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# The effects of gypsy moth defoliation and climatic conditions on radial growth of deciduous trees

Robin Naidoo

Department of Biology McGill University, Montreal

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#### **General abstract**

I investigated the effect of defoliation by the gypsy moth, Lymantria dispar L. (Lepidoptera: Lymantriidae) on the radial growth of tree species that differ in their acceptability as hosts for gypsy moth larvae. Annual growth rings were measured from 1950 to 1992 on increment cores taken from three species: red oak (Ouercus rubra L.), a preferred species, sugar maple (Acer saccharum Marsh.), an acceptable species, and white ash (Fraxinus americana L.), an avoided species. The number of gypsy moth larvae on these same individual trees had already been recorded from 1979 to 1992. To remove the potentially-confounding effects of climate on radial growth, I developed regression models of growth on climate in a pre-gypsy moth period (1950 to 1975), and then used these models to predict growth in a post-gypsy moth period (1978 to 1992). The residuals from these growth models were then examined with respect to gypsy moth numbers. The average number of gypsy moth larvae was a significant predictor of the residual growth of red oak in the post-gypsy moth period ( $R^2=0.72$ , p<0.0001). Growth residuals from the ash and maple climate models were uncorrelated with gypsy moth numbers. Since there were only two outbreaks during 1979 to 1992, the strong relationship of oak residual growth to gypsy moth numbers suggests that herbivory by even endemic levels of gypsy moth larvae can have a significant negative effect on the radial growth of individual trees. In a second analysis, annual growth rings were measured from 1950 to 1992 on red oak and white ash trees from two different sites, a gypsy-moth infested site (Lake Hill), and a similar but more recently-infested site nearby (Sunrise). Regression models of growth at Lake Hill on growth at Sunrise were constructed for the pre-gypsy moth period, and then used to generate predicted growth values at Lake Hill during the post-gypsy moth period. Ash growth at both Lake Hill and Sunrise was similar throughout 1950 to 1992, including the post-gypsy moth period. For oak, however, the first gypsy moth outbreak at Lake Hill (from 1978 to 1980) resulted in an average yearly growth loss of 42%, relative to growth at Sunrise. The second gypsy moth outbreak, in 1989 and 1990, led to no apparent growth losses, probably because gypsy moths had become established at Sunrise by this time.

### Résumé

J'ai étudié l'effet de la défoliation par la spongieuse, Lymantria dispar (Lepidoptera: Lymantriidae), sur la croissance radiale d'arbres feuillus pour lesquels la spongieuse montre une préférence variable. J'ai extrait des carottes de trois espèces d'arbres: le chêne rouge (Quercus rubra L.), un hôte préféré, l'érable à sucre (Acer saccharum Marsh.), un hôte acceptable, et le frêne blanc (Fraxinus americana L.), un hôte évité. La largeur des cernes annuels a été mesurée pour les années 1950 à 1992; le nombre de chenilles de spongieuse sur chacun des arbres carottés avait déjà été mesuré pour la période 1979-1992. Afin d'enlever la contribution du climat, qui affecte aussi la croissance radiale des arbres, j'ai construit des modèles de régression multiple pour la croissance de 1950 à 1975 en utilisant des variables climatiques; durant cette période, la spongieuse était absente du site. J'ai ensuite utilisé ces modèles pour prédire la croissance radiale pour la période 1979-1992 durant laquelle la spongieuse était présente sur le site. Pour le chêne rouge, le nombre moyen de chenilles a expliqué 72% de la variance de la croissance radiale résiduelle (c'est-à-dire la croissance après que l'effet du climat ait été enlevé). Il n'y avait pas de relation entre le nombre de chenilles et la croissance radiale résiduelle pour l'érable à sucre et le frêne blanc. Des nombres épidémiques de spongieuse ayant été observés pendant seulement quatre années sur 14 durant la période 1979-1992, la relation entre la croissance radiale résiduelle du chêne et le nombre de chenilles suggère que même des niveaux endémiques de chenilles peuvent affecter négativement la croissance radiale des hôtes préférés. Dans une deuxième analyse, des carottes ont été prises dans deux sites: un premier infesté par la spongieuse depuis 1978 («Lake Hill») et un deuxième qui a été infesté beaucoup plus récemment («Sunrise»). La largeur des cernes annuels a été mesurée pour les années 1950 à 1992 chez deux espèces d'arbres, le chêne rouge (un hôte préféré) et le frêne blanc (un hôte évité). Des modèles de régression ont été construits pour la croissance radiale des arbres à Lake Hill pendant la période 1950-1975, en utilisant la croissance radiale à Sunrise comme variable indépendante. Ces modèles ont été utilisés pour prédire la croissance à Lake Hill dans la période où la spongieuse était présente (1978 à 1992). La croissance

radiale du frêne blanc à Lake Hill était semblable à la croissance du frêne à Sunrise, même après l'arrivée de la spongieuse à Lake Hill. Cependant, pour les chênes, la première épidémie de spongieuse à Lake Hill (1978-1980) a causé une réduction de croissance de 42% par rapport à la croissance des chênes à Sunrise. Une telle réduction n'a pas été mise en évidence pour la deuxième épidémie (1989-1990), probablement parce que la spongieuse avait déjà atteint Sunrise.

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### Preface

Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.

If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". **The thesis must include :** A Table of Contents, and abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest to the accuracy of such statements at the doctoral oral defense. Since the task of examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all authors of the co-authored papers.

The two chapters of this thesis will be submitted to peer-reviewed journals, and will be co-authored by myself and Martin J. Lechowicz. I did the field work, collected the radial growth data, ran the analyses, and wrote the manuscripts. Professor Lechowicz organized the collection of the gypsy moth data and worked with me to decide the appropriate analyses of the radial growth data.

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#### **General Introduction**

Detailed investigations into the role of phytophagous insects in forested ecosystems have revealed that insects play an important role in many different ecological processes. Tree-insect interactions can result in positive and negative effects for both individual tree growth and ecosystem functioning. Schowalter et al. (1986) review herbivory in forested ecosystems, while Huntly (1991) reviews the effects of herbivory on the dynamics of communities and ecosystems, both aquatic and terrestrial. Phytophagous insects can affect individual trees by feeding on foliage, thus reducing the photosynthetic area and potentially leading to deteriorations in the physiological condition of the tree, as well as losses in primary production and reproductive capabilities (Rafes 1970, Perry 1994). However, nominal (low-level) herbivory can also stimulate primary productivity and increase short-term nutrient cycling (Reichle et al. 1973, Mattson and Addy 1975, Schowalter 1981, Schowalter et al. 1986). Leaves damaged by herbivory have greater leaching rates, leading to increased nutrient losses, especially for nitrogen and potassium (Seastedt and Crossley 1984). Insects that feed on the phloem of a tree can remove up to four times their dry biomass per day, resulting in disrupted growth and nutrient loss (Raven 1983). Insects that feed on developing buds can alter tree growth and geometry (Horn 1971). Leaves that have been sucked on or pierced have elevated transpiration rates (Whittaker 1984), while defoliation by chewing insects can reduce leaf transpiration rates (Nielsen and Ejlersen 1977). Ecosystem responses to herbivory include changes in forest structure, community development, and successional status (Schowalter 1981, Schowalter et al. 1986), nutrient cycling (Mattson and Addy 1975, Schowalter 1981, Schowalter et al. 1986), litterfall (Seastedt and Crossley 1984), and watershed hydrology (Coulson and Witter 1984).

Of the many different types of forest insects (Whiteford 1972), the guild that feeds on the foliage of trees has been one of the most well-studied (see review by Schowalter *et al.* 1986). Defoliating insects can be broadly grouped into two classes: those that have relatively low and stable population sizes (non-outbreaking species), and those with population densities that are strongly bimodal (outbreaking or eruptive species). Non-outbreaking species comprise approximately 98-99% of all defoliating insects (Nothnagle and Schultz 1987, Hunter 1991). These species tend to be solitary feeders that start feeding in the summer, have low fecundities, and feed on few host species (Hunter 1991). Non-outbreaking species rarely cause serious defoliation to host trees, and thus have not been as well-studied as their outbreaking counterparts (Mason 1987). Nominal herbivory by non-outbreak species (or by endemic levels of outbreak species) typically removes 5-15% of the leaf area, or 3-8% of the annual foliage production, in temperate forest ecosystems (Mattson and Addy 1975, Schowalter *et al.* 1986). This level of herbivory does not usually impair growth in trees (Rafes 1970, Schowalter *et al.* 1986), although Varley and Gradwell (1962) showed that radial growth of oaks declined with increasing numbers of insect herbivores, even though the population was at endemic levels for six of the eight years studied. Relatively minor fluctuations in the level of chronic herbivory can also influence nutrient cycling and primary productivity (Reichle *et al.* 1973, Mattson and Addy 1975, Schowalter 1981).

Outbreaking species are usually spring-early summer feeders, are gregarious, have high fecundities, feed on many different host species, and are more likely to have larval defenses than are non-outbreaking species (Hunter 1991). During outbreaks, insect defoliation can often result in the removal of 100% of the foliage in a forest, leading to reductions in primary productivity (Rafes 1970, Kulman 1971, Mattson and Addy 1975). While much fewer in number than non-outbreaking species, outbreaking species have caused severe economic damage to the timber industry (e.g. Whiteford 1972), and thus have been the focus of much scientific research. Of these, the most well-studied North American species have been those with the most serious impacts on human society; these include such native insects as the Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough), eastern spruce budworm (*Choristoneura fumiferana* Clemens), and forest tent caterpillar (*Malacosoma disstria* Hubner), as well as the gypsy moth (*Lymantria dispar* L.), which is an introduced species. This thesis concerns the impact of gypsy moth caterpillars on tree growth, both during occasional outbreaks and during the longer intervals when the population is at endemic levels.

The natural range of the gypsy moth (Lepidoptera: Lymantriidae) extends from Japan and central China across Siberia to Europe and Northern Africa (Liebhold *et al.* 1995). In this area it is regarded mostly as a minor pest, although severe outbreaks have been recorded periodically since the 15th century (Montgomery and Wallner 1988). The most recent outbreaks occurred in the 1950's and 1960's, and resulted in widespread defoliation throughout Europe, particularly in the former Yugoslavia, where 70% of deciduous hardwoods were defoliated (Montgomery and Wallner 1988). Liebhold *et al.* (1995), however, state that gypsy moth populations have historically remained at endemic levels in certain areas of its natural range. Predation on gypsy moths in its natural range is mainly from several species of birds, although beetles have also been recorded as important predators (Montgomery and Wallner 1988). Diseases and a wide variety of parasitoids also contribute to the numerical behavior of gypsy moth populations in Eurasia (Montgomery and Wallner 1988).

The gypsy moth was accidentally introduced in Massachusetts in 1869 by a visiting French scientist who had been attempting to crossbreed silk-producing caterpillars (Dunlap 1980). After the initial introduction, it spread quickly throughout New England and adjacent states, despite periodic efforts to eradicate the insect (Dunlap 1980). The general area of infestation continues to enlarge at the rate of 21 km/year (Liebhold *et al.* 1995), and now encompasses an area from southern Quebec and Ontario west to Michigan, east to Nova Scotia, and south to Virginia. Efforts to control gypsy moth populations have mostly involved application of *Bacillus thuringiensis* (a biological insecticide), as well as chemical insecticides such as Gypchek® (Jobin 1995). The introduction of exotic parasitoids from the gypsy moth's native range has also been used in control attempts, although their use has yet to result in effective control (Liebhold *et al.* 1995). In the early 1990's, however, a Japanese fungus (*Entomophaga maimaiga*) first introduced in 1909 caused severe mortality in gypsy moth infestations of New England, and has since spread throughout the general area of gypsy.

The mechanisms leading to gypsy moth outbreaks have proven difficult to

elucidate, although outbreak epicenters are often located at xeric sites, where droughtstress is high and the soil is shallow and rocky (Bess et al. 1947, Houston 1981, Wallner 1987, Elkinton and Liebhold 1990). Drought-stressed trees are thought to be more susceptible to insect attack (Mattson and Addy 1975, Mattson and Haack 1987), and drought conditions are often associated with insect outbreaks (Wallner 1987, Elkinton and Liebhold 1990). Sites with an abundance of preferred tree species are more likely to be seriously defoliated than sites with non-preferred species (Bess et al. 1947, Houston and Valentine 1977, Kleiner et al. 1989). Sparse leaf litter is also considered favorable for the gypsy moth, since small mammal predators are less likely to be present at these sites (Bess et al. 1947). Once an outbreak begins at an epicenter or "primary focus", it may spread to secondary and tertiary foci (Wallner 1987, Liebhold and Elkinton 1989). Expansion into surrounding areas from a focal stand can occur over a number of years, thus maintaining area-wide outbreaks for up to a decade (Campbell and Sloan 1978), although how this spread occurs is still not clearly understood (Elkinton and Liebhold 1990). Outbreaks are always followed by a crash in population numbers, usually associated with the gypsy moth nuclear polyhedrosis virus (Elkinton and Liebhold 1990).

Damages during gypsy moth outbreaks can be divided into two categories: socioeconomic and ecological. Socioeconomic costs include timber losses (Dennis *et al.* 1986, Montgomery and Wallner 1988), costs of spraying and other control measures (Montgomery and Wallner 1988), loss of recreational appeal (Hollenhorst *et al.* 1993), property damage (Payne *et al.* 1973), and reduction in aesthetic values (White and Schneeberger 1981). Ecological costs include potential changes in stand composition (Campbell and Sloan 1977), understory composition (Collins 1961), growth of host trees (Minott and Guild 1925, Baker 1941), nutrient cycling (Grace 1986), and trophic interactions (Kasbohm *et al.* 1995). The severity of these damages will depend on the composition of the stand; although the gypsy moth will feed on the foliage of many different types of trees, host preferences vary among species, thus stands with lesspreferred species will not be as seriously affected as stands with preferred species. North American species typically preferred by gypsy moth larvae are members of the genera Salix, Populus, Betula, and especially Quercus, while Fraxinus and Juglans spp. are avoided (Lechowicz and Mauffette 1986). In southwestern Quebec, the area in which the study site for this thesis was located, preferred species are Quercus rubra, Ostrya virginiana, Populus grandidentata, and Amelanchier and Salix spp. Intermediate or acceptable hosts are Betula spp., Tilia americana, Prunus serotina, Populus tremuloides, Fagus grandifolia, Ulmus americana, and Acer saccharum. Avoided species include members of the genera Carya, Fraxinus, and Acer. (Mauffette et al. 1983).

The life cycle of the gypsy moth is well-understood. Adult females are flightless, and therefore remain at the site of pupation, usually on a tree trunk. Males locate females by pheromones the females release, and each male often mates with multiple females. Both male and female moths live for approximately one week, during which time no feeding occurs. Egg masses are laid by females in late summer, usually on tree trunks but also occasionally on the ground, on rocks, or on tree stumps (Leonard 1981). The egg masses remain attached to their substrate through the winter, during which time extremely cold temperatures and lack of insulation from snow cover can lead to very low hatching rates (Leonard 1972). The larvae hatch in the spring, usually in synchrony with the leaf expansion of preferred hosts (Hunter 1993). Newly-hatched larvae number from between 100 and 1000 per egg mass, and are about 3 mm long. After hatching, larvae spin silk threads which are used in wind-aided dispersal. Those larvae that are eventually deposited near potential host plants begin to feed on new leaves during the day, while resting under the leaves at night. This feeding pattern is reversed in later instars, when larvae switch to feeding at night and hiding under bark flaps or similar structures during the day. Male larvae have five instars and females have six instars, and the total increase in weight from hatching to last-instar can be a thousand-fold. Lastinstar females are the most voracious feeders, consuming as much foliage in this instar as in all previous instars combined. Each gypsy moth larvae consumes approximately 1 m<sup>2</sup> of foliage during the course of its life (Leonard 1981). Larvae commence pupation near the end of June; after a two-to-three-week pupation period, adult moths emerge

functional and ready to commence reproductive activity.

It is during the later instars that gypsy moth larvae consume damaging amounts of tree foliage. When population levels are high, trees may be completely stripped of foliage in early summer (Leonard 1981). This severe defoliation can have serious negative effects on the radial growth of trees. Defoliation decreases the photosynthetic biomass of a tree, and thus reduces the amount of photosynthate produced (Kulman 1971, Parker 1981, Schowalter et al. 1986). In temperate hardwood trees, production of earlywood (i.e. radial growth early in the growing season) is supported by stored reserves of photosynthate from the previous season (Ladefoged 1952, Kozlowski et al. 1991). A reduction in the photosynthate of the current year is therefore unlikely to affect earlywood production, especially when defoliation occurs only after earlywood production, as is the case for gypsy moth defoliation. Latewood or summer-early fall growth, however, is dependent on the current year's photosynthate, and so a reduction of photosynthate due to defoliation in the early summer can affect latewood production of the same year (Rafes 1970, Kulman 1971). In addition, trees that are severely defoliated early in the growing season (as is the case with gypsy moth defoliation) often produce a second flush of leaves in mid-summer (Heichel and Turner 1976, Wargo 1981). In doing so, resources must be diverted away from other metabolic pathways, including that of growth (Schowalter et al. 1986). Therefore severe gypsy moth defoliation would likely reduce radial growth of host trees by reducing the amount of latewood produced, due to: 1) a reduction in the amount of photosynthate produced; and 2) a reallocation of resources away from growth and into refoliation.

Although many different impacts of gypsy moth defoliation have been investigated, the effect of defoliation on radial growth has not been adequately quantified for hardwood trees of northeastern North America. Previous studies in this region have sought to estimate percent losses in growth after a gypsy moth outbreak based on growth prior to the outbreak (Minott and Guild 1925, Baker 1941, Brown *et al.* 1979, Wargo 1981, Twery 1987, May and Killingbeck 1995). These studies have ignored, however, the potentially-confounding influence of climate on growth, as drought conditions which also result in reduced radial growth are often associated with insect outbreaks (Koerber and Wickman 1970, Mattson and Haack 1987). Dendroecological techniques (Fritts 1976, Fritts and Swetnam 1989) provide the means to separate these two effects. In dendroecology, ecological events or processes are inferred from the radial growth chronology of trees. The first application of tree-ring chronologies was for the reconstruction of past climatic conditions, termed "dendroclimatology" (Fritts and Swetnam 1989). Since Fritts' (1976) seminal work on the subject, dendroecological techniques have been used to investigate the effects of decline (Tainter *et al.* 1984, Phipps and Whiton 1988, Bauce and Allen 1991, Payette *et al.* 1996), drought (Cook and Jacoby 1977, Jenkins and Pallardy 1995), pollution (Nash *et al.* 1975, Fox *et al.* 1986, Innes and Cook 1989), and flooding (Tardif and Bergeron 1993, Jean and Bouchard 1996), on the radial growth of trees. A dendroecological analysis has yet to be conducted for the impact of gypsy moth defoliation on hardwood trees, however, and this therefore is the subject of my thesis.

Several different dendroecological approaches are available for quantifying the impact of insect defoliation on radial growth (Rafes 1970). The first involves establishing growth-climate relationships for host species, and then comparing growth during years of defoliation to climate-predicted growth. It has been well-established that macroclimatic variables such as average monthly temperatures and monthly precipitation totals are strongly correlated with annual radial growth in deciduous trees (e.g. Fritts 1962, Pilcher and Gray 1982, Tainter *et al.* 1984, Bednarz and Ptak 1990, Bauce and Allen 1991, Han *et al.* 1991, Lane *et al.* 1993, Tardif and Bergeron 1993, Luken *et al.* 1994, Yin *et al.* 1994, Payette *et al.* 1996). Multiple regression techniques for establishing growth-climate relationships have been used extensively in these studies to quantify the effect of climate on growth. Once the variance in growth due to climate has been accounted for, the remaining variance can be related to insect defoliation. Rubstov (1996) used a similar method to determine radial growth losses due to gypsy moth defoliation in oaks growing in Eurasia.

Another method involves using the radial growth of trees at an uninfested site as a measure of the expected growth at the infested site in the absence of defoliation (Rafes 1970, Kulman 1971). Chronologies from both sites are developed, with growth depressions in infested trees relative to uninfested trees being attributed to defoliation. This method has been used to quantify the impacts of defoliation on growth for such insects as the western spruce budworm, *Choristoneura occidentalis* Freeman (Swetnam and Lynch 1989), eastern spruce budworm (Blais 1962), larch sawfly, *Pristiphora erichsonii* Hartig (Jardon *et al.* 1994), forest tent caterpillar (Gross 1991), and Douglasfir tussock moth (Brubaker and Greene 1979).

Both of the above methods are used in this thesis to examine the effect of gypsy moth defoliation on tree species of contrasting host preferences. In chapter 1, growthclimate relationships are developed using multiple regression models of growth on climate, and patterns in the remaining growth variance are examined to determine if gypsy moth defoliation may be the causative agent. In chapter 2, radial growth losses due to gypsy moth defoliation are estimated by comparing growth of trees at a chronically-infested site to growth of conspecific trees at a more recently-infested site. Both of these sites were at Mont St-Hilaire, one of the eight Monteregian Hills on the plains of the St-Lawrence River Valley in the vicinity of Montreal, Quebec. Mont St-Hilaire is covered by the largest remaining tract of northern old-growth deciduous forest (1200 hectares), and as such was designated a UNESCO Biosphere reserve in 1978 (see Maycock 1961 for a detailed description of the geology, soils, and flora of Mont St-Hilaire). The gypsy moth study sites were typical of those that experience severe and repeated defoliations, in that both were dry and rocky with shallow soil and a predominance of a favored host species, in this case Quercus rubra. (Rouse 1970, Lechowicz 1983). Although several other native defoliators are present at Mont St-Hilaire, including non-outbreaking species such as the Bruce spanworm (Operophtera bruceata Hulst), maple leafroller (Cenopis acerivorana Mack.), and ugly-nest caterpillar (Archips cerasivoranus Fitch), as well as the forest tent caterpillar (an outbreaking species), a search through the Forest Insect and Disease Survey records indicated that with the exception of a known tent caterpillar outbreak in 1953 (Martineau and Beique 1953), none of these insects were present in very high numbers. Mont St-Hilaire thus seems an ideal location to study the impact of an introduced defoliator on a native and relatively undisturbed forest community.

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# Chapter 1. The effects of climate and gypsy moth defoliation on radial growth.

#### Abstract

I investigated the effect of defoliation by gypsy moth, Lymantria dispar L. (Lepidoptera: Lymantriidae) on annual radial growth of preferred, intermediate, and avoided host trees: red oak (Quercus rubra L.), sugar maple (Acer saccharum Marsh.), and white ash (Fraxinus americana L.), respectively. Individual trees were censused for gypsy moth larvae from 1979 to 1992 in a chronically infested forest on a drought-prone site in southwestern Quebec. Annual growth rings were measured from 1950 to 1992 on increment cores taken from these same trees. To remove the potentially confounding impact of climate on growth, radial growth chronologies were divided into two periods: pre-gypsy moth (1950 to 1975) and post-gypsy moth (1978 to 1992). Regression models of radial growth on climate were developed for the pre-gypsy moth period, and these equations were used to generate predicted growth values for the post-gypsy moth period. Summer precipitation or modelled summer soil water was a limiting factor for radial growth in all three species. Modelled March soil water and mean January temperature were also positive predictors of radial growth for white ash and red oak, respectively. For oak, the average number of gypsy moth larvae per tree explained 72% of the variance in growth not explained by climate in the post-gypsy moth period. Ash and maple growth were not correlated with gypsy moth larval numbers, although ash experienced a large growth increase after the first gypsy moth outbreak. Maple growth in the post-gypsy moth period was similar to that in the pre-gypsy moth period. These results are consistent with gypsy moth host preferences, and suggest that annual radial growth in deciduous trees is affected by gypsy moth defoliation, especially in preferred hosts. More importantly, this is the first evidence that herbivory by even endemic levels of gypsy moth larvae can have a significant negative effect on the radial growth of individual trees, and underscores the potentially adverse consequences of gypsy moth infestations during non-outbreak years.

#### Introduction

The impact of defoliating insects on radial growth of hardwood trees has been studied extensively in Australia (e.g. Mazanec 1968, Readshaw and Mazanec 1969, Mazanec 1974, Morrow and LaMarche 1978), Europe (e.g. Klepac 1959, Ierusalimov 1965, Ljapcenkov 1966, Rafes 1970, Magnoler and Cambini 1973, Kucherov 1990, Rubtsov 1996) and North America (e.g. Minott and Guild 1925, Baker 1941, Rose 1958, Embree 1967, Brown et al. 1979, Gross 1991, May and Killingbeck 1995). Kulman (1971) provides a comprehensive review of defoliation by many insect species on the radial growth of their hosts. Despite this large body of literature, most studies do not make use of modern dendroecological techniques, as described by Fritts (1976) and later Fritts and Swetnam (1991). Dendroecological methods allow one to take into account internal and external conditions that affect annual radial growth in trees, such as climate and tree age, and then isolate the contribution of a single factor, such as insect defoliation, to radial growth. Several recent North American studies have used dendroecological techniques in investigating the effect of defoliation on radial growth, but these have focused on the impact of spruce budworm on its coniferous hosts (Swetnam and Lynch 1989, Krause and Morin 1995, Krause 1997). In the hardwood forests of northeastern North America, a dendroecological analysis has not been conducted for the gypsy moth, Lymantria dispar L., (Lepidoptera: Lymantriidae), a defoliator of particular concern (Jobin 1995, Liebhold et al. 1995).

The gypsy moth is an outbreaking polyphagous folivore that feeds on the leaves of many North American trees and shrubs (Doane and McManus 1980, Liebhold *et al.* 1995). Introduced from Eurasia to Massachusetts in 1869 (Dunlap 1980), the gypsy moth is now established in southern Quebec and Ontario west to Michigan, east to Nova Scotia, and south to Virginia. Along the southern and western borders of its range, the area of infestation is increasing at the rate of 21 km per year (Liebhold *et al.* 1995). Gypsy moth populations periodically outbreak and cause substantial damage to northeastern forests, especially to those dominated by their preferred hosts, the oaks, (*Quercus*) (Bess *et al.* 1947, Campbell and Sloan 1977, Jobin 1995). More specifically, gypsy moth outbreaks can result in changes in future stand composition (Campbell and Sloan 1977), understory vegetation (Collins 1961), and recreational appeal (Hollenhorst *et al.* 1993). There are also economic losses due to gypsy moth defoliation: timber losses were estimated at greater than \$72 million in Pennsylvania alone during massive gypsy moth outbreaks in 1981 (Montgomery and Wallner 1988), and homeowners are willing to pay substantial amounts to protect their shade trees from damage (Liebhold *et al.* 1995). Early reports suggested that the most severe economic consequence of gypsy moth defoliation is the loss in timber yield due to reduced growth (Minott and Guild 1925, Baker 1941), but this possibility has not been well-documented (but see Perry 1955, Twery 1987).

In particular, the effects of a chronic infestation on the long-term annual radial growth of host trees have not been adequately investigated, despite the economic, ecological, and aesthetic consequences of gypsy moth damage to northeastern forests. One reason for this could be that the sheer severity and scale of outbreaks (Dunlap 1980) have overshadowed the potential importance of light but continuous defoliation of host trees by endemic levels of gypsy moth larvae. The confounding nature of the growthinsect-climate interaction can also make separating the main effects of each factor difficult (Koerber and Wickman 1970). Studies of gypsy moth defoliation on tree growth in the northeastern United States have thus been of two types. Those that are short-term focus only on the effects of a heavy defoliation event on radial growth in the immediate post-defoliation period, and often use a pre-defoliation period of similar length to assess growth losses. Both time periods are short, usually less than five years in length (Kulman 1971, Brown et al. 1979, Wargo 1981, May and Killingbeck 1995). Longer-term studies have incorporated years of little or no defoliation as well as years of heavy defoliation, but have ignored the potentially confounding effects of climate while trying to quantify radial growth losses (macroclimatic conditions are well-known to influence radial growth of trees - e.g. Fritts 1976, Cook and Jacoby 1977, Pilcher and Gray 1982). Reference periods prior to defoliation are again used to establish the percentage growth loss due to gypsy moth herbivory, but potential differences in climate

between periods are ignored or only cursorily dealt with (Minott and Guild 1925, Baker 1941).

Compounding these problems is the fact that most studies have only examined the impact of gypsy moth defoliation on highly-preferred species, such as members of the oak genus, as well as white pine (*Pinus strobus* L.), a species preferred by late instars. While oaks and white pine are main food sources, it is well-known that gypsy moth larvae will feed on many other woody species, and studies have shown that hosts have different degrees of acceptability and palatability for feeding larvae (Lechowicz and Mauffette 1986, Hamilton and Lechowicz 1991). Even trees that co-occur at the same site can suffer markedly different levels of defoliation, with preferred hosts being completely defoliated while avoided hosts remain virtually untouched (Lechowicz 1983). Host species are also likely to have different growth-climate relationships, due to differences in morphological, ecological, and life history characteristics. To accurately assess possible growth losses in mixed hardwood stands of northeastern North America, a complete investigation of the long-term effects of gypsy moth defoliation on radial growth of host trees should incorporate both the influence of climatic conditions and the different levels of gypsy moth preference for host trees.

In this study I used dendroecological techniques to determine whether long-term radial growth differences of tree species in an infested forest are related to gypsy moth host preferences. Gypsy moth larvae are classified as spring - early summer feeders (Hunter 1991), and generally feed on foliage from early May until the beginning of July (Jobin 1995). Because the period of growth for hardwood trees in northeastern North America is from May to August (Fraser 1956, Ahlgren 1957), I predicted that gypsy moth defoliation would result in the reduction of radial growth in the same year that defoliation occurred, specifically by a reduction in the amount of latewood produced (earlywood production should already have ceased by the time defoliation was most severe). Trees that are severely defoliated early in the growing season often produce a second flush of leaves in mid- to late-summer (Heichel and Turner 1976, Wargo 1981), thus diverting resources away from latewood production and into refoliation. After

having established growth-climate relationships for the different tree species in the absence of gypsy moths, thirteen-year records of gypsy moth larval numbers on host trees were used to assess the impact of defoliation on host species of varying preferences.

#### Methods

#### Study area

The study site was the south slope of Lake Hill, one of seven small peaks that comprise Mont St-Hilaire (45° 32' N, 73° 09'W). Located in the St-Lawrence River Valley in the vicinity of Montréal, Québec, Mont St-Hilaire is covered primarily with old-growth deciduous forest, and is the largest remaining tract of the Great Lakes - St-Lawrence lowlands forest type that carpeted the valley prior to European settlement. As a unique ecological and historical site, Mont St-Hilaire was accorded UN Biosphere Reserve status in 1978, and access and activities on the mountain are restricted so that its undisturbed character is maintained. Forest types on the mountain include oldgrowth beech-sugar maple (*Fagus grandifolia* Ehrh. - *Acer saccharum* Marsh.) stands on deep moist soils, hemlock (*Tsuga canadensis* (L.) Carrière) on steep, rocky slopes, yellow birch (*Betula alleghaniensis* Britton) and red maple (*Acer rubrum* L.) swamps in depressions, and red oak (*Quercus rubra* L.) forests on dryer sites (Maycock 1961). Vascular plant diversity is also high, with over 500 species recorded (Maycock 1961), including several that are listed as endangered in Quebec.

The south slope of Lake Hill exhibits many of the characteristics that Houston and Valentine (1977) ascribe to sites prone to gypsy moth infestation. The soil is shallow and sandy or rocky, with an average depth of only 65 cm over bedrock (Rouse 1970). Although the peak is only 297 m high, many areas are quite steep with open canopies, resulting in scree slopes with little leaf litter. Radiant energy budgets have been calculated and compared for the north and south slopes of Lake Hill; the south slope has considerably higher air and soil temperatures, and is thus much drier than the north slope (Rouse 1970). This is reflected in the forest composition, where red oak, a drought-tolerant species, dominates the xeric forest on the south side, while on the mesic north side the predominant species are beech and sugar maple (Lechowicz 1983). Other important species on the south slope are sugar maple and ironwood (*Ostrya virginiana* (Miller) K. Koch), while white ash (*Fraxinus americana* L.), beech, white birch (*Betula papyrifera* Marsh.), and basswood (*Tilia americana* L.) are minor components.

#### Collection of gypsy moth data

The arrival and establishment of the gypsy moth in southwestern Quebec and at Mont St-Hilaire has been well-documented. Widely scattered patches of gypsy moth defoliation began to be observed in 1972 in parts of western Quebec near Mont St-Hilaire (Jobin 1995), but the first major area-wide outbreak was in 1977. The first record of gypsy moth infestation at Mont St-Hilaire was also in 1977, when 10 hectares of Burned Hill (a small peak adjacent to Lake Hill) were defoliated (Jobin 1978). In 1978, the area of severe defoliation increased to 259 hectares, 123 of which were on Lake Hill. It is likely that the gypsy moth first arrived at Mont St-Hilaire on Burned Hill, as vehicles from a public campground adjacent to the hill could have imported the moth from areas to the south or west. The initial invasion probably occurred in the midseventies, after which the population increased to an outbreak level and spread from Burned Hill to neighboring Lake Hill (Lechowicz 1983). The first outbreak ended in 1980, and was followed by a number of years during which gypsy moth numbers were very low. A second outbreak occurred at Lake Hill in 1989 and 1990.

The Lake Hill study site was established in 1979, the year after the first severe gypsy moth defoliation. Twenty-four 500 m<sup>2</sup> circular quadrats were randomly placed along four altitudinal isoclines on the south and southeast slopes of Lake Hill (Figure 1). In each quadrat, all trees with a DBH (diameter at breast height) greater than 8 cm were tagged and identified to species. A tarpaper skirt was placed around the trunk of each tree; such artificial hiding places are used by late-instar gypsy moths as daytime hiding places (Liebhold *et al.* 1986), and Odell and Godwin (1979) reported that 95% of the larvae feeding on oak congregated under similar tarpaper bands. The number of larvae

### Figure 1.

The Lake Hill study site at Mont St-Hilaire. In 1979, twenty-four 500 m<sup>2</sup> quadrats (represented as circles on the contour map) were established on the south-facing slope of Lake Hill to monitor the gypsy moth infestation. The larger the symbol, the greater the average number of larvae per tree was during 1979 to 1992. The difference in larval numbers between quadrats was mainly due to the percentage of red oak in the canopy (Pearson correlation coefficient, r=0.524, p=0.015).


under the tarpaper bands was thus recorded, usually on four separate occasions when late instars were present, each summer from 1979 through 1992.

#### Collection and analysis of radial growth data

I selected three tree species with contrasting host preferences to examine the influence of gypsy moth defoliation on radial growth. Red oak is a preferred host of the insect, white ash is avoided, and sugar maple is intermediate (Lechowicz 1983, Lechowicz and Jobin 1983). For each species, two increment cores were collected from all available individuals in the twenty-four quadrats. Cores were taken at breast height and at a 90° angle to each other, with one core taken from the upslope side of the tree. The DBH of each tree was also measured. Cores were air dried and then mounted onto wooden backings. Ash and oak cores were planed, and maple cores were sanded, in order to make the rings more visible. Cores were cross-dated visually by using signal years (Stokes and Smiley 1968); narrow rings in 1953, 1971, 1978, 1979, and 1988, and large rings in 1981 made unambiguous cross-dating possible in almost every oak and ash core. Unequivocal cross-dating of maple cores was more difficult, due to extreme suppression in some cases, and missing or additional rings in others. Any core that was damaged or that could not be cross-dated was removed from the analysis; 14 oak, 19 maple, and 12 ash trees thus had chronologies based on only one core. After crossdating, ring widths were measured to the nearest 0.01 mm using a dissecting microscope with a sliding vernier scale. The age of the tree (at breast height) was also recorded. For some cores, estimating the age was not possible, either because the tree's center was rotten or because the core was too far off the pith. Trees where at least one age estimate was not available were also removed from the analysis. The years 1950 to 1992 were measured on all cores; 1950 was the earliest year I could measure, since many trees had just grown to breast height in the preceding few years.

Three different radial growth chronologies were calculated: raw ring width, standardized ring index, and residual ring index. The raw ring width chronology was calculated simply by averaging annual ring widths over all trees, for each species. The standardized ring index for each core was computed by dividing annual ring widths by the core's mean ring width from 1950 to 1992. The resulting series were averaged over all cores and trees for each species to give the standardized ring index chronology. The residual ring index chronology was calculated in a similar way, except the core's mean ring width was subtracted from the annual ring widths. Many tree ring studies are interested mainly in the year-to-year variance in radial growth due to climate, and thus go to great lengths to remove other sources of variation such as long term growth trends, stand dynamics, etc. (e.g. Blasing *et al.* 1988, Innes and Cook 1989, Graumlich 1993, Payette *et al.* 1996). In this case, however, I was interested in the impact of gypsy moth defoliation on radial growth of host trees, which may have a long term effect. Thus nonclimatic trends that are normally removed in tree ring studies were in fact part of the focus of this study. Standardizing by the mean of a series ensures preservation of trends that may be of interest, while at the same time removes growth rate differences among individual trees and among species.

### Climate and gypsy moth analysis

For each chronology, 128 candidate variables were screened with Pearson correlation coefficients to identify potential growth-limiting climatic conditions. All candidate variables were calculated for the period beginning in September of the previous year and continuing until September of the current year. The variables included monthly average temperatures and precipitation totals, precipitation during different periods of the growing season, discrete climatic conditions such as winter thaw and drought lengths, and modelled monthly values of soil water. Studies on the effect of climatic conditions on radial growth of trees often report different climate variables as being limiting to growth, and all of the variables considered here have been correlated with growth (e.g. Fritts 1976, Pilcher and Gray 1982, Graumlich 1993, Lane *et al.* 1993, Yin *et al.* 1994, Jenkins and Pallardy 1995, Payette *et al.* 1996). Soil water values were modelled using ForHym, a process-based model of forest soil water content with inputs of monthly precipitation and temperature data, as well as descriptive site data such as forest type and soil depth (Yin *et al.* 1994). All climate records were obtained from the St-Hubert airport weather station, about 20 km northwest of the study site. From 1950 to

1992 several weather stations were in operation for short periods at Mont St-Hilaire. Data from these stations was collated and compared to St-Hubert data from the same time; regression analysis showed that the two data sets agreed to the point where correction factors for the St-Hubert data were unnecessary (Appendix I). The St-Hubert climate data is thus assumed to adequately represent conditions at Lake Hill.

To establish a baseline model of tree growth in the absence of gypsy moth, the period 1950 to 1975 was used to generate a regression model of radial growth based on climatic variables. The year 1975 was selected as an end point to this period because the status of the gypsy moth population on Lake Hill during the years immediately preceding the first outbreak in 1978 is not known. Since it is possible that the insect was present at very low levels in 1976 and 1977, these years were not used in any regression analyses. The years 1978 to 1992 were used as the post-gypsy moth period. From the initial set of candidate variables, the 20 with the highest Pearson correlation coefficients were selected, and from this pool a multiple regression model of growth with two climatic variables was developed for each chronology, using the SAS procedure RSQUARE (SAS Institute Inc. 1985). The final model was selected based on: 1) the coefficient of determination  $(R^2)$ ; and 2) the absence of differences in the two variables between the two time periods. T-tests were used to determine whether there were any significant differences in the means of the climate variables between the two periods. All variables used in regression models showed no significant differences between the two periods (Appendix II), thus conditions most limiting to growth were assumed to be equivalent.

The pre-gypsy moth regression models were then used to generate predicted radial growth values in the post-gypsy moth period. These were plotted against actual growth values, and the residuals (predicted subtracted from actual, i.e. the component of growth not explained by climate) were then examined with respect to gypsy moth numbers. The maximum number of larvae counted during one of the summer censuses was averaged over all trees for each species; this was then used as a correlate of gypsy moth defoliation (this maximum larvae measurement was highly correlated with the number of egg masses counted each year, and egg mass density has been shown to be related to defoliation by Liebhold *et al.* 1993). Larval counts were log transformed to normalize the data. Examination of the residuals from all regression equations revealed that they were normally distributed and showed no trend, thus satisfying the linear regression assumptions of normality and heteroscedasticity (Zar 1984).

## Results

#### Gypsy moth larvae data

The first gypsy moth outbreak at Lake Hill began in 1978, the year before larval counts on individual trees began (Figure 2). The dashed line represents estimates of maximum larval counts based on defoliation maps from aerial surveys (Jobin 1978) and research on larval population density at Lake Hill prior to 1979 (Madrid and Stewart 1979, Lechowicz 1983). The first outbreak lasted until 1980, after which larval numbers on oak dropped to levels slightly higher than those of maple and ash. The population began another increase in 1987, and reached epidemic levels in 1989 and 1990 before crashing once again. The average number of larvae on sampled trees varied greatly between species. Oaks were heavily attacked during the two outbreaks, averaging 104.5 larvae per tree, while maple averaged 14.0 and ash 3.1 larvae per tree. In the years between the two outbreaks, oak averaged 7.1, maple 2.5, and ash 0.5 larvae per tree. **Sampled trees** 

Sample sizes for the three species were quite different, because of differences in abundance at Lake Hill, and also because maple cores were difficult to cross-date, resulting in the exclusion of many maple trees. Final sample sizes were thus 156 trees for oak, and 39 trees for both maple and ash. Figure 3 shows the relationship of DBH with age (both in 1992) for the sampled trees. In terms of age in 1992, oak ranged from 45 to 171, maple from 49 to 155, and ash from 44 to 133 years old (at breast height). Many of the trees were between 45 and 60 years old, indicating a strong recruitment pulse at least 60 years ago on the south side of Lake Hill. DBH in 1992 varied from 10.7 to 60.8 cm in oak, 9.9 to 47.2 cm in maple, and 9.9 to 41.7 cm in ash.

## Figure 2.

Gypsy moth population levels at Lake Hill, Mont St-Hilaire. Solid lines and symbols are logged values of the mean maximum larval count per tree of each species (three to five larval counts were made each summer from 1979 to 1992; the maximum larval count refers to the highest count of each summer for an individual tree). Dashed lines are estimates of the same measure, using data from Jobin (1978), Madrid and Stewart (1979), and Lechowicz (1983).



# Figure 3.

The relationship of diameter at breast height and age for red oak (n=156), sugar maple (n=39) and white ash (n=39). Both measures were from 1992, the last year of gypsy moth larval counts. This measure of age is not the true age of each tree, since cores were taken from breast height, not from the base of each tree trunk.



### Radial growth chronologies

All chronologies had distributions not significantly different from normal distributions (Proc Univariate, SAS Institute Inc. 1985), therefore parametric statistics were used in all analyses involving the entire chronologies. Both the standardized and the residual chronologies showed almost perfect correspondence to the original raw ring width chronologies for each species (Pearson correlation coefficients ranged from 0.990 to 1.000, p<<0.0001). Between-tree differences in mean ring width were thus minimal, and in all subsequent analyses the original ring width chronologies were used.

Table 1 contains several statistics for the ring width chronologies of each species. The mean ring widths were very similar, ranging from 0.116 to 0.126 cm. The standard deviations of each species were also comparable (0.029 in maple and ash, and 0.028 in oak). Mean sensitivity, which measures the relative difference in width from one ring to the next (Fritts 1976), was similar for both oak and ash, but much higher for maple. The first-order autocorrelation, which measures the correlation between a ring width at time *t* and its predecessor at time *t*-1, was fairly high for both oak and ash, and much lower for maple. Both of these results are clearly visible in the chronologies: ash and oak tend to have multi-year periods where growth is either constant or slowly increasing or decreasing, whereas maple is much more prone to sudden year-to-year increases or decreases in growth.

### Differences in growth patterns

During the period 1950 to 1972, the three species show very similar growth patterns (Figure 4). All three species show a sharp drop in growth in 1953. This was most likely due to severe defoliation by the forest tent caterpillar, *Malacosoma disstria* Hubner, (Lepidoptera: Lasiocampidae). Starting in 1952, the worst outbreak on record of the forest tent caterpillar caused severe damage to many forest stands in Quebec (Martineau and Beique 1953). By 1953, defoliation of deciduous trees in a 3000 square mile area which included Mont St-Hilaire was almost complete, and thus was the likely cause of the severe reduction in growth, as climate conditions in 1953 were not especially harsh (Appendix II).

Chronology	Mean Ring width	Std. Dev.	Mean Sensitivity	1st Order Autocorrelation
Oak ring width (cm)	0.118	0.028	0.359	0.655
Maple ring width (cm)	0.116	0.029	0.630	0.239
Ash ring width (cm)	0.126	0.029	0.369	0.630

# Table 1.

Ring width chronology statistics for red oak, sugar maple, and white ash. Ring width and standard deviation are in cm. Mean sensitivity is defined by Fritts (1976) as a measure of the mean change from one yearly ring width value to the next, and varies from 0 (no difference) to 2. The first-order autocorrelation coefficient is a measure of the association between a ring width at year t and a ring width at year t - 1, averaged over the whole series.

## Figure 4.

Actual ring width (A), ring widths divided by mean (B), and subtraction of ring widths from mean (C) chronologies for red oak, sugar maple, and white ash. Chronologies are means over all trees in each species. Chronology A has centimeters as units, chronology B is dimensionless with a mean of 1.0, and chronology C has centimeters as units and a mean of 0. Chronologies are from 1950 to 1992. Means used to develop chronologies B and C were the mean ring widths for each tree during 1950 to 1992.



Following the tent caterpillar outbreak, maple and ash experienced a period of slow but constant growth during the 1960's. Oak growth showed a similar pattern, although growth after 1966 was higher than that of either ash or maple. All three chronologies were significantly correlated with each other in the pre-gypsy moth period of 1950 to 1975 (Pearson correlation coefficients, oak with maple: r=0.67, n=26, p<0.001; oak with ash: r=0.42, n=26, p<0.05; maple with ash: r=0.79, n=26, p<0.001). Beginning in 1973, however, a different pattern emerged. Oak began a steep growth decline that eventually ended with three years of low radial growth in 1978, 1979, and 1980. During these three years oak trees suffered heavy defoliation by outbreak levels of gypsy moths. After 1980 oak growth increased and eventually stabilized at a level significantly below its pre-gypsy moth average (Table 2). Ash and maple also experienced growth declines beginning in 1973. The ash decline was much less severe than that of oak, and was also less prolonged. Whereas oak growth stayed depressed from 1978 to 1980, ash growth rebounded immediately after 1978, and in fact increased to its highest level in 1981. Maple exhibited a decline intermediate to that of oak and ash, and like ash did not experience a prolonged growth depression. There was no significant difference between mean ring width before and after the gypsy moth infestation for either ash or maple (Table 2). The decoupling of the species' ring chronologies is reflected in the Pearson correlation coefficients for 1978 to 1992: although ash and maple were still significantly correlated, oak and maple and oak and ash were no longer significantly correlated (maple with ash: r=0.54, n=13, p<0.05; oak with maple: r=0.42, n=13, p>0.05; oak with ash: r=-0.27, n=13, p>0.05).

### **Climate model**

Table 3 shows the regression models developed for growth in the pre-gypsy moth period. The coefficient of determination ranged from 0.39 to 0.48, and the models were highly significant in all three cases. The main reason why the R<sup>2</sup>'s for the models were fairly low, especially for maple, is that the narrow 1953 year was not well-predicted from the regression equations (Figure 5). The tent caterpillar outbreak cannot be accounted for in the climate models, thus for all three species the 1953 ring width is far

Chronology	Mean ring width 1950-1975	Mean ring width 1978-1992	Percent change in ring width	
Oak ring width (cm)	0.134	0.094 *	- 30.5%	
Maple ring width (cm)	0.113	0.118	+ 4.4%	
Ash ring width (cm)	0.119	0.134	+12.6%	

## Table 2.

Differences in chronology statistics from pre-gypsy moth (1950 to 1975) and postgypsy moth (1978 to 1992) time periods. Correlations tested using Pearson correlation coefficients.

\* Significantly lower than mean of pre-gypsy moth period (t-test, p. 0.001)

Chronology (Y)	Climate predictors (X <sub>1</sub> & X <sub>2</sub> )	Regression equation	R <sup>2</sup>	Р
Oak ring width (cm)	1) Min. May temperature ( <sup>0</sup> C)	Y=0.1500-0.0060X1+0.0002X2	0.45	0.0009
Manla ring width (ana)	of growing season (mm)		0.20	0.0020
wapie ring woth (cm)	2) July rain (mm)	Y=0.0562+0.0004X1+0.0002X2	0.39	0.0032
Ash ring width (cm)	1) Modelled July soil water (cm) 2) Providus year's mean November	Y=-0.7165+0.0163X₁ -0.0415X₂	0.48	0.0008
	temperature (°C)			

# Table 3.

Climate models for pre-gypsy moth period (1950 to 1975), with 1953 included in analysis.

# Figure 5.

Actual (Y-axis) and predicted (X-axis) ring widths (cm), 1950 to 1975. Predicted values were generated using climate data (cf. regression equations in Table 3). Line of equality is also shown. Symbols are years.



below the predicted value. If 1953 is excluded from the analysis, slightly different models are generated, and the fit of the regressions is greatly improved (Figure 6, Table 4). Summer soil water values (or correlates thereof) are predictors in each model, with oak also having daytime high temperature in January as a positive predictor of growth, and ash having March soil water as a positive predictor of growth. Since excluding 1953 from the growth-climate relationship is justified on the basis of the known tent caterpillar outbreak, the regression models developed without 1953 were used to generate predicted values of growth in the post-gypsy moth period.

### Impact of gypsy moth

The growth-climate relationships for all three species were not as strong in the post-gypsy moth period (1978 to 1992) as they were in the pre-gypsy moth period (Figure 7). Oak growth in all years is lower than predicted, and there no longer appears to be a linear relationship between the predictor variables and growth. The greatest deviations of actual from predicted values are in years in which heavy gypsy moth defoliation occurred, i.e. the first outbreak, 1978, 1979, and 1980, and the second outbreak, 1989 and 1990. With the exceptions of 1988 and 1992, ash growth is equal to or greater than predicted growth, with very large positive deviations following the first outbreak in 1979, 1980, and 1981. Maple shows a much stronger growth-climate relationship in the post-gypsy moth period than the other two species, with the exception of a large negative deviation in 1988. Residuals from the climate model were uncorrelated with log-transformed maximum larval counts for both maple and ash (Pearson correlation coefficients, maple: r=-0.061, p=0.836; ash: r=0.202, p=0.488). For oak, however, log-transformed maximum larval counts were a significant predictor of oak residual growth (Figure 8), accounting for 72% of the variance unexplained by climate during 1979 to 1992.

# Figure 6.

Actual (Y-axis) and predicted (X-axis) ring width values (cm), 1950 to 1975, with 1953 excluded. Predicted values were generated using climate data (cf. regression equations in Table 4). Line of equality is also shown. Symbols are years.

.



Chronology (Y)	Climate predictors ( $X_1 \& X_2$ )	Regression equation	R <sup>2</sup>	Р
Oak ring width (cm)	1) June rain (mm)		0.69	0.0001
	2) Mean maximum	Y=0.1328+0.0003X1+0.0050X2		
	temperature in January ( <sup>o</sup> C)			
Maple ring width (cm)	1) June rain (mm)	Y=0.0580+0.0004X1+0.0003X2	0.62	0.0001
	2) July rain (mm)		 	
Ash ring width (cm)	1) Modelled July soil water (cm)	Y=-0.3287+0.0020X1+0.0017X2	0.58	0.0001
	2) Modelled March soil water (cm)			

# Table 4.

Climate models for pre-gypsy moth period (1950 to 1975), with 1953 excluded from analysis.

# Figure 7.

Actual (Y-axis) and predicted (X-axis) ring width values (cm), 1978 to 1992. Predicted values are from regression equations in Table 4. Line of equality is also shown. For oak, percent losses in radial growth from climate-predicted values during outbreak years are: 1978 - 56.0; 1979 - 42.8; 1980 - 48.4; 1989 - 29.6; and 1990 - 42.0.



# Figure 8.

Losses in oak growth attributable to defoliation by gypsy moth after the effects of climate have been removed.



# Discussion

#### Pre-gypsy moth growth

Radial growth of trees prior to the gypsy moth infestation (1950 to 1975) was characterized by relative synchrony among the three species. An important feature of this period was the brief but severe tent caterpillar outbreak in 1953 that led to a large reduction in growth for all three species. Unlike the gypsy moth, the forest tent caterpillar will feed preferentially on the foliage of red oak, sugar maple, and white ash (Craighead 1950). By calculating predicted growth values using the initial climate models that included 1953 (Table 3), I estimated the reduction in growth caused by tent caterpillar defoliation. The reduction in oak growth from the climate-predicted value in 1953 was lower than the reduction in oak growth during the gypsy moth outbreaks (27.9% versus 43.8%). For ash and especially maple, the 1953 tent caterpillar outbreak resulted in severe growth reductions (41.0% and 65.8%, respectively) while the gypsy moth outbreaks did not result in any reductions in growth. Tent caterpillar defoliation has been shown to cause severe reductions in radial growth in maple (Gross 1991), and defoliation from the same forest tent caterpillar outbreak was also noticeable in maple radial growth chronologies from several sites in western Quebec (Payette et al. 1996) and New York state (Bauce and Allen 1991). All three species recovered after 1953; there was no evidence of a long-term growth decline attributable to defoliation by this native folivore.

Another striking feature of the radial growth of all three species in the pre-gypsy moth period was their very low annual growth rates. Burns and Honkala (1990) report the following mean annual diameter growth rates for each species. Red oak averaged 0.5 cm over a range of sites and ages in the central United States, whereas dominant or co-dominant trees growing on good sites in the Appalachian mountains average 1 cm and trees growing on average sites had a mean of 0.6 cm. Sugar maple trees in the north-central United States averaged 0.25 cm diameter growth per year over ten years. In Michigan, trees with a DBH of 46 cm had a mean radial growth of 0.76 cm per year, trees with a DBH of 30 cm grew 0.89 cm, and trees with a DBH of 15 cm grew 1.02 cm. These rates are all for trees greater than 40 years old. White ash trees in Canadian plantations had a mean annual radial growth rate of 0.3 to 0.5 cm, while trees in mixed Appalachian hardwood stands had growth rates varying from 0.3 to 0.8 cm per year, depending on site quality. Diameter growth at Lake Hill (i.e. radial growth multiplied by two), with means of 0.236 cm, 0.232 cm, and 0.252 cm for red oak, sugar maple, and white ash, respectively, was clearly lower than any of the estimates given by Burns and Honkala (1990). Using their most conservative growth estimates, radial growth of red oak at Lake Hill was only 47% of red oak growth elsewhere. The equivalent estimates for sugar maple and white ash are 93% and 84%, respectively. This emphasizes the point that Lake Hill is a poor-quality growth site, especially for oak, and thus the invasion and subsequent outbreaks of gypsy moth at the site are consistent with the notion that gypsy moth outbreaks are more likely to occur and are more severe at poor-quality sites with stressed trees (Mattson and Addy 1975, Houston and Valentine 1977, Mattson and Haack 1987).

Summer soil water, or a correlate thereof, was an important predictor of radial growth for all three species in the pre-gypsy moth period. On a very dry, rocky slope such as Lake Hill, soil water in the summer is likely to be extremely limiting for growth. Many previous dendroecological studies have found correlates of summer soil water to be important predictors of radial growth (e.g. Lane *et al.* 1993, Yin *et al.* 1994, Jenkins and Pallardy 1995). Modelled soil water values were significant predictors for ash growth, but did not replace their concomitant precipitation values in climate models for oak and maple. This result is in disagreement with that of Yin *et al.* (1994), who found that replacing precipitation variables with modelled soil water values substantially increased the predictive power of regression equations for growth. This could be due to the nature of the Lake Hill site; the ForHym model is an aspatial model parameterized on a flat site with deep soil, whereas Lake Hill is a south-facing slope with shallow, rocky soil. Resultant modelled soil water values may not be as accurate as those for flat sites for which the model was developed.

Differences in predictor variables of growth for the three species can be

attributed to differences in life history or autecological traits, since all were growing at the same site. Of the three species, only red oak had a temperature variable as a predictor of growth. Red oak is at the northern limit of its distribution (Burns and Honkala 1990), and so may be more likely to suffer severe cold damage than sugar maple, a species with a somewhat more northerly range. Calmé et al. (1994) have shown that red oak seedlings are much less cold-tolerant than sugar maple seedlings, exhibiting 50% more shoot damage at -33 °C than sugar maple. Higher temperatures in January may thus indicate more favorable conditions for oak, as damage due to extremely low temperatures would be less severe. A multiple regression model for earlywood width in red oak from North Carolina had December and February temperatures as significant positive predictors (Tainter et al. 1984). The coefficient of determination  $(R^2)$  for the four-variable model was 0.464. A 5-variable multiple regression model for latewood width for the same oaks included July precipitation as a significant positive predictor. This model had an R<sup>2</sup> of 0.609. Response function analyses of the related oaks Q. robur L. and Q. petraea (Mattuschka) Liebl. showed that climate accounted for between 5 and 72% of the variance in annual radial growth, with about half of the models having significant response elements for summer precipitation (Pilcher and Gray 1982). My regression model of growth accounted for 69% of the variance in pre-gypsy moth radial growth, at the upper end of the range of R<sup>2</sup>'s reported in the literature for *Ouercus* species.

The percentage of variance in growth explained by the sugar maple model (62%) was also well within the range reported in the literature; studies on the effect of climate on maple radial growth had climate variables explaining from 19.5 to 65.7% (Payette *et al.* 1996), 24 to 79% (Lane *et al.* 1993), 49 to 90 % (Bauce and Allen 1991) and 83% (Yin *et al.* 1994) of the variance in radial growth. It should be noted that most of these growth models had far more predictor variables than my models; I chose to use only two predictors because the addition of even random variables to a multiple regression equation can artificially inflate the amount of variance explained by the model (Draper and Smith 1968). There was little consistency in predictor variables between literature

models for maple radial growth; many different climate variables from both the current and previous year were found to be significant predictors of growth, although six of the nine models for which standard climate variables were used did include some measure or correlate of summer soil water.

Radial growth in white ash was positively influenced by modelled soil water in March. This is somewhat surprising, considering that the last killing frost at Mont St-Hilaire is usually not until the first week of May. White ash is a ring-porous species, and is one of the last species to leaf out on Lake Hill (Lechowicz 1984). Because ringporous species such as ash and oak must rebuild vessels to replace those that cavitated in the winter, their period in full leaf is shorter and starts later than diffuse-porous species such as maple (Lechowicz 1984, Lechowicz and Ives 1989). However, cambial activity starts earlier in ring-porous than in diffuse-porous species (Wareing 1951), and precedes leaf emergence. The positive response of ash growth to modelled March soil water could indicate that formation of large vessels (the earlywood of tree rings) is already starting in March, and is favored by wetter conditions. Since the trees were growing on a south slope, it is likely that growth began earlier than it would have at sites of other aspects. Rouse (1970) has shown that the south slope of Lake Hill is free of snow three weeks earlier than the north slope, and also that average weekly temperatures in March can be almost 4 °C warmer on the south slope. While summer precipitation was a significant element in response function analysis of white ash radial growth in Kentucky, March precipitation was not (Luken et al. 1994). Another study reported that growing season moisture was related to white ash radial growth, but the growing season was defined as April through September, and thus did not include March precipitation (Han et al. 1991).

To summarize, summer precipitation or modelled summer soil water was a limiting factor for radial growth in all three species. For sugar maple June and July rain were the two most important predictors of radial growth, with high rainfall leading to increased growth. White ash had March and July soil water as positive predictors of radial growth. Red oak was the only species to have a temperature variable included in the regression models of growth on climate, with higher January temperatures leading to increased radial growth. June rain was also a positive predictor of growth.

## Post-gypsy moth growth

Oak radial growth after the invasion of the gypsy moth was lower than the climate-predicted values for all years between 1978 and 1992. Not only was radial growth much lower than predicted, but it was no longer linearly related to the climate variables identified as most limiting to growth in the pre-gypsy moth period. Rather, gypsy moth larval numbers, an indirect measure of defoliation on trees, seemed to be the primary influence on oak growth from 1978 to 1992. Previous studies that have investigated the effect of gypsy moth defoliation on tree growth in the northeastern U.S. have not quantified the relative effects of climate and larval defoliation. By obtaining a climate-predicted value for growth, the loss in radial growth due to larval defoliation can be more accurately assessed. In this study I obtained growth losses in outbreak years of between 29.6 and 56.0%, for an average of 43.8%. In a European study that also computed climate-predicted radial growth values, upland oaks experiencing near total defoliation from outbreaks of gypsy moth and other Lepidoptera suffered a loss in radial growth of about 40%, which is very close to my estimate (Rubtsov 1996). Both of these values are less than the 52.2% (Minott and Guild 1925) and 58.0% (Baker 1941) values reported for red, scarlet, black, and white oaks in New England following defoliation of 81 to 100% of the canopy. Over-estimation of the effect of gypsy moth defoliation on growth in these studies is likely, since drought conditions which are often associated with severe outbreaks also result in poor growth, and thus distinguishing between these two factors is difficult without quantifying both (Koerber and Wickman 1970). Baker (1941) also reports on additional plots of black and white oak where severe defoliation resulted in growth declines of only 33 to 43%. In these cases, however, years of heavy defoliation were not associated with drought conditions; rainfall was average or even above-average in these years, which likely mitigated the negative effects of gypsy moth defoliation. Other studies report radial growth losses of 32 to 50%, but no mention of climatic conditions is made in these cases, thus comparisons are difficult to make

(Brown et al. 1979, May and Killingbeck 1995).

In addition to quantifying the effect of climate on growth before looking at the impact of defoliation, this study provides the first evidence that long-term radial growth of preferred host trees at a chronically infested site can be limited by gypsy moth larvae. This suggests that even endemic levels of gypsy moth larvae feeding at low intensities can have a significant negative effect on radial growth, and underscores the potentially adverse consequences of gypsy moth infestations during non-outbreak years. For oaks, only one other study could be found that attempted to relate larval abundance of defoliators over a number of years to radial growth of host trees. In this case, the authors investigated the influence of temperature and rainfall on growth of *Quercus robur* L., but found no significant correlations. They then constructed an index of growth, using the mean growth rate of each tree, and developed a significant regression model for growth decreased linearly with increasing caterpillar density, even though only two of the eight years were years of heavy damage.

Average foliage losses due to endemic levels of gypsy moth herbivory can be estimated from larval counts and the average oak DBH. Whittaker and Woodwell (1967) developed a regression equation of leaf surface area on DBH for white oak (*Quercus alba* L.), a closely-related species of similar growth form to red oak. Using this equation and the average DBH of oak trees sampled at Lake Hill (20.8 cm), the average foliage area for oaks at Lake Hill was 56.2 m<sup>2</sup>. During non-outbreak years, there were on average 7.1 gypsy moth larvae per oak tree. Over the course of its development, a gypsy moth larva consumes approximately 1 m<sup>2</sup> of foliage (Leonard 1981). Oaks therefore lost on average 7.1 m<sup>2</sup>, or 12.8 % of their foliage during years when gypsy moth numbers on oaks were at non-outbreak levels. This estimate of foliage area loss is within the 5-15% range reported in studies reviewed by Schowalter *et al.* (1986). In these studies and in Rafes (1970), however, nominal herbivory had a negligible effect on radial growth. Low-intensity but chronic defoliation of host trees has thus been largely ignored or downplayed when discussing the impact of defoliating insects on radial

growth (Rafes 1970, Mattson and Addy 1975, Schowalter *et al.* 1986). This study, however, suggests that nominal herbivory does result in radial growth reductions of host trees.

Of the three species, maple's radial growth from 1978 to 1992 showed the least perturbation from growth patterns prior to the arrival of the gypsy moth. Maple growth did show a negative response to gypsy moth defoliation in 1978. This reduction was much less than that of oak, but larger than the reduction in ash growth, which is consistent with maple's classification as a host of intermediate preference for the gypsy moth. None of the other gypsy moth outbreak years had ring widths narrower than expected, and with the exception of 1988, most of the other years were equal to or greater than the climate-predicted growth. Maple growth in 1988 showed as much of a reduction from the climate-predicted values as did gypsy moth-reduced ring widths in oak. Maple rings in 1988 were extremely narrow, and often missing (R. Naidoo, personal observation), thus suggesting that some climatic condition not accounted for in the climate model was adversely affecting maple growth.

Ash growth from 1978 to 1992 showed a different pattern from either oak or maple. Ring widths in 1988 and 1992 were slightly narrower than predicted. All other years were equal to or greater than the predicted values, which themselves did not exhibit much year-to-year variability. However, the years 1979, 1980, and especially 1981, were much higher than predicted. Ash, as an avoided host, suffered little if any defoliation during the first gypsy moth outbreak of 1978 to 1980; larval counts were exceedingly low even while oak was being severely attacked. It is thus likely that the years of tremendous growth increases in ash can be attributed to the arrival of the gypsy moth. It has been well-established that in the aftermath of an insect outbreak, large quantities of nutrients, especially nitrogen, are returned to the forest floor (Mattson and Addy 1975). This is due to the exceptionally high concentration of nutrients in larvae bodies and frass, as well as the increased fall of leaves, twigs, and branches due to larval activity in the canopy. Grace (1985) reported that in a forest attacked by gypsy moth, nitrogen return in the form of larval frass was higher than that in leaf litterfall. White ash has been classified as a nitrogen-demanding tree (Stanturf *et al.* 1989), and has been shown to respond to nitrogen fertilization with an increase in radial growth (Ellis 1979, Stanturf *et al.* 1989). It is thus possible that increased availability of nitrogen in the form of a nitrogen pulse after the first gypsy moth outbreak allowed ash to experience a timelagged increase in radial growth. Several studies have observed growth increases in nondefoliated trees subsequent to heavy defoliation of preferred hosts in the same stand (Ierusalimov 1965, Kulman 1971, Wickman 1980, Campbell and Garlo 1982, Swetnam and Lynch 1989). Studies have also shown that compared to ash, sugar maple shows a much reduced or negligible growth increase when fertilized by nitrogen (Ellis 1979, Stanturf *et al.* 1989), which could explain this species' lack of growth response.

By comparing years of low growth in the pre-gypsy moth period with years where known insect defoliation occurred, it is possible to quantify the impacts of "extreme" climatic events relative to insect outbreaks. Both predicted and actual ring widths were very narrow for all three species in 1971, thus I considered this year to be typical of a year in which climatic conditions were extremely unfavorable for tree growth. If we compare growth in 1971 with the mean annual radial growth in the pre-gypsy moth period, we can obtain an estimate of the reduction in growth due to harsh climatic conditions. This estimate can then be compared to the reduction in growth (from climate-predicted values) due to insect defoliation. In the case of red oak, radial growth in 1971 was reduced by 24.9%, as compared to the much greater mean growth reduction of 43.8% in gypsy moth outbreak years. For sugar maple and white ash, the effect of gypsy defoliation on radial growth was negligible, therefore I used the growth reduction from tent caterpillar defoliation in 1953 as a general measure of the impact of insect defoliation on radial growth. Sugar maple had a growth reduction in 1971 of 29.8%. This reduction was much lower than the 65.8% reduction in 1953. White ash also had a lower growth reduction in 1971 than in 1953 (16.2% compared to 41.0%). Therefore while harsh climatic conditions in 1971 did result in growth losses for all three species, these losses were not as serious as those caused by defoliation from outbreak levels of folivorous insects.

# Conclusion

In a drought-stressed forest chronically infested by gypsy moth, radial growth patterns of three host species differed from expected values based on pre-infestation growth-climate relationships. These differences were related to the species' hostpreference classifications. Red oak, a preferred species, declined markedly in growth after the initial outbreak, and was no longer limited by the macroclimatic factors that were important to growth before the arrival of the insect. Instead, the number of attacking larvae, a correlate of the amount of defoliation host trees received, was the primary influence on growth, with high numbers of larvae leading to narrower ring widths. This suggests that nominal herbivory by endemic levels of gypsy moth can have a significant negative effect on radial growth of preferred tree species. Sugar maple, a host of intermediate preference, showed the least response to gypsy moth infestation, and had the strongest post-gypsy moth growth-climate relationship. White ash, an avoided host, showed no negative response to gypsy moth outbreaks, and in fact increased in growth during and shortly after the first such outbreak. This increase in growth was probably due to an increase in nitrogen return to the litter. Insect outbreaks, based on both gypsy moth and tent caterpillar defoliation, led to greater reductions in radial growth than did severe climatic conditions.

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# Chapter 2. Radial growth losses in preferred and avoided tree species during gypsy moth outbreaks.

# Abstract

I investigated the effect of defoliation by gypsy moth, *Lymantria dispar* L., (Lepidoptera: Lymantriidae) on radial growth of preferred and avoided trees: red oak (*Quercus rubra* L.), and white ash (*Fraxinus americana* L.), respectively. Individual trees were censused for gypsy moth larvae from 1979 to 1992 in a chronically-infested forest on a drought-prone site. Annual growth rings were measured from 1950 to 1992 on increment cores taken from these same trees, as well as from trees at a similar but more recently infested site nearby. Regression models of growth at the chronically-infested site on growth at the recently-infested site were developed. These were then used to generate predicted radial growth values in the absence of gypsy moth at the chronically-infested site. During the first outbreak at the chronically-infested site, gypsy moth defoliation led to a mean reduction in radial growth of 42%, a loss similar to what has been reported in other studies. Yearly larval counts from 1979 to 1992 at the chronically-infested site were uncorrelated with the residuals from the growth models, however. This could be because herbivory by endemic levels of gypsy moth was occurring at the recently-infested site.

# Introduction

The gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae) is an introduced forest insect that has become the most serious defoliator of hardwood trees in northeastern North America (Montgomery and Wallner 1988, Jobin 1995). Native to Eurasia, it was first introduced in Massachusetts in 1869 (Dunlap 1980), and has since increased its range north to Quebec, south to Virginia, west to Michigan, and east to Nova Scotia (Liebhold *et al.* 1995). The gypsy moth has been classified as a "sustained eruption" insect by Berryman (1987), meaning that outbreaks spread from local epicenters to cover large areas, and are sustained in a particular area for several years before the population returns to endemic levels. During these prolonged and widespread outbreaks, defoliation by larvae can have severe socioeconomic consequences, such as death of timber trees (Dennis *et al.* 1986), reduced timber yield due to growth reductions (Minott and Guild 1925, Baker 1941), and high costs to homeowners for the protection of shade trees (Liebhold *et al.* 1995). Defoliation by outbreak levels of gypsy moth can also lead to changes in stand composition (Campbell and Sloan 1977), understory vegetation (Collins 1961), and recreational appeal (Hollenhorst *et al.* 1993).

Despite the clear socioeconomic and ecological effects of gypsy moth outbreaks, the impact of gypsy moth defoliation on radial growth of host trees in northeastern North America has not been adequately investigated. Several approaches to quantifying gypsy moth herbivory on radial growth have been used in the past by researchers. In North American studies, the average radial growth over a certain time period before a defoliation event was compared to average growth after defoliation (Minott and Guild 1925, Baker 1941, Kulman 1971, Brown *et al.* 1979, Wargo 1981, May and Killingbeck 1995). Reduction of growth in the post-defoliation period compared to the predefoliation period was attributed to gypsy moth herbivory. The weakness in this method is that potentially confounding differences in climatic conditions between periods are not accounted for. Many insect outbreaks coincide with drought-stress conditions which themselves can lead to radial growth reductions (Koerber and Wickman 1970), therefore the relative magnitude of each factor on growth is difficult to ascertain.

More modern studies using dendroecological techniques (Fritts and Swetnam 1989) have used two different but equally valid approaches to determine growth losses resulting from insect outbreaks. The first approach involves developing radial growth models based on climatic variables. Macroclimatic conditions are known to influence radial growth at many sites (e.g. Fritts 1976, Cook and Jacoby 1977, Pilcher and Gray 1982). After accounting for the effect of climate, the residual variance in growth can be examined to determine if any trends are due to insect herbivory (Rubtsov 1996). The alternate and more commonly used approach is to use radial growth chronologies of nonhost species, or of uninfested trees of the same species, as a baseline growth record. Any large growth depressions in the growth chronology of infested trees can then be attributed to insect defoliation (e.g. Kulman 1971, Swetnam and Lynch 1989, Jardon et al. 1994, Krause 1997). Neither of these dendroecological approaches have been used to quantify the effect of gypsy moth defoliation on growth of hardwood trees in northeastern North America. Chapter 1 used the climate model approach to investigate this problem. This second chapter will discuss the use of chronologies of non-infested trees in determining the impact of gypsy moth defoliation on radial growth.

My method involved the use of two nearby and similar stands with different histories of infestation. The "chronically-infested" stand was infested well before the "recently-infested" stand. This chronically-infested stand has been studied intensively, and population levels of the gypsy moth over a thirteen-year period were recorded at the level of individual trees. Radial growth patterns of host trees at this site were compared to conspecific trees at the recently-infested site, to determine if any differences in growth were due to gypsy moth defoliation.

# Methods

#### Study site

The field site was located at Mont St-Hilaire, Quebec, Canada (45° 32' N, 73° 09'W). Much of Mont St-Hilaire is covered by old-growth deciduous forest, making it the largest remnant of Great Lakes-St Lawrence Lowlands forest that previously dominated the St-Lawrence valley. Different types of forest stands are found on Mont St-Hilaire, including old-growth beech-sugar maple (*Fagus grandifolia* Ehrh. - *Acer saccharum* Marsh.) on deep moist soils, hemlock (*Tsuga canadensis* (L.) Carrière) on steep, rocky slopes, yellow birch (*Betula alleghaniensis* Britton) and red maple (*Acer rubrum* L.) swamps in depressions, and red oak (*Quercus rubra* L.) on dryer sites (Maycock 1961). Vascular plant diversity is also high: over 500 species have been recorded (Maycock 1961), including several that are endangered in Quebec.

Two stands at two different sites were selected for sampling. The first was a site infested by gypsy moth since the mid-1970's called Lake Hill (alternately referred to as the "chronically-infested site"). The Lake Hill site is on the outer face of Mont St. Hilaire, while the second site, called Sunrise, is a hill within the interior basin on the mountain (see map in Maycock 1961). The Sunrise site has only recently been infested, and will be referred to as the "recently-infested site". These sites were selected because of their similar characteristics: both stands are on dry, rocky, south-facing slopes, with stony and shallow soil that has an average depth of 65 cm to bedrock (Rouse 1970). Red oak is the dominant tree species in both stands. Ironwood (Ostrya virginiana (Miller) K. Koch) and sugar maple are other important species, while white ash (Fraxinus americana L.), basswood (Tilia americana L.), and beech (Fagus grandifolia Ehrh.) are minor components. The lower slope of both sites consists mostly of sugar maple and beech; higher up, red oak becomes the predominant species while beech disappears entirely. In many places the uppermost flanks are covered with very small and slowgrowing oak trees with open canopies; scree slopes where leaf litter is sparse are also common. Both sites thus exhibit many of the characteristics that Houston and Valentine (1977) ascribe to sites prone to gypsy moth infestation.

The history of the arrival and subsequent invasion of the gypsy moth has been well-documented for both Mont St-Hilaire and southern Quebec. While pockets of light to severe defoliation have been recorded in southwestern Quebec since 1972, the first area-wide outbreak in the vicinity occurred in 1977 (Jobin 1995). This was also the first year that substantial defoliation was noted on Mont St-Hilaire. Ten hectares of an oak stand on Burned Hill, a small peak adjacent to Lake Hill, were severely defoliated in 1977. The next year, the area of heavy defoliation had increased to 259 hectares, of which 123 were on Lake Hill (Lechowicz 1983). The first outbreak at Lake Hill ended in 1980, and was followed by a number of years during which gypsy moth numbers were very low. During these years the gypsy moth continued to spread over the mountain, as a second outbreak in 1989 and 1990 resulted in severe defoliation not only at Lake Hill but also at several other sites (M.J. Lechowicz, unpublished data). While no severe defoliation was reported on Sunrise, it is likely that the moth had become established there by the time of the second outbreak at Lake Hill, and perhaps sooner, although no means of establishing population levels at Sunrise exists. Gypsy moths were definitely present in 1996 on Sunrise (R. Naidoo, personal observation). Because of the uncertainty concerning the status of the moth, the Sunrise site can only be regarded as an uninfested site for the years of the first outbreak at Lake Hill, during which time I can be reasonably certain that no gypsy moths were present.

In 1979, twenty-four permanent 500 m<sup>2</sup> quadrats were established along four altitudinal isoclines at Lake Hill to monitor the gypsy moth infestation. Within these quadrats, all trees with a diameter at breast height (DBH) of greater than 8 cm were identified to species and given a permanent identification tag. Each summer from 1979 to 1992, gypsy moth larvae resting under tarpaper bands around the trunk of each tagged tree were counted on three to five separate occasions. Tarpaper bands are used as daytime hiding places by late-instar larvae (Liebhold *et al.* 1986), and Odell and Godwin (1979) reported that 95% of larvae feeding on oak trees congregated under these artificial concealments.

#### Collection and analysis of radial growth data

I selected two species with contrasting host preferences to examine the influence of gypsy moth defoliation on radial growth. Red oak is a preferred host of the insect, while white ash is avoided (Lechowicz and Mauffette 1986). At the Lake Hill site two increment cores were taken from all available ash and oak trees for which records of gypsy moth larvae existed. At Sunrise, two cores were collected from randomly selected trees along three altitudinal transects. Transects were run perpendicular to the slope and continued along the entire south side of the slope, so that the whole area was sampled with approximately equal intensity. Trees below 8 cm in DBH were not sampled. All cores were taken at breast height and at a 90° degree angle to each other, with one core taken from the upslope side of the tree. The DBH of each tree was also recorded.

Cores were air dried, then mounted onto wooden backings and planed, in order to make the rings more visible. Cores were cross-dated visually by using signal years (Stokes and Smiley 1968); narrow rings in 1953, 1971, 1978, 1979, and 1988, and large rings in 1981 made unambiguous cross-dating possible in almost every oak and ash core. Any core that was damaged or that could not be cross-dated was removed from the analysis. Because of this, 5 oak and 12 ash from Lake Hill had chronologies based on only one core; the equivalent numbers for Sunrise were 3 oak and 5 ash. After crossdating, ring widths were measured to the nearest 0.01 mm using a dissecting microscope with a sliding vernier scale. The age of the tree (at breast height) was also recorded. For some cores, estimating the age was not possible, either because the tree's center was rotten or because the core was too far off the pith. Trees where at least one age estimate was not available were also removed from the analysis. The years 1950 to 1992 were measured on all cores; 1950 was the earliest year I could measure, since many trees had just grown to breast height in the preceding few years. Since there were many more increment cores from Lake Hill oaks, due to their prevalence in the gypsy moth quadrats, a random sample of 41 oak trees was selected to be analyzed, matching the 41 oaks sampled at Sunrise. Final sample sizes for ash were 39 at Lake Hill, and 44 at Sunrise.

In addition to the raw ring width chronology (i.e. the mean ring width over all

trees and years for each species and each site), two other chronologies were calculated. The standardized ring index was calculated for each core by dividing the ring width of each year by the mean ring width from 1950 to 1992. This was done for all cores and trees in each species and at each site, and was then averaged over each species and each site to give the standardized ring index chronology. The residual ring index chronology was calculated in a similar manner, except that instead of dividing by the mean, the mean was subtracted from each ring width. In both the standardized and residual ring chronologies, the mean was used instead values from a hypothetical growth curve to preserve as much trend as possible. The focus of many dendrochronological studies is purely the year-to-year climate effects, and so in these studies growth curves are fit to the raw chronologies to remove as much non-climatic growth trend as possible (e.g. Blasing et.al. 1988, Innes and Cook 1989, Graumlich 1993, Payette et.al. 1996). In my case. I wanted to preserve potential trends, since it is possible that the arrival of the gypsy moth at Mont St-Hilaire would cause a long-term growth response in its hosts. By dividing or subtracting the mean, this is accomplished, while at the same time overall growth rate differences (i.e. fast-growing versus slow-growing trees) are removed. Growth models

To investigate the impact of gypsy moth defoliation on growth, I first constructed a regression model of Lake Hill growth based on Sunrise growth during the time period before the arrival of the gypsy moth. I set this "pre-gypsy moth" period to begin in 1950, the first year measured on increment cores, and end in 1975. I selected 1975 as an endpoint to the pre-gypsy moth period because gypsy moths may have been present at low numbers on Lake Hill before the first outbreak in 1978. I thus excluded the years immediately preceding the first outbreak, 1976 and 1977, from any regression analysis because of this uncertainty. These pre-gypsy moth regression equations were then used to generate predicted values of radial growth in the post-gypsy moth period, 1978 to 1992. The variance in growth at Lake Hill not explained by Sunrise growth (i.e. the residuals, predicted Lake Hill ring indices subtracted from actual ring indices) was then examined with respect to gypsy moth defoliation. The maximum number of larvae recorded during one of the summer counts was averaged over all trees for each year, and this measure was used as a correlate of gypsy moth defoliation (this maximum larvae measurement was highly correlated with the number of egg masses counted each year, and egg mass density has been shown to be related to defoliation by Liebhold *et al.* 1993). Larval counts were log transformed to normalize the data. Preliminary examination of the residuals from the regression equations revealed a trend in the residuals from the ash growth model. The Lake Hill ash ring index chronology was thus square root transformed, and the residuals from this new model, as well as the original oak growth model, were normally distributed and showed no trend, thus satisfying the linear regression assumptions of normality and heteroscedasticity (Zar 1984).

## Results

The first gypsy moth outbreak on Lake Hill began in 1978, the year before larval counts on individual trees started (Figure 1). The dashed line represents estimates of maximum larval counts based on defoliation maps from aerial surveys (Jobin 1978) and research on larval population density at Lake Hill prior to 1979 (Madrid and Stewart 1979, Lechowicz 1983). The first outbreak lasted until 1980, after which larval numbers on oak dropped to levels slightly higher than those of ash. The population began another increase in 1987, and reached epidemic levels in 1989 and 1990 before crashing once again. The average number of larvae on sampled trees varied greatly between species. Oaks were heavily attacked during the two outbreaks, averaging 113.0 larvae per tree, while ash averaged only 3.1 larvae per tree. In the years between the two outbreaks, oak averaged 8.0, and ash 0.5, larvae per tree.

The relationship of DBH with age (both in 1992) for the sampled trees is shown in Figure 2 (Lake Hill ) and Figure 3 (Sunrise). Oak age ranged from 45 to 171 and ash age from 44 to 133 years old in 1992 (at breast height) at Lake Hill. DBH in 1992 varied from 10.7 to 60.8 cm in oak, and 9.9 to 41.7 cm in ash, at Lake Hill. At Sunrise, oak age ranged from 46 to 200 and ash age from 60 to 159 years old in 1992. DBH in 1992 at

Gypsy moth population levels at Lake Hill. Solid lines and symbols are the logged average maximum larval count for each species. Dashed lines are estimates of the same measure from other data sources (see text).



The relationship of diameter at breast height (DBH) and age for red oak (n=41), and white ash (n=39) at Lake Hill. Both measures were from 1992, the last year of gypsy moth larval counts. Regression equations of DBH on age are also given for each species.



The relationship of diameter at breast height (DBH) and age for red oak (n=41), and white ash (n=44) at Sunrise. Both measures were from 1992, the last year of gypsy moth larval counts at Lake Hill. The regression equation of white ash DBH on age was not significant; the equation for red oak is given.



Sunrise was between 14.2 and 43.4 cm for oak, and 13.7 and 35.3 cm for ash. Oaks at both sites were divided into relatively discrete age classes, indicating recruitment was not continuous but rather in pulses, presumably following disturbance events.

#### **Ring chronologies**

The three types of growth chronologies for Lake Hill and Sunrise are shown in Figures 4 (oak) and 5 (ash). The standardized and residual chronologies were almost identical between sites for both species. The raw ring width chronologies, however, had greater differences between sites than did the two indices. This indicates that there were differences in the mean growth rate of trees between the two sites, and therefore I removed these differences by using the standardized ring index series in all analyses.

Table 1 contains several statistics for the ring index chronologies. The mean ring index in the pre-gypsy moth period was similar within each species at both sites; no significant differences between the Lake Hill and Sunrise stands were detected for oak (t-test; t=0.35, p=0.73) or ash (t=0.14, p=0.89). There were also no significant differences in mean ring index between sites during the post-gypsy moth period (oak: t-test, t=-0.38, p=0.71; ash: Mann-Whitney Rank Sum test, T=218, p=0.56). However, the mean ring index for oak was lower in the post-gypsy moth period than in the pre-gypsy moth period for both Lake Hill and Sunrise (Table 1). The 1st order autocorrelation, which measures the correlation between a ring index at time t and its predecessor at time t-1, was significant for the ash chronologies at both sites. Because this autocorrelation results in a reduction of the number of truly independent observations, I chose a conservative significance level of 0.005 for all subsequent analyses involving ash.

During the period 1950 to 1977, both species show very similar growth patterns (Figures 4B and 5B). The most noticeable feature of this time period is the sharp drop in growth in 1953. This drop was observed at both sites and in both species, and was most likely due to severe defoliation by the forest tent caterpillar, *Malacosoma disstria* Hubner (Lepidoptera: Lasiocampidae). Starting in 1952, a region-wide tent caterpillar outbreak caused severe damage to forests in much of southwestern Quebec (Martineau

Ring width (A), division of ring widths by mean (B), and subtraction of ring widths from mean (C) chronologies for red oak at Lake Hill and Sunrise. Chronology A has centimeters as units, chronology B is dimensionless with a mean of 1.0, and chronology C has centimeters as units and a mean of 0. Chronologies are from 1950 to 1992.

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Ring width (A), division of ring widths by mean (B), and subtraction of ring widths from mean (C) chronologies for white ash at Lake Hill and Sunrise. Chronology A has centimeters as units, chronology B is dimensionless with a mean of 1.0, and chronology C has centimeters as units and a mean of 0. Chronologies are from 1950 to 1992.



Chronology	Mean ring index 1950 - 1975	Mean ring index 1978 - 1992	1st order autocorrelation 1950 - 1975
Lake Hill oak ring index	1.107	0.819***	0.34
Sunrise oak ring index	1.088	0.838***	0.33
Lake Hill ash ring index	0.964	1.038	0.69**
Sunrise ash ring index	0.957	1.039	0.54**

## Table 1

Ring index means for pre- (1950 to 1975) and post- (1978 to 1992) gypsy moth periods, and the first-order autocorrelation in the pre-gypsy moth period. The first-order autocorrelation coefficient is a measure of the association between a ring width at year t and a ring width at year t - 1, averaged over the time series (in this case 1950 to 1975).

- \*\*\* Mean ring index in post-gypsy moth period significantly greater than index in pre-gypsy moth period (t-test, p<.0001)
- **\*\*** Significant first-order autocorrelation present in chronology (p<.005)

and Beique 1953). By 1953, Mont St-Hilaire was within a 3000 square mile area in which most deciduous trees were completely defoliated. This defoliation is thus the likely cause of the very narrow growth ring observed in all trees in 1953, since climatic conditions were not especially severe that year (Appendix II).

Following this sharp drop in 1953, oak growth at both sites recovered and was fairly synchronous until 1977. The only exception was in the first half of the 1960's, where oak growth at Sunrise was slightly but consistently higher than at Lake Hill. For the most part, however, oaks at both sites seemed to be growing in the same manner, presumably due to a common response to macroclimatic conditions. In 1977, however, oak growth at Lake Hill dropped below oak growth at Sunrise, and stayed at a much lower level for the next three years. These years, 1978 to 1980, were the years of the first gypsy moth outbreak at Lake Hill. After the outbreak, growth of oak at Lake Hill rebounded, eventually surpassing Sunrise growth for a three year-period in the mideighties before once again returning to approximately the same level.

Ash growth between sites was remarkably consistent throughout the entire length of the chronology, and did not exhibit any marked divergences, even after the arrival of the gypsy moth. Chronologies from both sites were characterized by relatively slow and consistent growth rates until 1972, after which a large increase occurred at both sites. This increase in growth lasted until 1981, after which time more normal levels of growth were once again observed.

#### **Growth models**

The growth models of Lake Hill ring index on Sunrise ring index for 1950 to 1975 are shown in Figure 6. Both models predicted a significant amount of variance in Lake Hill ring index, although the fit for ash was better than it was for oak. The model of ash growth was significant (p=0.0001) at the conservative 0.005 level. The actual ring index values in the post-gypsy moth period were then compared to predicted values generated from the pre-gypsy moth models (Figure 7). For oak there was no significant correlation between predicted and actual values (Figure 7A), indicating that the pre-

Actual (Y-axis) and predicted (X-axis) ring index values, 1950 to 1975, for red oak (A) and white ash (B). Predicted values were generated from given regression equations, where y=predicted Lake Hill ring index, and x=Sunrise index. Line of equality is also shown. Symbols are years.



Actual (Y-axis) and predicted (X-axis) ring index values, 1978 to 1992, for red oak (A) and white ash (B) at Lake Hill. Predicted values were generated using regression equations from Fig. 6. Line of equality is also shown.



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gypsy moth regression equation was unable to predict radial growth at Lake Hill after the invasion of the gypsy moth. With the exception of 1985, 1986, and 1987, all years were below the Sunrise-predicted values. In contrast, ash actual values were significantly correlated (again at the 0.005 level) with predicted values (Figure 7B). Residuals (actual ring index - predicted ring index, i.e. the component of Lake Hill growth variance not explained by Sunrise growth) for both species were not correlated with gypsy moth maximum larval counts (oak: Pearson correlation coefficient, r=-0.07, p=0.80; ash: Pearson correlation coefficient, r=0.05. p=0.87).

## Discussion

Radial growth in the pre-gypsy moth period was quite synchronous within species at both sites, although oak exhibited a different pattern than that of ash. The steep drop in growth in 1953 was evident in both species, however, and was likely due to forest tent caterpillar defoliation. The same tent caterpillar outbreak also resulted in growth reductions in 1953 in maple radial growth chronologies from several sites in western Quebec (Payette *et al.* 1996) and New York State (Bauce and Allen 1991). Red oak and white ash are both preferred hosts of the forest tent caterpillar (Craighead 1950), whereas white ash is avoided by the gypsy moth (Lechowicz and Mauffette 1986). Ash at both Lake Hill and Sunrise had very narrow growth rings in 1953. In contrast, ash radial growth at Lake Hill was unaffected by heavy gypsy moth defoliation. After the tent caterpillar outbreak, both species at both sites rebounded to pre-defoliation levels; there was no long-term growth depression.

Both ash chronologies exhibited a minor release, lasting from 1972 to 1981, before radial growth again returned to pre-release levels. Oaks did not show a similar growth release, and in fact began to decline at about the same time that ash began increasing in growth. It is possible that these two events are related; the decline in oak growth rate may have resulted in more favorable growth conditions for ash. These could include increased nutrient availability due to a reduction in root competition, and increased light availability due to crown reduction in oak. It is also possible that the oak decline resulted in favorable conditions for the subsequent invasion of the gypsy moth, as stressed trees are known to be more susceptible to outbreaks than healthy ones (Mattson and Haack 1987). A concomitant, though less severe growth decline also occurred in oaks at Sunrise, which suggests that macroclimatic conditions were involved in both declines. Some consideration, however, must be given to the possibility that gypsy moths were already present at Lake Hill during the decline period, although not at outbreak levels. The analysis discussed in Chapter 1 showed that modest but continuous gypsy moth defoliation at Lake Hill was negatively correlated with oak radial growth. The much more severe decline at Lake Hill could thus have been caused by endemic levels of gypsy moth herbivory at that site, herbivory which oaks at Sunrise did not experience.

The lack of correlation between actual and predicted radial growth in oak indicates that gypsy moth did affect growth at Lake Hill compared to the recentlyinfested stand at Sunrise in the post-gypsy moth period (1978 to 1992). During the years of the first outbreak, 1978 to 1980, losses in radial growth at Lake Hill relative to growth at Sunrise were 52.0, 36.5, and 37.5%, respectively, for an average of 42.0%. This is only slightly less than the 49.1 % loss reported for the same outbreak using a climate model to generate predicted oak growth (Chapter 1). Both of these values are slightly lower than other estimates reported for loss in radial growth due to gypsy moth defoliation in the northeastern United States. These were 52.2% (Minott and Guild 1925) and 58.0% (Baker 1941) losses for red, scarlet, black, and white oaks in New England following defoliation of 81 to 100% of the canopy. These older studies estimated the loss in radial growth by using an average measure of growth before the outbreaks as an estimate of predicted radial growth in the absence of gypsy moth. The weakness in this approach is that it fails to account for the often combined and concomitant negative effect of drought stress on host trees (Koerber and Wickman 1970, Mattson and Haack 1987). Thus a certain percentage of the decline attributed to gypsy moth defoliation in these studies is likely due to the associated drought stress that often

coincides with outbreaks of defoliating insects. Baker (1941) described additional plots of black oak and white oak for which climatic conditions as well as growth declines were observed. On these plots growth losses due to severe defoliation were only 33 to 43%. These lower estimates were likely due to the average or even above-average rainfall in these years, which could have mitigated the negative effects of gypsy moth defoliation. Other studies have reported radial growth losses of 32 to 50%, but no mention of climatic conditions were made in these cases, thus comparisons are difficult to make (May and Killingbeck 1995, Brown *et al.* 1979).

In addition to the North American studies cited above, much work on the effect of defoliation by the gypsy moth on radial growth has been done in Europe. Various authors have reported on radial growth losses for different host species, although most of them have followed a procedure similar to that of Minott and Guild (1925) and Baker (1941). Klepac (1959) reported a 30% loss of radial growth in Quercus robur after one year of severe defoliation. The mean radial growth loss in cork oak, Q. suber, was 33 to 39%, after three consecutive years of defoliation (Magnoler and Cambini 1973). In Rumania, complete defoliation of unspecified oaks by gypsy moth resulted in radial growth losses of 30 to 40% (Kulman 1971). Three to four years of complete defoliation in Hungary reduced annual radial growth by more than 50% in several species of oak (Kulman 1971). In a comprehensive review of Russian work on the subject, Rafes (1970) summarized available data on defoliation effects on radial growth, breaking insects into different feeding groups and classifying responses to defoliation based on forest type. For spring-summer defoliating insects in oak forests similar to those at my sites, the mean percentage radial growth loss after a year of heavy defoliation was 30%, and after two years was 65%. Defoliation after one year on oaks in Europe seemed to result in smaller losses in radial growth than losses reported from North America, perhaps because co-evolution of trees and gypsy moths in the insect's natural range have produced defenses or responses not found in the relatively new hosts of eastern North America. However, repeated defoliations in Europe seem to cause more severe damage than what was observed at my site after several years of outbreak levels of gypsy moth.

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Unlike the first outbreak, there was no appreciable impact of gypsy moth defoliation on the radial growth of oaks at Lake Hill compared to those at Sunrise during the second outbreak (1989 to 1990). In chapter 1, growth of oak trees in the years of the second outbreak was much reduced compared to the climate-predicted values. Since macroclimatic conditions should be similar between sites, it is likely that by 1989 gypsy moths had invaded the Sunrise site, resulting in depressed Sunrise growth and thus a weakening of the growth response to gypsy moth defoliation in the Lake Hill chronologies. Gypsy moth outbreaks spread from local epicenters or foci into surrounding areas over a number of years (Campbell and Sloan 1978, Wallner 1987, Liebhold and Elkinton 1989, Elkinton and Liebhold 1990). The spread of the gypsy moth from the initial epicenter on Burned Hill to Sunrise would thus have occurred after the first outbreak on Lake Hill, but likely before the second outbreak. Although there was no record of severe defoliation at Sunrise in 1990, other sites of approximately equal distance from Burned Hill were defoliated (M.J. Lechowicz, unpublished data), therefore it is reasonable to assume that gypsy moth larvae would have colonized Sunrise by this time. By 1984, radial growth of oaks at Sunrise had dropped below those of oaks at Lake Hill. Growth of oaks at Sunrise continued to be less than or equal to that of oaks at Lake Hill until the end of the chronology in 1992. Thus the radial growth record of oaks at Sunrise suggests that gypsy moth had probably arrived there by the mid-1980's, and contributed to the weakening of the gypsy moth defoliation signal at Lake Hill by defoliating oaks at Sunrise, thereby reducing radial growth. Because no severe reduction in growth comparable to the 1978-1980 gypsy moth outbreak at Lake Hill occurred, it is likely that oaks at Sunrise experienced herbivory by only endemic numbers of larvae. However, as shown in Chapter 1, chronic defoliation by even endemic levels of gypsy moth larvae contributed to radial growth reductions of oaks at Lake Hill, therefore this is the likely reason for the lower mean annual radial growth of oaks at Sunrise after the arrival of the gypsy moth at Mont St-Hilaire.

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## Summary

Gypsy moth defoliation on red oak, a preferred host species, resulted in radial growth losses (relative to climate-predicted values) both during outbreaks and also during years when the population was at endemic levels. Although some studies have reported radial growth declines during gypsy moth outbreaks, these generally did not take into account the confounding nature of the growth-climate-insect interactions. In this thesis I performed two different analyses that removed the influence of climate on radial growth before examining potential growth losses due to gypsy moth defoliation.

In chapter 1, models of radial growth on climate were developed and used to account for the variance in growth due to climate. Once this had been accounted for, the remaining variance in growth was analyzed with respect to gypsy moth defoliation. These analyses were performed for red oak (a preferred species), sugar maple (an acceptable or intermediate species), and white ash (an avoided species). Herbivory by gypsy moth larvae during outbreak years resulted in an average radial growth loss of 43.8% in red oak. More importantly, over a 14-year period during which time the gypsy moth population was mostly at an endemic level, the number of gypsy moth larvae on red oak was a significant predictor of radial growth. This result disagrees with most studies in the literature, which report that nominal herbivory has little impact on radial growth. Sugar maple and white ash showed no such growth-insect relationships.

In chapter 2, an alternative method was used to account for the effect of climatic conditions on growth. Trees from a similar site that had only recently been infested were used to generate predicted values of what growth would have been at the infested site had gypsy moth not arrived there. From this analysis, the estimate of radial growth loss in red oak at the infested site for the first outbreak was 42 %. The climate-based analysis of chapter 1 resulted in a growth loss of 49.1 % for the first outbreak, thus the two estimates agree fairly well with each other. Unlike the first chapter, however, the second outbreak at the infested site led to no apparent growth losses relative to the more recently infested site. This is most likely because gypsy moths had already arrived at the recently-infested site, and so herbivory on trees there would have decreased growth and thus reduced or eliminated apparent growth losses at the chronically infested site.

Climatic conditions were also a major influence on tree growth for each of the species studied. The climate regression models in chapter 1 predicted a highly significant proportion of the variance in radial growth before the arrival of the gypsy moth at the site. In chapter 2, growth before the arrival of the gypsy moth was quite synchronous between sites, and the regression models of growth at Lake Hill on growth at Sunrise were also highly significant. However, climatic conditions declined in importance once the gypsy moth arrived at Lake Hill, as reflected in the resultant breakdown in both types of models for red oak. Climate models for sugar maple and white ash were much more robust to the arrival of the gypsy moth, as was the Lake Hillon-Sunrise growth model for ash. Growth-climate relationships were thus modified by the arrival of the gypsy moth in proportion to the host preference of the species; climate models no longer predicted red oak growth, but sugar maple was still relatively wellpredicted, and ash was also well-predicted, with the exception of higher-than-predicted growth values following the first gypsy moth outbreak. The one discrepancy between models occurs in the interpretation of this ash release following the first gypsy moth outbreak at Lake Hill. While growth at Lake Hill appeared to be much greater than climatic conditions would suggest, growth of ash at Sunrise during the same time was only slightly lower than their conspecifics at Lake Hill. While gypsy moth may have had a role in the elevated growth of ash at Lake Hill, especially in 1980, it is also probable that some macroclimatic condition not in the climate regression models acted in concert with the nitrogen pulse explained in Chapter 1.

While gypsy moth defoliation did not have an adverse effect on maple and ash growth, defoliation by the forest tent caterpillar resulted in large reductions in growth during a massive outbreak in 1953. In this case, growth losses in maple and ash were similar to growth losses experienced by oak during gypsy moth outbreaks. This is consistent with tent caterpillar feeding preferences, since unlike the gypsy moth, the forest tent caterpillar will feed preferentially on the foliage of all three species. In each tree species, growth losses due to insect defoliation were more severe than growth losses in a harsh climatic year, with insect outbreaks resulting in approximately twice as much of a growth reduction as harsh climatic conditions. This illustrates the importance of both native and introduced defoliating insects to forest trees in northeastern North America, and suggests that insect defoliation may be an important contributor to background noise for researchers looking for signals of various types in dendroecological studies.

## Appendix I

# Comparison of climatic conditions at Mont St-Hilaire versus St-Hubert airport.

All climate data was taken from the St-Hubert airport weather station (45° 32' N, 73° 25' W, altitude=27 m). This station was the closest available weather station to Mont St-Hilaire. However, Yin *et al.* (1994) have expressed concern that in many studies, climatic conditions at "nearby" weather stations are in fact quite different from those at the study site. We thus examined whether this was in fact the case for climate data from St-Hubert and Mont St-Hilaire.

All climate data was obtained from Environment Canada. Our contact person was Jennifer Milton, a meteorologist at the Scientific Services Division of the Atmospheric Environment Service of Environment Canada (telephone: (514) 283-2264; fax: (514) 283-1296). For the St-Hubert weather station, climate data were available for the entire period in question (1950 to 1992). For Mont St-Hilaire, two weather stations were operating on the mountain for different lengths of time during the period 1950 to 1992. The "Mont St-Hilaire" station was in operation from 1960 to 1969, and the "Mont St-Hilaire - McGill" station was in operation from 1967 to 1974. Both stations were very close together in terms of position:

MSH: 45° 33' N, 73° 09' W, alt=173.7 m MSH - McGill: 45° 33' N, 73° 10' W, alt=198.1 m

The raw climate data obtained from all three stations were daily maximum temperature, daily minimum temperature, daily rainfall, and daily snowfall. From these daily values, monthly temperature averages and monthly precipitation totals were calculated. The few months of overlap between both Mont St-Hilaire stations showed very close correspondence of both temperature averages and precipitation totals, therefore data from both stations were combined together and plotted against St-Hubert values to determine if significant climate differences existed between both sites.

Figures 1 and 2 show minimum and maximum average monthly temperatures, respectively, of Mont St-Hilaire versus those of St-Hubert. In each case, an extremely tight fit is observed (R<sup>2</sup>'s of 0.996 and 0.998, respectively). In the case of the maximum monthly temperatures, those at Mont St-Hilaire appear to be slightly cooler than those at St-Hubert, but the difference was small enough that we considered it unnecessary to use the regression equation to transform the St-Hubert values. For my climate models of tree growth, this slight depression of Mont St-Hilaire temperatures relative to St-Hubert temperature would not have had any impact, since the variance in temperature at both sites appears to be almost identical.

Figures 3 and 4 show monthly totals of rain and snow, respectively. Here the fit is not quite as tight as for the temperature relationships. This is to be expected, since the occasional localized precipitation event could conceivably occur at one site and not the other. The rainfall data was log transformed to reduce heteroscedasticity. For snowfall we fit a 2nd order polynomial curve to the data as well as the linear regression. Large deviations from St-Hubert predicted values in both rain and snow were examined with respect to other climatic variables, to determine whether some functional basis for extreme discrepancies could be found, but these were uncorrelated with other conditions such as total summer precipitation and average summer temperature. The R<sup>29</sup>s were still extremely high for the linear regressions for both rain and snow, and we therefore decided once again to stick with the original St-Hubert values rather than attempt any transformation.

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Minimum monthly temperatures (°C) at the Mont St-Hilaire and St-Hubert weather stations.



Maximum monthly temperatures (°C) at the Mont St-Hilaire and St-Hubert weather stations.

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Total monthly rainfall (mm) at the Mont St-Hilaire and St-Hubert weather stations. Values were logged transformed due to heteroscedasticity in the original data.



Monthly snow totals (mm) at the Mont St-Hilaire and St-Hubert weather stations.



## **Appendix II**

## Climatic conditions from 1950 to 1992

This appendix describes the average monthly climatic conditions during the period 1950 to 1992, and also shows the temporal patterns of the climate variables used in the radial growth climate models. All climate data was obtained from Environment Canada. Our contact person was Jennifer Milton, a meteorologist at the Scientific Services Division of the Atmospheric Environment Service of Environment Canada (telephone: (514) 283-2264; fax: (514) 283-1296).

The first two figures are the twelve-month average temperature (Figure 1) and precipitation curves (Figure 2) at the St-Hubert weather station. This data was assumed to represent climatic conditions at Mont St-Hilaire (see analyses in Appendix I). The temperature curve clearly reflects the cold winters, warm summers, and large annual temperature range typical of a moist continental climate. Precipitation is highest in the summer months, due to the invasion of maritime air masses.

The next two figures (Figures 3 and 4) are those of the climate variables used in the regression equations of radial growth on climate in chapter 1. In each case, no long term trend is visible in the series. Pre- and post-gypsy moth patterns are similar, thus changes in radial growth patterns after the arrival of the gypsy moth at Mont St-Hilaire cannot be attributed to changing climatic conditions. Differences between variable means of the two different periods were also not significant:

> June rain: t-test, t=0.152, df=39, p=0.88 July rain: t-test, t=0.939, df=39, p=0.35 January temperature: t-test, t=-0.519, df=39, p=0.61 March soil water: t-test, t=-0.338, df=39, p=0.74 July soil water: t-test, t=0.603, df=39, p=0.55

Long-term average monthly temperatures (monthly values averaged over 1950 to 1992).



Long-term average monthly precipitation totals (monthly totals averaged over 1950 to 1992).



June rain (A) and July rain (B) from 1950 to 1992. Vertical lines indicate the pre-gypsy moth (1950 to 1975) and post-gypsy moth (1978 to 1992) periods. Mean values are also given for each period.



Daytime January temperature (A), modelled March soil water (B), and modelled July soil water (C) from 1950 to 1992. Vertical lines indicate the pre-gypsy moth (1950 to 1975) and post-gypsy moth (1978 to 1992) periods. Mean values are also given for each period.



## **Appendix III**

## The ForHym model - predicting soil water content

The development of regression equations to model the effects of climate on radial growth in trees has been used by Yin *et. al.* (1994), among others. In contrast to other researchers, however, they used a measure of soil water content in these regression equations, in addition to more common climate variables such as monthly temperatures and totals of precipitation. By doing this, they explained a greater proportion of variance than when climate variables alone were used in the models. In a preliminary analysis, I used only measures of precipitation or temperature in the regression equations that modelled the effect of climate on radial growth before the arrival of the gypsy moth on Lake Hill. By using a measure of soil water content in regression models, I hoped to get a better prediction of radial growth for the pre-gypsy moth period.

To obtain this estimate of soil water content, I wanted to use the ForHym model described by Arp and Yin (1992). I requested a copy of the model, but Professor Arp suggested instead that I visit his lab at the University of New Brunswick, where I would be able to consult with members of his lab who were experienced in the use of the model. The visit to UNB was quite brief. I arrived at Paul Arp's lab on Tuesday after lunch, and by Friday afternoon had completed the work to be done. This work included the following:

#### 1) Inputing the required data

The model in its current form is much more sophisticated than the one presented in Arp and Yin (1992). In addition to the hydrology module, the model now contains a module on soil temperature (ForStem), and on radiation (ForRad). Initially, I wanted to go through the model and develop at least a general understanding of how it worked, but I quickly realized that there would not be enough time to do that while at UNB. I first concentrated on getting the data into the model and having it run correctly. The data requirements were mostly as discussed in Arp and Yin (1992), and will not be discussed here in great detail. The main variables to enter were monthly average temperature, monthly total precipitation, and monthly snow fraction of precipitation. Other inputs were mainly site descriptors, such as percent cover by deciduous versus coniferous trees, soil depth, soil type, forest region, etc.

#### 2) Checking the predictions with observed measurements

Since I had no long-term soil water data to compare with the model's predictions, Professor Arp suggested that I obtain discharge data from nearby streams. Since the ForHym model has a stream discharge module, comparing predicted discharge with measured discharge would give at least some indication of the accuracy of the soil water predictions. The nearest stream with discharge data was Rivière des Hurons, with the measuring station being at 45° 29' 25"N, 73° 11' 13"W. This stream runs around the east and south sides of Mont St-Hilaire in the surrounding lowlands. The data were obtained from Environment Canada (1992).

The model predictions of stream discharge were quite good (Figure 1), although over the long term there is less predicted streamflow than there was observed. Professor Arp and Dr. Fan-Rui Meng suggested that this could be for two reasons: 1) since the stream is not on the mountain but in the agricultural lowlands, there is less evapotranspiration than on the forested slope of Lake Hill, and so more runoff; and 2) Arp suggested that Mont St-Hilaire would receive more precipitation than at St-Hubert (from where all climate data was taken), due to orographic precipitation, and thus there is actually more precipitation than is being inputed into the model. This "missing" precipitation could be why the model predicts less streamflow than is observed. Both Professor Arp and Dr. Meng thus suggested that the model is making reasonably good predictions, and that no modifications were necessary to force a better correspondence between the predicted and actual values. He emphasized that his model has produced very accurate predictions for all sites it had been tested at, and saw no reason why Mont

Discharge at Rivière des Hurons from 1973 to 1990. Dotted lines are model predictions, solid lines are measured values. The two lines heading upwards represent the predicted and actual cumulative discharge.



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St-Hilaire would be any different. He also stressed that ForHym was an aspatial model that generated predictions for any given point in the watershed. He believed that the processes involved were general enough that these predictions would be quite accurate no matter where the specific point was located. He believed the model would capture the important variability in soil water content with regard to tree growth, and suggested that whatever variability was not captured was unimportant to trees, as they were adapted to it. He did not see the need to modify the model for any effect of slope, as the slope will only enhance general predictions given by the model.

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## **Appendix IV**

## The Art of Coring

I explain here the process by which increment cores (small pieces of wood used by dendroecologists to count and measure rings) were taken from deciduous hardwood trees, with particular reference to sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), and white ash (*Fraxinus americana*). Texts by Maeglin (1979) and Stokes and Smiley (1968) were useful references for detailed information on the collection and preparation of increment cores.

## I. Pre-expedition essentials

#### a) Materials

- Haglofs increment borers (30 cm and 35 cm lengths, retailed by Canadian Forestry

Ltd., 100E Hymus, Pointe-Claire, H9R 1E4, (514) 697-1100)

- Extra extractors
- Masking tape (approximately 2 cm width)
- Core carrier
- Yellow straws used in McDonald's restaurants
- Permanent marker
- Clipboard and pencil
- Work gloves
- Caulking (simple mastic) and caulking gun
- Turpentine and rag
- Leather belt
- Metal bike spoke
- Forest gear (e.g. hiking boots, rain gear, etc.)
- Flagging tape

## **b)** Preparation

Certain preparations before heading into the field will ensure that the coring process goes as smoothly as possible. To construct an effective core carrier, find a sturdy plastic container long enough to contain McDonald's straws, e.g. tupperware, juice container, etc. Construct a lid that is easily secured but also easy to open, using cardboard, a garbage twist-tie, and duct tape. Be sure there is a way of securing the container to your belt or belt buckle.

Before going into the woods, one end of the straws should be sealed using masking or duct tape. The straws will be used to store the increment cores. Extractors (the component of the increment borer used to extract the core from the tree) should be made conspicuous with flagging tape, as they can easily be dropped and lost in the woods. You should have either a belt with loops able to contain several instruments, or a fanny pack. In case of rain, carry a clear plastic bag to place over your clipboard. When cutting the nozzle of the caulking tube, be sure to make a hole small enough to fit into a hole the diameter of the borer shaft.

## II. The pith of the matter - how to extract an increment core from a tree

The perfect core contains all the trees' rings from the bark to the pith (centre), and is straight, clean, and unbroken.

#### a) Selecting a starting place on the trunk

Before taking a core, look all around the tree trunk and get a feel for where the pith is. Hitting the pith can be very difficult, as it is not always where you would expect it to be, and the margin for error is very small. Trees that are asymmetrical make this even more difficult. Select a spot without any noticeable knots or lumps; for trees with ridged bark, select a spot in a furrow between two ridges, as it is easier for the shaft to penetrate into the wood under these conditions. If on a slope, the easiest place to take a core is from the upslope side, as you can put all your weight into the effort. When two

increment cores are to be taken from a tree, my procedure was to take one from the upslope side and one at a 90° angle from the upslope side. Some authors, however, have recommended taking cores at 180° angles. Before coring, be sure to secure the extractor in a safe place on your belt or in the zipper of your fanny pack.

#### b) Taking the core (for righties; reverse hands for lefties)

For optimal ease of entry, the right elbow should be pointing towards the ground, with the forearm perpendicular to the tree trunk and forming an "L" with the upper arm. The borer should be grasped in the centre of the handle, with the shaft between the index and middle fingers; the shaft should thus be an extension of the forearm. The left hand should grasp the shaft near the bit, to prevent wavering of the bit as it enters the wood. Apply tremendous force towards the tree, keeping the shaft and bit straight, and start turning the borer clockwise (cw). Continue to turn the borer with the right hand and steady the shaft with the left, until it is no longer possible to turn with only one hand; the bit should now be firmly entered in the wood.

Now grasp the handle with both hands and continue to turn cw until the tip has penetrated past the assumed depth of the pith. A good way to check on how far the shaft has entered the tree is to insert the extractor into the shaft until it touches the core inside; the length of extractor left outside the shaft is equivalent to the length of shaft penetration. Compare this length to the actual tree diameter to see how much farther the shaft should be entered.

## c) Extracting the core

Once the shaft has penetrated to the assumed depth of the pith, insert the extractor into the shaft, and ease it under the core up to the end of the borer. You may experience some difficulty in slipping the extractor under the core; try sliding the extractor in on the side or above the core to counter this. Sometimes a good push is needed to get the extractor fully to the end of the shaft. Once this has been done, snap the handle back counter-clockwise (ccw) in a quick motion, in order to break the core

from the tree. A sharp cracking sound indicates a successful break. In trees where the centre is rotting, the cracking sound will not be produced. You can now retrieve the core by slowly removing the extractor from the shaft. This may require some force, in order to disengage the extractor from the tip of the borer. Take care not to lose any loose bits of bark by placing your free hand under the leading edge of the extractor (the bark often breaks loose from the rest of the core). Place the core pith-down into a straw, and seal the top with tape. Label the straw as necessary and place it in the core carrier for safe transportation. Back the corer out of the tree by turning the handle ccw.

#### d) Repair procedure

This two-step final treatment is necessary to prevent future fungal infection or insect attack on cored trees, although Shigo (1986) recommends leaving the hole unplugged. Coring can cause wounds that lead to long columns of discoloured and decayed wood (Shigo 1986). Disinfection is accomplished by wiping the hole and its edge with turpentine. Caulking is then spread over the hole to seal it. Make sure to spread the caulking over the entire hole, and use a stick or the edge of the nozzle to firmly adhere the material around the edge of the opening.

## III. Trouble-shooting

## a) I'm having trouble extracting the core from the shaft. What can I do?

This occurs when the core is jammed into the borer, or when the extractor's edge has become blunted. After repeated failures (> 5) to extract the core, you may decide to back the borer out of the tree and use the bike spoke to push it out. This is a last resort; do not use often as the spoke may blunt the tip of the borer.

#### b) The first few rings of the core are always broken. Why is this happening?

The borer is wavering too much during the initial entry. Make sure you are holding the shaft steady as you turn it. Apply more force towards the tree and turn more slowly. If you are experiencing immense difficulty in the initial entry of borer into wood, the bit may require sharpening.

#### c) My cores are always rough, ragged, and dirty. How can I prevent this?

Proper maintenance of the increment borer is the key to obtaining clean, smooth cores. After coring many oak trees, the inside of the borer shaft may become stained black with tannin. This is what leads to the dark residue on the cores. Roughness or raggedness of cores can be prevented by sharpening the leading edge of the extractor, and the inner edge of the borer bit; sharpen both of these with the conical stone in the sharpening kit.

#### d) My borer is stuck in the tree and will not back out.

This problem occurs mainly in larger oaks (DBH 25 cm or greater), and is preceded by a change in the sound made by the borer while turning, as well as (and more importantly) by a feeling that the borer is now penetrating something the equivalent of butter, not wood. The bit is caught in soft rotten wood; continued progress of the shaft pithward will lead to the hollow centre of the tree and thus the feeling of no resistance whilst turning. Once the bit has entered into hollow space, or wood that is very mushy, the track made by the grooved edges of the bit is no longer solid enough to allow reversal of the shaft from the tree. It is better to stop at the first signs of softness in order to avoid serious problems.

A good first step in removing a stuck borer is to put a small piece of masking tape on the shaft, as close as possible to the bark of the tree. This will allow you to detect the slightest backward movement of the shaft. The overriding objective is to pull the bit of the borer back into non-rotten wood, so that you can then back it out in the normal fashion. To do so, you need to apply as much force as possible away from the tree, while turning the borer no more than 30 degrees ccw per "jerk". This will hopefully re-engage the bit in hard wood. Repeat 3 or 4 times. If the progress assessor does not move, you must pull even harder, while turning less. The key point is to minimize the turning of the borer, as each turn wears down the wood and hampers the re-engagement of the bit.

If all of this is of no avail, you will have to use a hammer and chisel to carve out

the borer (a painstaking task that is not good for the tree!).

## **IV. Post-coring maintenance**

#### a) Cleaning

Kerosene (1-K specification), a bike spoke, and a cloth are needed. Cut the margin of a sturdy cloth 10 cm longer than the length of the bike spoke; its width should be about 0.75 cm. Dip the whole cloth margin in kerosene. Fold the tip of the cloth over the end of the spoke (about 1 cm) and push into the wider end of the borer. Continue pushing it all the way into the borer. Then pull the cloth back out of the borer in a rotational fashion, thus ensuring a complete cleansing of the entire internal surface. The spoke will not reach all the way through the borer; you must therefore insert the cloth into the narrower end of the borer and twist (without using the spoke). Finally, wipe the extractor clean using a normal cloth soaked with kerosene.

#### b) Sharpening

You need a sharpening kit (retailed by Canadian Forestry Ltd.) with three types of stones: flat india, tapered, and conical. Follow the diagrammatic instructions given with the kit. In my experience, brand new increment borers rarely need to be sharpened; I extracted over 800 increment cores from oak, ash, and maple without any decline in performance.

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# Appendix V

# Key computer files used in M.Sc.

These files are compressed into an archived diskette. Professor Lechowicz and myself have copies of this archive. All files are PC format; the file extensions indicate the program used to create them:

wk3 - Lotus for Windows, version 1.0 a

ssd - SAS (version 6.03) data set file

prn - text (ASCII) file

numerical extension (e.g. 001) - text (ASCII) file

1) Tree-ring files: (Measured ring widths are from 1950 to 1992)

a) Lake Hill ash:

avgash2.wk3 - average yearly raw ring widths, mean ring width, DBH, and age for all ash trees

ash-stan.wk3 - yearly raw ring widths, standardized ring widths, residual ring widths, and first differences of natural logs for all ash cores

b) Lake Hill maple:

avgmap2.wk3 - average yearly raw ring width, DBH, and age for all maple trees map-stan.wk3 - yearly raw ring widths, standardized ring widths, residual ring widths, and first differences of natural logs for all ash cores

c) Lake Hill oak:

- avgoak2.wk3 average yearly raw ring widths, mean tree ring width, mean ring width pre-gypsy moth, mean ring width post-gypsy moth, DBH, age, ageclass, and quadrat of all oak trees
- oak-stan.wk3 yearly raw ring widths, standardized ring widths, residual ring widths, and first differences of natural logs for all oak cores

oak-rand.wk3 - yearly raw ring widths, standardized ring widths, residual ring widths, and first differences of natural logs for a random sample of oak trees used in Chapter 2

## d) Sunrise:

- sun-avg.wk3 yearly ring widths, DBH, and age for all ash and oak trees at Sunrise
- sun-stan.wk3 yearly raw ring widths, standardized ring widths, residual ring widths, and first differences of natural logs for all oak and ash cores at Sunrise

#### 2) Climate files:

climate2.ssd - contains all climate variables used in regression analysis

- 50-92.prn daily min. temp., max. temp., and precipitation at St-Hubert weather station from 1950 to 1992
- msh-gaul.001 files contain daily max temp (001), min temp (002), rain (010), and snow (011) data for the Mont St-Hilaire / Gault weather station, 1976-79
- msh-gaul.002
- msh-gaul.010
- msh-gaul.011
- msh-mcg.001 files contain daily max temp (001), min temp (002), rain (010), and snow (011) data for the Mont St-Hilaire / McGill weather station, 1967-74

msh-mcg.002

msh-mcg.010

msh-mcg.011

msh.001 - files contain daily max temp (001), min temp (002), rain (010), and snow (011) data for the Mont St-Hilaire weather station, 1960-69 msh.002

msh.010

msh.011

weather.wk3 - Comparisons of monthly weather data of Mont St-Hilaire stations with St-Hubert station

## 3) Gypsy moth files:

gmquad1.wk3 - Files contain DBH, maxlarv, eggmass, and quadrat for all trees in Lake Hill quadrats

gmquad2.wk3

yearlarv.wk3 - Contains maxlarv and eggmass counts for all Lake Hill oak trees used in M.Sc. analysis, 1979 to 1992

larvae-3.wk3 - Contains average maxlarv value for Lake Hill ash, maple, and oak, 1979 to 1992

#### 4) Regression analysis:

- chronos.ssd SAS file with average yearly raw ring widths, standardized ring widths, residual ring widths, and first differences of natural logs chronologies for Lake Hill ash, maple, and oak
- chronos.wk3 contains chronologies for all three Lake Hill species, as well as predicted values and residuals from climate values, and gypsy moth counts
- chronos2.wk3 contains chronologies for Lake Hill and Sunrise ash and oak, as well as predicted Lake Hill values and gypsy moth counts







IMAGE EVALUATION TEST TARGET (QA-3)







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