the climate at any one station is related to that at the neighbouring ones, the measures at each of the 20 stations are not independent Such autocorrelation amongst variables tends to exaggerate the presence of relationships (Cliff and Ord 1981)

The possible importance of the overwintering temperature in determining the susceptibility of a region to outbreaks can be further seen by comparing the mean minimum overwintering temperatures at each station (Fig 9) to the spatial pattern of outbreaks (Fig 2) This shows that there have been few outbreaks in the north-central part of the province, where temperatures often

drop below −40°C and yet where expanses of suitable host exist

## Discussion

The conclusions of past studies that have suggested the importance of the larval feeding temperature in determining year to year changes in abundance have been primarily based upon observations through one or two outbreaks at only one or two locations (Hodson 1941, Blais et al 1955, Witter et al 1975, Hodson 1977) Our analysis suggests that, while temperatures at the time of larval feeding and during the winter may influence the rate of increase of outbreaks in some places and in some years, they cannot account for the pattern of outbreaks across the entire province over a 41-yr period Witter et al (1975), studying forest tent caterpillars near International Falls, Minnesota, observed a similar situation In two years with winter temperatures below −43°C populations declined, but populations also declined in years with warmer winters Populations increased following both warm (1967) and cold (1969) springs Populations also declined following both warm (1970 and 1971) and cool (1968) springs A recent study of the cyclic dynamics of the western tent caterpillar, *Malacosoma californicum pluviale*, observed synchronous population declines among sites with different weather conditions This argues against particular weather conditions being necessary for synchronous, periodic population fluctuations (Myers 1990) Furthermore, our analysis shows that ro-
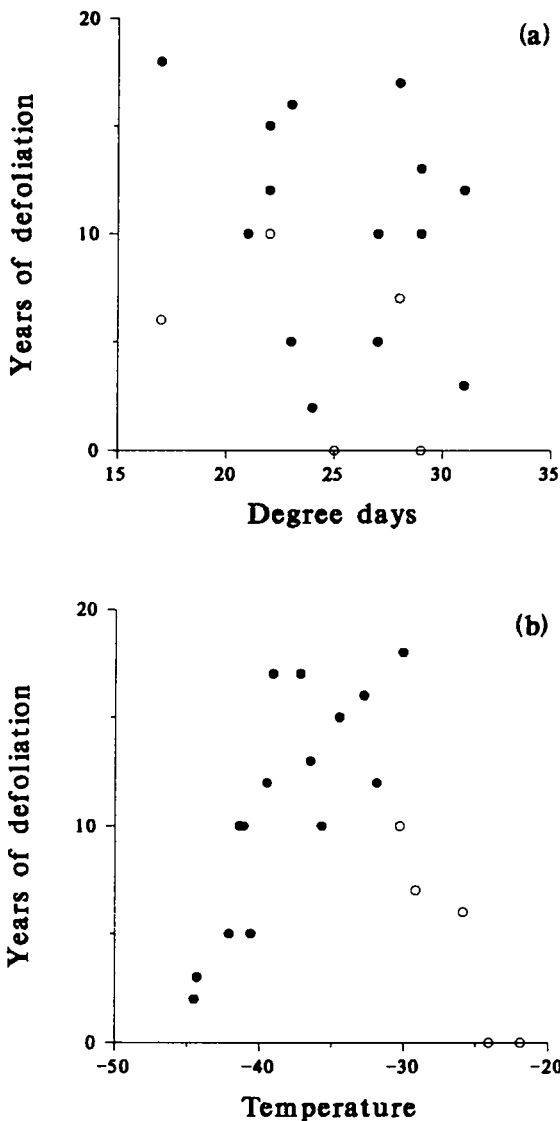
useable sites  Strong spatial autocorrelation of both over-wintering temperatures and feeding degree-days occurred for stations closer than 100 km apart (Daniel 1990), and this was a consideration in choosing sites for weather records  Variation in the altitude and conditions between the location of the weather station and the areas surveyed for defoliation undoubtedly occurred  A possible example of mismatch between the site for collection of temperatures and tent caterpillar defoliation is in northeastern Ontario (Fig  2) where two outbreaks have occurred in 41 yr and yet the mean minimum temperature is low  Caterpillar populations on hillsides may not be exposed to the same temperatures as weather stations in the valleys in this area  Further analyses of topography and weather would be interesting but are beyond this study

While there is no apparent relationship between the long-term mean larval feeding temperature and the severity of outbreaks across the province, there is some indication of a relationship between the minimum over-wintering temperature and severity of outbreaks  The north-central part of the province, with annual minimum temperatures that frequently fall below −40°C, has shown little defoliation from 1948 to 1988  This relationship between the minimum overwintering temperature and the susceptibility of an area seems, at first, to contradict the findings of the interannual analysis  However it is possible that, while winter mortality rates are rarely high enough to be the primary cause of outbreak collapses throughout most of the province, they may be high enough in the north-central part of the province to generally always prevent densities from reaching levels that would cause noticeable defoliation  Given fecundities of c  150 to 200 eggs per adult (Hodson 1941, Witter et al 1975) and a sex ratio of c  1 1 (Sippell 1957, Witter 1979), generation mortality rates of close to 99% are required to bring about a decline in abundance  The highest reported overwintering mortality rate for pharate forest tent caterpillar is 65%, which occurred in a year with a minimum temperature of −43°C (Witter et al

Fig  8  Relationship between the number of years of defoliation and the long-term climate, 1948–88, for the 20 climate stations (a) mean feeding degree-days, (b) mean minimum overwinter-ing temperature  Open circles represent the stations within the non-forested part of southern Ontario

bust hypotheses such as that predicting a warm year within 4 yr of a population outbreak are not useful since it is very likely that any year will be preceded by a warm year within 4 yr

There will always be weaknesses arising from analyses of survey data done over a large geographic scale  An example here is potential variation in the temperatures measured at the weather station and temperatures at the site of the caterpillar population  In this study it was necessary to use weather stations with complete records for the 41 yr study period. This limited the number of

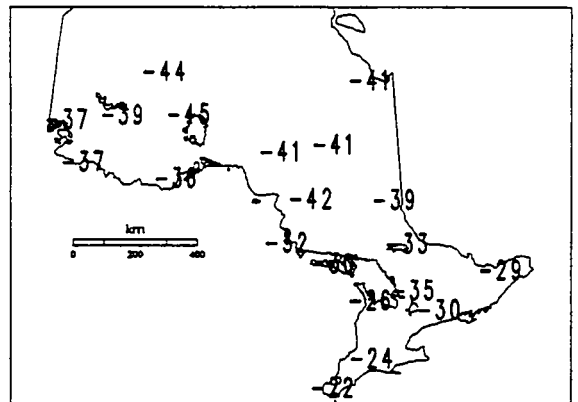

Fig  9  The mean of the minimum overwintering temperature, 1948–88, for each of the 20 climate stations

1975) Furthermore, the supercooling point of −40°C provides only an indication of the temperature at which mortality becomes significant The direct effect of low temperatures on egg mortality is not known The lethal limit of low temperatures for hibernating insects is not fixed The probability of freezing increases as the temperature decreases and the exposure time increases (Salt 1961) As such, areas which experience only brief periods of temperatures < −40°C may still have quite high egg survival Eggs within areas with longer, more frequent periods of exposure, such as the north-central part of the province, will have a higher probability of freezing This might further explain the reduced susceptibility of such areas to defoliation

If the distribution of minimum winter temperatures does influence the susceptibility of regions to forest tent caterpillar outbreaks, one would also expect it to be important in determining the long-term pattern of outbreaks for other forest defoliators One example of a forest insect showing a similar relationship between temperature and outbreaks is the winter moth, *Operophtera brumata*, in Scandinavia MacPhee (1967) has shown that winter moth egg mortality increases significantly when temperatures are near its supercooling point of −35°C, with 10% mortality occurring at −32 2°C and 100% mortality −36 7°C When the long-term pattern of defoliation by the winter moth in Norway and Sweden (from 1862–1967) was compared to the distribution of mean minimum winter temperatures, outbreaks were found to be concentrated within regions with mean minimum winter temperatures above −33°C (Tenow 1972) Furthermore, within larger areas of defoliation there were often belts of undamaged forest along rivers and lakes, where higher overwintering mortality was attributed to local accumulations of cold air (Tenow 1981)

This suggests that extreme cold is more likely to influence the geographical distribution of outbreaks than the cyclic pattern of population density The study of Witter (1979) showed clearly how egg mortality following an extremely cold winter could reduce the rate of increase of a forest tent caterpillar population without causing a population collapse This is likely to be the normal effect of weather on the forest tent caterpillar it contributes to variation in densities reached among sites and among outbreaks, but does not normally influence the periodicity of the population dynamics Whether extreme weather conditions could synchronize populations remains a possibility (Moran 1953) While populations in different regions of Ontario varied in the extent of defoliation, they appeared to remain more or less synchronous This pattern and the occurrence of particularly extensive outbreaks, as occurred in the early 1950's, remain to be explained

Recently Roland (1993) analyzed a subset of the data on forest tent caterpillar defoliation in Ontario to investigate the relationship between forest fragmentation and the duration of caterpillar outbreaks He did not include the non-forested areas of southern Ontario nor the

more northern areas in which the mean of the minimum overwinter temperatures was < −40° C In remaining areas he found that the duration of outbreaks was related to the amount of forest edge More forest edge was associated with prolonged outbreaks There was also an indication of outbreaks being shorter in areas with more aspen He suggested that warmer temperatures on the forest edge during larval development could play a role in the duration of outbreaks Our analysis shows more years of defoliation in forested areas with warmer winter temperatures, and these were the sites primarily studied by Roland

In conclusion, a warm spring has a high probability of occurring by chance in the 4 yr before the peak of population density of a forest insect such as the forest tent caterpillar that fluctuates with a 10 to 13 yr periodicity. We find no consistent association between either warm or cool springs and increase or decrease in defoliation by forest tent caterpillars in Ontario Winter temperatures below the supercooling point may influence the distribution of tent caterpillars, and may sometimes reduce egg hatch in some areas However, cold winter temperatures do not have a consistent effect on population dynamics Populations of forest insects may be synchronized periodically by widespread weather conditions, although it is difficult to test this possibility

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