# Temperatures Experienced by Emerald Ash Borer and Other Wood-boring Beetles in the Under-bark Microclimate

by

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# AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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# Abstract

Most studies of under-bark microclimate have been restricted to observations of a few coniferous trees in wooded southern latitudes. This limitation is worrying because of emerging wood-boring pests that specialize on deciduous trees in Canada, such as emerald ash borer (*Agrilus planipennis*). Using a large data set that includes 60 ash trees spread across both urban and woodlot sites in 6 different Ontario locations, I found that the under-bark microclimate of deciduous trees can provide wood-boring beetles with an environment in which temperatures which differ from air temperature. On average, daily minimum under-bark temperatures are significantly warmer than air temperatures in the winter months. At temperatures low enough to cause substantial cold-temperature mortality to emerald ash borer, the difference between under-bark and air temperature can be large. In addition, I observed that the difference between daily minimum under-bark and air temperature can vary, and consequently that assumptions of a constant level of difference between the two are not valid. In the spring season, I found that daily under-bark temperature maxima on the south side of the tree are significantly warmer than air temperature maxima. This difference lead to faster predicted development times for beetles in the southern under-bark microclimate of urban trees as compared to predictions based on air temperature, suggesting that city trees may impact overall population dynamics.

While it is clear that under-bark temperatures differ from air temperatures, and are important to predicting possible range and population growth of wood-boring insects, large scale measurements of microclimate conditions are not feasible. I tested the ability of a simple Newtonian cooling model to predict under-bark temperature extremes using weather station data. While the model did not predict daily under-bark temperature maxima accurately, predictions of minima were quite accurate (1.31˚C average root mean squared error), especially when compared to the errors from assuming under-bark temperature is the same as air temperature (3.20˚C average root mean squared error). I recommend use of the Newtonian cooling model to predict under-bark temperature minima of deciduous and coniferous trees.

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# Chapter 1

# Introduction and literature review

## 1.1 Introduction

Temperature can impact many aspects of an insect's life, including oviposition, development rate, longevity, and mortality (Gilbert and Raworth 1996). However, many insects do not live in direct exposure to the ambient climate, but instead occupy microhabitats like a bird's nest, fungi, or wood. For example, wood-boring beetles spend a large portion of their lives inside the phloem, cambium, and hardwood of their host trees (Gaumer and Gara 1967, Ungerer et al. 1999, Cappaert et al. 2005).

There is evidence that this under-bark microclimate has the effect of shielding wood-boring insects from extreme temperature minima, and that air temperatures are different from under-bark temperatures generally (Bartos and Amman 1989, Bolstad et al. 1997, Tran et al. 2007). However, some previous studies of the difference between air and under-bark temperature are based on small data sets (e.g. Powell 1967, Bartos and Booth 1994), while others ignore the variability of the difference between air and under-bark temperature (Bolstad et al. 1997, Ungerer et al. 1999), or only consider data from part of the year (Tran et al. 2007).In addition, all studies I am aware of only consider under-bark temperature of coniferous trees at latitudes further south than those in Canada, and do not consider any trees in an urban environment.

In this chapter, I will review the cold temperature mortality and temperature-dependent development of insects, with a specific focus on wood-boring beetles and the relationship of these factors to the under-bark microclimate, with an emphasis on emerald ash borer (*Agrilus planipennis*). Following this, I present two studies in publication format: an empirical study of under-bark temperatures, and a model to predict these temperatures from weather station data. In chapter 2, using a large data set, I will illustrate that the daily winter minimum under-bark temperature tends to be warmer than air temperature, and that the magnitude of the difference between the two is not constant. I will also show that at temperatures which would cause substantial cold-temperature mortality, the difference between air and under-bark temperature can be large. In addition, I will show that springtime daily under-bark maxima on the south side of the tree tend to be warmer than air temperature, and that for trees in an urban environment, this can lead to faster development times for beetles in that microclimate. In chapter 3, using a Newtonian cooling model I will predict daily under-bark temperature minima and maxima of ash trees at northern latitudes, and show that this model gives estimates of minimum under-bark temperature with smaller errors than assuming that air temperature is reflective of under-bark temperature

## 1.2 Literature review

### 1.2.1 Cold temperatures and insect mortality

Insects are typically classed as being “freeze avoiding” or “freeze tolerant” (Sinclair et al. 2003). Freeze avoiding insects cannot survive the formation of ice crystals in their body fluids, and undergo physiological changes to avert freezing; freeze tolerant insects can survive the formation of ice crystals in their body tissues (Zachariassen 1985). The point at which freezing of body fluids occurs is called the supercooling point (SCP), so freeze tolerant insects can survive reaching the SCP, and freeze avoiding ones cannot.

It is also known that some freeze avoiding insects (e.g. peach-potato aphids) experience some mortality at temperatures above the SCP (Clough et al. 1990, Bale 1996). Wood-boring insects such as emerald ash borer (*Agrilus planipennis*) and mountain pine beetle (*Dendroctonus ponderosae*), however, do not experience significant levels of mortality from exposure to temperatures above the SCP (Bentz and Mullins 1999, Crosthwaite et al. 2011). Response to temperatures above the SCP does not appear to be widely reported, and could prove to be important to population growth if such temperatures cause relatively high levels of mortality.

For many insect species, there is a significant amount of seasonal variation in the SCP (Danks 2005). This is the case for wood-borers like emerald ash borer and mountain pine beetle, which have cooler SCPs in the winter than in other times of the year (Bentz and Mullins 1999, Crosthwaite et al. 2011), but not for others like the southern pine beetle (*Dendroctonus frontalis*), and some southern populations of eastern five spined ips (*Ips grandicollis*) (Lombardero et al. 2000).Wood-boring beetles tend to be freeze avoiding, with a wide range of super-cooling points across and even within species. Mean SCP of southern pine beetles can range from -7˚C to -20˚C depending on time of year and latitude (Tran et al. 2007), and the mean SCP of 4 wood-boring beetle species (*D. frontalis*, *I. grandicollis*, *Ips perotti*, and *Ips pini*) in mid-latitude North American locations range from -5.05˚C to -13.41˚C (Lombardero et al. 2000). Mountain pine beetles have an SCP as high as -2˚C and as low as -35˚C, depending on the time of year, and emerald ash borer can have SCPs as warm as -11.1˚C and as cold as -35.3˚C (Crosthwaite et al. 2011).

Lombardero et al. (2000) performed experiments to determine if short or long term acclimation to cold temperatures had any impact on the SCP of four wood-boring beetle species. The authors found that giving the beetles either a short or long time to adjust to a cooler temperature before subjecting them to extreme cold did not significantly affect the SCP of the beetles. For emerald ash borer, exposure to relatively warm temperatures (10˚C and 15˚C) did produce an increase in the beetles' SCP relative to those kept at a cooler temperature, but the difference only became significant after a week or more, and only increased the SCP by about 2 to 5 degrees, still remaining below -20˚C (Sobek-Swant et al. 2011). Such a prolonged warm period followed by such cold temperatures seems very unlikely in the locations where the beetle is present, meaning that deacclimation to cold temperatures may not be important for this particular species.

The effects of cold temperatures on the survival on individuals insects can determine can determine the latitudinal limit of an insect's range (Bale et al. 2002). For example, southern pine beetles live as far north as its cold tolerance will allow (Ungerer et al. 1999). It was predicted in that study that an increase in annual minimum temperature of just 3˚C would permit a northern range increase of 170km.

### 1.2.2 Temperature-dependent development of insects

The temperature also affects the timing and rate of insect development (Davidson 1944, Howe 1967, Lactin et al. 1995, Gilbert and Raworth 1996, Gillooly et al. 2002). Up to a maximum temperature threshold, insects develop more quickly at warmer temperatures than at cooler ones (Gilbert and Raworth 1996). For wood-boring beetles, temperature begins playing an important role from the egg stage of the life cycle, and it is common for different life stages to have different developmental thresholds and times. Developmental rates of the various life stages of southern pine beetle have different responses to increased temperatures, but all appear to be reasonably well-approximated by a linear function between about 10˚C and somewhere between 25˚C and 30˚C (Wagner et al. 1984, Ungerer et al. 1999). Similar trends are reported for the Asian longhorn beetle (*Anoplophora glabripennis*) (Keena 2006, Keena and Moore 2010), emerald ash borer(Lyons and Jones 2005)mountain pine beetle(Bentz et al. 1991), and European spruce bark beetle (*Ips typographus*) (Wermelinger and Seifert 1998).

One simple way of expressing the way that temperature affects development for a given species is degree day accumulation. One degree day corresponds to 24 hours spent at 1˚C above a (typically species-specific) developmental threshold. As a sample calculation, if an insect has development time of 5 degree days with a 10˚C threshold, then it has to spend 5 days at 11˚C, or 2.5 days at 12˚C, or 1 day at 11˚C and 2 at 12˚C, and so on. In the general case, degree day accumulation can be calculated as:

$$DegreeDays = \sum_{i} Y_i (T_i - X)$$

Where $i$ is the time in days, $T_i$ is the temperature (in ˚C) held constant over time the day, $X$ is the developmental threshold, and $Y_i$ has value of 0 if $T_i > X$, and 1 otherwise. This formula can be adjusted to account for temperatures that vary over a shorter time period (e.g. an hour).

One problem with using degree day accumulation is that beyond an upper limit, increases in temperature no longer produce an increase in development rate, and further increases can negatively impact it (Logan et al. 1976). However, the increase in development rate with temperature is often linear (or approximately linear) across a wide range of temperatures (Logan et al. 1976, Bentz et al. 1991, Lyons and Jones 2005, Keena and Moore 2010). The linearity across much of the temperature range is especially relevant for wood-boring beetles, where the under-bark microclimate tends to have cooler maxima than the surrounding air during the warmer part of the year (Tran et al. 2007). Protection of beetles from temperature maxima may not occur in all cases (Bolstad et al. 1997), and hence a more robust model of temperature-dependent development may be needed for some species and environments. However, for some cases at least, the especially high temperatures that cause a decrease in development rate will not often be reached in the under-bark microhabitat. Hence, the use of degree-day accumulation models is reasonable, particularly for northerly locations where maximum temperatures tend to be lower. So, while it appears that modeling temperature-dependent development using degree day accumulation is no longer considered physiologically accurate because of insects' response to very high temperatures (Logan et al. 1976, Lamb 1992, Lactin et al. 1995), using degree day accumulation to predict development times for wood-boring beetles in the field should not be problematic, once the difference between under-bark and air temperature is accounted for (Bentz et al. 1991, Bolstad et al. 1997).

Temperature also influences voltinism, the number of generations per year. Some species like *Dendroctonus adjunctus* are strictly univoltine (Gaylord et al. 2006), whereas others like mountain pine beetle, southern pine beetle, and European spruce bark beetle can have multiple generations in a year, with the timing of the generations affected by the temperatures the beetles experience (Powell et al. 2000, Gaylord et al. 2006, Jonsson et al. 2009). Others, like emerald ash borer are typically univoltine, but can also be semi-voltine (one generation every other year) depending on rate of development, which depends on temperature (Wei et al. 2007). Number and timing of generations has impacts on population dynamics (Logan and Bentz 1999, Jonsson et al. 2009), and also affects pest management practices like monitoring and trapping of the beetles (Gaylord et al. 2008). The shift from fewer generations per year to more can be devastating to a forest, increasing the probability of beetle outbreaks (Coulson 1979). For example, mortality rates of susceptible trees due to southern pine beetle can skyrocket from their endemic rate of less than 1 or 2 percent (Waring et al. 2009) to levels that make this pest one of the most ecologically destructive forest pests in North America (Ayres and Lombardero 2000).

### 1.2.3 Under-bark microclimate

The under-bark microclimate affects the temperatures experienced by wood-boring beetles, meaning that air temperature often does not give an accurate indication of the temperature regimes they encounter in the field (Bartos and Booth 1994, Bolstad et al. 1997, Tran et al. 2007). Many economically important species, such as mountain pine beetle, southern pine beetle, and emerald ash borer spend the winter months in the phloem and outer cambium area of the trees they inhabit (Powell 1967, Ungerer et al. 1999, Cappaert et al. 2005). Understanding this difference between air and under-bark temperature is key to applying physiological data to population predictions of wood-boring beetles. Failure to consider the effect of under-bark microclimate can result in inaccurate predictions of emergence times and cold temperature mortality (Tran et al. 2007, Gaylord et al. 2008).

Existing studies of under-bark temperature and wood-boring beetles appear to have mainly been concerned with mountain pine beetle and southern pine beetle, and hence have mostly examined the under-bark temperature of coniferous trees. In addition, all studies have focused on trees in a forest or woodlot setting. I am aware of no studies that consider the difference between under-bark and air temperature in an urban environment. Urban locations could potentially offer dispersing beetles an overwintering midpoint between two distant woodlots. In addition, if under-bark winter temperature minima are warmer in urban locations than in woodlot ones, then the urban environment might offer wood-boring beetles a reservoir from which to disperse the year after an extreme cold temperature event.

The two largest studies on the difference between under-bark and air temperature were done by Bolstad et al. (1997) and Tran et al. (2007). Concerned with mountain pine beetle, Bolstad et al. monitored temperature of cut pine bolts year-round in a high elevation (>2700m) area, as well as the under-bark temperature of 4 live trees year-round at 2 different sites (>2200m elevation). The authors reported that the daily phloem minima of live trees was 2.1˚C and 1.6˚C warmer than the daily air temperature minimum on the north and south side of the tree, respectively. The mean difference between under-bark temperature of cut pine bolts and air temperature was smaller, averaging just 0.58˚C on the south side, and negligible on the north side.

Tran et al. (2007), studying southern pine beetle, examined the under-bark temperature of 9 trees across 5 sites of lesser elevation, with time series ranging in length from 17 to 89 days from February to August, and one time series of length 3 days in December. Modeling minimum winter temperatures, Tran et al. (2007) found a larger degree of thermal buffering from daily minima (1.5-3.9˚C on average, and as high as 9.2˚C).

It should be noted that an average difference between daily under-bark and air temperature minima of, for example, 1˚C may not necessarily mean that the difference between daily air and under-bark temperature is constantly 1˚C; the difference may be significantly more or less for any given day. This means that a model which assumes a constant level of buffering from minimum air temperatures may not necessarily reflect those experienced.

In addition to the interest in determining under-bark temperature minima relating to winter mortality, there is also interest in determining the warmer under-bark temperatures the beetles experience, in order to determine development times, emergence times, and voltinism. In a study of spring emergence of a variety of wood-boring beetles, (Gaylord et al. 2008) found that degree day accumulation of air temperatures produced inaccurate estimates of spring flight initiation of several species of *Dendroctonus*. The authors posit that the inaccurate estimates may stem from differences between under-bark and air temperatures. Studies that use observed or modeled hourly phloem temperatures rather than air temperature to predict development times in the field report accurate results (Bentz et al. 1991, Yurk and Powell 2010). In both studies, after modeling temperature-dependent development rates for the various life stages of mountain pine beetle, the authors used observed phloem temperatures to accurately predict the development time from oviposition through adult emergence.

Bolstad et al. (1997) observed that air temperature tended to have cooler daily maxima than under-bark temperature, while Tran et al. (2007) observed the opposite effect, even when controlled for seasons examined. The difference is of a large magnitude, with

Tran et al. (2007) reporting daily air temperature maxima being warmer by 2-6˚C on average, and Bolstad et al. (1997) reporting daily under-bark maxima being warmer by 6-8˚C on average. Such a stark contrast may be partially a result of the elevation differences between the two studies (close to 2000m), and is also likely the result of differences in solar radiation since Tran et al. (2007) report minimal difference between sunlit and shaded (i.e. south and north) aspects of a tree, whereas Bolstad et al. (1997) report an average difference of 3.8-10.2˚C, depending on the time of year.

### 1.2.4 Modeling under-bark temperature

Since air temperature does not accurately reflect under-bark temperature, there have been attempts to model temperature in the under-bark micro-habitat. In particular, mechanistic models which relate under-bark temperature to environmental variables and the physical properties of the tree have been used with varying degrees of success.

Complex models (e.g. Derby and Gates 1966, Potter and Andresen 2002) can require a lot of parameterization. These finite difference models break the tree up into several sections, each of which has a number of parameters that need to be estimated. Once these parameters are estimated, equations that relate to radiative, convective, and conductive heat transfer are used to calculate the under-bark temperature for a given time and point on the tree. Estimation or measurement of density, bark thickness, solar radiation, diameter, air temperature, solar angle of incidence, thermal conductivity, wind speed and direction, and air temperature can all be needed in order to properly use these complex models. The large number of parameters makes the use of these models not only intimidating, but very difficult over large and often heterogeneous environments.

To address this, alternative models have been used to predict under-bark temperature. Bolstad et al. (1997) predicted south side daily maximum under-bark temperature ($TP_{max}$) as:

$$TP_{\max} = T_{\max} + \Delta P_{\max} \times \frac{\Delta T}{\Delta T_{95}}$$

Where $T_{max}$ is the daily maximum air temperature, $\Delta P_{max}$ is maximum south phloem temperature minus north phloem temperature, $\Delta T$ is the daily maximum minus daily minimum air temperature, and $\Delta T_{95}$is the historical 95th percentile of $\Delta T$. North side phloem daily maxima were assumed to be equal to air temperature maxima, and north and south side minima were assumed to be 0.57˚C warmer than air temperature minima.

Apart from the problems with assuming a constant level of thermal buffering discussed above, the authors calculated average errors (observed minus expected values) in a way that does not accurately convey the magnitude of the errors. The authors simply averaged daily errors rather than first taking the absolute value of the errors, or squaring the errors. For large errors, this oversight has the effect of decreasing the magnitude of the average error. For example, suppose that on two consecutive days, the observed minimum under-bark temperature is 0˚C, and the predicted under-bark temperature for those days is -2.0˚C and +2.0˚C, sequentially. The average error as calculated by Bolstad et al. (1997) would be 0.0˚C, when in reality the error has an average magnitude of 2.0˚C.Nevertheless, the average errors reported by location range from: -2.9˚C to 1.3˚C, and -4.7˚C to -0.8˚C for south and north side daily maxima; -0.7˚C to 8.2˚C and -1.7˚C to 8.1˚C for south and north side daily minima.

In order to determine under-bark temperatures experienced by southern pine beetles, Tran et al. (2007) used a Newtonian cooling model. This mechanistic model related current under-bark temperature ($T_{t+\Delta t}$) to under-bark temperature an hour earlier ($T_t$), current air temperature ($A_{t+\Delta t}$), and a cooling constant ($K$).

$$T_{t+\Delta t} = T_t + K(A_{t+\Delta t} - T_t)$$

Calculating the root mean squared error (RMSE) by averaging the squared errors and then taking the square root, the authors gave a true indication of the magnitude of prediction error. The RMSE ranged from 0.6˚C to 1.7˚C, depending on which tree was measured, when all hourly data was considered, and from 0.6˚C to 1.5˚C when only daily minima were used to calculate RMSE. The magnitude of these errors is fairly small relative to the (underrepresented) errors reported by Bolstad et al. (1997).

While the model employed by Tran et al. (2007) does a good job of addressing the variable nature of the difference between air and under-bark temperature, one of the shortcomings of the study was the data set used to build and test the model. The data set contained 8 time series that ranged in length from 17 to 89 days, and captured observations from periods in February to August (and an additional time series of length 3 days in December). In particular, there is no (or almost no) data for every month from September through January. Despite that, the authors predicted under-bark temperature throughout the year (including September through January), and assumed that the magnitude of the errors and the nature of the air-under-bark temperature difference would be the same year-round. This assumption may or may not be incorrect, but was not tested.

### 1.2.5 Conclusions

A review of the literature indicates that temperature plays an important part in the lives of wood-boring beetles, impacting their development rate and winter mortality. This impact has a large effect on the population dynamics of the various species, many of which are invasive or native outbreak species of great economical and ecological import. As such, determining the temperatures experienced by wood-boring beetles in the under-bark microclimate is of great interest.

It is known that under-bark temperatures of woodlot and forest conifers differ from air temperatures generally. Daily minima tend to be warmer within the tree than in the air, and daily maxima are either warmer or cooler depending on the environment studied. Attempts have been made to model under-bark temperature. However, previous modeling efforts suffer from shortcomings, including excessive complexity, assumption of a constant level of thermal buffering, or application of the model to data outside the timeframe used to build and test the model.

The investigation of the differences between under-bark and air temperature minima may shed light on the possibility that cold winter temperatures which increase mortality or cool temperature maxima which delay development rates will limit the northern range of wood-boring beetle populations that are of economic interest. However, there is little information in the literature on the under-bark temperature of deciduous trees. This omission is worrying when many emerging pest species (e.g., emerald ash borer and Asian longhorn beetle) attack these tree species, and when one considers that their under-bark temperatures may be different than conifers because of differences in bark thickness and the fact that deciduous trees are devoid of foliage in the winter months. Literature review also revealed that most studies had been completed for southern wooded regions, and so future work should also include study sites at more northern latitudes and urban environments, which can experience different temperature extremes and patterns than southern and woodlot sites. In addition, an investigation of whether or not urban trees experience different temperature minima than woodlot ones will help discern whether or not beetles in an urban environment can act as a reservoir that protects the species from temperature-related decreases in population growth. Modeling efforts of under-bark temperature have been hampered by testing on small datasets, but the Newtonian model introduced by Tran et al. (2007) appears promising. If this model can be successfully applied to winter temperatures of woodlot and urban deciduous trees, then it seems likely that this simple approach could be applied to both deciduous and coniferous trees in a range of latitudes and longitudes in varying environments throughout the year.

# Chapter 2

# Characterization of temperatures experienced by wood-boring beetles in the under-bark microclimate

## 2.1 Overview

Most studies of under-bark microclimate have been restricted to observations of a few coniferous trees in wooded southern latitudes. I addressed this limitation in the literature using a large data set composed of ash trees in an urban and woodlot environment at 6 different Ontario locations. I observed that daily minimum under-bark temperatures of these deciduous trees are significantly warmer than daily minimum air temperatures in the winter, and that these differences can be important to predictions of overwintering mortality of wood-boring beetles during cold periods.  However, I found no significant difference between under-bark temperature minima in urban and woodlot environments, suggesting that urban heat island effects will not significantly influence beetle overwintering survival, at least for urban trees bordering a park or yard. The difference between air and under-bark temperature minima can vary considerably, and I observed that on 16% of days in the winter of 2008-09, minimum under-bark temperatures were more than 4˚C different than minimum air temperatures on the north side of woodlot trees (the most conservative value found). With such large differences relatively common, I conclude that assumptions of a constant level of thermal buffering between the under-bark microclimate and air temperature are not valid.

Similarly, maximum under-bark temperatures on the south side of trees were significantly warmer than air temperature maxima, but not for the north side of the tree. This difference lead to significantly faster predicted development times for beetles on the south side of urban trees than in the air. However, no difference between development times predicted using air temperature and under-bark temperatures was found for the south side of woodlot trees. Clearly, solar loading leads in faster development rates, and as a result, I suggest urban trees in exposed areas may alter the projected population dynamics of wood-boring insects in wider regions.

## 2.2 Introduction

Temperature can control an insect's development time, metabolism, voltinism, emergence period, and can cause mortality in its extremes (Davidson 1944, Bentz et al. 1991, Gillooly et al. 2002, Altermatt 2010). In particular, warm temperatures can control the development time of insects (Davidson 1944, Gilbert and Raworth 1996), and extremely cold temperatures can impact their distribution and survival (Ungerer et al. 1999, Bale et al. 2002). Extreme cold temperatures can cause the crystallization of insect body fluids, which is fatal for a large group of insects (i.e., "freeze-avoiding" species). Furthermore, a prolonged exposure to temperatures that are cold, but do not cause freezing of insect tissues (so-called "sub-lethal" temperatures), can negatively impact the survival of insects (Bale 1996, Somme 1996).Finally, experiencing elevated temperatures during a time of cold-hardiness can have a negative impact on the survival of some species (Irwin and Lee 2003, Sinclair et al. 2003).

One of the hurdles to applying knowledge of insect response to temperature in the natural environment is that insects are not necessarily exposed to air temperatures, and can instead shelter in a microclimate whose temperature differs from the air temperature. As a result, a strong understanding of the extreme temperatures experienced in a particular microclimate can be important to understanding how insect distributions will change in the face of climate change, or invasion of a new range (Ungerer et al. 1999, Lombardero et al. 2000, Sinclair et al. 2003).

Information about microclimate temperatures is particularly important in the study of wood-boring beetles, many of which are invasive or native outbreak species (e.g., emerald ash borer, Asian longhorn beetle, southern pine beetle, etc). These species can have drastic impacts on urban and forest trees, causing great ecological and economic damage (Waring et al. 2009). For example, the emerald ash borer has already killed tens of millions of ash trees in North America since its arrival in the early 1990s, and has the potential to devastate the ash population in the same proportion as Dutch Elm disease killed elms in the 1970s (Poland and McCullough 2006). Even worse, the combined impact of multiple species, including native pests or new arrivals, could severely change the composition of North America's forest and urban trees.

Many wood-boring insects spend the winter and spring months in the phloem and outer cambium of trees (Bolstad et al. 1997, Poland and McCullough 2006, Tran et al. 2007). This microclimate can shield wood-boring insects from air temperatures, potentially impacting both overwintering mortality and development time (Bartos and Amman 1989, Bolstad et al. 1997, Tran et al. 2007). However, data on the microclimate experienced by wood-boring insects in trees is rare, and is often reported as pooled means across several sites or locations. Previous studies have sometimes involved cut bolts rather than live trees (Bolstad et al. 1997), have limited sampling in the winter months (Tran et al. 2007), or a short sampling period (Derby and Gates 1966, Bartos and Amman 1989, Bartos and Booth 1994, Potter and Andresen 2002). Furthermore, it appears that previous large-scale studies have only considered conifers rather than deciduous trees. This distinction could be important because of the possibility that physical properties (e.g. bark thickness) and the lack of foliage on deciduous trees in the winter months may produce different under-bark temperatures than in conifers. In addition, I am aware of no previous studies that have considered street or ornamental trees in urban environments. If trees in an urban environment experience warmer temperature minima than those in a woodlot environment, then it is possible that urban sites could serve as a reservoir for wood-boring beetle populations, maintaining active populations even when nearby woodlots and forests experience large scale cold temperature mortality. Furthermore, if development time is quicker in urban environments than in woodlots, then urban emergence could drive population dynamics in a wider region.

In addition to these issues and unexplored factors, some models of under-bark temperature have assumed that the difference between the daily under-bark and air temperature minimum is of the same magnitude each day (e.g. Bolstad et al. 1997, Ungerer et al. 1999). Assumption of a constant level of thermal buffering (usually 0-1˚C) in a model has been shown to be less effective than modeling hourly under-bark temperature using a simple mechanistic model (Tran et al. 2007). The success of the mechanistic model may be due to the variability in the difference between under-bark and air temperature minima, which has not been fully described.

I examined the temperatures experienced in the under-bark microclimate, with a particular focus on overwintering mortality and temperature-dependent development of wood-boring beetles. With respect to cold temperatures, I considered how the daily minimum under-bark temperature differs from daily minimum air temperature on the north and south side of urban and woodlot deciduous trees, and examined the variability of the difference between under-bark and air temperature to see if the difference is well-approximated by a constant. I also examined the difference between daily under-bark and air temperature maxima in the spring season, and related the difference to the temperature-dependent development of wood-boring beetles. I used emerald ash borer (EAB) and ash trees (*Fraxinus sp.*) as a study system because of the ecological and economic impact of EAB in North America with regard to both urban and woodland forestry.

## 2.3 Methods

### 2.3.1 Data collection and sampling sites

I collected hourly temperature data from weather stations and under-bark temperature probes at six sites (Table 2.1) in Ontario, Canada, ranging from Sault Ste Marie in the north and west (46˚30'14.6"N, 84˚18'07.9"W) to Ottawa in the east (75˚39'29.2"W) and London in the south (43˚00'33.0"N). At each of the 6 locations, 5 trees (*Fraxinus americana* or *Fraxinus pennsylvanica)* were chosen in an urban site (yard or park-side street trees), and 5 trees were chosen in a woodlot setting, for a total of 60 trees across the 6 locations. On each tree, a HOBO 2x External Temperature Data Logger (product id: U23-003) was installed in the summer of 2008.One temperature probe was inserted at a height of 3m into the outer cambium area on the north side of the tree, and one at the same height on the south side. Hourly under-bark temperature was recorded over a period of approximately 2 years (starting in mid-summer 2008). Hourly air temperature over this time period was obtained from Environment Canada for nearby weather stations (Table 2.1). The Sault Ste Marie woodlot site was much farther than all other sites from the nearest weather station, so instead of using an air temperature series from Environment Canada, ambient temperature at the site was logged hourly using the same type of data logger as described above, but mounted on a pole, exposed to the air, and covered with a HOBO Radiation Shield (product id: RS3).

I defined winter seasons as December 2008 through February 2009 and December 2009 through February 2010. The spring seasons were from March through May in 2009 and 2010.In both seasons of both years, there was a datalogger failure rate of approximately 25%. For each of the available north and south under-bark time series and the associated air temperature time series, I calculated the mean of daily minimum temperature in the winter and mean of daily maximum temperature in the spring. All values were calculated using MATLAB software (version R2008a).

### 2.3.2 Data analysis – cold temperatures

I randomly selected one woodlot and one urban tree from each location in each winter. To determine if mean of daily minimum under-bark and air temperature are different, I used paired (by location) t-tests of the randomly selected trees. I used separate t-tests for urban and woodlot locations, the two winters, and for the north and south side of the tree. All tests of significance were done using SAS Software (version 9.1) and had 5 degrees of freedom.

I also compared minimum temperatures of urban and woodlot trees, using paired (by location) t-tests with the randomly selected trees, using separate tests for the north and south sides of the trees and for each winter.

Mean differences between minimum daily under-bark and air temperature are not necessarily indicative of the potential range of temperature differences (Tran et al. 2007).

Therefore, I addressed the assumption made by some authors that modeled the difference between daily minimum under-bark temperature as a constant (e.g. Bolstad et al. 1997, Ungerer et al. 1999). To challenge this, I pooled the difference between daily minimum under-bark and air temperature for all sites in the winter of 2008-2009, and the proportion of days where the difference between daily minimum air and under-bark temperature was more than ±2˚C was calculated, as was a similar statistic for a difference of ±4˚C.

In an effort to relate the difference between under-bark and air temperature minima directly to emerald ash borer physiology, I looked at the number of days in each location when minimum air or under-bark temperature was as cold as the approximate mean winter supercooling point of the species. Previous work indicates that this temperature is -30˚C, and that reaching it during the winter months would result in approximately 50% mortality (Crosthwaite et al. 2010).

### 2.3.3 Data analysis – warm temperatures

Using a randomly selected urban and woodlot tree from each location in each spring, I compared the mean of daily maximum under-bark and air temperature using paired (by location) t-tests, in an effort to determine if the there is a difference between under-bark and air temperature that could possibly affect development time.

In addition, I more directly related warm temperatures to emerald ash borer physiology, by calculating the median development time for male and female emerald ash borer using the life-stage-specific degree-day model described by Lyons and Jones (2005) using under-bark and air temperatures. I performed paired (by location) t-tests, comparing development time as calculated using under-bark and air temperature.

## 2.4 Results

### 2.4.1 Cold temperatures

All mean of daily temperature minima under-bark values were higher than those of their associated weather stations (Fig 2.1). These differences were highly significant for the north and south side of urban and woodlot trees in both winters ($T_5$>7.2, P<0.001 for each test), and ranged from 1.5˚C to 2.9˚C for the randomly selected trees. There was variability in this difference during the winter months (Fig 2.2). On the north and south side of urban trees, 60% and 68% of observed days had differences of more than ±2˚C, and 23% and 33% had a difference of more than ±4˚C. On the north and south side of woodlot trees, the difference was more than ±2˚C on 58% and 59% of days, and more than ±4˚C on 17% and 20% of days. However, a comparison of mean under-bark temperature minima (Table 2.2) in urban and woodlot locations showed no significant differences between these sites for either the north ($T_5$=-0.92, P=0.399; $T_5$=1.18, P=0.290) or south ($T_5$=2.28, P=0.072; $T_5$=1.76, P=0.139) side of the tree in either winter.

Under-bark or air temperatures as low as -30˚C (the emerald ash borer supercooling point) were not observed at any site during the second winter. During the first winter, this extreme was recorded for air temperature at North Bay on 3 days (twice during a 3-day cold snap, and once more about 10 days later). In addition, one day at the Sault Ste Marie urban site was this cold, and one day in Ottawa was nearly this temperature (-29.7˚C). In the under-bark microclimate, this mean supercooling point temperature was recorded in North Bay for all trees during the 3-day cold snap, but not observed 10 days later. Interestingly, during the cold snap, the microclimate in all trees was colder than the minimum air temperature (by as much as 4˚C). No Sault Ste Marie trees had under-bark temperature below -25.6˚C, but one Ottawa woodlot tree reached a minimum of -30.5˚C on the day that air temperature dropped to -29.7˚C.

### 2.4.2 Warm temperatures

The mean of daily maximum air temperature (Table 2.2) was not significantly different than the mean of daily maximum under-bark temperature on the north side of the tree for woodlot ($T_5$=-0.70, P=0.517; $T_5$=-0.79, P=0.465) or urban sites ($T_5$=1.79, P=0.133; $T_5$=0.77, P=0.475) in either spring. The difference between the south side of the tree and the air for this metric was significant for both urban ($T_5$=3.76, P=0.013; $T_5$=3.55, P=0.016) and woodlot ($T_5$=4.43, P=0.007 and $T_5$=4.42 P=0.007) trees in both spring seasons. However, there was no significant difference between mean of daily maximum temperature on the south side of urban and woodlot trees in either spring ($T_5$=-0.81, P=0.457; $T_5$=-0.62, P=0.564).

Because development times of males and females were so similar (Table 2.2), and because daily temperature maxima on the north side of the tree were not significantly different from air temperature, only tests involving females and the south side of the tree were performed. Median development time was significantly faster in the under-bark microclimate than in the air in urban sites in both years ($T_5$=-3.51, P=0.017; $T_5$=-8.85, P<0.001). This was not the case for woodlot trees ($T_5$=-1.95, P=0.109; $T_5$=-2.04, P<0.096). However, the development times of female emerald ash borer in the air and on the south side of the tree were variable between and within sites and locations (Fig. 2.3). In some cases, development times predicted using under-bark microclimate temperatures were over 30 days shorter than development times predicted from air temperatures, while in other cases predicted times were longer in the under-bark environment. Urban trees foster quicker development times at some locations, but this was not the case for every location, or even the same location in consecutive years.

## 2.5 Discussion

Using a large dataset including urban and woodlot ash trees at 6 locations from 2 years, I showed that mean daily under-bark temperature minima are significantly warmer than air temperature minima during the winter. While air temperature minima cold enough to cause substantial cold mortality to emerald ash borer were recorded, these temperatures did not necessarily correspond to lethal temperatures in the under-bark microclimate. However, there were times when under-bark temperature reached these extremes and air temperature did not. Therefore, these differences are not well-described as a thermal buffering constant and instead can vary considerably. Most importantly, a large proportion of differences between daily under-bark and air temperature minima tend to be greater than is assumed by some models. Finally, spring mean daily under-bark temperature maxima on the south side of trees were significantly warmer than air temperature maxima, and in an urban environment, this had the effect of speeding up the predicted development time of individual. These results all point to one thing: assuming under-bark temperature is the same as air temperature can lead to errors.

It has been known for some time that under-bark temperature can differ from air temperature. However, the nature of this difference has not been well-characterized, particularly over the winter months. Many studies of under-bark temperature include only the summer months, occasionally incorporating data from the spring or late winter. One of the important results to come out of these studies is that under-bark temperature minima tend to be warmer than air temperature minima (Powell 1967, Bartos and Amman 1989, Bartos and Booth 1994, Tran et al. 2007). However, of these studies, Tran et al. (2007) is the only one containing winter data (just 3 trees with data from February, and one with 3 days of data from December).

Previous studies (e.g. Powell 1967, Bartos and Amman 1989, Bolstad et al. 1997, Ungerer et al. 1999, Tran et al. 2007) have also only considered coniferous trees at lower latitudes than those included in this study. This is notable, because as the deciduous-feeding emerald ash borer (EAB) and Asian longhorn beetle loom large as threats to North America's deciduous trees, there is interest in the population dynamics of these invasive pests. Differences between coniferous and deciduous trees (e.g. bark thickness, winter foliage) and latitudes (different solar intensity, day length, temperature patterns) could mean that to assume under-bark temperatures for conifers at low latitudes and deciduous trees at higher latitudes is an error.

My findings relating to the difference between under-bark and air temperature were, for the most part, comparable to those found in studies involving coniferous trees in more southern latitudes, although not necessarily of the same magnitude. Bolstad et al. (1997) report a mean difference between winter under-bark and air daily temperature minima of 0.6˚C and 0.7˚C for the south side and north side of the tree. These values are smaller than the ones I observed. The differences between the results of the studies are probably due to the differences in methodology (the authors used cut bolts in an effort to approximate heavily infested trees) and macroclimate (high elevation Idaho vs lower elevation Ontario), rather than differences in the tree species (coniferous vs. deciduous). In fact, the authors briefly mention that on the 4 live trees they monitored, mean daily differences between under-bark and air temperature minima were closer to 2˚C.

I stress that although others have reported mean temperature differences between under-bark and air temperature minima, a failure to consider the variable nature of this difference can lead to large predictive errors. This was shown when modeling under-bark minima using hour data produced better estimates than assuming a constant level of buffering (Tran et al. 2007). It is worth noting that the mean values of the pooled differences between daily woodlot under-bark and air minima that I calculated were not far outside those reported elsewhere (~2˚C). However, a substantial number of days had differences with considerably larger differences, and so the assumption of a constant level of thermal buffering is not advisable. For example, Bolstad et al. (1997) took this approach and noted large errors in predicting daily under-bark temperature minima. Instead of assuming a constant level of buffering, I suggest the use of a mechanistic model with the ability to predict under-bark temperature minima, like the one used by Tran et al. (2007),which was shown to be superior at predicting under-bark temperature minima. However, I note that the model used therein was optimized on largely spring and summer data, so blind application of it to the winter season is not advisable.

Large differences between under-bark and air temperature during a cold spell (which I observed) could drastically impact predictions of overwintering mortality. With the knowledge that winter minimum under-bark temperatures tend to be warmer (frequently much warmer) than air temperature, consider the difference in context of a physiological model in order to establish its importance. The supercooling point is the temperature at which an insect's body fluids crystallize, and for many species of wood-boring beetles, when this temperature is reached, it results in the death of the insect (Ungerer et al. 1999, Lombardero et al. 2000, Crosthwaite et al. 2011). There is some variability in the supercooling point from individual to individual, even within species. Reported standard deviations of the supercooling point have been observed to range from 0.14˚C to 3.9˚C, with the bulk of the reported values tending to be less than 1.5˚C, particularly when month or season are controlled for (Ungerer et al. 1999, Lombardero et al. 2000, Regniere and Bentz 2007, Tran et al. 2007, Crosthwaite et al. 2011).Now, consider a (simplified) hypothetical population of wood-boring beetles with a normal distribution of supercooling points (mean: -10.0˚C; std dev: 1.0˚C). Within the physiological model, we wish to estimate the proportion of beetles that died due to cold exposure over the winter, when the minimum winter air temperature reached was -11.0˚C. If the physiological model were to assume that the beetles are directly exposed to air temperature, it would predict that 84% of them would die. However, if the under-bark microclimate is 2.0˚C warmer than the air temperature during the cold bout, the beetles would only experience a minimum temperature of -9.0˚C, resulting in just 16% mortality. The difference between these two outcomes on a physiological model could have great impacts on model predictions of spread and population dynamics for the ensuing months (or longer). In practice, wood-boring beetles can experience a change in supercooling point over the course of a winter, and prolonged exposure to sub-lethal temperatures can cause mortality, but this simple example illustrates the importance of the tree's ability to buffer the insects from cold temperatures.

With respect to warm temperatures, our results affirm those of Bolstad et al. (1997) who found that daily temperature maxima were warmer than the air on the south side of the tree, and not warmer than air on the north side (at least in the spring months). The magnitude of the difference found by Bolstad et al. (1997) was more than twice than what was observed here, and I stress again that assuming a constant level of difference between daily air and under-bark temperature maxima is not advisable. The finding that under-bark maxima were warmer than air temperature maxima contrasted the findings of Tran et al. (2007), who observed the opposite. It seems likely that in a particularly densely wooded forest, shading of tree trunks from solar radiation could produce the effect the authors observed. In order for this trend to be present in the winter months, it would probably have to be a coniferous forest, as defoliation of deciduous trees would expose them to some solar radiation.

Another unique aspect of this study is that I examined trees in an urban environment. It is interesting that the difference between under-bark and air maxima was enough to produce significantly shorter mean development times in urban trees, but not in woodlot ones. It may be that this effect is present for woodlot trees, but not with the same consistency and magnitude as it is for urban trees. In any case, there were no locations in either year where development of emerald ash borer was more rapid in woodlots than in urban sites by more than a few days (Fig. 2.2), so first capture of the beetle in an urban setting could signal the time to begin woodlot monitoring for emergence.

Characterization of urban under-bark temperatures is also useful to city foresters, informing monitoring and management efforts in cities (and surrounding areas), where tree species that are hosts for wood-boring beetles often make up a large proportion of the urban tree population (MacFarlane and Meyer 2005, Nowak et al. 2001). Urban trees could potentially play an important role in wood-boring beetle population dynamics. In particular, urban trees could serve as a midpoint between two distant woodlots, and it was unknown whether or not urban settings could serve as a reservoir for wood-boring beetles during the winter months, shielding them from harsh minimum temperatures and then allowing for early dispersal in the spring. While development times differed between these sites, there was no systematic difference between winter minimum temperatures in urban and woodlot sites. This winter ‘reservoir effect’, if it exists, is probably not very large in magnitude.

It should be noted, however, that urban trees chosen were not typically street trees from the city center. They often bordered a park or yard on one side. Similarly, woodlots were not chosen from especially rural areas, and in some cases were situated just outside of what would be classified as an urban environment. These two factors may have minimized the difference between locations described as “urban” and “woodlot”.

The use of a very large data set has allowed me to illustrate that mean winter daily under-bark temperature minima in deciduous trees are significantly warmer than air temperature minima. This is also true for maximum spring temperatures on the south side of trees, which can have an impact on development times of wood-boring beetles. The magnitudes of the difference between under-bark and air temperature minima can be biologically significant relative to the variability in wood-boring insects’ cold tolerance. In particular, large differences between under-bark and air temperature during cold periods would have major implications for predictions of overwintering mortality, and by extension, distribution and spread modeling. Since cold temperature can be a northern range-limiting factor for wood-boring beetles (Ungerer et al. 1999), understanding the temperatures they experience in the field can be key to studying how populations' ranges will shift in the face of ongoing climate change or upon invasion into a new area. I stress that the assumption of a constant level of difference between air and under-bark minimum (or maximum) temperatures is a flawed one. The level of thermal buffering can vary greatly, necessitating that a mechanistic model of under-bark temperature does not include such an assumption.

**Table 2.1** Sampling locations and distance to weather stations. *The woodlot Sault Ste Marie site was too far from the weather station, so an ambient logger was installed.

| **Site** | **Latitude** | | **Longitude** | | **Approx Distance to weather station (km)** | |
|---|---|---|---|---|---|---|
| | **Urban** | **Woodlot** | **Urban** | **Woodlot** | **Urban** | **Woodlot** |
| Kingston | N55˚15’5” | N44˚14’11” | W76˚36’29” | W76˚31’44” | 7 | 2 |
| London | N43˚00’44” | N43˚00’42” | W81˚16’22” | W81˚16’8” | 10 | 10 |
| North Bay | N46˚19’25” | N46˚19’49” | W79˚25’57” | W79˚25’2” | 4 | 3 |
| Ottawa | N45˚22’50” | N45˚22’14” | W75˚39’30” | W75˚40’21” | 7 | 6 |
| Sault Ste Marie | N46˚30’15” | N46˚13’31” | W84˚18’18” | W83˚57’53” | 16 | 0* |
| Toronto | N43˚39’16” | N43˚39’27” | W79˚35’04” | W79˚35’19” | 5 | 4 |

**Table 2.2** Values of the mean winter minimum (˚C), mean spring maximum (˚C), and mean development time (days from Jan 1), averaged across the 6 randomly selected trees in each site type or across weather stations. Air temperature values are slightly different for urban and woodlot sites at the Sault Ste Marie location where an ambient logger was installed at the woodlot.

| **Season** | **Measure** | **Urban** | | | **Woodlot** | | |
|---|---|---|---|---|---|---|---|
| | | **North** | **South** | **Air** | **North** | **South** | **Air** |
| **Winter 08-09** | **Mean Daily Min** | -10.3 | -9.4 | -12.3 | -10.2 | -9.8 | -12.2 |
| **Winter 09-10** | **Mean Daily Min** | -7.1 | -6.9 | -8.9 | -7.4 | -7.2 | -8.9 |
| **Spring 2009** | **Mean Daily Max** | 11.2 | 13.4 | 10.4 | 10.2 | 13.9 | 10.5 |
| **Spring2010** | **Mean Daily Max** | 14.8 | 16.7 | 14.1 | 13.8 | 17.1 | 14.1 |
| **Year 1** | **Development Time (Male/Female)** | 195/193 | 189/187 | 204/203 | 206/205 | 198/198 | 204/203 |
| **Year 2** | **Development Time (Male/Female)** | 176/174 | 171/169 | 182/181 | 183/182 | 175/173 | 182/181 |

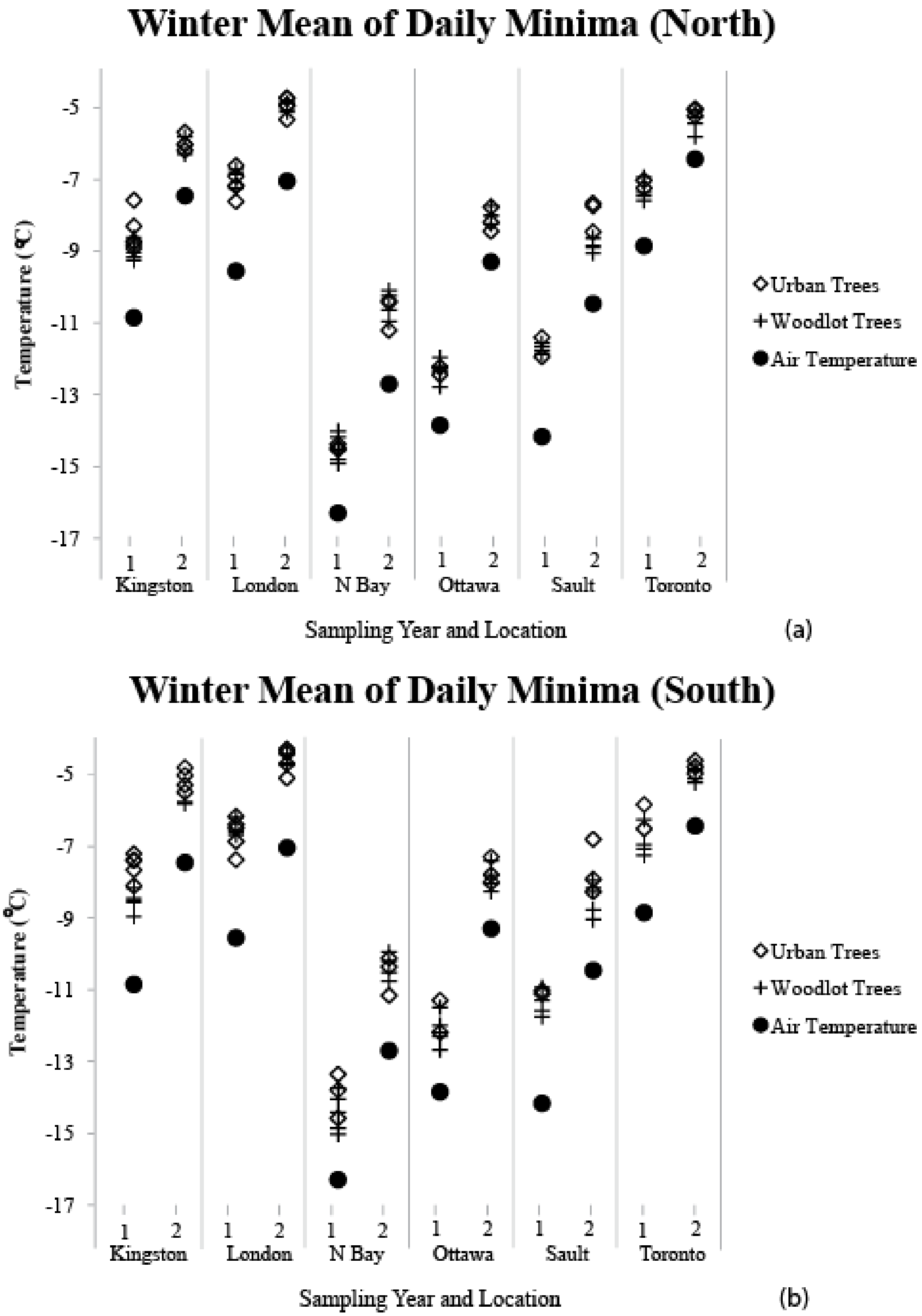

**Figure 2.1** Mean of daily temperature minima for the winter seasons on the north (a) and south (b) side of the trees and air temperature. ‘1’ refers to winter 2008-09 and ‘2’ refers to winter 2009-10.

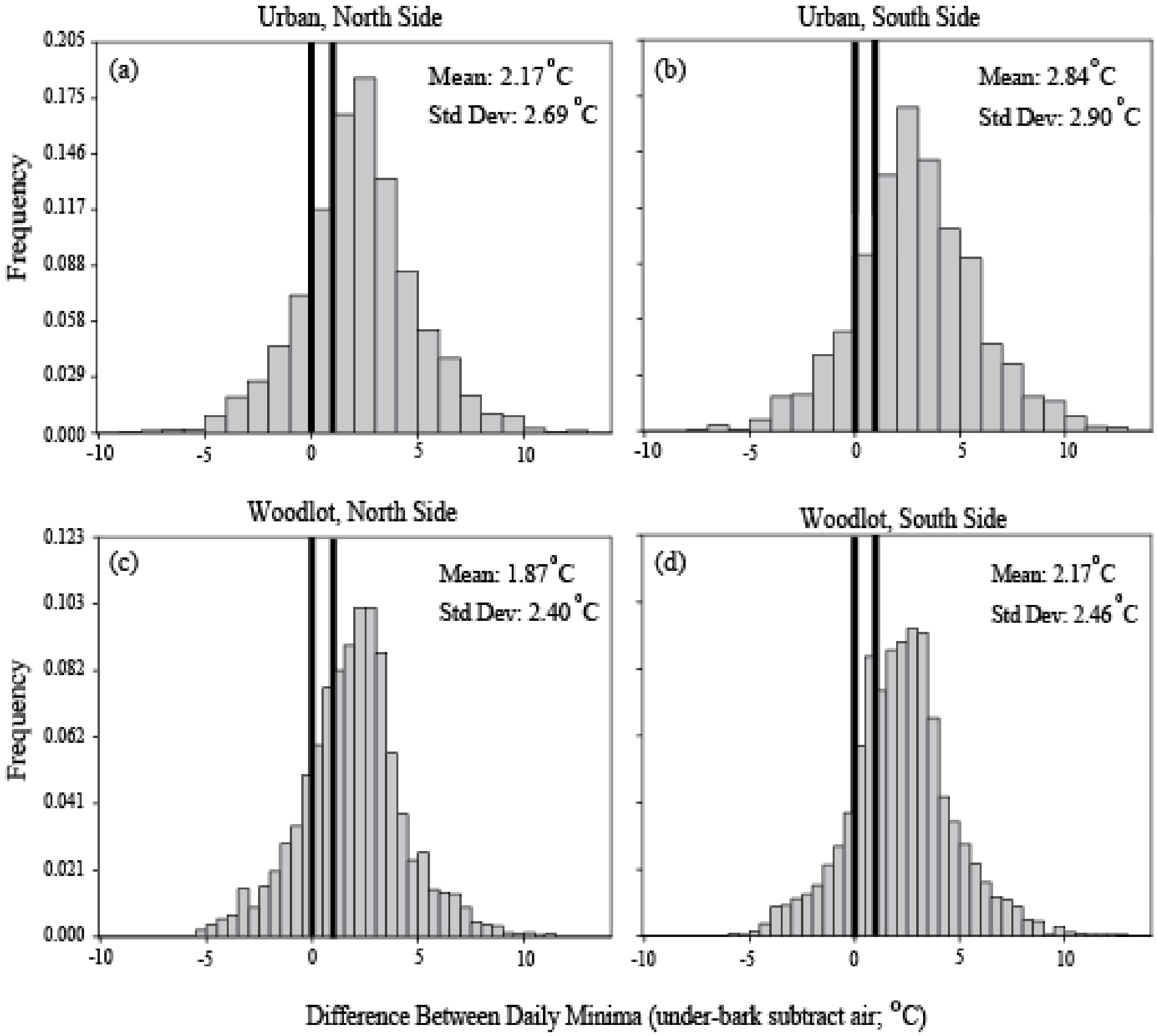

**Figure 2.2** Histograms of the difference between daily under-bark and air minima for the winter of 2008-09. Values from all urban (a and b) and woodlot (c and d) trees have been pooled for the north and south side of the tree. The area between the thick lines represents the range difference assumed by the models in Bolstad et al. (1997) and Ungerer et al. (1999).

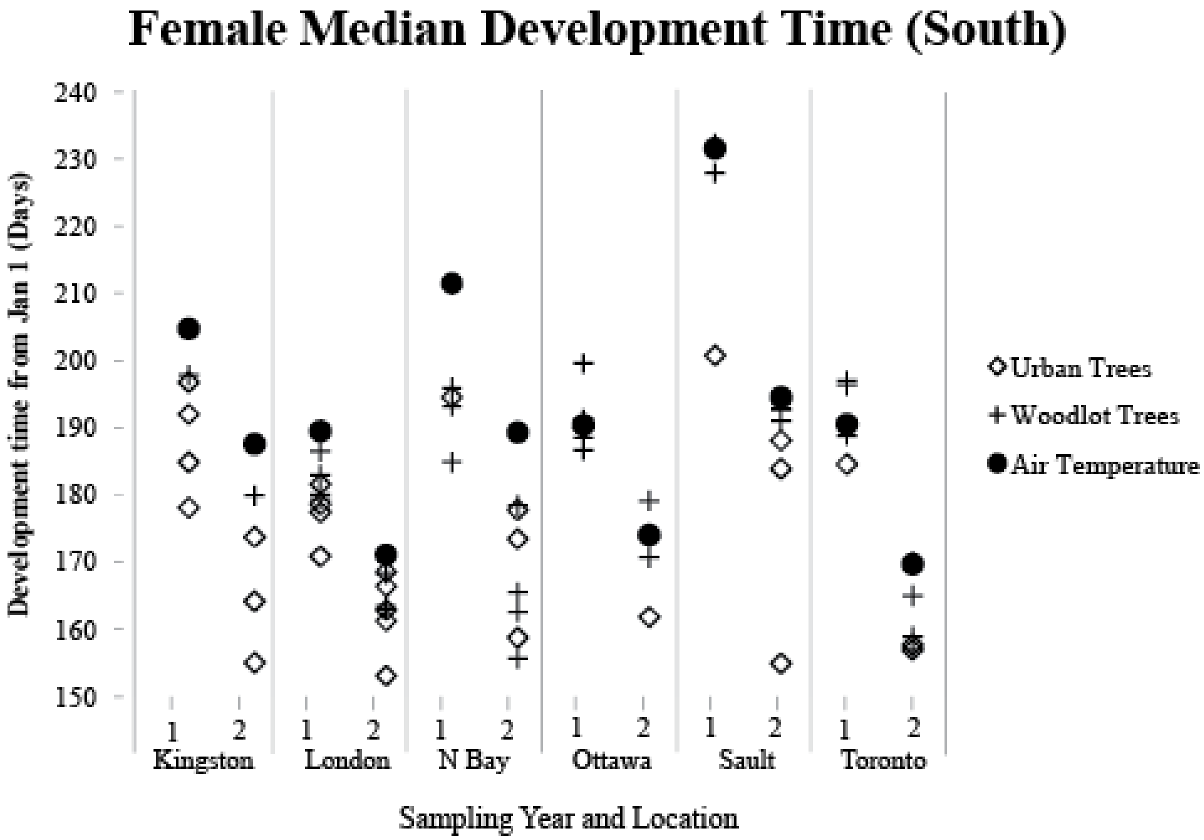

**Figure 2.3** Median development time as calculated for females on the south side of the tree and exposed to the air. Although the pattern is not consistent, it is clear that females in urban trees can potentially have expedited development.

# Chapter 3

# Cold temperature and emerald ash borer: Modeling the under-bark temperature of ash trees in Ontario

## 3.1 Overview

Extreme temperatures can cause mortality in wood-boring beetles when it gets cold enough that the beetles' body fluids freeze. Because of this, winter temperature minima can control the range of wood-boring beetles and other insects. However, wood-boring beetles which spend the winter months in the under-bark microclimate (e.g. emerald ash borer, mountain pine beetle) may experience minimum temperatures that tend to be warmer than air temperature minima. However, the magnitude of the difference between under-bark and air temperature minima is variable, meaning that models of under-bark temperature cannot assume a constant level of thermal buffering.

I used a Newtonian cooling model to predict the under-bark temperature minima of ash trees in Ontario. The model was parameterized and tested using hourly temperature data from two winters for 24 different ash trees in urban and woodlot sites across 6 different locations, in order to capture a wider range of temperature extremes and patterns experienced by emerald ash borer or other deciduous-feeding wood-boring beetles. Average model prediction errors (1.31˚C root mean squared error) were much smaller than errors associated with assuming no difference between air and under-bark temperature minima (3.20˚C root mean squared difference). Modifications of the Newtonian cooling model to account for elevation, urban heat islands, and solar radiation did not offer any improvement in model fit.

An attempt was made to model daily temperature maxima, but even when the model was modified to include solar radiation, it was not accurate at predicting daily temperature maxima, possibly because of complex shading and heating patterns that can occur during warmer parts of the day in urban and woodlot environments. I conclude that this model is suitable for modeling minimum under-bark temperature across a range of latitudes and longitudes for both deciduous and coniferous trees in urban and woodlot settings.

## 3.2 Introduction

Extreme temperatures can determine the limit of an insect’s range and distribution (Ungerer et al. 1999, Lombardero et al. 2000, Bale et al. 2002, Battisti et al. 2005). For example, Ungerer et al. (1999) found that southern pine beetle maintained populations as far north as their susceptibility to cold temperatures would allow. Wood-boring insects, however, experience a sheltered microclimate that differs from air temperatures (Bartos and Amman 1989, Bolstad et al. 1997, Tran et al. 2007). An understanding of these under-bark temperatures is particularly important for predicting the possible range and spread of novel forest pest species. For example, emerald ash borer (EAB), whose range now extends into locations in Ontario and Quebec, Canada (Co-operative Emerald Ash Borer Project, 2011), may be limited in its spread by extreme cold. There are physiological studies regarding the effects of cold on EAB mortality (Crosthwaite et al. 2011, Sobek-Swant et al. 2011), however, to relate these studies to predicted range, under-bark temperatures must be determined.

Some earlier studies show that at night, when minimum temperatures are most likely, the under-bark temperature is warmer than that of the surrounding air (Powell 1967, Bartos and Amman 1989, Bartos and Booth 1994). However, these studies do not report the magnitude of the difference, and take place over the late spring and summer months. In a study that did include data from the winter, Bolstad et al. (1997) observed that mean daily under-bark minima on the south side of the tree were on average about 2.1˚C warmer than air temperature minima. In modeling under-bark temperature minima, the authors of that study and ones that followed from it (notably Ungerer et al. 1999) discounted the variability in the difference between under-bark and air temperature minima. However, there is typically larger variability in the difference of these temperatures (Section 2.5; Tran et al. 2007), and Bolstad et al. (1997) noted that prediction errors of daily minimum temperatures were particularly large.

Since large-scale monitoring of under-bark temperature is both costly and impractical, a more feasible approach is to use widely available air temperature data to predict the under-bark temperature of trees. There are several models of under-bark temperature, but some of these may require large data collection efforts regarding individual tree properties efforts for parameterization. For example, finite difference models used by Derby and Gates (1966) and Potter and Andersen (2002) divide the tree up into a number of sections and estimate a number of parameters for each section. Then, using equations relating to different sources of heat transfer, the authors can calculate under-bark temperature for a desired point and time. However, use of these models can require estimation or measurement of density, bark thickness, solar radiation, diameter, air temperature, solar angle of incidence, thermal conductivity, wind speed and direction, and air temperature, making the models very thorough, but ultimately difficult to apply to a large and heterogeneous area or long time scale.

A simpler method for modeling under-bark temperature was introduced by Tran et al. (2007). The authors used a Newtonian convective cooling model to predict under-bark temperature of pine trees, with the goal of applying the findings to southern pine beetles, and found reasonably good agreement between predicted and measured temperatures. Model predictions were compared to observed data from February through August of one year. It is unclear how this simple model performs with other tree species (e.g. deciduous trees), environments (e.g. urban sites), and climatic conditions (e.g. more northern locations), and it is not known how accurate under-bark temperature predictions will be over the winter time period in full (December through February). It is conceivable that under-bark temperature of urban trees may be more difficult to predict than those in a woodlot environment because of the increased exposure of urban trees. Also, although I expect the model to perform well on northern deciduous trees, the cooling constant may be different than those of conifers at more southerly latitudes, and if the model is particularly sensitive to this parameter estimate, it will have implications for the model's application to a wide area.

I applied this Newtonian cooling model to the problem of predicting the under-bark temperatures experienced by emerald ash borer. I used a large set of data collected from weather stations and 60 ash trees in six different Ontario locations across 2 years, in order to evaluate the model's ability to predict under-bark temperature extremes across a number of trees, latitudes, and landscape features. I focused on the ability of the model to predict daily minimum under-bark temperatures, but did examine its performance on daily maxima as well. In addition, I tested modifications of the Newtonian cooling model to account for factors that might affect under-bark microclimate, such as urban heat islands, elevation, and solar radiation.

## 3.3 Methods

### 3.3.1 Temperature data

In the six Ontario locations described in Chapter 2, temperature dataloggers were installed (HOBO 2x External Temperature Data Loggers - product id: U23-003) with two temperature probes inserted into the outer cambium of the north and south side of the tree at a height of 3m. At each location, there were 5 trees in an urban environment and 5 trees in a woodlot environment, for a total of 60 trees. The data loggers recorded the under-bark temperature on the north and south side of the trees at hourly intervals from September 2008 through March 2010. During winter (Dec-Feb) many of the dataloggers failed, leaving 49 time series for winter 2008-2009, and 47 for winter 2009-2010, with at least 2 urban and 2 woodlot series for each location in each year.Hourly air temperature data was collected from Environment Canada’s National Climate Data and Information Archive for each of the locations. Since the Sault Ste Marie woodlot location was farther away from the nearest weather station (50km), a datalogger that recorded hourly ambient air temperature was also installed at the woodlot site.

I split the under-bark temperature data into a model building set and a testing set. The model building set consisted of one urban and one woodlot time series, both of which were randomly chosen from each location from each year. The testing set had a similar make-up, resulting in the model building set and testing set consisting of 24 time series each. Series from the south side of the tree were used in order to provide a conservative estimate of the probability that the under-bark environment underwent cold temperatures that are lethal to emerald ash borer.

### 3.3.2 Newtonian cooling model

Following Tran et al. (2007), I used a Newtonian convective cooling model (equation 1) to predict under-bark temperature. Convective heat transfer occurs when a solid and the gas or liquid around it are at different temperatures. This simple model only requires the estimation of one parameter: the cooling constant, *K*. The model relates current under-bark temperature to earlier under-bark temperatures and the current temperature of the air via the cooling constant as:

$$T_{t+\Delta t} = T_t + K(A_{t+\Delta t} - T_t) \qquad (1)$$

where$T_t$ is the under-bark temperature of the tree at time *t*, $\Delta t$ is a time step of one hour, $A_t$ is the air temperature of a nearby weather station at time *t*, and *K* is a cooling constant that is related to the physical properties of the tree (e.g. diameter, density, water content, etc)..

The model was applied to the model building set with a range of values of *K* from 0.05 to 0.28in intervals of 0.01. The range was chosen to include all values of *K* used by Tran et al. (2007) for which they had hourly data. I used an initial condition of $T_0$ = 0˚C, and the model was given 48 time steps (hours) to converge. A value of *K* was selected based on minimizing the residual sum of squares of the model-building set, and the model with that value of *K* was run on the testing set.

### 3.3.3 Model selection and fit

As in Tran et al. (2007), I measured model fit using root mean squared error (RMSE) of daily minimum under-bark temperature. The units (˚C) of this measure are easily interpretable, making it easy to relate the magnitude of prediction error to EAB physiology, and previous use of this metric gives a baseline for comparison of model accuracy. RMSE is calculated as:

$$RMSE_j = \sqrt{\frac{\sum_{i=1}^{m}(O_i - E_i)^2}{m}}$$

where $RMSE_j$ is the root mean squared error of time series $j$, $O_i$ is the observed minimum under-bark temperature on day $i$, $E_i$ is the modeled minimum under-bark temperature for day $i$, and $m$ is the number of days in the time series after the model was given 48 hours to converge. I then calculated average model fit across all time series in the data set of interest, either the model building set during model construction, or the testing set during model validation.

The model fit for individual trees was also examined in order to ensure that improvement in average model performance did not come at the expense of applicability to certain trees. I expected the optimal value of $K$ for a given tree to be negatively related to tree diameter at breast height (DBH) (Tran et al. 2007). That is, trees with larger diameters will respond more slowly to changes in air temperature. To test this, I linearly regressed the optimal value of $K$ for each tree in the model building set on its DBH, which was measured at the beginning of the experiment, and again after the first growing season.

I also calculated a statistic similar to RMSE to measure how far off predictions would be if I simply assumed that under-bark temperature was the same as air temperature. Across the testing set I calculated the root mean squared difference (RMSD) between daily minimum under-bark and air temperature, similarly to RMSE, except instead of modeled temperature I used air temperature. A comparison of the two statistics gives a direct indication of the difference between actual under-bark temperature, air temperature and modeled under-bark temperature.

Finally, to compare model variants, I calculated Akaike's information criterion (AIC) for each and compared them. AIC was calculated as:

$$AIC = n \times \ln\left(\frac{RSS}{n}\right) + 2z$$

where *n* is the number of data points, *RSS* is the residual sum of squares of minimum daily under-bark temperature, and *z* is the number of parameters in the model. The model selected was the one with the smallest AIC value (Akaike 1974, Burnham and Anderson 2002).

### 3.3.4 Modified Newtonian models

Urban areas often experience warmer temperatures than nearby rural areas because of urban heat island (UHI) effects (Oke 1982). All weather stations used in this study were not deep within an urban zone, and were situated in open spaces with good air flow. When the weather station recording air temperature is outside of the urban zone, but the tree is within the zone, there may be a difference in air temperature that needs to be accounted for. I included UHI effects in the model by the addition of a constant value to weather station temperatures for urban sites. The constant used was 2.1˚C, which is the mean urban heating effect for a city of similar latitude (Todhunter 1996). Under-bark temperature was calculated as:

$$T_{t+\Delta t} = T_t + K([A_{t+\Delta t} + 2.1 \times U] - T_t)$$

where *U*=1 indicates an urban tree and *U*=0 a woodlot tree. (2)

The difference in elevation between the trees and their nearby weather stations can also cause air temperature differences, with higher elevations tending to be cooler at a rate of 9.8˚C per 1000m: the dry adiabatic lapse rate (Kittel and Kroemer 1980). This temperature difference was accounted for by subtracting 9.8˚C from the weather station temperature for every 1km difference in elevation between the tree and the weather station, meaning that under-bark temperature was calculated as:

$$T_{t+\Delta t} = T_t + K([A_{t+\Delta t} - V \times 9.8] - T_t) \qquad (3)$$

where $V$ is the difference in elevation (in km) between the tree and its corresponding weather station.

For equations 2 and 3, the parameter $K$ was re-fitted on the range of 0.05 to 0.28 in increments of 0.01, and a value was chosen that minimized the average RMSE of daily minimum under-bark temperatures across the model-building set.

In addition to convective heating and cooling, trees also experience temperature change as a result of incoming solar radiation. Using solar radiation data, solar heating was incorporated into the Newtonian model as:

$$T_{t+\Delta t} = T_t + K(A_{t+\Delta t} - T_t) + S_{t+\Delta t} \times C \qquad (4)$$

where $S_t$ is the solar radiation reading at time t in watts*m$^{-2}$, and $C$ is the solar constant used to relate incoming solar radiation to a change in temperature. Analysis of the solar model was completed only for Toronto, Ontario, as that was the only location with reliable hourly solar radiation data. The model building set was taken to be the Toronto series from the winter of 2008-2009 and the testing set was all Toronto series from winter 2009-2010.Parameterization of this modified model initially involved simultaneously fitting *K* on the range of 0.05 to 0.28 in increments of 0.01, and *C* on the range of 0.0005 to 0.1 in increments of 0.0005.

### 3.3.5 Modeling daily maxima

The basic Newtonian model (equation 1) was also parameterized using the daily maxima rather than the minima (*K* ranging from 0.05 to 2.0), as was the solar model (equation 4; *K* ranging from 0.05 to 0.28 and *C* ranging from 0.0005 to 0.1), in order to determine model performance in predicting warm temperature extremes. The AIC and average RMSE of daily under-bark maxima for these models were calculated, and RMSE was compared to the RMSD between air and under-bark daily maximum temperatures.

## 3.4 Results

The basic Newtonian convective cooling model produced more accurate estimates of daily minimum under-bark temperature than using the air temperature (AIC=1142.6 vs. 4913.1; Table 3.1; e.g. Figure 3.1). For the simple Newtonian cooling model, the optimal value of the cooling constant *K* was 0.11, which produced an average RMSE across the testing set of 1.31˚C, with a single series RMSE maximum of 2.42˚C, and a minimum 0.65˚C. When I assumed that under-bark temperature was the same as air temperature, I calculated an average RMSD of 3.20˚C across the testing set, with a single series maximum of 4.76˚C, and a minimum of 1.83˚C. For every individual tree, the RMSE of the basic model was smaller than the RMSD between air and under-bark temperature. The 95% confidence interval for under-bark temperature predictions was ±2.59˚C. Small changes in the value of *K* did not produce significant changes in the average RMSE across the model building set, and there was a clearly singular optimal value of *K* (Figure 3.2).

There was a significant linear relationship between the optimal value of *K* for each individual tree in the model-building set and the tree diameter at breast height (estimated slope=0.002, estimated intercept=0.191, $R^2 = 0.51$; F-test$_{22,1}$; $P<0.001$). Including this relationship in the Newtonian cooling model gave it the form:

$$T_{t+\Delta t} = T_t + (0.191 - 0.002 DBH_i) \times (A_{t+\Delta t} - T_t)$$

Running this model across the testing set, however, produced no significant improvement in model fit (AIC=1144.6), because the model is fairly insensitive to small changes in the value of *K*, and the adjusted $R^2$ value of the regression between K and DBH was small.

The Newtonian convective cooling model modified for the effects of urban heat islands performed poorly when compared to the basic model. With an optimal value of *K*=0.14, the AIC was 1909.3, giving it a worse fit than the basic model. The average RMSE across the testing set was 1.57˚C with a single series minimum of 0.64˚C and a maximum of 2.87˚C. Similarly to the basic model, small changes in the value of *K* did not produce a significant change in model fit.

Adding the effects of elevation also offered no improvement in model performance. The optimal value of *K* was 0.12, producing an AIC of 1208.6, and an average RMSE of 1.33˚C across the testing set. The maximum RMSE for a single series was 3.03˚C, and the minimum was 0.67˚C.

The model that incorporated the effects of solar radiation for the Toronto data also did not offer improved performance in the prediction of minimum temperatures. For this model the optimal values for *K* and *C* were 0.12 and 0.001. The basic Newtonian cooling model produced an AIC of -1157.22 across the Toronto testing set, whereas the incorporation of solar radiation gave an AIC of -212.7.

## 3.5 Discussion

Using the Newtonian cooling model, I was able to successfully predict minimum under-bark temperatures for a large sample of trees widely distributed across Ontario in both urban and woodlot environments. Successful use of this model indicates that the minimum temperature conditions of the under-bark microclimate can be easily predicted using regularly collected climate data. I also illustrated that assuming that under-bark temperature is the same as air temperature leads to errors of a relatively large magnitude (3.20˚C vs. 1.31˚C).

More complex models of under-bark temperature exist (e.g. Derby and Gates 1966, Potter and Andresen 2002). While I do not doubt their efficacy, the complex nature of the models can make parameterization very difficult, especially if one wishes to apply these models over a large area where tree and tree stand variables are not constant. In contrast, this simple mechanistic model is easily parameterized and is robust to differences between trees and locations.

The performance of the Newtonian cooling model on ash trees was similar to previous performance on coniferous trees (e.g., Tran et al. (2007) observed a RMSE of daily minimum under-bark temperature of about 1˚C for pine trees). The difference in model performance can partially be attributed to climate and tree species differences, as well as the fact that the authors used the optimal value of $K$ for each individual tree, whereas I used a single value of K for all trees. A regression of the optimal value of $K$ on tree diameter was significant, but use of individual parameters for each tree did not significantly improve model performance. If I had used the optimal value of *K* for each individual tree, the average RMSE across the model building set would have been 1.17˚C as opposed to 1.31˚C using a single value of *K* for all trees. This small improvement suggests that there is no need to try and parameterize this model for each tree individually.

Some studies have discounted the fact that the difference between under-bark and air temperature minima can vary from day-to-day (e.g. Ungerer et al. 1999, Bolstad et al. 1997). However, over the course of a winter, the difference between under-bark and air temperature can vary considerably, with 16-33% of days having a difference between under-bark and air temperature minima over 4˚C (Section 2.4.1), suggesting that an assumption of a constant difference between air and under-bark temperature minima is not recommended. Moreover, Tran et al (2007) have shown that this mechanistic model is more effective than assuming a constant level of buffering.

Simple modifications of the Newtonian cooling model by including elevation, urban heat island effects, or solar radiation produced no improvement in model performance (Table 3.1). It tends to be coldest at night when there is a lack of solar radiation, which may explain the reason that solar radiation did not improve model prediction of daily minima. It should also be noted that the area of this study did not have exceptionally large differences in elevation between weather stations and their associated nearby trees. Only one site had a difference of more than 100m (North Bay; approx 150m difference), and even there the inclusion of elevation did not improve the model. Elevation could become a very important variable in high relief areas. In such locations, it would be advisable to use a spatial interpolation technique that incorporates elevation (Bolstad et al. 1997, Tran et al. 2007).

Daily under-bark temperature maxima were not accurately predicted by the simple model, or the model variant which included solar radiation. Interestingly, Tran et al. (2007) did not seem to have had this same issue, reporting a RMSE of hourly temperature of approximately 1˚C, meaning that even if errors are higher on average for the maxima (not reported), they are unlikely to be of the same magnitude that we observed (>4˚C on average). This difference may be due to the application of the model in deeply wooded areas versus more open and urban sites, characteristic of our study, where solar loading has a larger influence. However, if that were the case, it still remains unclear why the inclusion of solar radiation did not improve model performance. I suspect that the complex and intermittent local shading, characteristic of structures in populated areas may explain some of this failure.

To put the prediction error of the model in the context of a specific species, the emerald ash borer, I considered the variability in the EAB supercooling point (SCP). The SCP is the temperature at which the beetles' body fluids freeze, and reaching this critical temperature results in 100% mortality (Crosthwaite et al. 2011, Sobek-Swant et al. 2011). The variability in the SCP can be compared to the error in under-bark temperature predictions to evaluate the magnitude of model uncertainty. The SCP of EAB has a standard deviation of 3.2˚C across the time period of December to February (Crosthwaite et al. 2011 unpublished data). This variability in SCP is much larger than the RMSE of daily minimum under-bark temperature predictions made using the basic Newtonian model (1.31˚C) (Figure 3.3). Having model errors smaller than SCP variability minimizes the effect of under-bark temperature prediction errors on estimated proportion of EAB mortality.

I suggest that the Newtonian cooling model can be widely applied to predict the minimum temperatures in the under-bark microclimate for a wide variety of tree species and wood-boring pests. For example, the errors of this model are smaller than the variability in emerald ash borer super cooling point. The model is easy to parameterize, does not need to be calibrated for individual trees, can accommodate both deciduous and coniferous trees, is robust across urban and wooded locations, and offers good performance across a range of spatial locations and seasons. This simple tool makes the application of physiological models of species range a practical and accurate alternative to climate driven niche-based approaches.

**Table 3.1** Parameterized models and their respective error values of minimum under-bark temperature predictions. The basic Newtonian cooling model performed best. The 'All sites' column includes data from the entire model-testing set; the 'Only Toronto' column includes all trees from Toronto in the 2009-10 winter.

| **Model description and number** | **Optimal equation** | **Avg RMSE/D (˚C)** | |
|---|---|---|---|
| | | **All sites** | **Only Toronto** |
| No model; air temperature | $T_{t+\Delta t} = A_{t+\Delta t}$ | 3.20 | 2.00 |
| Basic Newtonian cooling model (Eq 1) | $T_{t+\Delta t} = T_t + 0.11(A_{t+\Delta t} - T_t)$ | 1.31 | 0.76 |
| Newtonian model with urban heat island (Eq 2) | $T_{t+\Delta t} = T_t + 0.23([A_{t+\Delta t} + 2.1 \times U] - T_t)$ | 1.57 | 1.23 |
| Newtonian model with elevation (Eq 3) | $T_{t+\Delta t} = T_t + 0.12([A_{t+\Delta t} - V \times 9.8] - T_t)$ | 1.33 | 0.69 |
| Newtonian model with solar radiation (Eq 4) | $T_{t+\Delta t} = T_t + 0.12(A_{t+\Delta t} - T_t) + S_{t+\Delta t} \times 0.001$ | N/A | 0.90 |

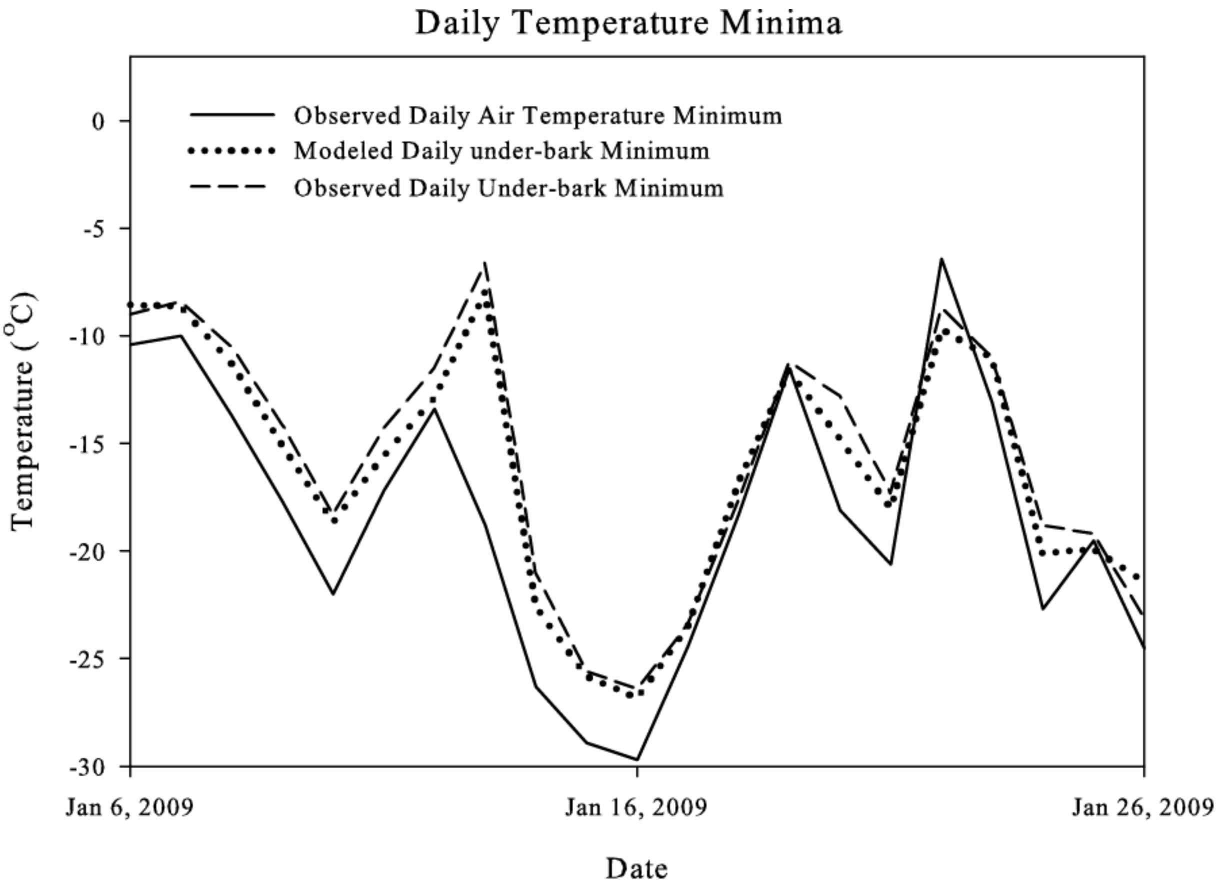

**Figure 3.1** Daily minima for observed air and observed under-bark temperature, as well as modeled under-bark temperature for an urban tree in January of 2009 in Ottawa, Ontario. The modeled under-bark temperature minima are much closer to the observed under-bark minima than the air temperature minima are.

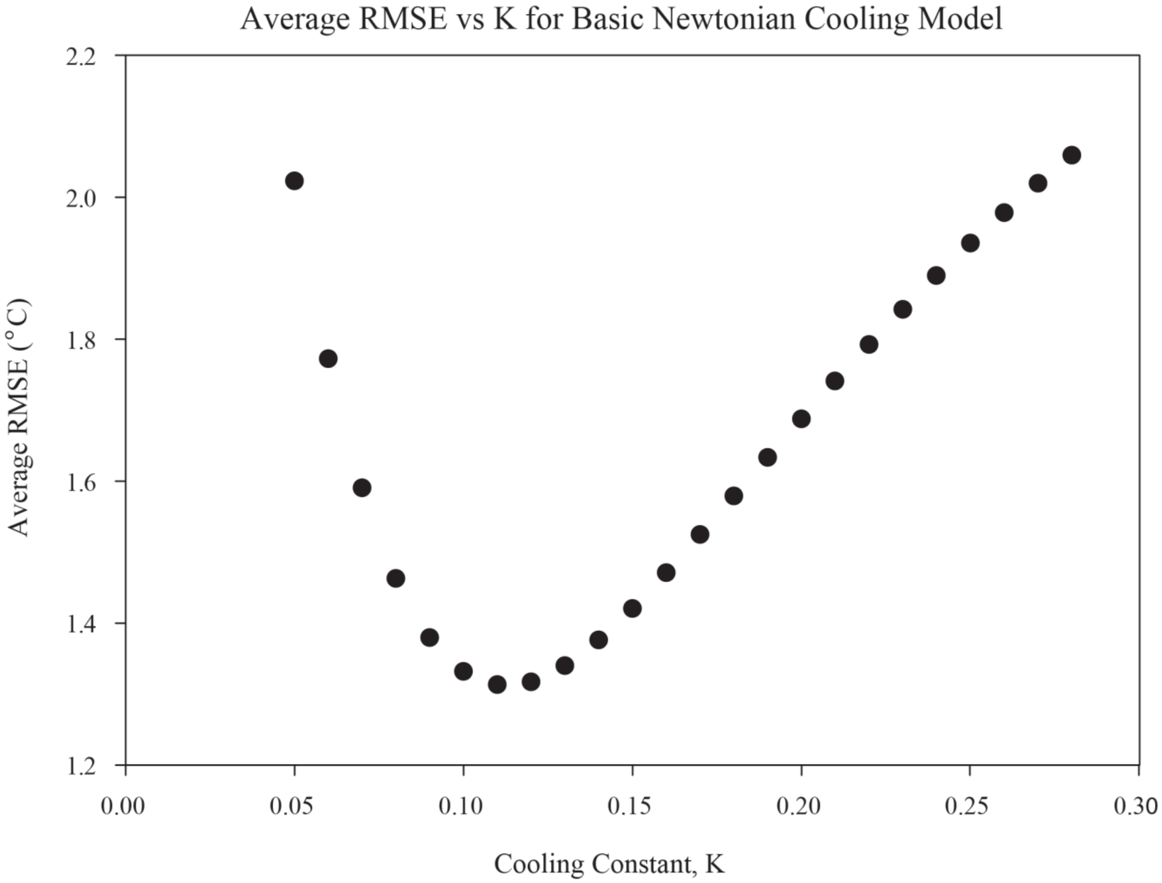

**Figure 3.2** Average RMSE vs cooling constant for the basic Newtonian model (equation 1). Note the well defined minimum at K=0.11.

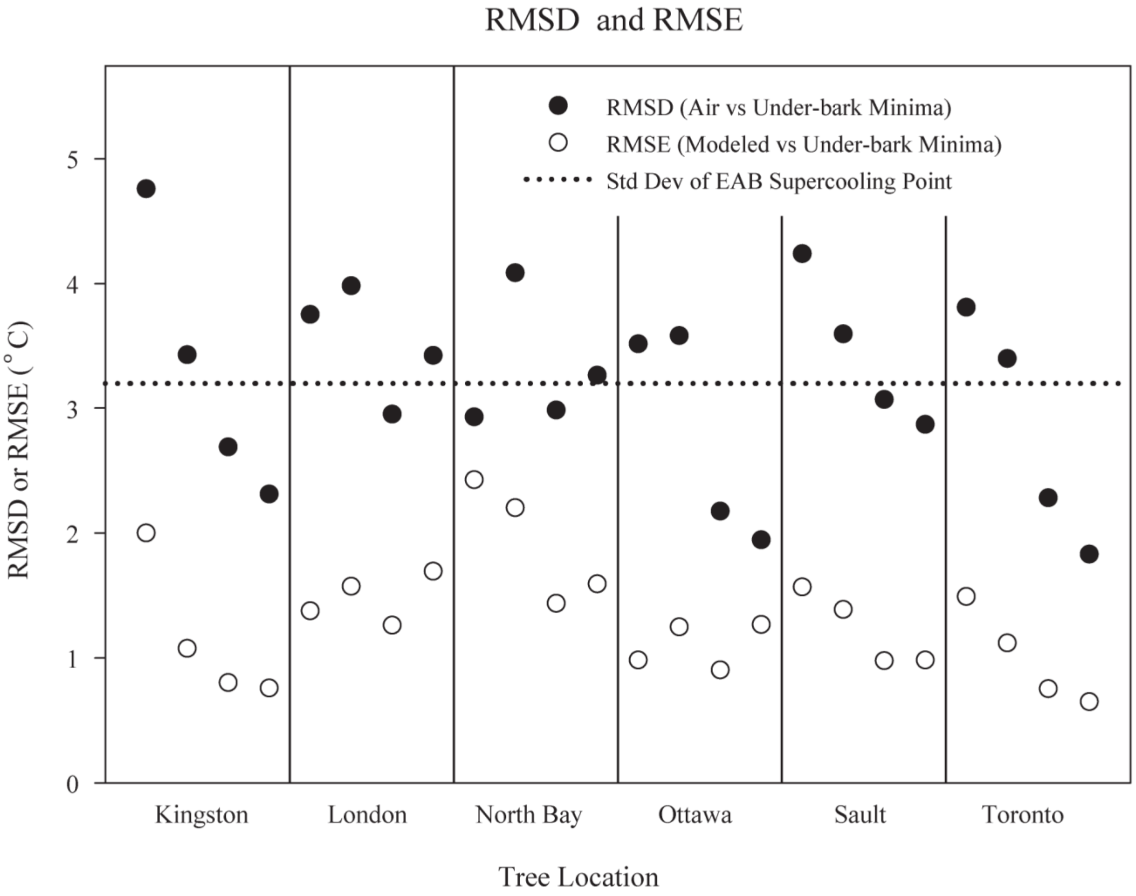

**Figure 3.3** A comparison of the Root Mean Squared Difference (where under-bark temperature is assumed to be the same as air temperature) and Root Mean Squared Error (where under-bark temperature is modeled) by location. All values of RMSE are below their associated RMSD, and below the line indicating standard deviation of emerald ash borer super cooling point.

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