

## ABSTRACT

DALE, ADAM GARLAND. The Effects of Urban Habitats on the Fitness and Abundance of an Herbivorous Pest of Street Trees, and their Subsequent Effects on Tree Condition and Ecosystem Services. (Under the direction of Dr. Steven Frank.)

Trees in urban areas provide services like air filtration, carbon sequestration, and temperature reduction that benefit human and environmental health. Unfortunately, herbivorous pests are often more abundant and damaging in urban than rural habitats. This phenomenon has been documented for over a century, however, we still have a poor understanding of the factors that cause it. The purpose of this work is to investigate the ecological interactions that affect herbivorous pest abundance and fitness on urban trees with the ultimate goal of developing integrated pest management strategies to address them.

Scale insects are one of the most ubiquitous and difficult to control insect pests in urban landscapes. In the southeastern U.S., the gloomy scale, *Melanaspis tenebricosa* (Hemiptera: Diaspididae), is the most important insect pest of *Acer* spp. street trees, most commonly *A. rubrum*. *Acer* is the most commonly planted genus of landscape tree in the eastern U.S. and *A. rubrum* is among the most common street tree species in the southeast. Since scale insects are difficult to control, management often includes frequent insecticide applications, which pose environmental and human health risks, particularly in populated urban areas. Therefore, investigating the underlying ecology driving greater scale insect abundance in urban habitats may not only broaden our understanding of urban ecology, but help develop cultural management practices that contribute to safer, more sustainable pest management and more productive urban forests.

As urbanization increases, vegetation is replaced by impervious surfaces. Previous research in urban landscapes where vegetation complexity was reduced has attributed elevated pest abundance to reduced regulation by natural enemies. However, reducing vegetation complexity also makes cities much warmer and drier than surrounding natural habitats. Throughout this research, I investigate how urban habitat characteristics like impervious surface and vegetation influence temperature, drought, and natural enemy abundance, in regulating the abundance of *M. tenebricosa* on *A. rubrum* street trees.

Using an existing gradient of urban temperatures and vegetation complexity within metropolitan Raleigh, NC, I determine that scale insect abundance increases with warming, rather than by reduced biological control. Working towards a mechanism for this response, I find that warmer temperatures increase scale insect fecundity and population growth rates. I also determine that as urban temperatures increase, *A. rubrum* drought stress increases. In fact, I experimentally determine that drought stress and urban warming additively benefit *M. tenebricosa* fitness by increasing body size and fecundity. As warming, drought stress, and *M. tenebricosa* abundance increase, tree condition is also dramatically reduced. Additionally, photosynthetic rate does not change with temperature on watered trees, whereas photosynthesis on drought-stressed trees declines with temperature due to stomatal closure. This difference in carbon assimilation translates to less growth on drought stressed street trees. My research supports previous findings about the effects of urban areas on insect pests and plants, but elucidates underlying mechanisms and provides evidence that these drivers act in concert rather than independently.

To minimize the risk of infestation and damage associated with impervious surfaces, urban warming, and pest damage, I develop impervious surface thresholds that define the most and least suitable planting sites for *A. rubrum* in urban landscapes. I also create a simple method by which landscape professionals can accurately estimate groundcover type around a planting site, thereby assisting urban planners and practitioners. Urbanization is rapidly increasing throughout the distribution of this pest and climate change projections show increased warming and drought. Therefore, my results suggest that beneficial habitat is expanding for *M. tenebricosa*. Urban foresters and landscape professionals can use information like this to mitigate the effects of urbanization on pests and trees by creating urban landscapes that are more resilient to future change.

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The Effects of Urban Habitats on the Fitness and Abundance of an Herbivorous Pest  
of Street Trees, and their Subsequent Effects on Tree Condition and Ecosystem  
Services

by  
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## **DEDICATION**

I dedicate this to my family, who has supported me unconditionally since my beginning. I also dedicate this to my nieces and nephews, who I hope can learn to appreciate the ecology that surrounds them, and to pursue their dreams, no matter how unrealistic they may seem.

## **BIOGRAPHY**

Adam Dale, born and raised in North Carolina, graduated from Ragsdale High School in Jamestown, NC in 2007. In August 2007, Adam began his undergraduate degree at North Carolina State University to study biological sciences in preparation for dental school. For three years during his undergraduate program, he worked as a laboratory assistant in an entomology lab, where he learned about insects and ecology and found his passion for those fields. Adam graduated with his bachelor's of science in biological sciences in December 2011. In January 2012, he began a master's program in the entomology department at NC State University under the direction of Dr. Steven Frank. Towards the end of his second year, Adam transitioned his graduate program to pursue a Ph.D. His doctorate research focused on the ecology of herbivorous insect pests that live and feed on trees within cities. The ultimate goals of his project were to determine ecological interactions that regulate the abundance of these pests, determine the effects that pests and urban areas have on street trees, and develop strategies to manage them.

Following graduation in December 2015, Adam will move to the University of Florida, where he will continue researching the ecology of urban landscapes and developing strategies to make them more resilient to pests and future change.

## **ACKNOWLEDGEMENTS**

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First and foremost, I thank Steve Frank, who has been integral not only to this research, but also my personal and professional development. I also thank Sarah Frank, who I am sure convinced Steve to keep me around even when he had his doubts. I thank Barbara Fair, who taught me a lot about arboriculture, the green industry, and provided me with great opportunities to broaden my experience. I thank my committee members, George Kennedy and Melissa McHale, for broadening my knowledge, making me think critically, and better preparing me for a future career in science. My officemate, Elsa Youngsteadt, has provided countless assistance, advice, discussion, and direction that without, I would have had a much more difficult and less educational graduate degree. My lab-mate, Emily Meineke, inspired me to pursue an urban ecology project when I began graduate school, and has provided valuable direction, discussion, and friendship throughout my time here. I thank my family and friends who have always believed in me and given me the support to stay motivated and pursue my interests. I could not ask for better parents who have supported me and given me every opportunity that I could want. My Aunt Jan has inspired me to become a scientist since I knew what a scientist was, and has been central to my career path. Last, but certainly not least, I thank Katie Maslanka, who has had to deal with me the most over the past four years. Your support, patience, and love have kept me focused and driven to do my best.

## TABLE OF CONTENTS

<b>LIST OF TABLES</b> .....	vii
<b>LIST OF FIGURES</b> .....	ix
<b>CHAPTER 1: Urban warming trumps natural enemy regulation of herbivorous pests</b> .....	<b>1</b>
Abstract .....	2
Introduction.....	4
Methods .....	7
Results .....	15
Discussion .....	19
Acknowledgements .....	24
References .....	25
Tables and Figures .....	31
<b>CHAPTER 2: The effects of urban warming on herbivore abundance and street tree condition</b> .....	<b>41</b>
Abstract .....	42
Introduction.....	44
Methods .....	46
Results .....	54
Discussion .....	57
Acknowledgements .....	63
References .....	64
Tables and Figures .....	69
<b>CHAPTER 3: Forecasting the effects of heat and pests on urban trees: Impervious surface thresholds and the ‘Pace to Plant’ technique</b> .....	<b>76</b>
Abstract .....	77
Introduction.....	78
Materials and Methods .....	80
Results .....	85
Discussion .....	88
Acknowledgements .....	92
References .....	93
Figures .....	97
<b>CHAPTER 4: Urban warming and drought stress combine to increase pest fitness and abundance on street trees</b> .....	<b>102</b>
Introduction.....	102
Materials and Methods .....	104
Results .....	109
Discussion .....	113
References .....	116
Figures .....	120

**CHAPTER 5: The effects of urban warming, drought, and an herbivorous pest on street tree physiology and growth ..... 125**

Introduction..... 125

Materials and Methods ..... 128

Results ..... 134

Discussion ..... 138

References ..... 143

Tables and Figures ..... 148

## LIST OF TABLES

### Chapter 1

Table 1. Correlations between each vegetation structural complexity strata predicting meant tree canopy temperature and mean <i>Melanaspis tenebricosa</i> abundance .....	31
Table 2. Model fit indices used to help determine the best model for path analysis .....	31
Table 3. Total (direct + indirect) effects of explanatory variables (side headings) on response variables.....	32
Table 4. Total (direct + indirect) effects of explanatory variables on response variables when using Shannon's H diversity index as a measure of vegetation structural complexity. Total effect, standard error, t-value, and p-value are listed per cell. Effects indicate the magnitude of the explanatory variable's effect on the response. T-values are representative of the importance of the relationship. Bolded numbers are significant (P<0.05) .....	33

### Chapter 2

Table 1. Parameter estimates table of multiple regression analyses .....	69
Table 2. Parameter estimates table of multiple logistic regression predicting tree condition.....	70
Table 3. Pearson Chi-squared test.....	70
Table 4. Contingency table comparing tree condition to surface temperature division .....	71

### Chapter 5

Table 1. ANCOVA of mean tree canopy temperature, <i>M. tenebricosa</i> abundance, and watering treatment predicting DBH growth and total stem elongation over two years. Interactions were not significant so they were removed. Bolded values are significant (P<0.05). .....	148
Table 2. ANCOVA of tree canopy temperatre, <i>M. tenebricosa</i> abundance, and watering treatment predicting leaf-level services during 2014, 2015, and the two year mean. Interactions were included if significant or nearly significant. Bolded values are significant and italicized values are nearly significant (P<0.05). .....	149-50

Table 3. ANCOVA of mean tree canopy temperature and watering treatment predicting *A. rubrum* xylem water potential during the 2014 and 2015 growing seasons. Interactions were not significant so they were removed from the model. Bolded values are significant ( $P < 0.05$ )..... 150

## LIST OF FIGURES

### Chapter 1

Figure 1. Photographs of a *M. tenebricosa* - infested red maple tree in an urban landscape. Close-up of a twig heavily infested with *M. tenebricosa* (left). Red maple street tree located in a simple urban habitat composed of turf and impervious surface in Raleigh, North Carolina, USA (right) ..... 34

Figure 2. Thermal map of surface temperature measurements in the Raleigh, North Carolina metropolitan area on 18 August 2007. Temperatures range from 30°C to 36°C, designated by the darkest blue and red regions, respectively. White circles with black dots indicate selected red maple study sites. Inset map in the upper left corner illustrates the regional location of Raleigh, North Carolina in the southeastern United States..... 35

Figure 3. Model 3 path diagram illustrating the direct effects of each exogenous (circles) and endogenous (rectangles) variable in our study system. Dashed arrows show the hypothesized direct biotic effects (enemies hypothesis) regulating *M. tenebricosa* abundance. Solid arrows show the hypothesized direct abiotic effects (temperature) regulating *M. tenebricosa* abundance. Asterisks indicate relationship is significant ( $P < 0.05$ ) ..... 36

Figure 4. Relationship between seven-month mean temperature and mean egg count per female on four dates in 2013. (A) 1 April,  $y = 12.30X - 215.7$ . (B) 16 April,  $y = 12.59X - 211.9$ . (C) 23 April,  $y = 8.871X - 135.8$ . (D) 12 May,  $y = 14.46X - 231$ . All regression models are statistically significant ( $P < 0.05$ ) . 37

Figure 5. Relationship between seven-month mean temperature and (A) the ratio of second- to first-generation adult *M. tenebricosa* ( $y = 0.428X - 7.79$ ) and (B) mean adult female *M. tenebricosa* body size ( $y = 0.127X - 1.301$ ). Both regression models are statistically significant ( $P < 0.05$ )..... 38

Figure 6. Model 1 path diagram illustrating the direct effects of each exogenous (circles) and endogenous (rectangles) variable in our study system. Unlike the selected model, this model includes path coefficients from impervious surface cover to parasitoid and predator abundance. Dashed arrows show the hypothesized direct biotic effects (enemies hypothesis) regulating *M. tenebricosa* abundance. Solid arrows show the hypothesized direct abiotic effects (temperature) regulating *M. tenebricosa* abundance. Asterisks indicate relationship is significant ( $P < 0.05$ ) ..... 39

Figure 7. Model 2 path diagram illustrating the direct effects of each exogenous (circles) and endogenous (rectangles) variable in our study system. Unlike the selected model, this model excludes coarse vegetation

groundcover from the analysis. Dashed arrows show the hypothesized direct biotic effects (enemies hypothesis) regulating *M. tenebricosa* abundance. Solid arrows show the hypothesized direct abiotic effects (temperature) regulating *M. tenebricosa* abundance. Asterisks indicate relationship is significant ( $P < 0.05$ ) ..... 40

## Chapter 2

Figure 1. Thermal map of Raleigh, NC on August 18 2007. Temperature ranges from 24 to 36 °C designated by the darkest blue and red regions, respectively. (a) Study site selection for *M. tenebricosa* abundance survey, water potential measurement, growth measurements, and condition rating. (b) City-wide red maple street tree dataset of over 8000 trees overlaid on a surface temperature thermal image of Raleigh, NC ..... 72

Figure 2. Linear regression of seven-month mean temperature and log mean scale abundance per 0.6 m of maple twig ( $\log(y) = -29.95 + 1.65x$ ). Regression model is statistically significant ( $P < 0.05$ ) ..... 73

Figure 3. Linear regression of mean August 2013 tree canopy temperature and mean stem water potential (MPa) ( $y = 5.53 - 0.31x$ ). Regression model is statistically significant ( $P < 0.05$ ) ..... 73

Figure 4. Since scale insect abundance was the most important predictor in our multiple logistic regression model, we use simple logistic regression to illustrate the relationship between scale insect abundance and tree condition. Points represent recorded measures of *M. tenebricosa* abundance on the x-axis but are not associated with y-axis cumulative probabilities. Colored sections are associated with the cumulative probabilities on the y-axis as they change across measured *M. tenebricosa* abundance on the x-axis..... 74

Figure 5. Pairwise comparison (a) of the number of trees with “Poor” and “Excellent” condition ratings between “Warm” and “Cool” median temperature classification ( $P < 0.0001$ ). Pairwise comparison (b) of the number of trees with “Poor” and “Excellent” condition ratings between “Hot” and “Cold” quartile temperature classification ( $P < 0.0001$ ) ..... 75

## Chapter 3

Figure 1. (a) Thermal map of surface temperatures in Raleigh, NC taken on 18 August 2007. Each point represents a randomly selected *A. rubrum* street tree ( $N = 82$ ). (b) Zoomed in image of a single street tree placed onto a map of surface temperatures and impervious surface ground cover classification. Each ring around the tree represents one of the 13 radii for which percent impervious surface was calculated..... 97

Figure 2. Four designed landscape scenarios illustrating the ‘Pace to Plant’ technique. In each diagram, the tree or planting site is located at the intersection of the transects. Circle diameters are equal to 40 m and road widths equal 9 m. White dashes represent steps onto impervious surface and black dashes represent steps onto pervious surface. The number of white dashes equals the percent impervious surface estimate for each scenario ... 98

Figure 3. Simple linear regression of (a) percent impervious surface (125 m radius) and tree canopy temperature, (b) tree canopy temperature and *M. tenebricosa* abundance, and (c) percent impervious surface cover (60 m radius) and *M. tenebricosa* abundance ..... 99

Figure 4. Probability curves illustrating the change in probability of finding a given tree condition rating as percent impervious surface around a planting site increases from 0 to 100%. Threshold lines are the average point at which each radius from the tree predicts a change in tree condition for all 13 measured radii. Each symbol indicates a different measured radius from the tree. Different colors represent different tree condition ratings ..... 100

Figure 5. (a) Simulated paced estimate of impervious surface on x-axis correlated with the calculated actual percent impervious surface from four landscape scenarios. (b) ‘Pace to Plant’ estimate of percent impervious surface cover on x-axis correlated with the GIS calculated percent impervious surface at a 20 m radius. (c) ‘Pace to Plant’ estimate of percent impervious surface cover on x-axis correlated with log transformed *M. tenebricosa* abundance ..... 101

## Chapter 4

Figure 1. ANCOVA regression plot of tree canopy temperature and watering treatment (W=watered, UW=unwatered) predicting mean xylem water potential (MPa). Temperature and watering treatment significantly predict xylem water potential ( $P < 0.05$ ) (Watered  $R^2 = 0.18$ , Unwatered  $R^2 = 0.41$ ) ..... 120

Figure 2. (a) ANCOVA regression plot of tree canopy temperature predicting mean *M. tenebricosa* adult female body size of individuals from each watering treatment (W=watered, UW=unwatered). Temperature and watering treatment significantly predict mean body size ( $P < 0.05$ ) (Watered  $R^2 = 0.31$ , Unwatered  $R^2 = 0.37$ ). (b) ANCOVA regression plot of tree canopy temperature predicting mean number of embryos per individual *M. tenebricosa* adult female on each watering treatment. Temperature and watering treatment significantly predict the mean number of embryos produced per individual ( $P < 0.05$ ) (Watered  $R^2 = 0.27$ , Unwatered  $R^2 = 0.17$ ). ..... 121

Figure 3. (a) ANCOVA regression plot of tree canopy temperature predicting 2015 *M. tenebricosa* abundance on trees from both watering treatments (W=watered, UW=unwatered). Mean temperature, but not watering treatment or their interaction, significantly predicted *M. tenebricosa* abundance ( $P < 0.05$ ) (Watered  $R^2 = 0.20$ , Unwatered  $R^2 = 0.74$ ). (b) ANCOVA regression plot of mean tree canopy temperature predicting the *M. tenebricosa* log10 population growth ratio of individuals on watered and unwatered trees. There was no significant relationship between variables ( $P > 0.05$ ) (Watered  $R^2 = 0.19$ , Unwatered  $R^2 = 0.00$ ) ..... 122

Figure 4. (a) Mean *M. tenebricosa* abundance on watered and unwatered study trees over the next 15 years. The effect of time, watering treatment, and their interaction was significant ( $P < 0.05$ ). Mean *M. tenebricosa* abundance was significantly different between watering treatments beginning in the fourth year ( $P < 0.05$ ). (b) *Melanaspis tenebricosa* abundance on watered and unwatered trees at different temperatures and levels of initial abundance. H\_H\_UW represents the warmest, unwatered tree with the greatest initial *M. tenebricosa* abundance. H\_H\_W is the warmest, watered tree with the greatest initial *M. tenebricosa* abundance. C\_L\_UW represents the coolest, unwatered tree with the lowest initial *M. tenebricosa* abundance. C\_L\_W is the coolest, watered tree with the lowest initial *M. tenebricosa* abundance. 123

Figure 5. (a) Hypothetical time series of mean *M. tenebricosa* abundance on watered and unwatered trees over the next 15 years assuming an equal, low initial population size of 10 individuals. The effect of time, watering treatment, and their interaction is significant ( $P < 0.05$ ). Mean *M. tenebricosa* abundance is significantly different between watering treatments beginning in the second year ( $P < 0.05$ ). (b) *Melanaspis tenebricosa* abundance on watered and unwatered trees at different temperatures and levels of initial abundance. H\_H\_UW represents the warmest, unwatered tree with the greatest initial *M. tenebricosa* abundance. H\_H\_W is the warmest, watered tree with the greatest initial *M. tenebricosa* abundance. C\_L\_UW represents the coolest, unwatered tree with the lowest initial *M. tenebricosa* abundance. C\_L\_W is the coolest, watered tree with the lowest initial *M. tenebricosa* abundance. 124

## Chapter 5

Figure 1. ANCOVA regression plots of tree canopy temperature regressed with mean xylem water potential for each watering treatment. (a) 2014 mean tree canopy temperature predicting 2014 mean water potential (Watered  $R^2 = 0.26$ , Unwatered  $R^2 = 0.39$ ). (b) 2015 mean tree canopy temperature predicting 2015 mean water potential (Watered  $R^2 = 0.16$ , Unwatered  $R^2 = 0.32$ ). W = watered and UW = unwatered trees ..... 151

Figure 2. Time series of mean xylem water potential during each summer month of the two-year study. W = watered and UW = unwatered trees.

Asterisks indicate a significant difference between watering treatments (P<0.05). Error bars are standard error of mean values..... 152

Figure 3. ANCOVA regression plots of tree canopy temperature predicting leaf-level services for 2014 (left column), 2015 (middle column), and the two-year means (right column). (a-c) photosynthesis rate, (d-f) stomatal conductance rate, and (g-i) transpiration rate. R<sup>2</sup> values are embedded within each plot. W = watered and UW = unwatered trees ..... 153

Figure 4. Repeated measures ANOVA of mean leaf-level services and photosystem damage during 2014 and 2015 per watering treatment. (a) photosynthesis rate, (b) stomatal conductance rate, (c) transpiration rate, and (d) F<sub>v</sub>/F<sub>m</sub> value. Asterisk indicates significant difference between treatments (P<0.05). Error bars are standard error of the mean ..... 154

Figure 5. ANCOVA regression plots of two-year mean tree canopy temperature regressed with tree growth for each watering treatment. (a) Mean temperature predicting two-year DBH growth (Watered R<sup>2</sup> = 0.03, Unwatered R<sup>2</sup> = 0.05). (b) Mean temperature predicting two-year total stem elongation (Watered R<sup>2</sup> = 0.08, Unwatered R<sup>2</sup> = 0.29). W = watered and UW = unwatered trees. .... 155

## CHAPTER 1: Urban warming trumps natural enemy regulation of herbivorous pests

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## Abstract

Trees provide ecosystem services that counter negative effects of urban habitats on human and environmental health. Unfortunately, herbivorous arthropod pests are often more abundant on urban than rural trees, reducing tree growth, survival, and ecosystem services. Previous research where vegetation complexity was reduced has attributed elevated urban pest abundance to decreased regulation by natural enemies. However, reducing vegetation complexity, particularly the density of overstory trees, also makes cities hotter than natural habitats. We ask how urban habitat characteristics influence an abiotic factor, temperature, and a biotic factor, natural enemy abundance, in regulating the abundance of an urban forest pest, the gloomy scale, (*Melanaspis tenebricosa*). We used a map of surface temperature to select red maple trees (*Acer rubrum*) at warmer and cooler sites in Raleigh, NC. We quantified habitat complexity by measuring impervious surface cover, local vegetation structural complexity, and landscape scale vegetation cover around each tree. Using path analysis, we determined that impervious surface (the most important habitat variable) increased scale insect abundance by increasing tree canopy temperature, rather than by reducing natural enemy abundance or percent parasitism. As a mechanism for this response, we found that increasing temperature significantly increases scale insect fecundity and contributes to greater population increase. Specifically, adult female *M. tenebricosa* egg sets increased by approximately fourteen eggs for every 1° C increase in temperature. Climate change models predict that the global climate will increase by 2-3° C in the next 50-100 years, which we found would increase scale insect abundance by three orders of

magnitude. This result supports predictions that urban and natural forests will face greater herbivory in the future, and suggests that a primary cause could be direct, positive effects of warming on herbivore fitness rather than altered trophic interactions.

## Introduction

Trees are essential to urban habitats because they provide ecosystem services such as air filtration, temperature reduction, carbon sequestration, and enhanced aesthetic value (Oke et al. 1989, Nowak & Dwyer 2000, Dawe 2011) that improve human health (Donovan et al. 2013). Unfortunately, herbivorous arthropods are often more abundant on urban than rural trees (Hanks & Denno 1993a, Speight et al. 1998, Raupp et al. 2010), reducing tree health (Zvereva et al. 2010) and the ecosystem services they provide. However, the factors that increase herbivore abundance in urban areas are not well understood (Raupp et al. 2010).

For decades, ecologists have debated the importance of abiotic and biotic factors in regulating herbivore abundance and distribution (Hunter et al. 1992). Andrewartha and Birch (1948) proposed that abiotic factors, such as rainfall, temperature, and humidity regulate herbivore distribution. In contrast, Hairston et al. (1960) argued for the importance of biotic factors such as predation and parasitism. Most research on herbivores in urban environments has focused on the hypotheses of Hairston et al. (1960), attributing increased herbivore abundance on urban plants to ineffective biological control by natural enemies (Frankie & Ehler 1978, Kahn & Cornell 1989, Hanks & Denno 1993a, Tooker & Hanks 2000, Shrewsbury & Raupp 2000, 2006). However, the influences of abiotic components of urban environments on herbivores, such as the urban heat island effect, have not been examined. In this study, we investigate how heat, a ubiquitous abiotic factor in cities, and natural enemies, a biotic factor, affect scale insect fitness and abundance on urban street trees. The relative influence of natural enemies and urban heat on pest populations

is of direct relevance to management of these trees because the management implications differ depending on which factor is most important. As cities expand and the global climate changes, the extent of urban warming will increase and natural areas will experience warming similar to that of cities; therefore, temperature may be highly important and influential in both urban and natural habitats.

The enemies hypothesis predicts that increased habitat complexity will support more natural enemies, which then more intensively regulate herbivore populations (Root 1973). This prediction is consistent with the importance of biotic regulation proposed by Hairston et al. (1960) and has been supported by studies in natural (Maron & Harrison 1997, Hawkins et al. 1999), agricultural (Letourneau 1987, Bianchi et al. 2006), and urban landscapes (Hanks & Denno 1993a, Tooker & Hanks 2000, Frank & Shrewsbury 2004, Shrewsbury & Raupp 2000, 2006). Specifically, in urban landscapes Shrewsbury and Raupp (2006) used a vegetation structural complexity index to rate urban yards as simple or complex based on the amount and frequency of vegetation. They found that azalea lace bug, *Stephanitis pyrioides* (Scott) (Hemiptera: Tingidae), abundance was greater in yards with simple vegetation, compared to yards with complex vegetation. This greater pest abundance was attributed to lower predator abundance in simple urban yards. Shrewsbury and Raupp (2000) also found that sun exposure was greater in simple yards and one of the best predictors of lace bug abundance. Others have associated greater pest abundance and damage with sun exposure in natural (Louda et al. 1987, Moore et al. 1988) and urban habitats (Kahn & Cornell 1989). Direct sun

exposure increases temperature yet the effect of habitat complexity on natural enemies has never been separated from habitat effects on temperature.

Urban habitats are up to 10° C warmer than surrounding rural habitats (Oke 1973, Kim 1992) as a result of anthropogenic heat sources, increased impervious surface, and reduced vegetation cover (Nowak & Dwyer 2000). As vegetation cover is reduced, it is either replaced by or exposes impervious surfaces (Nowak & Greenfield 2012), which absorb and reradiate heat from solar radiation and anthropogenic heat sources (Oke et al. 1989) resulting in what is referred to as an urban heat island effect. Warmer temperatures can decrease arthropod development time and increase survival and fitness (Kozłowski 1992, Berger et al. 2008). Therefore, increased herbivore abundance in urban habitats may be attributable to temperature effects on arthropod physiology. Only one study has directly examined the influence of heat on arthropod pest abundance in urban habitats: Meineke et al. (2013) found that soft scale insect (Hemiptera: Coccidae) abundance varied 13-fold across a 2.4° C urban temperature gradient. However, this study focused on the effects of temperature without directly addressing the cause of temperature differences among study sites. Our goal is to separate the effects of habitat complexity on temperature from its well-documented effects on natural enemies, to examine the relative importance of abiotic and biotic factors in regulating pest abundance on urban trees.

Over a century ago, Metcalf (1912) documented greater abundance of gloomy scale, *Melanaspis tenebricosa* (Comstock) (Hemiptera: Diaspididae), on urban street trees, compared to rural street trees in Raleigh, NC. Since then, in

concert with the loss of elm and chestnut trees to pests, maples have become one of the most commonly planted genera of street trees in eastern North America (Raupp et al. 2006). *Melanaspis tenebricosa* persists as the most important pest of red maple in the southeastern U.S. but is rarely found on trees outside of urban areas (Metcalf 1922, Frank et al. 2013). The injurious effects of *M. tenebricosa* feeding on tree health are apparent and widespread in urban habitats (Frank et al. 2013) but the forces driving increased abundance are not well understood.

We examined the contributions of impervious surface groundcover, coarse vegetation groundcover, and local vegetation structural complexity to temperature and natural enemy abundance, and, in turn, the influence of temperature and natural enemy abundance on *M. tenebricosa* abundance. Our hypothesis was that simple habitats with more impervious surface cover and less vegetation cover would be warmer and have greater *M. tenebricosa* abundance than more complex habitats with less impervious surface cover. To identify mechanisms by which warming could increase scale insect abundance we examined the relationship between temperature and *M. tenebricosa* parasitism, fecundity, and population increase. Our hypothesis was that parasitism would not be affected by temperature but that *M. tenebricosa* fecundity and population growth would increase as temperature increased.

## Methods

### Study system and species

Red maples (*Acer rubrum*) are deciduous trees indigenous to the eastern United States (Nesom 2006). *Melanaspis tenebricosa* is a key native pest of red

maple trees in the southeastern United States (Metcalf 1922). These scale insects live on the trunk and branches (Figure 1) of maple trees, where they extract fluids from within woody tissues (Metcalf 1922, Frank et al. 2013). They are univoltine and overwinter as mated adult females, with immature stages active for 6 – 8 weeks beginning in late spring (Metcalf 1922). Scales accumulate on the bark, causing discoloration, premature leaf drop, branch dieback, and occasionally tree death (Metcalf 1922, Frank et al. 2013). There are several predators that attack immature stages of armored scale including: Coccinellidae (Coleoptera), Dolichopodidae (Diptera), Syrphidae (Diptera), Anthocoridae (Hemiptera), Geocoridae (Hemiptera), Chrysopidae (Neuroptera), and Hemerobiidae (Neuroptera) (Drea & Gordon 1990). Gloomy scales are also parasitized by at least five species of parasitoid wasps from the families Aphelinidae, Encyrtidae, and Signiphoridae (Miller & Davidson 2005, Dale & Frank unpublished data).

## Study Sites

We conducted field studies on red maple trees at 26 sites throughout the Raleigh, NC metropolitan area. Study sites varied across a gradient of vegetation and ground cover from a parking lot tree planted in 16 m<sup>2</sup> of soil, to street trees in turf planting strips (Figure 1) and trees in residential front lawns. Sites were selected using a thermal map constructed from surface temperature measurements in band 6 of Landsat-5 World Reference System 2 (WRS-2) path 16, row 35 images acquired on August 18, 2007 (Figure 2; Meineke et al. 2013). We overlaid a map of red maple locations (provided by the Raleigh Parks and Recreation Department) in ArcMap

(ArcGIS Desktop 10, Redlands, CA) and selected 13 red maples within relatively hot sites and 13 within relatively cool sites of the thermal map (Figure 2).

#### Vegetation structural complexity

We define vegetation structural complexity as an index of the amount and structure of vegetation at each study site based on the frequency of vegetation in three-dimensional space (Erdelen 1984, Shrewsbury & Raupp 2000). We quantified three-dimensional vegetation structural complexity around each study tree using methods described by Shrewsbury and Raupp (2000). With the tree in the center, we measured and marked a 10 x 10 m area around each study tree. The vertical dimension of this area consists of five vegetation strata layers, creating a 500-unit<sup>3</sup> grid. These layers are ground cover (e.g., turf, English ivy), annuals/perennials, shrubs, understory tree species, and overstory tree species (Shrewsbury & Raupp 2000). We recorded immature overstory tree species as part of the understory. We assigned each box within the grid a 1 or 0 based on the presence or absence of vegetation. Ratings could reach a maximum of 500, representing the most structurally complex vegetation. Vegetation complexity ratings measure the quantity of vegetation in a habitat but do not account for the distribution of vegetation among strata. As a second measure of structural complexity, we used Shannon's diversity indices to calculate an index of vegetation complexity at each site (Primer v6). Using this index, we treated vegetation strata as a "species" and box counts within each strata as "abundance". In addition to including total structural complexity scores in our path analysis we analyzed the correlation between each strata and *M*.

*tenebricosa* abundance and mean site temperature to assess the importance of each strata.

#### Ground cover

To examine the habitat around each study site on a larger scale, we analyzed the ground cover around each tree in ArcMap (ArcGIS10®) using impervious surface and coarse vegetation groundcover data in Raleigh, NC (Bigsby et al. 2013). Bigsby et al. (2013) delineated six groundcover types at a 1 m resolution, which included tree, water, road, building, grass, and bare ground classifications. We used impervious surface and coarse vegetation cover because these classifications comprised greater than 97% of the groundcover within 100 m of each of our study trees. Impervious surface includes building footprints as well as pavement and asphalt such as parking lots, roads, and sidewalks. Coarse vegetation includes large, woody flora such as shrubs and trees, which are supportive of pest and natural enemy populations and were the most important vegetation strata in predicting site temperature and scale insect abundance at the local scale. Each classification was represented as a shape file in ArcMap (ArcGIS10®), along with a shape file of our 26 trees as points. We created a buffer zone around each tree with a radius of 100 m (Sperry et al. 2001), calculated the total area of each groundcover within the buffer zone, and divided by the total area of the buffer zone to determine percent groundcover type around each tree.

### *Melanaspis tenebricosa* abundance

To measure *M. tenebricosa* abundance, we pruned one haphazardly selected 0.15 m terminal twig from each of four cardinal directions on each of our 26 study trees using a 3.66 m pole pruner. We collected twigs on four dates in 2012 when scales were active (5 and 20 April; and 3 and 18 May) and examined them under a dissecting microscope to record scale abundance and life stage per 0.6 m length of twig.

### Natural enemy abundance

Using methods similar to Raupp et al. (2001), we surveyed the abundance of flying natural enemies at each of our study sites with 7.6 x 12.7 cm yellow sticky cards (Olson Products, Medina, OH). We hung sticky cards in the lower canopy of each tree and replaced them every two weeks from April through July 2012.

To determine which parasitoids were attacking *M. tenebricosa*, we collected 0.5 m scale-infested twigs, placed them in vials with a cotton ball stopper, and kept them in an environment chamber at 27° C ( $\pm 0.5$ ) (Percival Scientific Inc., Perry, IA). We collected emerged parasitoids, preserved them in 80% ethanol, and identified them to genus. After this, we could distinguish between parasitoids that attack *M. tenebricosa* and other parasitoids present at each site. We recorded the abundance of these *M. tenebricosa* parasitoids collected on yellow sticky cards.

To determine predator abundance, we counted and identified to family all generalist predators that were collected on yellow sticky cards and known to feed on scale insects.

## Tree canopy temperature

Thermal mapping gave approximate site surface temperatures on 18 August 2007. To determine actual tree canopy temperatures, we placed iButton thermochron (Dallas Semiconductor of Dallas, TX) remote temperature loggers within the canopy of each study tree. Using methods similar to Meineke et al. (2013), we placed thermochrons in iButton wall mounts (Dallas Semiconductor of Dallas, TX) within 59 ml portion containers (Dart Container Corporation Mason, MI) and fastened them to the undersides of branches approximately 4.5 m above ground using zip ties. iButtons recorded the temperature every hour from April 2012 to April 2013. Due to loss of iButtons, complete 12-month temperature readings were only available for 22 of the 26 sites. Therefore, we used 7 months for which all sites had complete data. These months in chronological order from 2012 to 2013 are: June, July, August, September, February, March, and April.

## Path analysis

We hypothesize causal pathways that include direct and indirect contributions of biotic and abiotic factors to *M. tenebricosa* abundance (Figure 3). Based on this hypothesis, we constructed path diagrams and conducted a path analysis (Grace 2008) using PROC CALIS (SAS® 9.3). We fitted three potential models including different combinations of exogenous and endogenous variables and their potential associations but selected one for analysis. We chose this model based on concurrence with our a priori hypothesized associations and variables of interest in addition to goodness of fit indices, Akaike Information Criterion (AIC), Schwarz Bayesian Criterion (SBC), and model parsimony. We did not use Chi-square values

for goodness of fit because our variables are not independent and identically distributed. Our model predicts that habitat characteristics influence natural enemy abundance and site temperature, both of which influence scale insect abundance (Figure 3) based on the enemies hypothesis and our temperature hypothesis, respectively. We treated vegetation structural complexity (local scale) and percent groundcover type (landscape scale) as continuous, exogenous variables influencing site temperature, predator abundance, and parasitoid abundance (Figure 3). Temperature, predator abundance, parasitoid abundance, and scale insect abundance were treated as endogenous variables with the former three contributing to scale insect abundance (Figure 3). We repeated the above analyses replacing the vegetation structural complexity rating with Shannon's H indices for complexity.

#### Percent parasitism of *M. tenebricosa*

To examine the efficacy of parasitoids across study sites, we collected 4.8 m of scale-infested twigs from the canopy of each study tree and placed them in a rearing tube. Using methods adapted from Tooker and Hanks (2000), we constructed rearing tubes out of cardboard mailing tubes and placed a clear glass vial in the cap at one end. This end had a light source so that emerging parasitoids would fly into the vial. Every two weeks, over a twelve-week period, we collected, counted, and identified parasitoids from the tubes. Percent parasitism was calculated for each site by dividing the number of parasitoids that emerged by mean scale insect abundance per 4.8 m of twig as previously determined per 0.6 m length of twig. The rearing tube percent parasitism distribution followed a zero-inflated

Poisson distribution so we analyzed the data using PROC GENMOD ZEROMODEL (SAS® 9.3).

As a second measure of percent parasitism, we collected scale-infested twigs on 18 December 2012 and examined them for parasitized *M. tenebricosa*. We removed scale covers and recorded the presence of a parasitized scale insect, parasitoid larva, parasitoid pupa, or parasitoid adult. We calculated percent parasitism at each site by dividing the number of parasitized scales by the number of scales examined. The distribution of the data also followed a zero-inflated Poisson distribution so we analyzed the data using PROC GENMOD ZEROMODEL (SAS® 9.3).

#### *Melanaspis tenebricosa* fecundity and population increase

To determine if temperature affects scale insect fecundity, we dissected 8 gravid adult females per site on four dates in 2013: 1, 16, and 23 April; and 12 May. We selected two females per twig among four twigs collected from each tree. We placed eggs from dissected females on a glass microscope slide and counted them under a phase contrast compound light microscope. *Melanaspis tenebricosa* eggs were hatching at cold and hot sites on the final sampling date, indicating the end of egg development. We constructed a model treating mean egg count per female per site and mean seven-month temperature as continuous variables and examined their relationship using simple linear regression (JMP, Version 10. SAS Institute Inc., Cary, NC).

We also calculated the ratio of recently developed live *M. tenebricosa* adult females in December 2012 to live adult females prior to egg hatch in April 2012 as a measure of population increase across one generation. We treated population increase ratios as continuous response variables correlated with seven-month mean temperature (JMP, Version 10. SAS Institute Inc. Cary, NC).

Larger female insects often produce eggs earlier in development, are more fecund, and survive better than smaller females (Kozłowski 1992, Berger et al. 2008). As a general measure of fitness, we determined body length of adult female *M. tenebricosa* from the pygidium to the anterior end of 8 individuals from each study site on four dates in 2013: 1, 16, and 23 April; and 12 May. As in the fecundity survey, we selected two females per twig among four twigs collected from each tree. We treated mean body size as a continuous response correlated with seven-month mean temperature using simple linear regression (JMP, Version 10. SAS Institute Inc., Cary, NC).

## Results

### Habitat analysis

Vegetation structural complexity ratings ranged from 42 to 315 out of 500 with a mean ( $\pm$ SD) of 178 ( $\pm$ 66.3) and were distributed across two to five vegetation strata. Shannon's H vegetation structural complexity indices ranged from 0.31 to 1.44 with a mean of 0.93 ( $\pm$ 0.28). Individually, understory and overstory strata significantly predicted site temperature and *M. tenebricosa* abundance (Table 1), providing further support for our coarse vegetation groundcover analysis. We used

total vegetation structural complexity in our path analysis for statistical power and because it equally predicts site temperature and *M. tenebricosa* abundance while including all other strata (Table 1). Impervious surface cover ranged from 3.95% to 78.5% with a mean of 33.6% ( $\pm 22.9$ ) and coarse vegetation cover ranged from 13.1% to 94.6% with a mean of 52.4% ( $\pm 29.2$ ).

#### Arthropod abundance

Mean *M. tenebricosa* abundance includes all life stages and ranged from 0 to 2241 live individuals per 0.6 m of twig with a mean ( $\pm$ SD) of 444.0 ( $\pm 683.7$ ).

We identified five parasitoid wasp morphotypes as natural enemies of *M. tenebricosa*. Four of these were identified to genus and one was identified to subfamily. These were: *Signiphora* (Signiphoridae), *Encarsia* (Aphelinidae), *Ablerus* (Aphelinidae), *Coccidoctonus* (Encyrtidae), and *Coccidoxinoides* (Encyrtidae). Of these, *Signiphora*, *Encarsia*, and *Ablerus* were collected on yellow sticky cards. Over 94% of all gloomy scale parasitoids collected on sticky cards were *Encarsia* spp. However, all three genera were included in the metric of parasitoid abundance used in the path analysis.

We identified generalist predators in the families Aleoarthridae, Anthocoridae, Chrysopidae, Coccinellidae, Dolichopodidae, Forficulidae, Geocoridae, Phlaeothripidae, and Syrphidae on yellow sticky cards. We also recorded spiders (Araneae) and one specialist predator, the scale picnic beetle, *Cybocephalus nipponicus* (Coleoptera: Nitidulidae).

## Tree canopy temperature

Seven-month mean hourly tree canopy temperature ranged from 18.26°C to 20.12°C with a mean ( $\pm$ SD) of 19.17°C ( $\pm$ 0.44).

## Path analysis

All three potential path models fit well and displayed similar associations between variables (Supplemental 1 & 2); however, we present the one that fully tests our a priori hypotheses and includes all measured variables (Table 2, Figure 3). Results for each model suggest that only impervious surface and temperature are significantly associated with and significantly predict *M. tenebricosa* abundance. Replacing vegetation structural complexity with Shannon's H indices in the analysis produced the same significant relationships between impervious surface, temperature, and scale insect abundance corroborating the strength of these responses (Supplemental 3). For all models, all non-significant path coefficients exhibit minor to no difference in coefficient values and in all cases do not change significance. In addition, goodness of fit indices were acceptable for all models and close enough to one another to permit selection of any model based on these values (Table 2). As such, we chose the full model that most completely represents our hypotheses and the linear relationships between variables. We found no evidence of nonlinearity in the relationship between explanatory and response variables in our model. Direct effect path coefficients represent the direct contribution of an explanatory variable to the response variable when keeping all other variables constant (Figure 3). Indirect effects represent the effect of an explanatory variable on

a response through its effect on other variables. The total effects equal the sum of direct and indirect effects and represent the total contribution of an explanatory variable to a response (Table 3).

The strongest effect in our path model was the total positive effect of mean temperature on *M. tenebricosa* abundance ( $t=4.62$ ,  $P<0.0001$ ) (Table 3). The total effect of percent impervious surface cover was significantly positively associated with mean temperature ( $t=4.45$ ,  $P<0.0001$ ) (Table 3), which is consistent with other studies associating ground cover and temperature (Oke 1973, Hart & Sailor 2009, Jenerette et al. 2011). Impervious surface was also significantly positively associated with *M. tenebricosa* abundance ( $t=3.08$ ,  $P=0.002$ ) due to its strong, positive association with temperature (Table 3). To the extent that it showed a trend, vegetation structural complexity was negatively, but not significantly associated with mean temperature, almost certainly due to its inverse relationship with impervious surface cover. However, this trend disappeared when Shannon's H indices were included in the path analysis. There was no correlation between habitat complexity and natural enemies or natural enemies and *M. tenebricosa* abundance (Table 3). No other exogenous or endogenous variables had significant direct, indirect, or total effects on one another in our path model.

#### Percent parasitism of *M. tenebricosa*

Rearing tube percent parasitism was low with a mean of 0.72% ranging from 0 to 4.4% and was not related to seven-month mean temperature (Wald  $X^2=0.07$ ,  $df=1$ ,  $P=0.79$ ), vegetation complexity (Wald  $X^2=0.01$ ,  $df=1$ ,  $P=0.91$ ), or coarse

vegetation cover (Wald  $X^2=0.05$ ,  $df=1$ ,  $P=0.82$ ). Percent parasitism of *M. tenebricosa* determined by removing scale covers was slightly higher, ranging from 0 to 12.5% with a mean of 2.22% but also not related to temperature (Wald  $X^2=0.01$ ,  $df=1$ ,  $P=0.93$ ), vegetation complexity (Wald  $X^2=0.00$ ,  $df=1$ ,  $P=0.96$ ), or coarse vegetation cover (Wald  $X^2=0.01$ ,  $df=1$ ,  $P=0.94$ ).

#### *Melanaspis tenebricosa* fecundity and population increase

Simple linear regression revealed the strongest association between mean egg count per female and seven-month temperature on the first sampling date ( $R^2=0.72$ ,  $P<0.0001$ ) (Figure 4A). On the final date there was still a significant positive correlation between mean egg count per female and seven-month temperature ( $R^2=0.20$ ,  $P=0.04$ ) (Figure 4D). In addition, the slope of the regression equation was greatest for the final survey date ( $y=14.46X - 231$ ) (Figure 4D), suggesting the strongest effect of temperature on egg count.

The ratio of second-generation adults to first-generation adults was significantly positively correlated with seven-month site temperature ( $R^2=0.32$ ,  $P=0.02$ ) (Figure 5a). There was also a significant positive association between seven-month site temperature and body size ( $R^2=0.44$ ,  $P=0.0008$ ) (Figure 5b).

#### Discussion

For over a century, scientists have observed greater pest abundance on urban trees compared to trees in natural habitats (Putnam 1880, Metcalf 1912). We found that *M. tenebricosa* abundance increased in response to urban heat, supporting our hypothesis that the abiotic factor, temperature, is more important than

the biotic factors we measured. Trees in the hottest urban habitats had three orders of magnitude more *M. tenebricosa* than the trees in the coldest urban habitats; some had up to 2241 individuals per 0.6 m of twig. We conclude that in our study, urban habitat characteristics such as high impervious surface cover increase herbivore abundance by making the habitat warmer, rather than less suitable for natural enemies as proposed in other studies. As urban areas become warmer and continue to expand, the direct abiotic effects of warming on herbivore fitness, particularly scale insects, may be greater than the effects of warming on trophic interactions.

Warmer temperatures increase insect metabolic activity, which can increase body size (Ray 1960), while also decreasing development time and increasing fecundity (Yasuda 1983, Kozłowski 1992). *Melanaspis tenebricosa* is univoltine (Metcalf 1922), so shorter generation time does not explain differences in abundance. However, increases in abundance could be due to increases in fecundity. Female *M. tenebricosa* were significantly larger and produced more eggs in warmer than cooler urban habitats. Our first survey for egg set revealed the strongest association between temperature and egg count, suggesting that scale insects at warmer urban sites produce eggs earlier in the season. This association weakened over time but remained significant and at the time of immature emergence, individual *M. tenebricosa* egg sets increased by approximately fourteen eggs for every 1°C increase in temperature. This increase in fecundity is corroborated by an over four times greater population increase on warmer than cooler trees. Thus, greater fecundity provides a feasible mechanism through which

warming could increase *M. tenebricosa* population growth and density on urban trees.

Vegetation structural complexity and ground cover did not increase natural enemy abundance or efficacy as predicted by the enemies hypothesis. In fact, we found a nearly significant, negative association between vegetation structural complexity and parasitoid abundance (Table 3). Parasitoid abundance was greater in simpler habitats where scale insect abundance was also high, which is likely explained by a density-dependent response of parasitoids to their herbivore hosts (Holling 1959, 1961, Waage 1983). Percent parasitism was not affected by vegetation structural complexity or ground cover, similarly to Hanks and Denno (1993a) who attributed scale insect abundance in simple urban landscapes, in part, to a lack of generalist predators. In our system, *M. tenebricosa* abundance was not associated with generalist predator abundance. Although natural enemies have been shown to regulate scale insects and other pests (Luck & Dahlstein 1975, McClure 1977, Clarke et al. 1992, Raupp et al. 2001), we did not find evidence to support the enemies hypothesis or the role of natural enemies in regulating *M. tenebricosa* abundance.

Our results may shed light on other studies that have found a negative relationship between vegetation structural complexity or groundcover and herbivore abundance without identifying a strong biotic mechanism (Hanks & Denno 1993a, Shrewsbury & Raupp 2000, Tooker & Hanks 2000). For example, Tooker and Hanks (2000) found greater pine needle scale, *Chionaspis pinifoliae* (Hemiptera: Diaspididae), abundance in simple impoverished habitats near impervious surface

cover compared to complex wooded habitats despite higher parasitoid abundance and parasitism in the impoverished habitats. Shrewsbury and Raupp (2000) found that light exposure, most strongly influenced by the overstory tree strata, predicted azalea lace bug abundance better than other habitat components such as plant diversity. Our results suggest that the overstory, as well as the understory tree strata most strongly influence site temperature. It is plausible that in these and similar studies that the simple urban habitats were warmer than the more complex ones. Herbivorous pest abundance and impervious surface cover have been associated in other studies (Sperry et al. 2001, Speight et al. 1998), but a mechanism behind this was never identified. Our study integrates temperature into existing theory about the effects of habitat and urbanization on biotic interactions.

Plant stress caused by characteristics of urban habitats has been predicted to increase herbivore abundance in some cases by increasing plant nutritional quality, decreasing defense, or both (Mattson 1980, White 1984, Miller et al. 2006). Increasing impervious surface cover can increase plant water stress (Berrang et al. 1985) and temperature (Hart & Sailor 2009). However, water stress has generally been found to reduce survival and abundance of armored scales (Cockfield & Potter 1986, Hanks & Denno 1993a, b) and other sap feeding insects (Koricheva et al. 1998, Huberty & Denno 2004) and thus does not explain the greater abundance of these pests on urban trees. For example, Hanks and Denno (1993a) found that survival of armored scale cohorts decreased on drought-stressed trees and did not explain why there were more scales on stressed urban trees compared to trees in wooded areas. Therefore, we suspect that scale insects at our hot sites thrived in

spite of, not because of, host-plant water stress.

Climate change is predicted to affect ecosystems via direct effects on the organisms present and by disrupting trophic interactions (McKinney 2002). Urban trees and their herbivores have lived in warmer temperatures for decades. Our results support the hypothesis that warming increases herbivore, specifically *M. tenebricosa* and likely other scale species, abundance directly, more than by disrupting biotic control by natural enemies. Within the next century, the global climate is projected to increase by 2-3° C (Meehl et al. 2007, Hansen et al. 2010). The warmest trees in our study were less than 2° C warmer than the coolest trees and had over 2000 more scale insects per 0.6 m of twig. Trees cool urban habitats through transpiration and by providing shade (Oke et al. 1989). Pests decrease these services by reducing plant photosynthesis and growth (Cockfield et al. 1987, Schaffer & Mason 1990, Vranjic & Ash 1997, Zvereva et al. 2010), especially at warmer temperatures (Zvereva et al. 2010). This likely occurs in our system because *M. tenebricosa* feeding causes branch dieback and premature leaf drop (Metcalf 1922, Frank et al. 2013). Although our study was limited to one herbivore pest, our results suggest that as cities become warmer, herbivores will reduce plant health and the ecosystem services they provide. Mitigation of this reduction may include planting trees that are less susceptible to known urban pests (Lacan & McBride 2008) or increasing vegetation complexity in urban habitats to maximize plant ecosystem services.

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Table 1. Correlations between each vegetation structural complexity strata predicting mean tree canopy temperature and mean *Melanaspis tenebricosa* abundance.

Vegetation strata	Seven-month mean temperature			Mean <i>M. tenebricosa</i> abundance		
	df	<i>r</i>	<i>P</i>	df	<i>r</i>	<i>P</i>
Ground cover	24	0.10	0.61	24	0.05	0.82
Annuals/perennials	24	0.32	0.11	24	0.32	0.11
Shrubs	24	0.08	0.69	24	0.12	0.57
Understory tree	24	0.62	0.0007	24	0.41	0.04
Overstory tree	24	0.49	0.01	24	0.42	0.03
Total complexity	24	0.57	0.002	24	0.40	0.045
Shannon's <i>H</i>	24	0.49	0.01	24	0.47	0.02

Notes: Degrees of freedom (df) =  $N - 2$ , where  $N$  is number of plots. Correlation coefficient (*r*) and *P* indicate strength of correlation and significance, respectively.

Table 2. Model fit indices used to help determine the best model for path analysis.

Model	<i>N</i> var.	<i>N</i> par.	GFI	Adjusted GFI	AIC	SBC	BCFI	RMSEA
1	7	21	0.77	0.06	77.54	103.96	0.76	0.40
2	6	18	0.86	0.02	52.7	75.35	0.74	0.43
3	7	21	0.82	0.29	67	93.42	0.85	0.32

Notes: Abbreviations are *N* var., number of variables; *N* par., number of parameters; GFI, goodness-of-fit index; AIC, Akaike information criterion; SBC, Schwarz Bayesian criterion; BCFI, Bentler comparative fit index; RMSEA, root mean square error of approximation. The adjusted GFI is a goodness-of-fit index that is adjusted for the degrees of freedom of the model.

Table 3. Total (direct + indirect) effects of explanatory variables (side headings) on response variables.

Variables	Total effect	SE	<i>t</i>	<i>P</i>
<b>Mean temperature</b>				
Mean temperature	0	0	0	0
Parasitoid abundance	0.22	0.25	0.86	0.39
<i>M. tenebricosa</i> abundance	0.63	0.14	4.45	<b>&lt;0.0001</b>
Predator abundance	-0.32	0.29	-1.08	0.28
<b>Parasitoid abundance</b>				
Mean temperature	0	0	0	0
Parasitoid abundance	0	0	0	0
<i>M. tenebricosa</i> abundance	-0.19	0.18	-1.08	0.28
Predator abundance	0	0	0	0
<b>Predator abundance</b>				
Mean temperature	0	0	0	0
Parasitoid abundance	0	0	0	0
<i>M. tenebricosa</i> abundance	-0.008	0.16	-0.05	0.96
Predator abundance	0	0	0	0
<b>Percent coarse vegetation</b>				
Mean temperature	0	0	0	0
Parasitoid abundance	-0.14	0.23	-0.58	0.56
<i>M. tenebricosa</i> abundance	0.03	0.06	0.48	0.63
Predator abundance	-0.18	0.27	-0.66	0.51
<b>Percent impervious surface</b>				
Mean temperature	0.59	0.13	4.62	<b>&lt;0.0001</b>
Parasitoid abundance	0.13	0.15	0.84	0.40
<i>M. tenebricosa</i> abundance	0.38	0.12	3.08	<b>0.002</b>
Predator abundance	-0.19	0.18	-1.04	0.30
<b>Vegetation complexity</b>				
Mean temperature	-0.28	0.14	-1.93	<i>0.05</i>
Parasitoid abundance	-0.34	0.18	-1.84	<i>0.07</i>
<i>M. tenebricosa</i> abundance	-0.12	0.11	-1.08	0.28
Predator abundance	0.01	0.22	0.06	0.95

*Notes:* Total effect, SE, *t*, and *P* value are listed per cell. Effects indicate the magnitude of the explanatory variable's effect on the response; *t* values are representative of the importance of the relationship. Values in boldface type are significant ( $P < 0.05$ ) and values in italics are nearly significant.

Table 4. Total (direct + indirect) effects of explanatory variables on response variables when using Shannon's H diversity index as a measure of vegetation structural complexity. Total effect, standard error, t-value, and p-value are listed per cell. Effects indicate the magnitude of the explanatory variable's effect on the response. T-values are representative of the importance of the relationship. Bolded numbers are significant (P<0.05).

	Effect / Standard Error / t-value / p-value					
	Mean	Parasitoid	Predator	%	%	Shannon's
	Temp.	abund.	abund.	Coarse	Imperv.	Diversity
				Veg.	surface	Index
Mean	0	0	0	0	0.65	-0.18
Temp.					0.13	0.15
					5.16	-1.18
					<b>&lt;0.0001</b>	0.24
Parasitoid	0.33	0	0	-0.15	0.22	-0.13
abund.	0.25			0.24	0.17	0.20
	1.35			-0.61	1.29	-0.66
	0.18			0.54	0.20	0.51
<i>M.</i>	0.61	-0.19	-0.008	0.03	0.39	-0.10
<i>tenebricosa</i>	0.14	0.18	0.16	0.07	0.12	0.11
abund.	4.48	-1.08	-0.05	0.47	3.18	-0.88
	<b>&lt;0.0001</b>	0.28	0.96	0.64	<b>0.001</b>	0.38
Predator	-0.19	0	0	-0.23	-0.12	0.28
abund.	0.28			0.27	0.18	0.21
	-0.67			-0.85	-0.66	1.36
	0.50			0.39	0.51	0.17



Figure 1. Photographs of a *M. tenebricosa* - infested red maple tree in an urban landscape. Close-up of a twig heavily infested with *M. tenebricosa* (left). Red maple street tree located in a simple urban habitat composed of turf and impervious surface in Raleigh, North Carolina, USA (right).

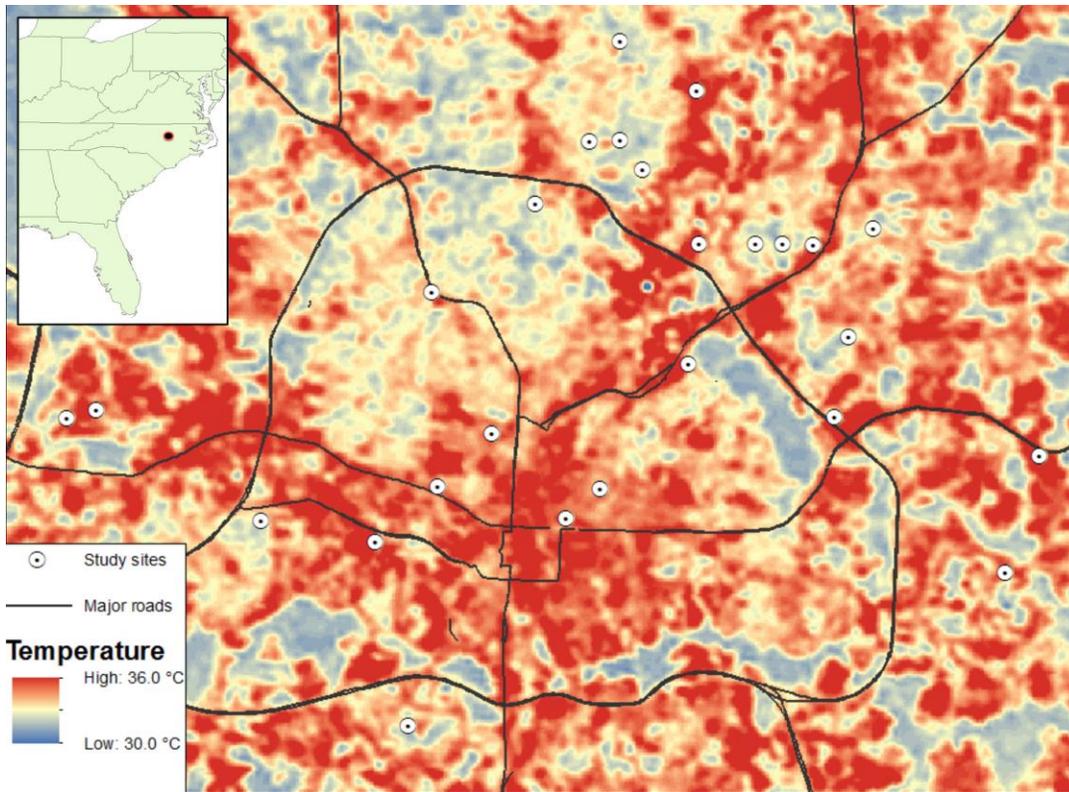


Figure 2. Thermal map of surface temperature measurements in the Raleigh, North Carolina metropolitan area on 18 August 2007. Temperatures range from 30°C to 36°C, designated by the darkest blue and red regions, respectively. White circles with black dots indicate selected red maple study sites. Inset map in the upper left corner illustrates the regional location of Raleigh, North Carolina in the southeastern United States.

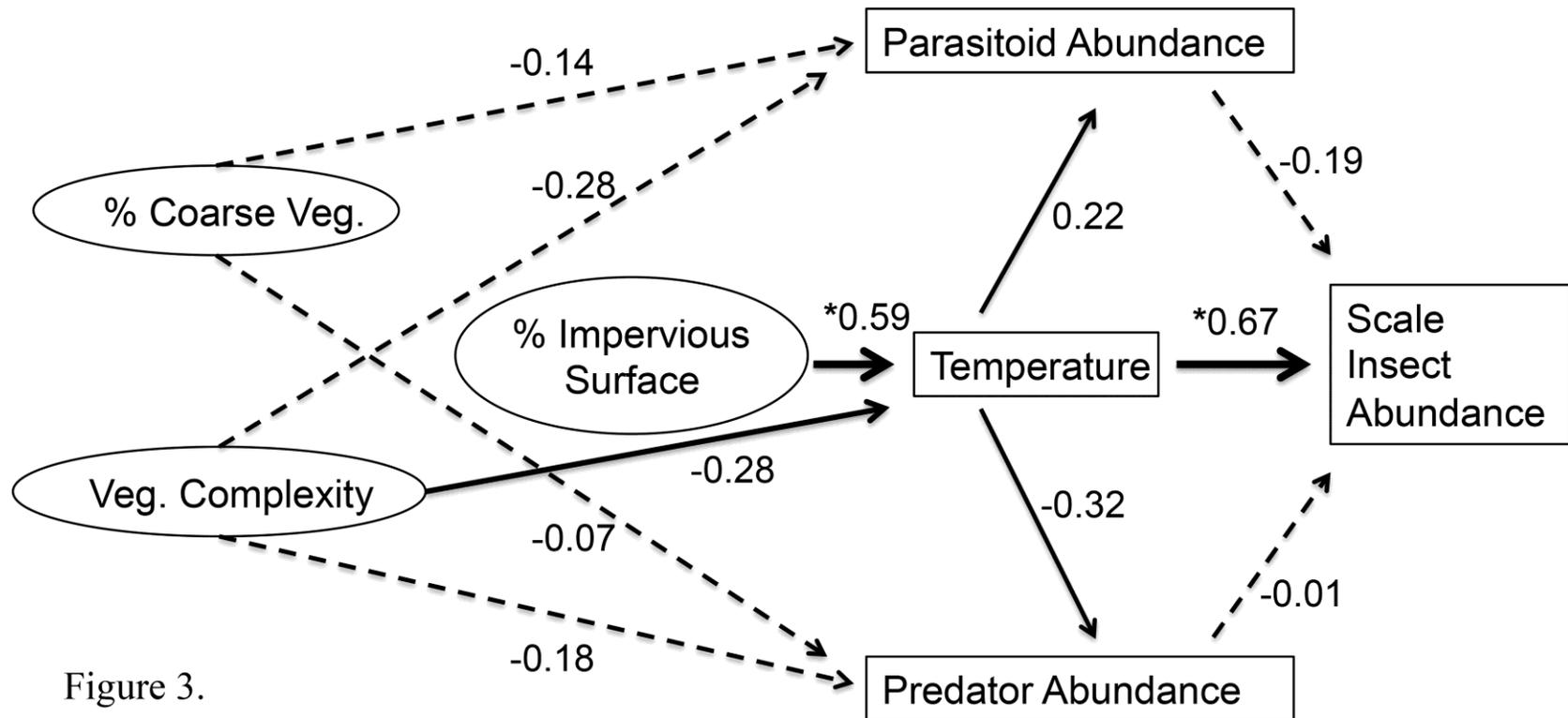


Figure 3.

Figure 3. Model 3 path diagram illustrating the direct effects of each exogenous (circles) and endogenous (rectangles) variable in our study system. Dashed arrows show the hypothesized direct biotic effects (enemies hypothesis) regulating *M. tenebricosus* abundance. Solid arrows show the hypothesized direct abiotic effects (temperature) regulating *M. tenebricosus* abundance. Asterisks indicate relationship is significant ( $P < 0.05$ ).

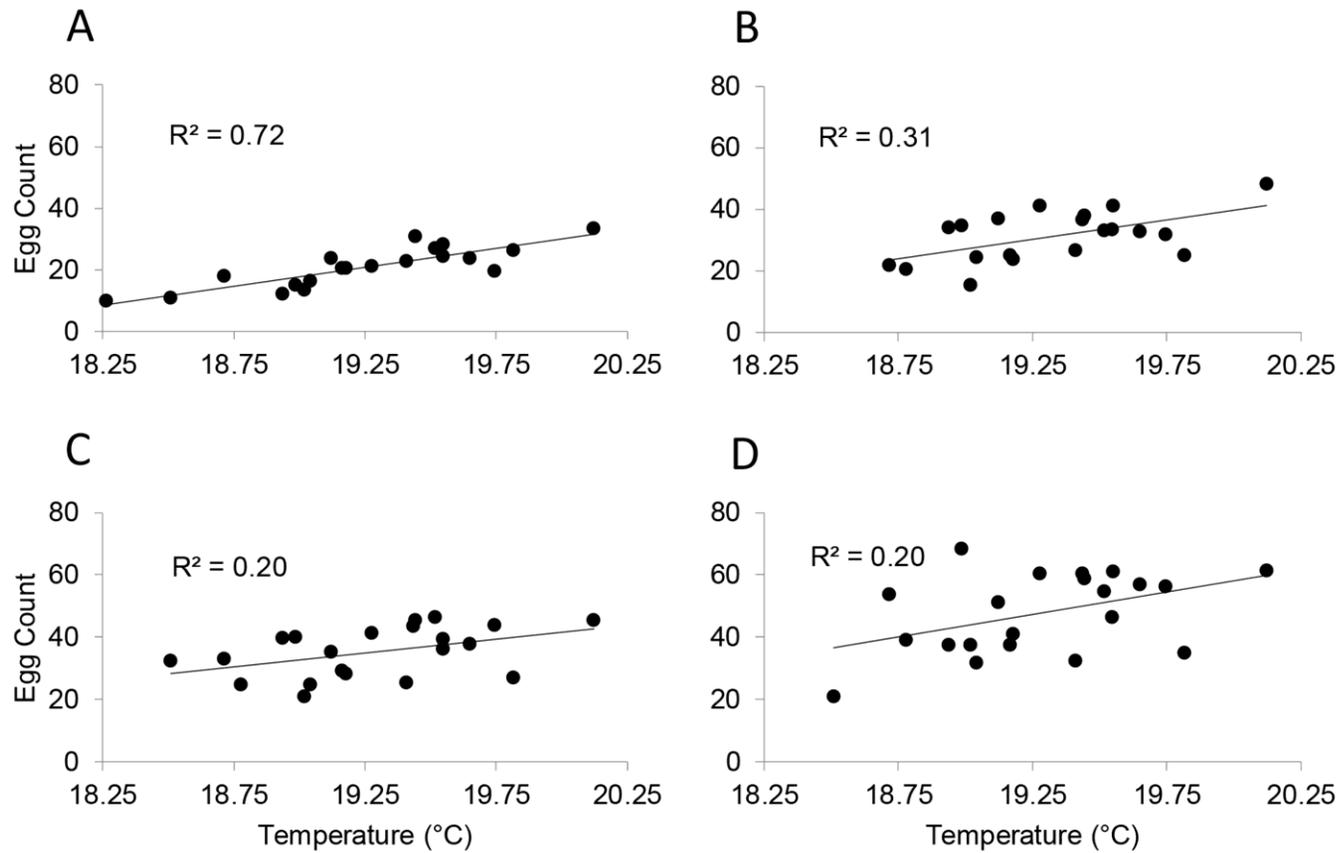
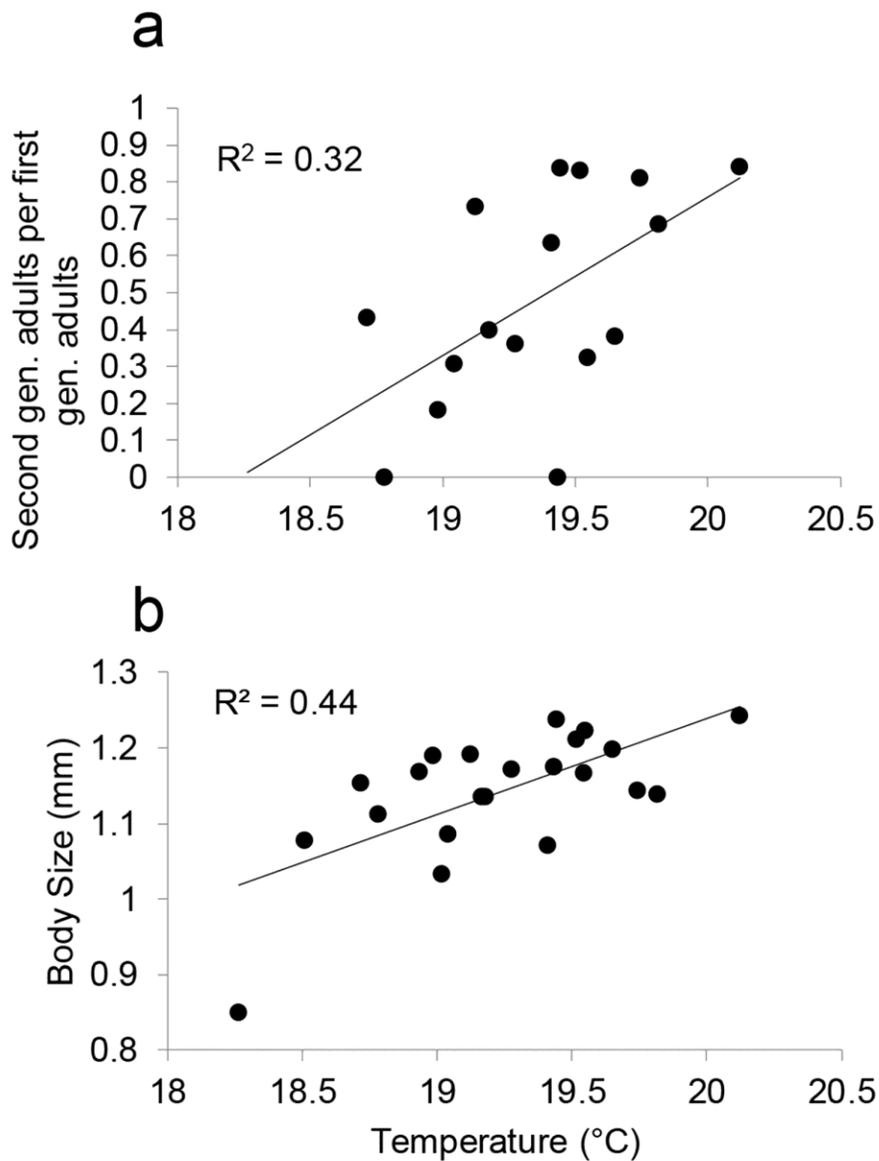


Figure 4.

Figure 4. Relationship between seven-month mean temperature and mean egg count per female on four dates in 2013. (A) 1 April,  $y=12.30X - 215.7$ . (B) 16 April,  $y=12.59X - 211.9$ . (C) 23 April,  $y=8.871X - 135.8$ . (D) 12 May,  $y=14.46X - 231$ . All regression models are statistically significant ( $P<0.05$ ).



**Figure 5.**

Figure 5. Relationship between seven-month mean temperature and (A) the ratio of second- to first-generation adult *M. tenebricosos* ( $y = 0.428x - 7.79$ ) and (B) mean adult female *M. tenebricosos* body size ( $y = 0.127x - 1.301$ ). Both regression models are statistically significant ( $P < 0.05$ ).

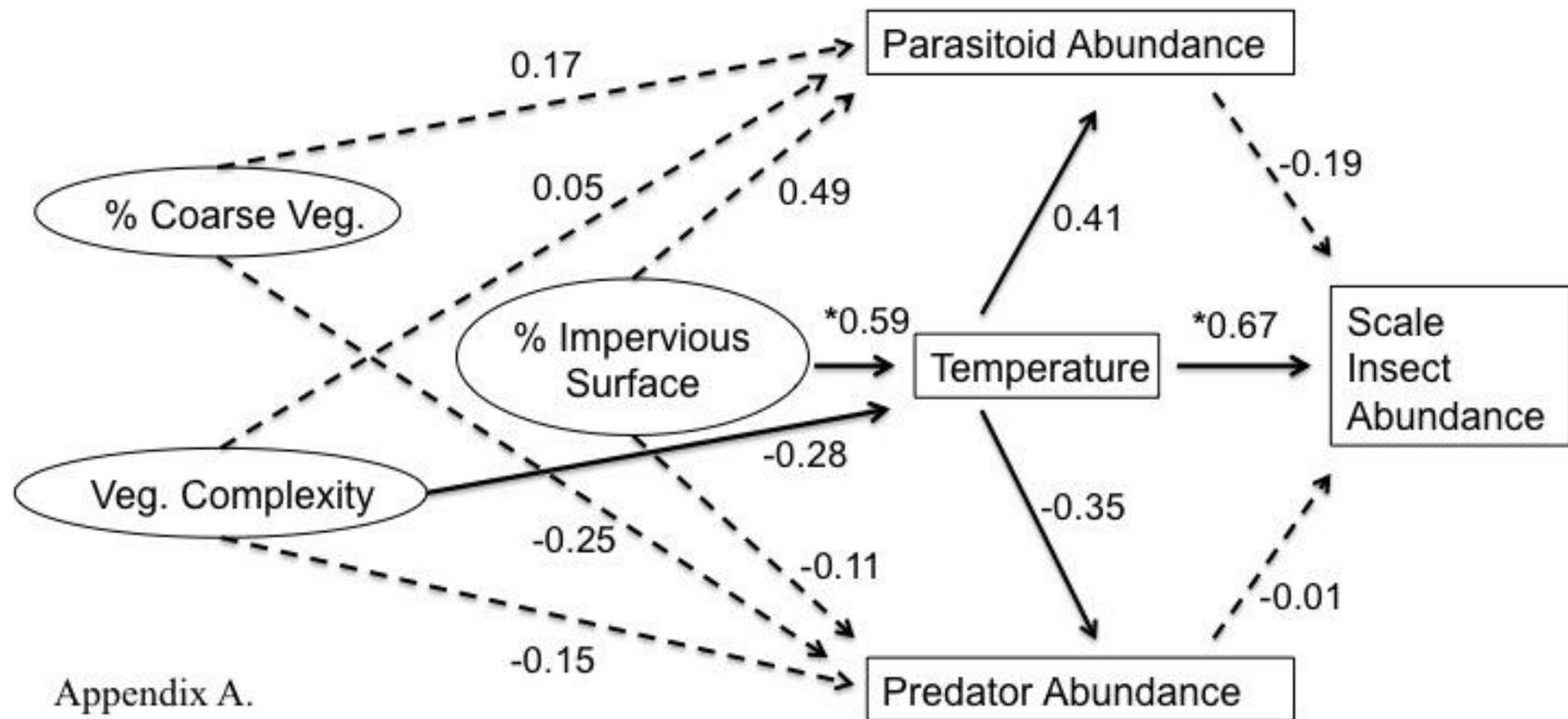
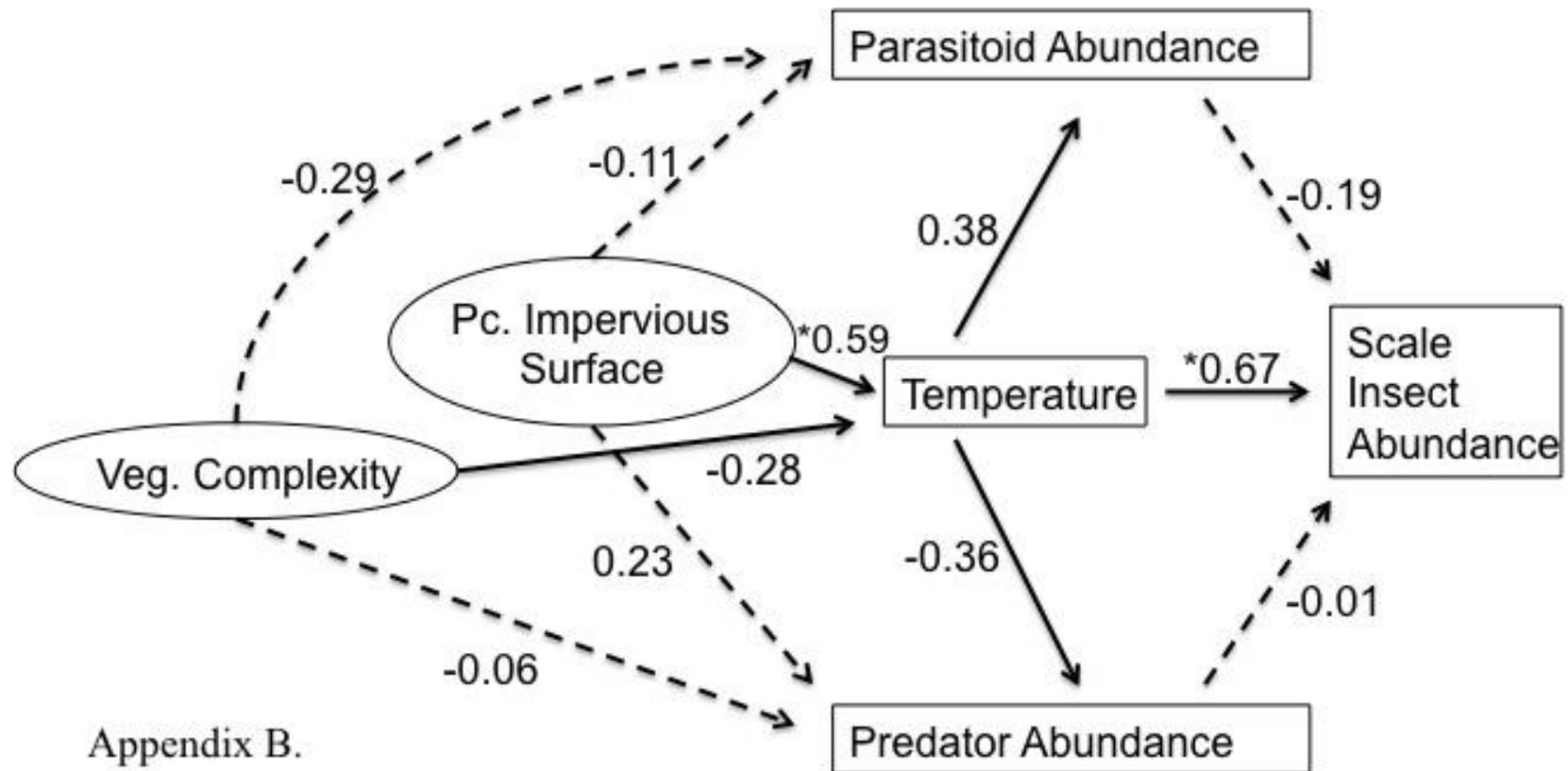


Figure 6. Model 1 path diagram illustrating the direct effects of each exogenous (circles) and endogenous (rectangles) variable in our study system. Unlike the selected model, this model includes path coefficients from impervious surface cover to parasitoid and predator abundance. Dashed arrows show the hypothesized direct biotic effects (enemies hypothesis) regulating *M. tenebricosa* abundance. Solid arrows show the hypothesized direct abiotic effects (temperature) regulating *M. tenebricosa* abundance. Asterisks indicate relationship is significant ( $P < 0.05$ ).



Appendix B.

Figure 7. Model 2 path diagram illustrating the direct effects of each exogenous (circles) and endogenous (rectangles) variable in our study system. Unlike the selected model, this model excludes coarse vegetation groundcover from the analysis. Dashed arrows show the hypothesized direct biotic effects (enemies hypothesis) regulating *M. tenebricosa* abundance. Solid arrows show the hypothesized direct abiotic effects (temperature) regulating *M. tenebricosa* abundance. Asterisks indicate relationship is significant ( $P < 0.05$ ).

## **CHAPTER 2: The effects of urban warming on herbivore abundance and street tree condition**

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*Key words:* *Melanaspis tenebricosa*, *Acer rubrum*, urban forest, urban ecology, temperature, climate change, street trees, tree inventory

## Abstract

Trees are essential to urban habitats because they provide services that benefit the environment and improve human health. Unfortunately, urban trees often have more herbivorous insect pests than rural trees but the mechanisms and consequences of these infestations are not well documented. Here, we examine how temperature affects the abundance of a scale insect, *Melanaspis tenebricosa* (Comstock) (Hemiptera: Diaspididae), on one of the most commonly planted street trees in the eastern U.S. Next, we examine how both pest abundance and temperature are associated with water stress, growth, and condition of 26 urban street trees. Although trees in the warmest urban sites grew the most, they were more water stressed and in worse condition than trees in cooler sites. Our analyses indicate that visible declines in tree condition were best explained by scale-insect infestation rather than temperature. To test the broader relevance of these results, we extend our analysis to a database of more than 2700 Raleigh, US street trees. Plotting these trees on a Landsat thermal image of Raleigh, we found that warmer sites had over 70% more trees in poor condition than those in cooler sites. Our results support previous studies linking warmer urban habitats to greater pest abundance and extend this association to show its effect on street tree condition. Our results suggest that street tree condition and ecosystem services may decline as urban expansion and global warming exacerbate the urban heat island effect. Although our non-probability sampling method limits our scope of inference, our results present a gloomy outlook for urban forests and emphasize the need for management tools. Existing urban tree inventories and thermal maps could be used

to identify species that would be most suitable for urban conditions.

## Introduction

Trees provide ecosystem services that mitigate the negative effects of urban habitats on human and environmental health (Oke et al. 1989, Pataki et al. 2006, Donovan et al. 2013). For example, trees reduce urban temperatures, filter air, fix carbon, and reduce energy use through photosynthesis, transpiration, and by providing shade (Oke et al. 1989, Boyd et al. 2013). Unfortunately, many herbivorous pests are more abundant and damaging on urban trees than in natural habitats (Putnam 1880, Metcalf 1912, 1922, Raupp et al. 2010). In addition, abiotic stress such as heat and drought are often more severe in urban habitats (Kim 1992, Coffelt and Schultz 1993, Raupp et al. 2010). Individually, herbivory or abiotic stress can reduce tree photosynthesis, growth, and survival (Cockfield et al. 1987, Schaffer and Mason 1990, Vranjic and Ash 1997, Brightwell and Silverman 2009, Zvereva et al. 2010). Although not as well documented, these stresses likely occur in concert with one another and combine to reduce tree health and the services trees provide.

Heat is a ubiquitous abiotic stress within urban habitats. Cities can be up to 10 °C warmer than surrounding rural areas due to impervious surface cover, anthropogenic heat sources, and low vegetation cover (Oke 1973, Kim 1992). Warmer temperatures increase vapor pressure deficits (Jenerette et al. 2009), which create greater atmospheric demand for water via transpiration (Whitlow and Bassuk 1988, Álvarez et al. 2011). Furthermore, heat and impervious surfaces reduce soil moisture, limiting the amount of water available to roots (Katul et al. 2003, Jenerette et al. 2009). Thus, greater transpiration demand may not be met because warmer temperatures and dry soils can also limit stomatal conductance (McDowell et al.

2008, Álvarez et al. 2011). Therefore, trees stressed by heat and water deficits may not grow optimally, which limits the services they can provide.

Warmer temperatures also increase herbivorous pest abundance on urban trees by increasing insect fecundity and survival (Meineke et al. 2013, Dale and Frank In press). Dale and Frank (Dale and Frank In press) found that an armored scale insect, *Melanaspis tenebricosa* (Comstock) (Hemiptera: Diaspididae), produced 52% more eggs per adult female with a 1.6° C increase in average site temperature. This contributed to three orders of magnitude more scale insects on street trees at warmer urban sites. Herbivore feeding, particularly by sap-feeding insects, increases water stress (Cockfield and Potter 1986), and reduces tree photosynthesis (Cockfield et al. 1987), growth (Vranjic and Ash 1997, Brightwell and Silverman 2009), and aesthetic quality (Frank et al. 2013). Thus, on trees that are already stressed by warmer urban temperatures, herbivore feeding may further reduce plant vigor and services (Zvereva et al. 2010).

Our hypothesis was that urban heat increases *M. tenebricosa* abundance and that these two factors concurrently increase tree water stress and reduce tree condition. To test this hypothesis, we first determined how temperature affects *M. tenebricosa* abundance on red maple (*Acer rubrum*) street trees. To determine how temperature and pest abundance affect tree stress and growth, we measured tree midday water potential, DBH, and branch growth at various levels of scale insect abundance and temperature. Lastly, we used a standardized method for rating tree condition and a citywide tree inventory to compare trees at various levels of scale insect abundance and temperature within the city. Understanding how urban

conditions reduce street tree condition is essential to our understanding of these ecosystems and managing their resources.

## Methods

### *Study System: A. rubrum and M. tenebricosa*

Maple trees are among the most common street trees in North Carolina (Personal observation) and the eastern United States (Raupp et al. 2006). Red maples are deciduous, bottomland tree species indigenous to the eastern United States (Nesom 2006). Gloomy scale, *M. tenebricosa*, is a native armored scale insect that lives on the trunk and branches of maple trees, where it feeds on cambial parenchyma cells (Beardsley and Gonzalez 1975). Heavily infested trees exhibit darkened, discolored bark, twig and branch dieback, and eventually die (Metcalf 1922). These scale insects are more abundant on urban than rural red maple trees, and in the southeastern U.S. have been the most important pest of red maple street trees for over a century (Metcalf 1922, Frank et al. 2013).

### *Study Sites*

We conducted field studies on red maple trees at 26 sites throughout the Raleigh, NC metropolitan area. All study trees were property of the city of Raleigh, NC. We were granted permission to conduct research on these trees by the Raleigh Parks, Recreation, and Human Resources department. We used a GIS street tree inventory map of city-owned red maples (provided by Raleigh Parks, Recreation, and Human Resources) throughout Raleigh, NC in ArcMap (ArcGIS Desktop 10,

Redlands, CA). Sites were selected using a Landsat thermal image acquired on 18 August 2007, prepared as described in (Meineke et al. 2013) and overlaid with the tree inventory map (Figure 1b). The thermal map illustrates variation in surface temperature throughout the city, ranging from 24 to 36 °C and designating relatively cool and hot regions as a gradient of blue to red, respectively. We selected 13 red maples within the hottest regions and 13 within the coolest regions of the thermal map, each separated by more than 400 m (Figure 1a). Due to the mechanisms that cause urban sites to experience warmer and cooler temperatures, there are inherent differences in study site vegetation and impervious surface cover (Dale and Frank In press).

*Objective 1: Determine the effect of temperature on M. tenebricosa abundance*

Thermal mapping was used for initial tree selection and gave relative site surface temperatures when the image was taken on 18 August 2007. To determine actual tree canopy temperatures, we placed iButton thermochron DS1921G (Dallas Semiconductor of Dallas, TX) remote temperature loggers within 59 ml portion containers (Dart Container Corporation Mason, MI) and fastened them to the underside of a branch within the canopy of each study tree.. This method protected iButtons from direct sunlight and precipitation. iButtons recorded temperature every hour from April 2012 to April 2013. Due to loss of iButtons, complete 12-month temperature readings were only available for 22 of the 26 sites. Therefore, we used 7 months for which all sites had complete temperature data. These months in

chronological order from 2012 to 2013 were: June, July, August, September, February, March, and April.

To measure *M. tenebricosa* abundance, we pruned one haphazardly selected 0.15 m terminal twig from four cardinal directions on each of our 26 study trees as described in [23]. To avoid biased selection, twigs were chosen based on length, presence of live foliage, and at a height of at least 3 meters at which point *M. tenebricosa* are not visually discernable. We collected twigs on four dates in 2012: 5 and 20 April, and 3 and 18 May. Twigs were examined under a dissecting microscope to record scale insect abundance per 0.6 m. In a previous study [23], we determined the importance of temperature in predicting scale insect abundance as it was influenced by several other exogenous variables in a path model. Here we were interested in the direct effect of temperature on scale insect abundance so we could then understand the effects of scale insect abundance and temperature on trees in Objectives 2 and 3. We tested the effect of mean 7-month tree canopy temperature on *M. tenebricosa* abundance using simple linear regression (JMP, Version 10. SAS Institute Inc., Cary, NC). Residuals of the simple regression of mean 7-month temperature predicting mean *M. tenebricosa* abundance followed a non-normal distribution (Shapiro-Wilk  $W=0.902$ ,  $P=0.017$ ). As such, scale insect abundance data were  $\log_{10}(x+1)$  transformed to improve normality of the residuals. The resulting model followed the form:

$$\log(y_i) = a + b_1x_1 \quad \text{Eq. 1}$$

where  $\log(y_i)$  is the observed response in  $\log_{10}$  transformed *M. tenebricosa* abundance for the  $i^{\text{th}}$  tree;  $a$  is the y-intercept parameter to be estimated;  $b_1$  is the slope parameter to be estimated; and  $x_1$  is mean 7-month tree canopy temperature.

*Objective 2: Determine how temperature and M. tenebricosa abundance affect tree water potential and growth*

Plant water potential is among the most accurate measures of plant moisture stress (McCutchan and Shackel 1992, De Swaef et al. 2009). It quantifies the amount of transpiration-driven negative pressure required to pull water up from the roots to the leaves (Scholander et al. 1965). Water-stressed plants require greater force to move water throughout their vascular system (Scholander et al. 1965) and have a more negative water potential. Midday water potential is a measure of the peak stress level that a plant experiences during the day (McCutchan and Shackel 1992). We measured midday water potential from noon to 3:00 pm on 5, 7, 8, and 9 August 2013 with a pressure chamber (PMS Instrument Company, Albany, OR). Site sampling order was randomized. We collected one 25 cm twig with 10 to 30 fully expanded leaves from sun-exposed locations approximately 5.5 m above ground from the north and south side of each tree canopy. Weather conditions were similar for each day with a mean midday temperature of approximately 31 °C, relative humidity of approximately 70% (Carolina 2013) and mostly sunny skies. We recorded xylem water potential within 5 minutes of twig abscission. We used multiple linear regression to determine how mean 7-month tree canopy temperature, *M. tenebricosa* abundance, and their interaction affect water potential (Eq. 2) in JMP

10.0. We also used multiple linear regression to test this hypothesis using two other temperature metrics in place of 7-month temperature to determine the temporal scale at which the urban environment affects tree stress: mean August temperature (Eq. 3) and midday temperature (Eq. 4) during the time of sampling. The resulting models were:

$$y_i = a + b_1 \log(x_1) + b_2 x_2 + b_3 \log(x_1)x_2 \quad \text{Eq. 2}$$

$$y_i = a + b_1 \log(x_1) + b_2 x_2 + b_3 \log(x_1)x_2 \quad \text{Eq. 3}$$

$$y_i = a + b_1 \log(x_1) + b_2 x_2 + b_3 \log(x_1)x_2 \quad \text{Eq. 4}$$

where  $y_i$  is the observed response in mean water potential for the  $i^{\text{th}}$  tree;  $a$  is the y-intercept parameter to be estimated;  $b_i$  is the slope parameter to be estimated;  $\log(x_1)$  is  $\log_{10}$  transformed mean *M. tenebricosa* abundance;  $x_2$  is mean 7-month tree canopy temperature (Eq. 2), mean August tree canopy temperature (Eq. 3), or mean midday tree canopy temperature (Eq. 4); and  $\log(x_1)x_2$  is the interaction term between temperature and *M. tenebricosa* abundance.

As a second evaluation of tree stress, we determined annual growth by measuring change in diameter at breast height (DBH). DBH measurements were conducted in accordance with National Forest Service guidelines (USDA 2007) and taken at exactly 1.4 m above the highest ground on each study tree in June 2012 and July 2013. We calculated change in DBH as a measure of annual tree growth, which is reflective of tree vigor and carbon sequestration. Change in DBH was  $\log_{10}(x+1)$  transformed to meet assumptions of linear regression analysis. In addition, change in DBH was dependent upon initial DBH. Therefore, we conducted a partial correlation by including the residuals of the correlation between initial DBH and

change in DBH as a predictor variable. We used multiple linear regression to determine how mean seven-month temperature, *M. tenebricosa* abundance, and their interaction affect change in DBH over one year in JMP 10.0. The resulting model was:

$$\log(y_i) = a + b_1 \log(x_1) + b_2 x_2 + b_3 \log(x_1)x_2 + b_4 x_4 \quad \text{Eq. 5}$$

where  $\log(y_i)$  is the observed response in  $\log_{10}$  transformed change in tree DBH for the  $i^{\text{th}}$  tree;  $a$  is the y-intercept parameter to be estimated;  $b_i$  is the slope parameter to be estimated;  $\log(x_1)$  is  $\log_{10}$  transformed mean *M. tenebricosa* abundance;  $x_2$  is mean 7-month tree canopy temperature;  $\log(x_1)x_2$  is the interaction term between temperature and *M. tenebricosa* abundance; and  $x_4$  is the residuals of the correlation between initial DBH and change in DBH.

Since change in DBH is often a slow progression of growth over a single year, we measured annual stem elongation as a historical assessment of resource allocation to above ground growth (Johns et al. 2013). We randomly selected and pruned one twig from 8 sides of the canopy from each study tree. In late fall of 2013 we located and measured the distance from the apical tip to the most recent bud scar (2013 growth) and the distance from bud scar to previous bud scar, accounting for 2012 and 2011 growth. We then calculated mean annual growth over the past three years for each tree. We used multiple linear regression to determine how mean seven-month temperature, *M. tenebricosa* abundance, and their interaction affect mean annual stem elongation in JMP 10.0. The resulting model was:

$$y_i = a + b_1 \log(x_1) + b_2 x_2 + b_3 \log(x_1)x_2 \quad \text{Eq. 6}$$

where  $y_i$  is the observed response in 3-year mean annual stem elongation for the  $i^{\text{th}}$  tree;  $a$  is the y-intercept parameter to be estimated;  $b_i$  is the slope parameter to be estimated;  $\log(x_1)$  is  $\log_{10}$  transformed mean *M. tenebricosa* abundance;  $x_2$  is mean 7-month tree canopy temperature; and  $\log(x_1)x_2$  is the interaction term between temperature and *M. tenebricosa* abundance.

*Objective 3: Determine how temperature and M. tenebricosa abundance affect tree condition*

To qualitatively rate overall tree condition, each study tree was rated following the protocol used by the Raleigh Parks, Recreation, and Human Resources department, similar to that used by Berrang et al. (Berrang et al. 1985). These condition ratings are: Excellent, good, fair, poor, and dead. “Dead” trees were those with brittle branches and no live foliage but were not included in our study. “Poor” trees had many dead branches, broken branch tips, a broken central leader, exposed roots, and/or crispy leaves. “Fair” trees had some dead branches, wilted leaves, and less severe symptoms than poor trees. “Good” trees had no significant dead branches, no injuries, and may have sparse or coarse foliage. “Excellent” trees were defined as those with healthy foliage and full canopies. We recruited two volunteers in addition to a primary investigator to conduct tree condition evaluations on each of our study trees. For each tree, condition was recorded as the most common rating (shared by at least 2 of 3 observers). Using this method, we used multiple logistic regression to determine how seven-month temperature, scale insect

abundance, and their interaction affect tree condition in JMP 10.0. The multiple logistic regression model was:

$$p(y_i) = \frac{e^{a+b_1 \log(x_1)+b_2x_2+b_3 \log(x_1)x_2}}{1 + e^{a+b_1 \log(x_1)+b_2x_2+b_3 \log(x_1)x_2}} \quad \text{Eq. 7}$$

where  $p(y_i)$  is the observed probability of a change in tree condition for the  $i^{\text{th}}$  tree as temperature and scale insect abundance change;  $a$  is the y-intercept parameter to be estimated;  $b_1$  is the slope parameter to be estimated;  $\log(x_1)$  is  $\log_{10}$  transformed mean *M. tenebricosa* abundance;  $x_2$  is mean 7-month tree canopy temperature; and  $\log(x_1)x_2$  is the interaction term between temperature and *M. tenebricosa* abundance.

To determine if temperature affects street tree condition across the entire city, we analyzed tree condition ratings for 2780 city-owned red maple trees in Raleigh, NC. Starting with a tree inventory of over 8000 city-owned red maple trees created by the Raleigh Parks, Recreation, and Human Resources department (Figure 1b), we compared tree condition ratings to projected site surface temperatures. The thermal map projected surface temperature values representative of daily maximum August temperature at a 30 x 30 m resolution. In multiple instances, a 30 x 30 m thermal polygon contained more than one red maple tree. To prevent pseudo replication by selecting trees within the same polygon, we used ArcMap GIS software to randomly select one red maple tree within each discriminant polygon of the thermal map. We used Hawth's tools for spatial ecological analysis to randomly select one tree within each temperature polygon containing one or more red maple trees. Interpolated site temperature values were then extracted at each selected point and compiled in an attribute table with corresponding tree condition ratings and

DBH measurements. We selected trees to fall within the DBH range of our study trees (15.2 to 50.8 cm) to control for the effect of age on condition rating and to homogenize the inventory with our sample trees.

Due to a lack of fit in logistic regression and since Landsat surface temperature projections are discrete values, we classified temperature values into categorical variables for comparison with tree condition rating. Temperature values for the remaining 2780 trees were divided at the median (29.26 °C) into “warm” and “cool” temperature classifications. The citywide data separated at the median represent a more conservative analysis of temperature effects on tree condition since they mostly include medium temperature trees. Because of this, we also classified the upper and lower quartile of the citywide distribution as “hot” and “cold”, respectively. This gives a more similar representation of our subsample and shows temperature extremes that will become more common as urban warming couples with global climate change. “Excellent” and “poor” ratings were compared between temperature classifications because they were the most confidently rated tree conditions. We conducted contingency analyses and Pearson’s chi square tests to test the hypothesis that tree condition is dependent on site temperature using JMP 10.0.

## Results

### *Objective 1: Determine how temperature affects M. tenebricosa abundance*

Mean *M. tenebricosa* abundance included all life stages and ranged from 0 to 2241 live individuals per 0.6 m of twig with a mean ( $\pm$ SD) of 444 ( $\pm$ 683.66). Seven-

month mean tree canopy temperature ranged from 18.3 to 20.1°C with a mean of 19.2°C ( $\pm 0.44$ ). Mean log *M. tenebricosa* abundance per 0.6 m of twig was significantly ( $\alpha = 0.05$ ), positively correlated with seven-month mean tree canopy temperature (Figure 2, Table 1).

*Objective 2: Determine how temperature and M. tenebricosa abundance affect tree water potential and growth*

Mean midday stem water potential ranged from -1.21 to -3.10 MPa with a mean ( $\pm$ SD) of -2.19 MPa ( $\pm 0.39$ ). Multiple linear regression revealed no association between midday tree canopy temperature and mean tree water potential, mean *M. tenebricosa* abundance, or their interaction (Table 1). Based on multiple linear regression, mean August temperature was significantly associated with mean water potential but *M. tenebricosa* abundance was not (Figure 3, Table 1). There was a nearly significant interaction between mean *M. tenebricosa* abundance and mean August temperature in predicting mean water potential (Table 1), suggesting that the effect of temperature on water potential may not be independent of scale insect abundance. Multiple linear regression using mean 7-month temperature revealed a significant association with mean water potential, while mean *M. tenebricosa* abundance was not (Table 1). As temperature increased, mean water potential significantly decreased. There was also a nearly significant interaction between 7-month temperature and *M. tenebricosa* abundance in predicting water potential (Table 1). Variance inflation factors (VIF) for each tested model did not suggest an effect of collinearity on the output (VIF < 3).

Change in DBH ranged from 0 to 4.3 cm with a mean ( $\pm$ SD) of 1.3 cm ( $\pm$ 1.08). The full model predicting change in DBH was significant and explained approximately 91% of the variation in the dataset (Table 1). Change in DBH was positively associated with mean 7-month tree canopy temperature, but we detected no effect of *M. tenebricosa* abundance, or its interaction with temperature (Table 1). Although collinearity is a potential influence, VIF values for the full model did not suggest an effect of collinearity on the results ( $VIF < 2$ ). Three-year mean annual stem elongation ranged from 0.08 to 0.49 m with a mean of 0.27 m ( $\pm$ 0.11) and was not associated with mean 7-month tree canopy temperature, mean *M. tenebricosa* abundance, or their interaction (Table 1).

*Objective 3: Determine how temperature and M. tenebricosa abundance affect tree condition*

Landsat surface temperatures correlated well with 7-month mean iButton tree canopy temperatures ( $r = 0.76$ ), supporting our use of Landsat surface temperature as a proxy for tree canopy temperature. The full logistic regression model predicting tree condition was significant and explained 44% of the variation in the model (Table 2). *Melanaspis tenebricosa* abundance was significantly associated with tree condition, while seven-month temperature and the interaction between the two were not (Table 2). As *M. tenebricosa* abundance increased, the probability of finding a tree in poor condition significantly increased while the probability of finding a tree in excellent condition significantly decreased (Figure 4). These results suggest that

temperature does not contribute any additional value to predicting the variation in tree condition that *M. tenebricosa* is able to predict on its own.

Global contingency analysis of tree condition and site temperature divided at the median showed that there was a significant difference in the likelihood of tree condition rating between warm and cool sites (Table 3). Pairwise comparison of excellent and poor condition trees revealed that trees in warm sites are significantly more likely to be in poor condition than those in cool sites (Figure 5a, Table 3). In addition, over 63% of trees in poor condition were located in warm sites (Table 4).

The upper quartile included sites greater than or equal to 30.68° C and lower quartile sites were less than or equal to 27.74° C. Global contingency analysis of these data also showed a significant difference in the likelihood of tree condition ratings between hot and cold sites (Table 3). Pairwise comparison of excellent and poor condition trees revealed that trees in hot sites were significantly more likely to be in poor condition when compared to those in cold sites (Figure 5b, Table 3). Hot sites had over twice as many trees in poor condition than cold sites (Table 4). Detecting such a difference in both median and quartile analyses further supports the suggestion that temperature is associated with tree condition.

## Discussion

Many herbivorous pests including lacebugs (Shrewsbury and Raupp 2000), mites (Kropczynska et al. 1986), caterpillars (Coffelt and Schultz 1993), soft scales (Meineke et al. 2013), and other armored scales (Hanks and Denno 1993, Tooker and Hanks 2000) are more abundant and damaging in urban than rural habitats

(Putnam 1880, Metcalf 1922, Raupp et al. 2010, Cuevas-Reyes et al. 2013).

Although the mechanisms underlying this phenomenon are not well understood (Raupp et al. 2010), mounting evidence points to high urban temperatures as an important factor (Meineke et al. 2013, Dale and Frank In press). We acknowledge that our non-probability sampling method limits the scope of inference from our sample to the total street tree population. Despite this limitation, our results suggest that urban warming increases scale insect abundance on street trees (Figure 2). Moreover, our results suggest that warming and scale insect abundance each contribute to reducing red maple street tree condition. Meineke et al. (Meineke et al. 2013) found that a soft scale insect was more abundant on warmer than cooler street trees due to an increase in scale insect survival. In a previous study, we found that *M. tenebricosa* in warmer urban habitats are more fecund than those in cooler urban habitats, leading to greater population growth rates (Dale and Frank In press). Greater survival, fecundity, and potentially other direct effects of temperature contribute to greater herbivore abundance on warmer street trees.

Heat can induce drought stress in trees by reducing soil moisture content and increasing vapor pressure deficits (Cregg and Dix 2001, Jenerette et al. 2009), which leads to a greater demand for transpiration (Whitlow and Bassuk 1988, Álvarez et al. 2011) but also stomata closure and lower photosynthesis rates (McDowell et al. 2008). In addition, impervious surfaces replace soil volume that tree roots would otherwise exploit for water and nutrient uptake. As predicted, we found that trees in warmer urban habitats were significantly more water stressed than those in cooler urban habitats (Figure 3). Although not addressed in this paper,

impervious surfaces and urban habitats also create conditions such as soil compaction that can increase water stress (Smiley 2006). Such conditions are likely also worsened by warmer temperatures. Water stress can have negative effects on tree health by causing xylem embolism and subsequent cavitation within vascular tissue, which can reduce tree condition (Sperry and Tyree 1988). We have determined that scale insect abundance is positively associated with temperature but our results may suggest that it is also influenced by water potential (Table 1). Such a relationship is supported by Cockfield and Potter (Cockfield and Potter 1986) who found a strong interaction between plant water stress and scale insect abundance on euonymus plants, as well as Hanks and Denno (Hanks and Denno 1993) who found that street tree water stress negatively affected the fitness of an armored scale insect.

In some cases plant stress can lead to greater herbivore abundance (Mattson 1980, White 1984, Miller et al. 2006, McDowell et al. 2008). For example, White (White 1984) demonstrated that stressed plants circulate greater free amino acid content throughout their vascular system, which herbivores are able to exploit during feeding. However, this primarily applies to foliar-feeding insects (White 1984). Plant water stress most often reduces the fitness of sap feeding insects (Cockfield and Potter 1986, Koricheva and Larsson 1998, Huberty and Denno 2004). Hanks and Denno (Hanks and Denno 1993) found that armored scale insect survival and abundance declined with increasing water stress on street trees. *Melanaspis tenebricosa*, in addition to other armored scale insects, feed on parenchyma cells within the cambium of trees, which does not provide direct access to vascular

circulation as in other sap-feeding insects (Beardsley and Gonzalez 1975, Miller and Davidson 2005). The mechanism behind the plant stress – herbivore relationship in our system remains unknown but is an important area for future research and may explain some of the remaining variation in *M. tenebricosa* abundance.

Warmer urban temperatures are often associated with less vegetation cover and greater sun exposure (Shrewsbury and Raupp 2000, Dale and Frank In press). These conditions can increase tree growth rates by increasing photosynthesis and carbon sequestration, especially when ample water and nutrients are available (Way and Oren 2010). Despite greater water stress at warmer temperatures, we found a significant increase in DBH growth rate as tree canopy temperature increased (Table 1), suggesting that conditions were below that which negatively affects growth. Spring and summer 2013 were also abnormally wet, with rainfall approximately 34% above normal (Carolina 2013). We suspect that this drastic increase in water availability may have reduced water stress and temperature compared to other years, allowing growth to continue where conditions would otherwise be limiting. In addition, DBH is only one component of growth and may not be representative of overall tree condition, especially at a scale as small as we found, and among trees of different ages. Stem elongation is extremely variable and dependent on sunlight exposure, competition for dominance among stems, and position within the canopy (Lambers et al. 1998). In addition, plants in poor health or that have lost tissue to herbivores sometimes compensate with greater growth on the remaining tissue (McNaughton 1983). Since *M. tenebricosa* causes branch dieback, trees with more

scales may have fewer branches than cool trees but equal growth in the branches they do have.

We found that scale insect abundance and significant reductions in tree condition coincide with a less than 2 °C increase in temperature (Figure 2, Figure 4), which global warming is predicted to exceed within this century (Christensen et al. 2007, Meehl et al. 2007, Hansen et al. 2010). Heat and scale insect abundance each contributed to reduce the condition of red maples. Although trees in poor condition comprised only 10% of red maple street trees, they were significantly more likely to be in warmer urban sites, which based on our results, may have had more *M. tenebricosa*. This difference was even significant when temperatures were divided at the median, where half of the trees were at medium temperatures. Our quartile analysis shows that the upper temperature extremes have over twice as many trees in poor condition than cooler sites, which represent conditions that may become more common as urban and global warming progress. Moreover, nearly 90% of red maple street trees are in less than excellent condition, which may reflect the unsuitability of urban habitats for red maple trees.

Management of urban forests is important but difficult due to the diversity of plants, organisms that attack them, and the conditions in which trees are planted. Different tree species have different habitat requirements based on provenance and evolutionary histories. Therefore, some trees are more suitable for street tree plantings than others. In addition, our results and others (Shrewsbury and Raupp 2000, Tooker and Hanks 2000, Meineke et al. 2013, Dale and Frank In press) illustrate that certain areas within cities are more prone to greater herbivore

abundance and damage. Although our study is limited to one tree species, our results suggest that satellite images, tree inventories, and GIS methods similar to ours can be useful for selecting tree species and suitable planting sites. As urbanization and climate change progress, such techniques may be critical to sustaining and managing productive urban forests.

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**Table 1.** Parameter estimates table of multiple regression analyses

	R <sup>2</sup>	F	df	Est.	SE	t	P	VIF
Scale abund.*	0.42	17.12	24				<b>0.0004</b>	
Intercept			24	-29.95	7.66	-3.91	<b>0.0007</b>	
7-month temp.			24	1.65	0.40	4.14	<b>0.0004</b>	
Midday water potential	0.19	1.68	22				0.199	
Intercept			22	11.31	17.75	0.64	0.531	
Scale abund.*			22	0.58	1.04	0.56	0.583	2.52
Midday temp.			22	0.34	0.61	0.55	0.588	2.62
Interaction			22	-0.51	0.40	-1.28	0.214	1.09
Midday water potential	0.49	7.10	22				<b>0.0016</b>	
Intercept			22	-66.08	25.02	-2.64	<b>0.015</b>	
Scale abund.*			22	-0.42	0.71	-0.58	0.565	1.84
August temp.			22	3.55	1.02	3.47	<b>0.002</b>	1.90
Interaction			22	-1.49	0.76	-1.97	0.062	1.04
Midday water potential	0.36	4.09	22				<b>0.0189</b>	
Intercept			22	-61.2	36.47	-1.68	0.107	
Scale abund.*			22	0.09	0.76	0.12	0.906	1.71
7-month temp.			22	4.38	1.94	2.25	<b>0.035</b>	1.73
Interaction			22	-3.27	1.62	-2.01	0.056	1.02
Change in DBH	0.92	62.76	21				<b>&lt;0.0001</b>	
Intercept			21	-0.94	0.38	-2.46	<b>0.023</b>	
Scale abund.*			21	0.01	0.008	1.41	0.174	1.81
7-month temp.			21	0.06	0.02	2.80	<b>0.011</b>	1.74
Interaction			21	-0.03	0.02	-1.70	0.105	1.04
Residuals Initial by change in dbh			21	0.97	0.07	14.08	<b>&lt;0.0001</b>	1.06
3- yr ann. stem elong.	0.09	0.69	22				0.567	
Intercept			22	17.72	48.02	0.37	0.716	
Scale abund.*			22	1.10	1.01	1.09	0.287	1.71
7-month temp.			22	-0.49	2.56	-0.19	0.850	1.73
Interaction			22	1.02	2.14	0.48	0.637	1.02

\*Scale abund. refers to log<sub>10</sub> transformed *M. tenebricosa* abundance; significant results are bolded

R<sup>2</sup> = coefficient of determination; F = F-statistic; df = degrees of freedom; Estimate = parameter estimate; SE = standard error; t = t-statistic; P = p-value; VIF = Variance inflation factor

Table 2. Parameter estimate table of multiple logistic regression predicting tree condition

	R <sup>2</sup>	df	Estimate	SE	χ <sup>2</sup>	P
Tree Condition	0.44	9			29.13	<b>0.0006</b>
Intercept		9	-21.76	71.56	0.09	0.761
<i>M. tenebricosa</i> abund.		9	-2.54	1.29	3.90	<b>0.048</b>
7-month temp.		9	1.43	3.75	0.15	0.702
<i>M. tenebricosa</i> abund. x 7-month temp.		9	1.46	3.47	0.18	0.674

Table 3. Pearson Chi-squared test.

Tree condition division		N	df	Pearson χ <sup>2</sup>	P
Median	Global	278	4	24.09	<b>&lt;0.0001</b>
	Pairwise	578	1	17.13	<b>&lt;0.0001</b>
Upper & lower quartiles	Global	139	4	32.39	<b>&lt;0.0001</b>
	Pairwise	249	1	28.23	<b>&lt;0.0001</b>

\*Significant results are bolded

Table 4. Contingency table comparing tree condition to surface temperature division.

Count		Poor	Excellent
Column %			
Row %			
<hr/>			
Median division			
	Warm	179	136
		63.25	46.10
		56.83	43.17
	Cool	104	159
		36.75	53.90
		39.54	60.46
Upper & lower quartile division			
	Hot	94	42
		70.15	36.52
		69.12	30.88
	Cold	40	73
		29.85	63.48
		35.40	64.60
<hr/>			

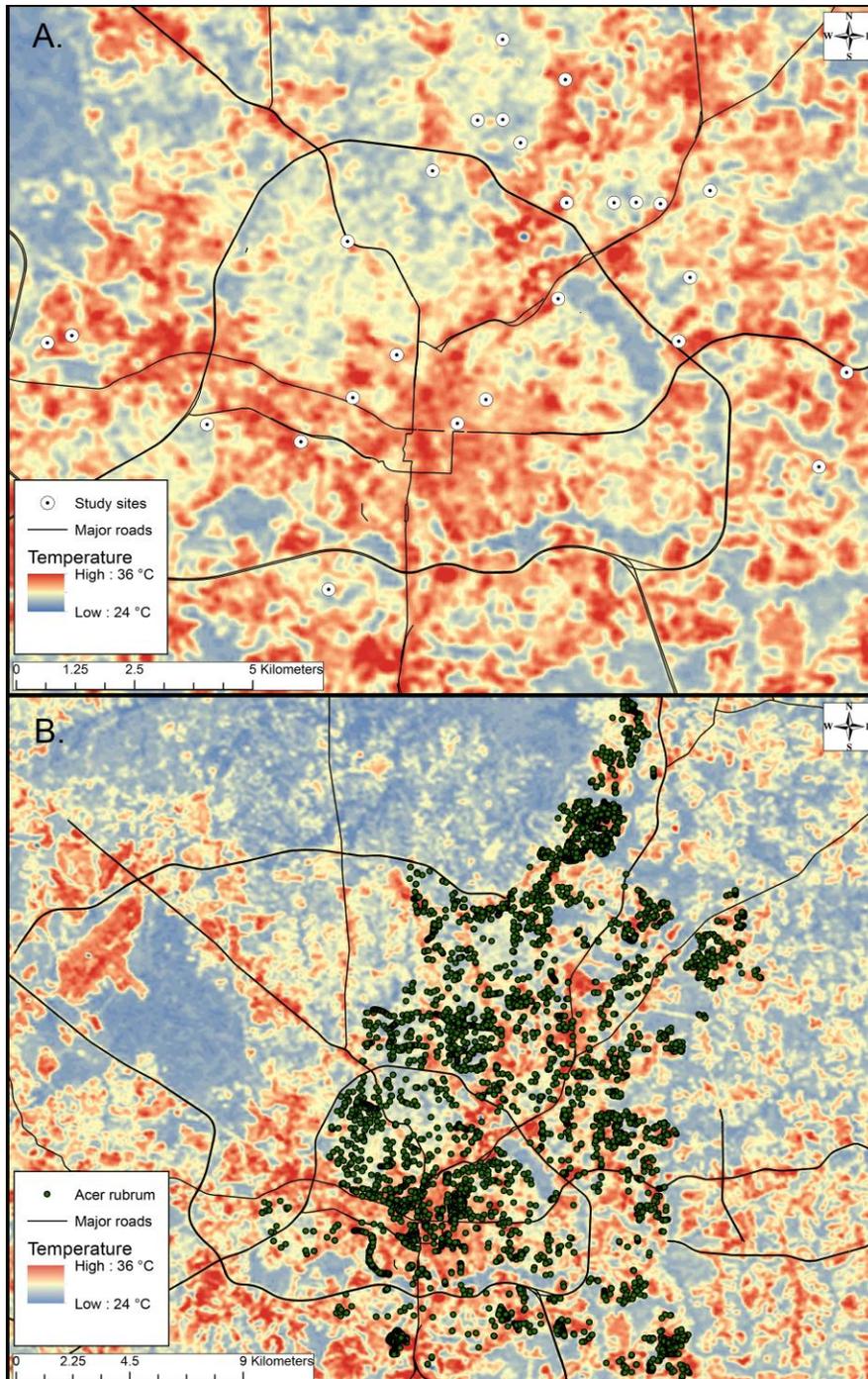


Figure 1. Thermal map of Raleigh, NC on August 18 2007. Temperature ranges from 24 to 36 °C designated by the darkest blue and red regions, respectively. (a) Study site selection for *M. tenebricosa* abundance survey, water potential measurement, growth measurements, and condition rating. (b) City-wide red maple street tree dataset of over 8000 trees overlaid on a surface temperature thermal image of Raleigh, NC.

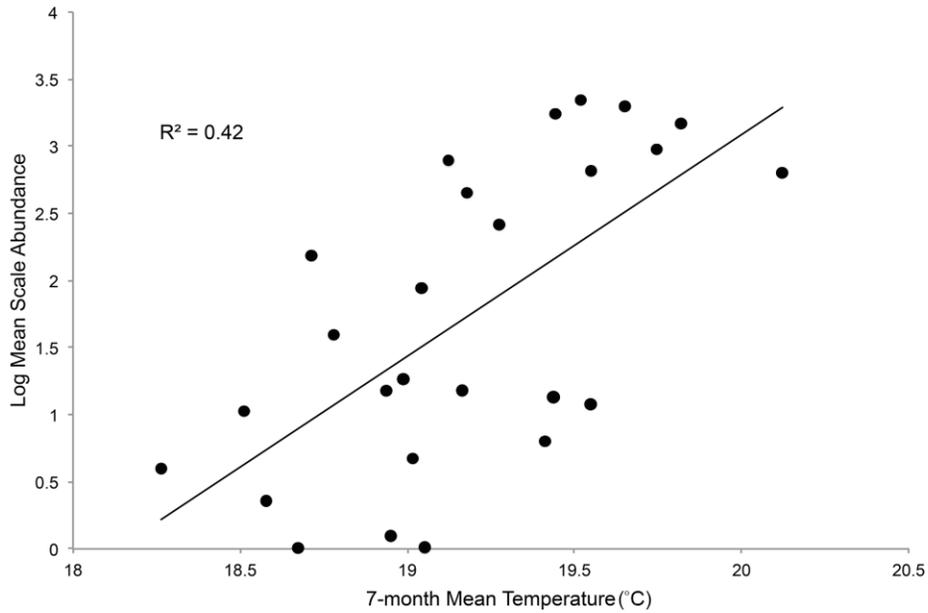


Figure 2. Linear regression of seven-month mean temperature and log mean scale abundance per 0.6 m of maple twig ( $\log(y) = -29.95 + 1.65x$ ). Regression model is statistically significant ( $P < 0.05$ ).

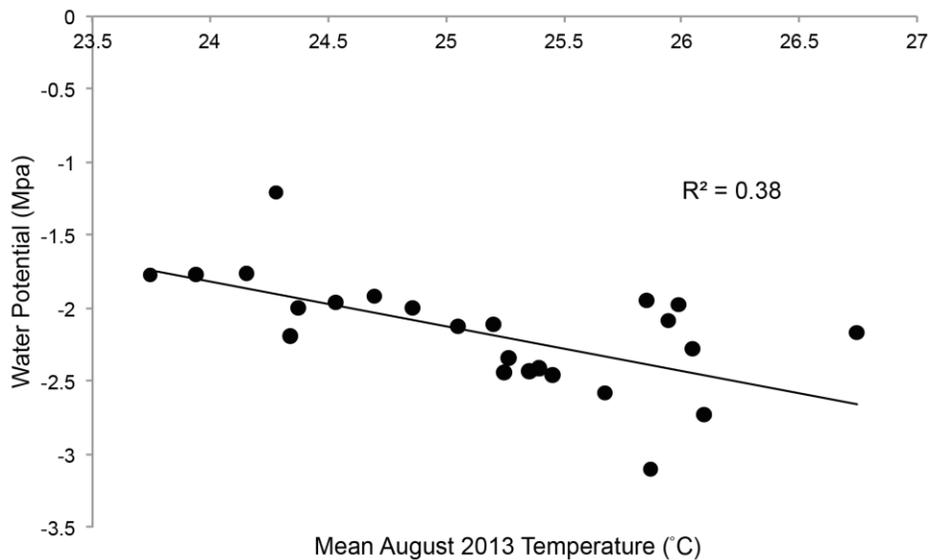


Figure 3. Linear regression of mean August 2013 tree canopy temperature and mean stem water potential (MPa) ( $y = 5.53 - 0.31x$ ). Regression model is statistically significant ( $P < 0.05$ ).

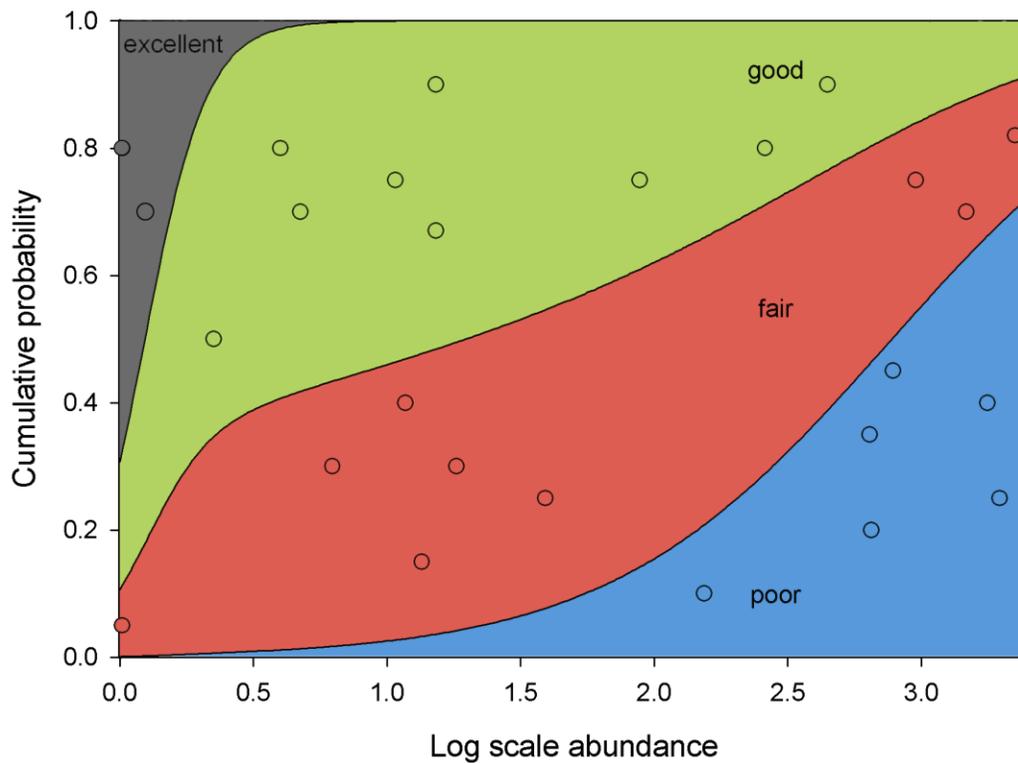


Figure 4. Since scale insect abundance was the most important predictor in our multiple logistic regression model, we use simple logistic regression to illustrate the relationship between scale insect abundance and tree condition. Points represent recorded measures of *M. tenebricosa* abundance on the x-axis but are not associated with y-axis cumulative probabilities. Colored sections are associated with the cumulative probabilities on the y-axis as they change across measured *M. tenebricosa* abundance on the x-axis.

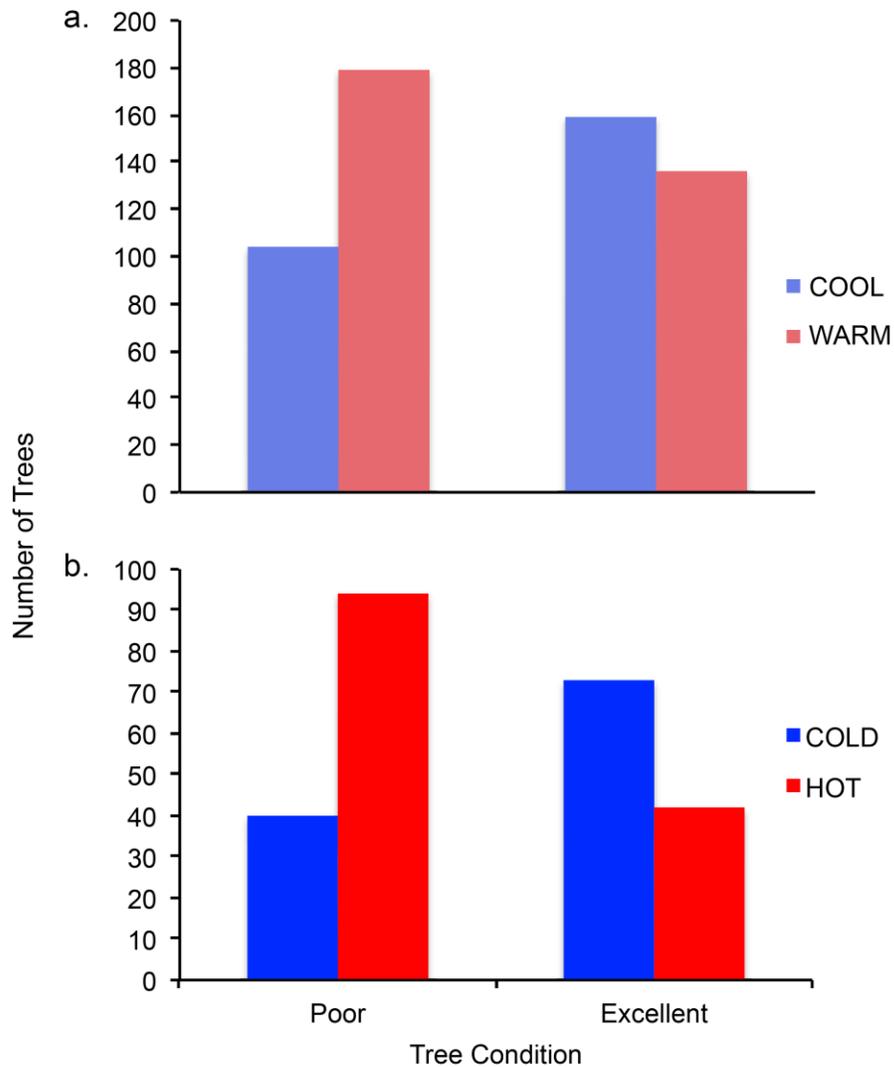


Figure 5. Pairwise comparison (a) of the number of trees with “Poor” and “Excellent” condition ratings between “Warm” and “Cool” median temperature classification ( $P < 0.0001$ ). Pairwise comparison (b) of the number of trees with “Poor” and “Excellent” condition ratings between “Hot” and “Cold” quartile temperature classification ( $P < 0.0001$ ).

### **CHAPTER 3: Forecasting the effects of heat and pests on urban trees: Impervious surface thresholds and the 'Pace to Plant' technique**

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## Abstract

Trees provide ecosystem services that benefit humans and the environment. Unfortunately, urban trees often do not provide maximum services due to abiotic stress and arthropod herbivores and borers. These problems often originate from trees being planted in unsuitable conditions. Cities are warmer than natural areas because impervious surfaces absorb and reradiate heat. Higher temperatures can increase pest insect abundance and water stress and reduce street tree condition relative to natural forests. For example, the gloomy scale insect (*Melanaspis tenebricosa* Comstock (Hemiptera: Diaspididae)), a pest of red maple (*Acer rubrum*) street trees, is more abundant in warmer than cooler urban sites. *Acer rubrum* at warmer urban sites with more *M. tenebricosa* are typically in poor condition. Here, we demonstrate these relationships and illustrate how impervious surface cover can be used to predict the condition of *A. rubrum* street trees. Then we develop impervious surface thresholds that define suitable planting sites, that can be used by individuals with access to GIS software. We also present the 'Pace to Plant' technique, that can be used by landscape professionals to quickly estimate impervious surface cover around a planting site. Our thresholds predict future tree condition based on planting site impervious surface cover. Our hope is that more informed planting will minimize pest infestations and maximize the future vigor and performance of street trees.

## Introduction

Trees provide services such as carbon sequestration, temperature reduction, and air and water filtration that benefit people and the environment (Oke et al. 1989, Tzoulas et al. 2007, Donovan et al. 2013, Nowak et al. 2013). These services are even more important within cities because over half of the world population and 80% of the U.S. population inhabit them (Alig et al. 2004, W.H.O. 2014). Maximizing these services in urban forests is challenging because urban habitats are dynamic and stressful. For example, it has been documented for over a century that herbivores are more abundant and damaging in cities than surrounding natural habitats (Putnam 1880, Metcalf 1912, Tooker and Hanks 2000, Raupp et al. 2010). The first step in urban landscape integrated pest management (IPM) is planting the appropriate tree species for the conditions at specific urban sites (Raupp et al. 1985, Raupp et al. 1992). Unsuitable urban conditions can increase tree stress and pest abundance, limiting the ecosystem services trees provide (Coffelt et al. 1993, Vilagrosa et al. 2003, Nowak et al. 2004, Litvak et al. 2012, Boyd et al. 2013, Savi et al. 2014).

Impervious surfaces are those that are impenetrable to water such as asphalt, concrete, and brick. These surfaces create roads, parking lots, and buildings, which absorb sunlight and release it as heat, creating what is called the urban heat island effect (Oke 1973, Kim 1992, Nowak and Dwyer 2000). Impervious surface cover around a planting site can stress plants by limiting root growth, raising temperatures, and creating drought-like conditions (Oke et al. 1989, Nowak et al. 1990, Graves 1994, Leibowitz 2012, Savi et al. 2014). Herbivorous arthropod pests can benefit

from the resulting plant stress and from warming itself (White 1984, Herms and Mattson 1992, Huberty and Denno 2004, Raupp et al. 2010, Meineke et al. 2013, Dale and Frank 2014b, Youngsteadt et al. 2014). For example, abundance of mimosa webworm (*Homadaula anisocentra*) and horse chestnut scale (*Pulvinaria regalis*) on urban trees increased with the amount of impervious surface surrounding a tree (Speight et al. 1998, Sperry et al. 2001). Dale and Frank (2014b) found a similar pattern with a scale insect pest, *Melanaspis tenebricosa*, but determined that temperature, rather than impervious surface itself, was the primary factor driving pest abundance. Herbivorous arthropods, particularly sap-feeding insects, can reduce woody plant photosynthesis, growth, and reproduction, so preventing infestations or reducing pest abundance is important for sustaining urban tree health (Zvereva et al. 2010).

Scale insects are among the most damaging and difficult to manage arthropod pests of landscape plants (Adkins et al. 2010, Raupp et al. 2010). In the southeastern U.S., *Melanaspis tenebricosa* (Comstock) (Hemiptera: Diaspididae) is the most important pest of red maple (*Acer rubrum*) street trees (Metcalf 1912, Frank et al. 2013). *Melanaspis tenebricosa* is a native, univoltine (one generation per year), armored scale insect that lives on the bark and feeds on vascular fluids of trees, primarily *Acer* spp. (Metcalf 1922). This host plant association is important because *Acer* is the most commonly planted genus of street tree in the eastern U.S., including North Carolina (Raupp et al. 2006). *Melanaspis tenebricosa* are drastically more abundant in urban than natural forests (Metcalf 1912, Youngsteadt et al. 2014), and up to 200 times more abundant at warmer than cooler urban sites due to

greater body size, reproduction, and population growth (Dale and Frank 2014b). High *M. tenebricosa* abundance on *A. rubrum* street trees causes branch dieback, canopy thinning, premature leaf drop, and bark discoloration, which may reduce the services they provide (Dale and Frank 2014a, Savi et al. 2014).

We examine the relationship between impervious surface cover, temperature, scale insect abundance, and tree condition, with the goal of using impervious surface cover to predict tree condition and select appropriate planting sites. Here, our objectives are to 1) document the relationship between impervious surface and *A. rubrum* condition; 2) develop impervious surface thresholds that landscape architects can use when specifying *A. rubrum* on landscape plans; and 3) develop a technique that landscape professionals can use on site to make informed decisions. Historically, thresholds have been used in IPM to effectively manage pests, however, few are established for urban landscapes (Raupp et al. 1988, Coffelt and Schultz 1990, Raupp et al. 1992, Coffelt and Schultz 1993). The IPM decision-making tools we present here will help planners and urban forest managers get the right tree in the right place to reduce future maintenance costs and increase tree survival and services.

## Materials and methods

### Study system and design

This study was conducted in Raleigh, NC, U.S., from 2012 through 2014. Our study sites were selected using a Geographic Information System (GIS)–based street tree inventory created by the Raleigh Parks, Recreation, and Cultural

Resources department. We overlaid *A. rubrum* street trees from this inventory onto a Landsat thermal image of surface temperatures in Raleigh, NC acquired on 18 August 2007 and prepared as described in Meineke et al. (2013). Two subsamples of *A. rubrum* street trees were selected from the inventory and pooled for analyses (Figure 1a). Fifty-eight trees were selected in 2012 by dividing Raleigh into 4 km<sup>2</sup> sections and randomly selecting *A. rubrum* from the hottest and coldest regions of each section as described in Youngsteadt et al. (2014). Twenty-four additional *A. rubrum* were randomly selected in 2014 using the same method as Youngsteadt et al. (2014). All trees were between 15.2 and 50.8 cm in diameter at breast height (DBH).

#### Field measurements

Landsat thermal images provide only a snapshot of surface temperatures useful for site selection. To monitor ambient air temperatures experienced by trees during the study, we placed iButton thermochron DS1921G (Dallas Semiconductor of Dallas, TX) remote temperature loggers within 59 ml portion containers (Dart Container Corporation Mason, MI) and fastened them with a zip-tie to the underside of a branch, approximately 4.5 m above ground within the lower third of the canopy of each tree. iButton data loggers recorded ambient temperature every one to three hours depending on the tree subsample. Because all sites have daily temperature data for August, we used the average August temperature for all analyses; 24 of our site temperatures were recorded in August 2014, while the remaining 56 were

recorded in August 2013. Due to loss of iButton data loggers for unknown reasons in the field, we used 80 of our 82 sites for temperature analyses.

To determine *M. tenebricosa* abundance, we pruned one randomly selected 0.3 m terminal twig from four cardinal directions of each tree using a pole pruner as described in (Dale and Frank 2014a, b, Youngsteadt et al. 2014). In the laboratory, twigs were examined under a dissecting microscope to count live *M. tenebricosa* adult females per 0.15 m of twig.

Tree condition was rated as excellent, good, fair, or poor. Condition was assigned based on leaf condition, amount of branch dieback, central leader health, and other characteristics as described in Dale and Frank (2014a) and similar to Berrang et al. (1985). The City of Raleigh has assigned condition ratings to most tree species listed in the inventory as they have been assessed over the past 7 years. Within our dataset, which was selected from this inventory, 39 *A. rubrum* had condition ratings assigned to them by the city of Raleigh Urban Forestry Division, 26 were assigned condition ratings as part of a previous study in 2013, and 17 did not have condition ratings so they were left out (final *N* for condition analyses = 65) (Dale and Frank 2014a).

To determine the amount of impervious surface around each of our study trees, we used ArcMap (ArcGIS 10.2) to calculate the percent impervious surface cover within given radii of each tree. Impervious surface cover was delineated at a 1 m resolution as described in Bigsby et al. (2013) and included buildings, pavement, and asphalt such as parking lots, roads, and sidewalks. Using a shapefile of our study sites (N=82), we created circular buffer regions around each tree at 10, 15, 20,

25, 30, 35, 40, 45, 50, 60, 80, 100, and 125 m radii (Figure 1b). We calculated the total area (m<sup>2</sup>) within each buffer region that contained pixels scored as impervious in the raster image. Using the total area of impervious surface, we calculated the percentage of the buffer region that was composed of impervious surface at each radius.

### Statistical analyses

To determine the relationships between temperature, scale insect abundance, and impervious surface cover, we used simple linear regression (JMP Pro 11). We  $\log_{10}(x+1)$  transformed scale counts to meet assumptions of linear regression, as determined by inspecting plots of residuals. To determine how scale insect abundance or impervious surface cover at each radius predicted tree condition, we used simple logistic regression (JMP Pro 11). Using the probability formulas generated from the logistic regression for each radius, we calculated the likelihood of a given tree condition across a range of 0 to 100% impervious surface (Figure 4). To establish impervious surface cover thresholds, we calculated the average percentage of impervious surface cover for all measured radii at which the most likely condition changed from good to fair and fair to poor (Figure 4).

### Impervious surface estimation

To create a tool for on-the-ground application of our results, we developed the 'Pace to Plant' technique. After testing each measured radius from the tree as described previously, we decided that a 20 m radius provided the best balance of

accuracy and practicality. A 20 m radius predicts significant effects of impervious surface on tree condition rating while also being short enough for someone to walk. Using our method, one can walk 25 steps (approximately 20 m) from the planting site in four directions at 45° to the longest adjacent impervious edge, and estimate the percentage of impervious surface surrounding it (Figure 2). Once each of four paths has been walked, the total number of steps onto impervious surface is divided by the total number of steps taken (100) to give an estimate of the percentage of impervious surface surrounding the planting site.

To refine and test this technique, we created four hypothetical scenarios of urban planting sites (Figure 2). These scenarios do not encompass all possible site characteristics and may not conform to all urban planting regulations, but provided the necessary framework for technique development. Figure 2a, b, c, and d illustrate street tree plantings in a median strip, three-way intersection, four-way intersection, and a permeable island, respectively. Each scenario was designed with 9 m road widths and a tree planted 1 m from the curb, in compliance with Raleigh, NC street design regulations (City of Raleigh 2014). With these scenarios, we used basic geometry to calculate the area of impervious surface within a 20 m radius of the planting site and determined the impervious percentage of that area. With an architect's scale, we measured 25 equidistant points in four directions that were each equivalent to the 20 m radius representing a person's steps (Figure 2). Then we counted the number of points within the impervious areas and divided them by 100 to determine the impervious estimate.

To further validate our method, three individuals went to 15 *A. rubrum* street trees and estimated impervious surface cover using the 'Pace to Plant' technique. These 15 trees were selected to maximize technique validation efficiency and capture a large range of percent surrounding impervious surface cover. Following the 'Pace to Plant' estimations, we used ArcMap to calculate the percent impervious surface around the same *A. rubrum* street trees at the same radius. We took the mean of three paced estimates of impervious surface cover and compared them to the GIS calculation to see how well one predicted the other.

## Results

### Field measurements

August average tree canopy temperatures ranged from 23.20 °C to 26.96 °C with a mean ( $\pm$ SD) of 25.11 ( $\pm$ 0.85). For all 82 study trees, *M. tenebricosa* abundance per 0.15 m of twig ranged from 0 to 2241 live individuals with a mean of 261.21 ( $\pm$ 510.65). *M. tenebricosa* abundance increased with average August tree canopy temperature (simple linear regression,  $R^2 = 0.29$ ,  $P < 0.0001$ ) (Figure 3b).

Tree condition ratings included 6 excellent, 22 fair, 23 good, and 14 poor trees. *M. tenebricosa* abundance significantly predicted *A. rubrum* street tree condition ( $N = 65$ ,  $X^2 = 33.41$ ,  $P < 0.0001$ ). As scale insect abundance increased, the probability of finding a tree in poor condition significantly increased while the probability of finding a tree in good condition decreased.

Percent impervious surface cover was calculated at 13 different radii for each study site. At the smallest radius (10m), percent impervious surface ranged from 0 to

99.2% while at the largest radius (125m), percent impervious surface ranged from 3.8 to 72.7%. Percent impervious surface cover significantly predicted mean August tree canopy temperature at all radii ( $P < 0.01$ ). Tree canopy temperature was best predicted at the 125 m radius ( $R^2 = 0.22$ ,  $P < 0.0001$ ) (Figure 3a). For every percentage increase in impervious surface cover in the 125 m radius, tree canopy temperature increased by 0.02 °C. Since *M. tenebricosa* abundance increased with temperature, and temperature increased with impervious surface, we tested the relationship between *M. tenebricosa* abundance and percent impervious surface. We found that at all radii, as percent impervious surface cover increased, mean *M. tenebricosa* abundance per 0.15 m of twig also increased ( $P < 0.01$ ). Scale insect abundance was best predicted by percent impervious surface cover at a 60 m radius around the tree ( $R^2 = 0.48$ ,  $P < 0.0001$ ) (Figure 3c).

Given the relationships between impervious surface cover, *M. tenebricosa* abundance, and *A. rubrum* condition, we used impervious surface to predict tree condition rating. At all measured radii, percent impervious surface cover significantly predicted the likelihood of finding a tree in a given condition ( $N=65$ ,  $P < 0.01$ ). All condition ratings were significantly predicted from 40 to 125 m radii. Excellent, good, and poor condition ratings were significantly predicted from 15 to 35 m radii. Impervious surface cover at a 10 m radius only statistically predicts good and poor condition ratings (Table 1). The best predictor, based on goodness of fit indices, of tree condition rating was at a 100 m radius from the study tree ( $X^2 = 29.87$ ,  $P < 0.0001$ ).

For each model (10 – 125 m radius), we determined the most likely condition rating for every percentage increase in impervious surface. Our threshold calculations show that trees are most likely to be in good condition at sites with 0 to 32% impervious surface. Between 32 and 62% impervious surface, trees will most likely be in fair condition. At any percentage of impervious surface cover above 62%, trees will most likely be in poor condition (Figure 4).

#### Impervious surface estimation

Although the strongest relationship between impervious surface cover and tree condition was at a 100 m radius ( $X^2 = 29.87$ ,  $P < 0.0001$ ), this is too far and time consuming for people to walk around each planting site. Both 20 and 25 m radii from the tree were statistically significant predictors of tree condition ( $X^2 = 16.8$ ,  $P = 0.0008$ ;  $X^2 = 17.22$ ,  $P = 0.0006$ ) and are more practical to walk. To reduce the time and complexity of estimating impervious surface, we recommend measuring a 25-step radius from the planting site, which creates a 20 to 25 m radius circle around the planting site (depending on step length) and sums to 100 steps. Therefore, the number of steps on impervious surface is equal to the percent impervious surface around that planting site.

Based on calculations of four urban landscape scenarios, our simulated paced estimates are on average 1.6 percentage points less than the actual percent impervious surface (Figure 2). There was a strong, positive correlation between the actual and estimated percent area of impervious surface ( $R^2 = 0.96$ ,  $P = 0.0198$ ) (Figure 6a).

On average, our on-site validation using 25 steps overestimated impervious surface cover by 14% when compared to ArcGIS calculations. There was, however, a strong positive relationship between the two ( $R^2 = 0.74$ ,  $P < 0.0001$ ) (Figure 6b). In addition, our paced estimates more strongly predicted *M. tenebricosa* abundance ( $R^2 = 0.53$ ,  $P = 0.002$ ) than did GIS calculations at a 20m radius ( $R^2 = 0.29$ ,  $P < 0.0001$ ) (Figure 6c).

## Discussion

Urban forests are faced with many challenges that make optimal tree vigor and longevity difficult to achieve. Impervious surface cover limits root growth and root access to water and nutrients, while also increasing temperatures (Oke et al. 1989, Graves 1994). Our results indicate that greater impervious surface cover leads to warmer temperatures, greater *M. tenebricosa* abundance, and worse *A. rubrum* street tree condition. We identified thresholds of impervious surface cover for landscape architects and other planners to consider when designing a landscape with *A. rubrum*. Our 'Pace to Plant' technique provides a way for landscapers to assess sites when deciding which plant species are appropriate. These two tools should improve urban tree IPM and survival.

We focused on the effects of impervious surface cover on temperature and its subsequent effects on scale insect abundance and tree condition. Our larger data set corroborates Dale and Frank (2014a) and Youngsteadt et al. (2014) findings that *M. tenebricosa* abundance increases with temperature. However, percent impervious surface cover predicted *M. tenebricosa* abundance more strongly ( $R^2 =$

0.48) than did tree canopy temperature ( $R^2 = 0.29$ ) (Figure 3). This suggests that impervious surface affects trees and scale insects through more than increasing temperature, perhaps by increasing tree water or temperature stress (White 1984, Raupp et al. 2010, Savi et al. 2014). As a result, impervious surface is an even better tool than temperature for predicting *A. rubrum* tree condition and susceptibility to *M. tenebricosa*.

Percent impervious surface significantly predicted tree condition at all tested radii around the tree. It is important to note that the best model fits were at the largest radii, suggesting that impervious surface has a cumulative effect on tree condition. Therefore, when making planting decisions, one must consider ground cover at larger scales than the immediate planting site. Landscape architects have access to GIS software with which they can analyze groundcover on landscape scales. Using our results and impervious surface thresholds, these individuals have the knowledge and tools needed to avoid specifying *A. rubrum* in sites with greater than 32% impervious surface.

When at a site, smaller radii are more practical to measure. Therefore, we recommend an approximate 20 m radius (or 25 steps) from the planting site. At this distance, excellent, good, and poor condition ratings can be predicted with confidence (Table 1). In addition, 25 paces in four directions sums to 100, which allows for simple percent calculations. For cases where shrubs or buildings obstruct the walking pathway, we suggest estimating the number of steps taken up by that space. It is important to note that sites with relatively little surrounding tree canopy and other vegetation cover were more accurately estimated than those with more

surrounding vegetation cover. We suspect this means the GIS land cover map actually underestimates impervious surface because it is an aerial image that excludes impervious cover beneath tree canopies. Our 'Pace to Plant' technique more accurately estimates impervious surface cover because it accounts for groundcover beneath vegetation cover. This technique gives landscape professionals the tools to assess sites that have been specified for *A. rubrum* or to make their own specifications when planning a tree planting. These professionals often warranty the trees they plant, and that landscape architects specify. Therefore, ensuring the success of the tree could reduce costs and improve business.

The purpose of this technique is not to create definitive limitations for *A. rubrum* planting sites, but to make recommendations based on the probability of the future condition of a tree planted at a given site. Another important component to consider is the amount and structure of vegetation surrounding the planting site. Vegetation structural complexity, particularly tree canopy cover, affects site temperature and subsequent pest abundance (Shrewsbury and Raupp 2000, Tooker and Hanks 2000, Dale and Frank 2014b, Frank 2014). Vegetation complexity can also promote biological control by providing habitat refuges for natural enemies, although in previous research we found that temperature and impervious surface were more important in this system (Hanks and Denno 1993, Shrewsbury and Raupp 2000, Tooker and Hanks 2000, Frank and Shrewsbury 2004, Dale and Frank 2014b). Therefore, a site with more complex surrounding vegetation could buffer the effects of impervious surface.

Our 'Pace to Plant' technique provides a tool that landscape professionals can use to quickly and easily assess a planting site and reduce the risk of future tree failure or decline. These data and simulations are specific to *A. rubrum* in the southeastern U.S. However, based on the negative effects of impervious surface on other tree species, it is likely that these thresholds can be adapted for other tree species. Many problems with tree health originate at planting (Grabosky and Gilman 2004). One of the first steps of IPM in urban landscapes is correctly planting the appropriate tree in a given space to maximize its success and reduce future management costs (Raupp et al. 1985, Raupp et al. 1992, Grabosky and Gilman 2004). Using these impervious surface thresholds and the 'Pace to Plant' technique, landscape architects and other landscape professionals have the tools to plant the most common landscape tree in the eastern U.S. in more suitable locations or select a different tree.

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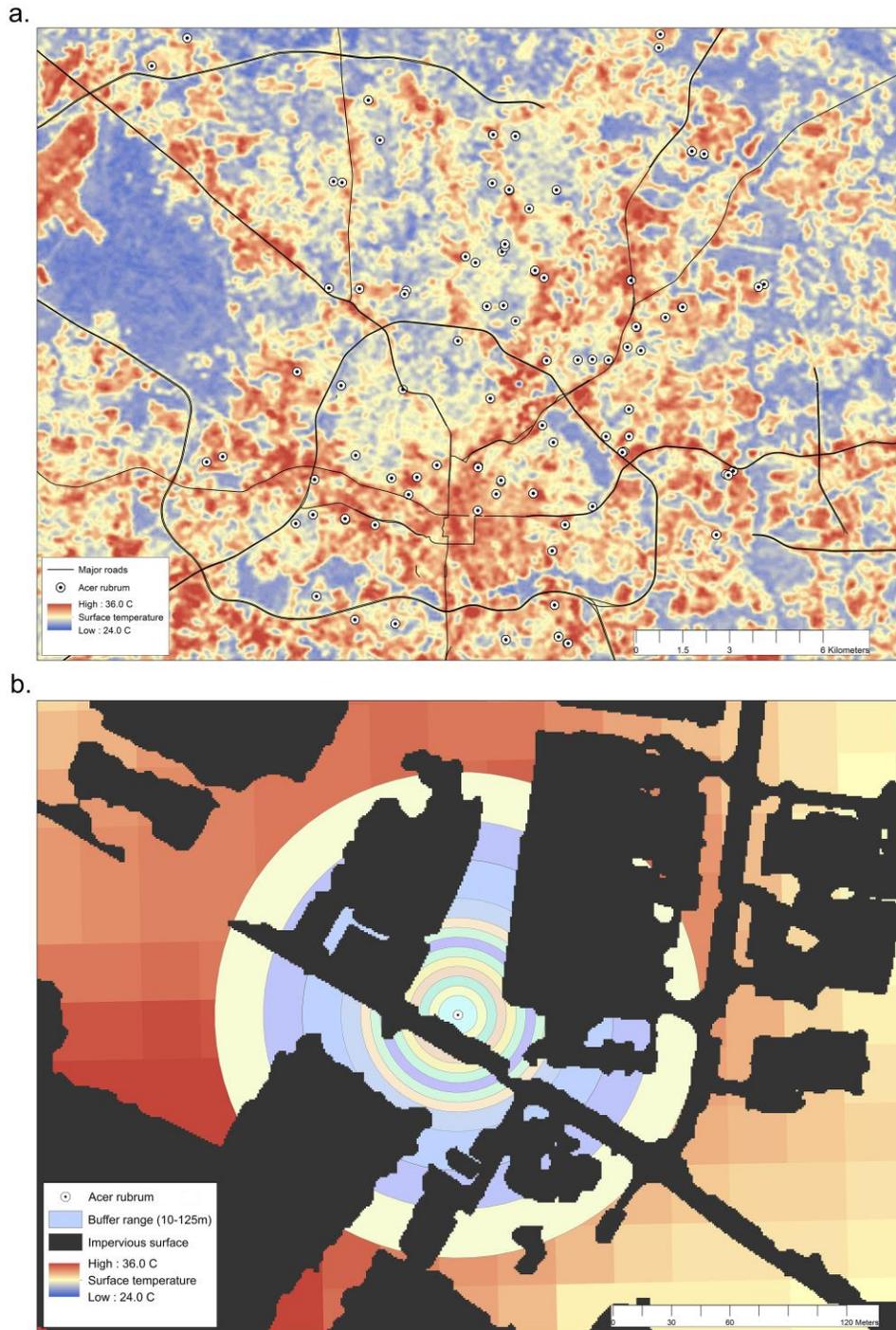


Figure 1. (a) Thermal map of surface temperatures in Raleigh, NC taken on 18 August 2007. Each point represents a randomly selected *A. rubrum* street tree (N = 82). (b) Zoomed in image of a single street tree placed onto a map of surface temperatures and impervious surface ground cover classification. Each ring around the tree represents one of the 13 radii for which percent impervious surface was calculated.

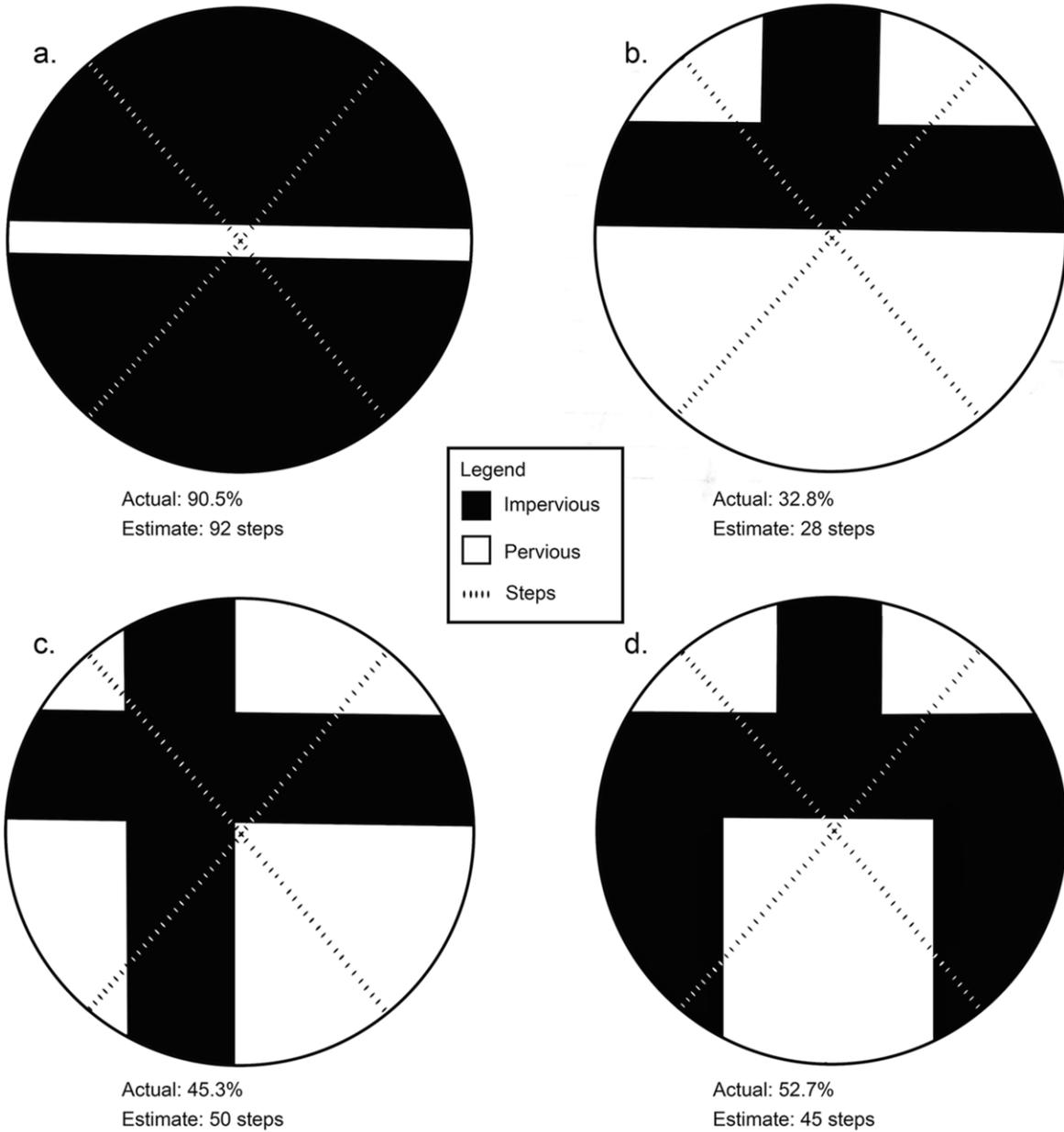


Figure 2. Four designed landscape scenarios illustrating the 'Pace to Plant' technique. In each diagram, the tree or planting site is located at the intersection of the transects. Circle diameters are equal to 40 m and road widths equal 9 m. White dashes represent steps onto impervious surface and black dashes represent steps onto pervious surface. The number of white dashes equals the percent impervious surface estimate for each scenario.

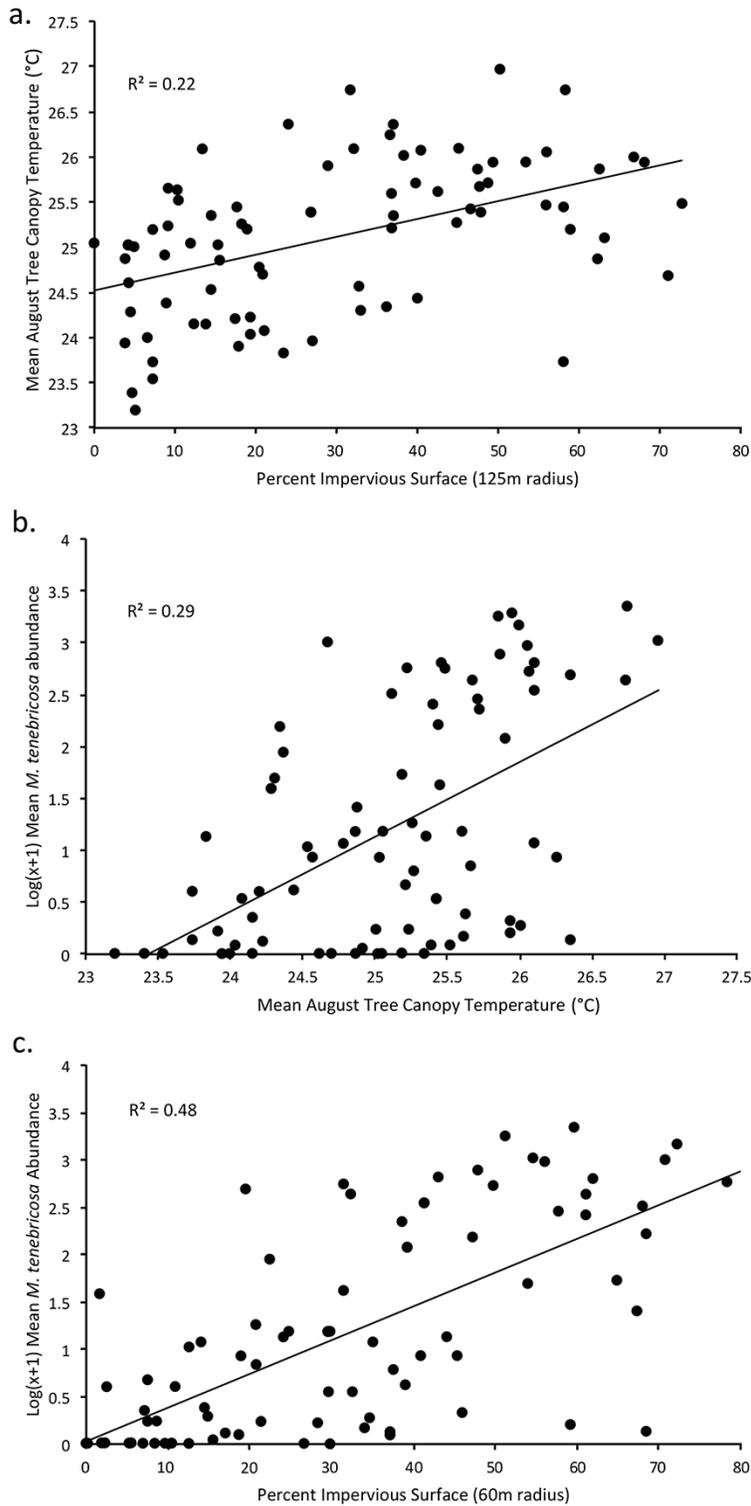


Figure 3. Simple linear regression of (a) percent impervious surface (125 m radius) and tree canopy temperature, (b) tree canopy temperature and *M. tenebricosa* abundance, and (c) percent impervious surface cover (60 m radius) and *M. tenebricosa* abundance.

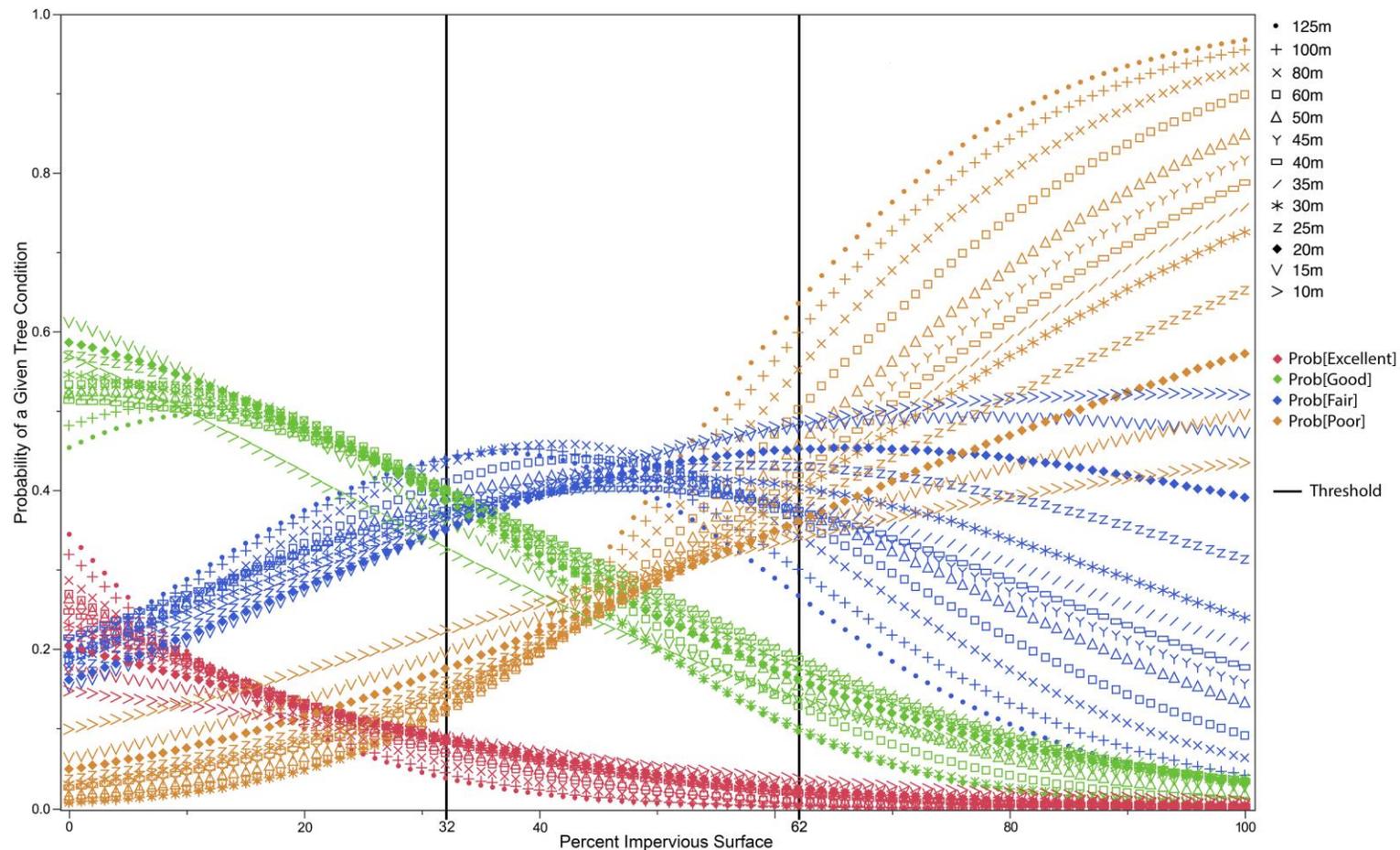


Figure 4. Probability curves illustrating the change in probability of finding a given tree condition rating as percent impervious surface around a planting site increases from 0 to 100%. Threshold lines are the average point at which each radius from the tree predicts a change in tree condition for all 13 measured radii. Each symbol indicates a different measured radius from the tree. Different colors represent different tree condition ratings

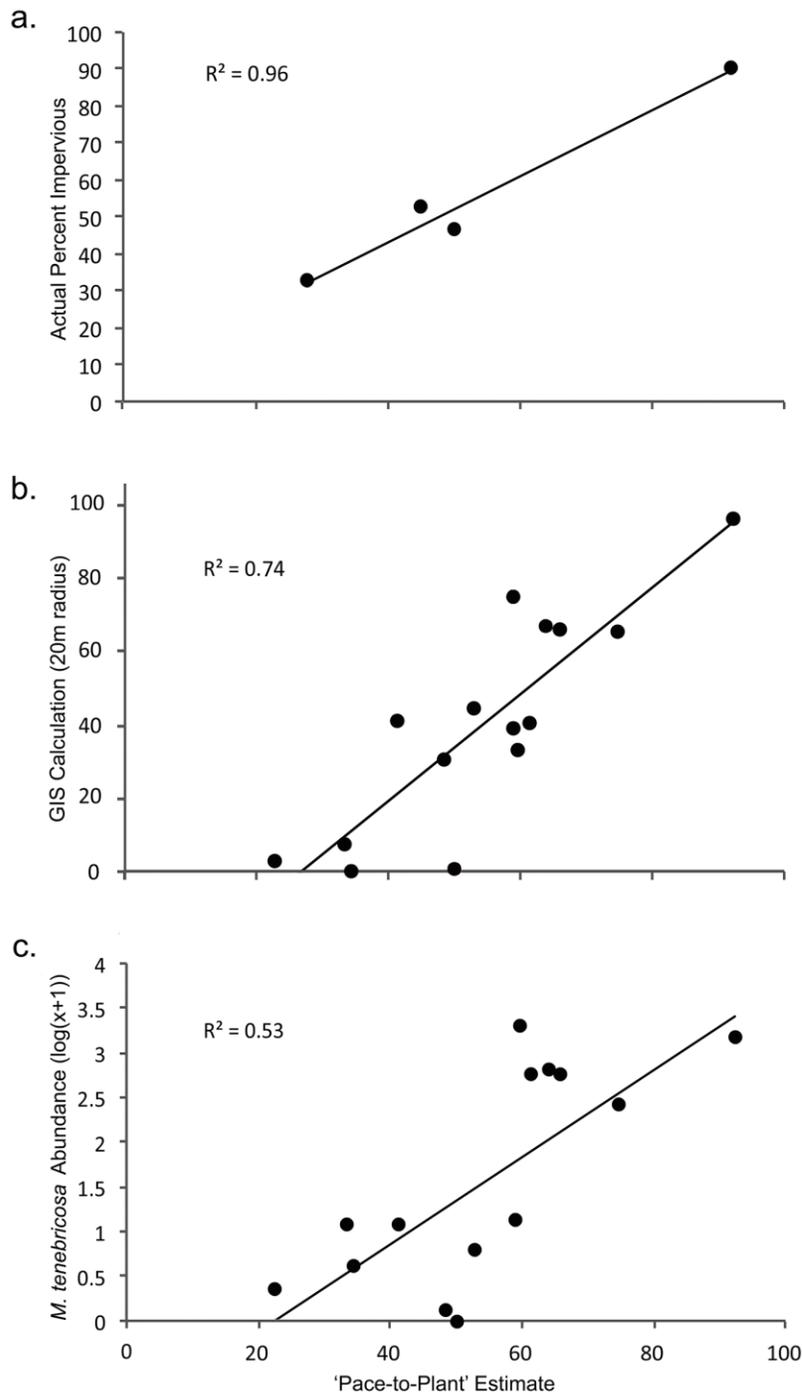


Figure 5. (a) Simulated paced estimate of impervious surface on x-axis correlated with the calculated actual percent impervious surface from four landscape scenarios. (b) 'Pace to Plant' estimate of percent impervious surface cover on x-axis correlated with the GIS calculated percent impervious surface at a 20 m radius. (c) 'Pace to Plant' estimate of percent impervious surface cover on x-axis correlated with log transformed *M. tenebricosa* abundance.

## CHAPTER 4: Urban warming and drought stress combine to increase pest fitness and abundance on urban trees

### Introduction

Urban forests are more susceptible than natural forests to chronic infestations and outbreaks of herbivorous arthropods (Raupp et al. 2010, 2012). The drivers of this are not fully understood but higher temperatures have been shown to play a primary role (Meineke et al. 2013, Dale and Frank 2014b). Temperature directly affects arthropod metabolism and development, which under warming, may lead to larger, more fecund individuals (Yasuda 1983, Kozlowski 1992, Berger et al. 2008). Dale and Frank (2014b) found that 2°C of urban warming increased the abundance of *Melanaspis tenebricosa* (Hemiptera: Diaspididae) on *A. rubrum* street trees. One mechanism for this was that *M. tenebricosa* on warmer trees were larger and produced up to three times as many offspring as those on cooler trees.

Urban warming is driven largely by impervious surface cover, which reduces water infiltration and availability to plant roots (Oke et al. 1989, Graves 1994). At the same time, urban warming induces drought stress by increasing the atmospheric demand for water (Mattson and Haack 1987, McIntyre 2000). The plant stress hypothesis proposes that drought can increase herbivore fitness and abundance by increasing the nutritional quality of plants and reducing plant defenses (White 1984). Sap-feeding pests in particular often show a positive response to drought stress (Koricheva et al. 1998, Herms 2002, Huberty and Denno 2004). Several studies link this hypothesis to urbanization by showing positive relationships between impervious surface cover and herbivore abundance or between drought, impervious surface,

and herbivores (Speight et al. 1998, Cregg and Dix 2001, Sperry et al. 2001, Raupp et al. 2010). For example, Cregg and Dix (2001) found that oak trees growing in downtown sidewalk tree pits were more drought-stressed and harbored more aphids and lace bugs than oaks planted in a nearby campus park with little impervious surface. Likewise, the density of *Pulvinaria regalis* on urban mulberry trees significantly increased as surrounding impervious surface cover increased (Speight et al. 1998).

The relationship between impervious surface cover and herbivores can be inconsistent, even among sap-feeders (Koricheva et al. 1998). Hanks and Denno (1993) found that drought stress reduced survival and fecundity of white peach scale (*Pulvinaria pentagonia*) on mulberry street trees compared to less stressed trees in woodlots. However, in this and other studies, the effects of plant stress and drought have been confounded with factors like vegetation complexity and temperature such that less stressed plants were also in more wooded, potentially cooler locations.

Climate change research suggests that abiotic factors like temperature, CO<sub>2</sub>, and drought often act in concert or antagonistically to affect herbivores, which makes single-factor empirical tests less meaningful (Robinson et al. 2012). Given the close association between urban warming, impervious surface cover, and drought stress, it is difficult to separate their effects in observational experiments. My objective was to determine how drought stress and warming interact to affect the fecundity and population growth of *M. tenebricosa*, a sap feeding scale insect pest. To do this, I manipulated water stress on *A. rubrum* street trees across an existing gradient of urban temperatures to decouple these effects on *M. tenebricosa*. Then I measured

*M. tenebricosa* body size, fecundity, and abundance over three generations to estimate the rate and mechanisms of population growth. Understanding the effects of warming and drought on urban plants and animals is important because urban forests support much of urban biodiversity and provide ecosystem services that benefit human and environmental health (McKinney 2002, Donovan et al. 2013, Nowak et al. 2013).

## Materials and methods

### Study organisms

*Melanaspis tenebricosa* is a native armored scale insect pest of *Acer spp.* trees, primarily *A. rubrum*, which is the most common genus of landscape tree in the eastern U.S. (Metcalf 1912, Raupp et al. 2006, Frank et al. 2013). *Acer rubrum* is a bottomland, softwood tree species native throughout eastern North America (Tirmenstein 1991). *Melanaspis tenebricosa* are drastically more abundant on *A. rubrum* in urban than natural forests throughout the southeastern U.S. (Metcalf 1912, Frank et al. 2013, Youngsteadt et al. 2014). These insects feed on parenchyma cells within the trunk and branches of trees. Heavily infested trees lose branches, prematurely drop leaves, and eventually die (Frank et al. 2013).

*Melanaspis tenebricosa* is univoltine. Mated adult females overwinter, then give live birth over a 6 to 8 week period beginning in May (Metcalf 1922, Frank et al. 2013). Newly emerged nymphs are mobile for merely hours before settling on the bark, where they become sessile, produce a waxy cover, and feed for the remainder of

their life. One would predict that a sessile insect unable to escape drought or heat should respond strongly to changes in abiotic conditions and host tree quality.

### Study system

All trees were property of the City of Raleigh, NC, USA and located in the right-of-way, which was up to 10 m from the street. To select study sites, I used ArcMap 10.2 to overlay a geocoded street tree inventory map created by the city of Raleigh onto a Landsat thermal image of surface temperature acquired on 18 August 2007 and prepared as described in Meineke et al. (2013). I created a grid of 2x2 km squares, divided the city into equal quadrants, and randomly selected three grid squares per quadrant. From each selected grid square I picked a pair of *A. rubrum* from the hottest and coldest sites, resulting in 48 trees at 24 randomly selected sites. Tree pairs at each site were at least 15 m and no more than 75 m apart. Since scale insects have to be measured and dissected to count embryos within a short time after collecting, I selected a subset of 22 trees from 11 sites due to the logistical constraints. The 11 sites were selected because they showed the greatest difference in xylem water potential between watered and unwatered trees during the summer of 2014. Tree diameter at breast height (DBH) ranged from 15.7 to 37.7 cm.

### Effect of temperature and water treatment on drought stress

To determine tree canopy temperature, I placed an iButton thermochron DS1921G (Dallas Semiconductor, Dallas, TX, USA) remote temperature logger 4.5

m above ground within each tree's canopy. iButtons were mounted on the underside of a lateral branch attached to an iButton wall mount within a 59-ml portion container (Dart Container Corporation, Mason, Michigan, USA) using a cable tie. iButtons recorded temperature every two hours from May 2014 through August 2014, the time period in which *M. tenebricosa* are most active and developing. Mean two-hour tree canopy temperature, henceforth referred to as tree canopy temperature, was calculated for the period May 2014 through August 2014 and used for all analyses of temperature.

At each site, one tree was watered and one tree was not. Ten watered trees with diameters of 15.7 to 31.8 cm had two TreeGator® slow-release watering bags (Spectrum Products Inc., Youngsville, NC) around their base. One tree was 37.7 cm in diameter and required three watering bags around its base. Each bag held approximately 75 liters and was filled twice per week from May through August 2014 and 2015, resulting in 300 liters of water per tree per week and 450 liters per week for one tree.

To determine how temperature and watering treatments affected tree drought stress, I used a pressure chamber (PMS Instrument Company, Albany, OR) to measure midday xylem water potential of each tree once during the second week of June, July, and August 2014. Midday water potential was measured during 1100 to 1500 each day. I removed one 15 to 20 cm terminal twig from sun-exposed locations approximately 5.5 m above ground on the north and south-facing sides of each tree. Weather conditions during each measuring period were mostly sunny and between

29 and 31°C. Three-month mean xylem water potential was calculated for each tree and used for analysis.

*Effect of temperature and water treatment on M. tenebricosa fitness and abundance*

To determine if *M. tenebricosa* were affected by temperature and the watering treatment, I measured adult female body size and fecundity, and calculated the ratio of third-generation adult females (counted September 2015) to first generation adult females (counted April 2014) on each tree.

To determine the effect of temperature and drought stress on *M. tenebricosa* fitness, I measured and dissected adult female *M. tenebricosa* under a dissecting microscope and counted the number of embryos developing within them immediately prior to birth as in Dale & Frank (2014b). On 6 May 2015, at the end of reproductive development, I collected one, 30.5 cm twig from each cardinal direction and selected an adult female every 15 cm beginning at the terminal end, totaling twelve individuals per tree. Using the same technique as Dale and Frank (2014b), I measured adult female *M. tenebricosa* length from the pygidium to the anterior end of the body. Then, I dissected each *M. tenebricosa* under a stereomicroscope, slide mounted the contents, and counted the developing embryos under a phase-contrast compound light microscope.

Finally, I determined live adult female *M. tenebricosa* abundance on each *A. rubrum* by pruning one 0.3 m live terminal twig, 5 m above ground, from each cardinal direction of the tree canopy as in Dale and Frank (2014a). *Melanaspis tenebricosa* were collected and counted under a dissecting microscope at the

beginning of the experiment in April 2014 and again in September 2015. To improve the normality of residuals, I  $\log_{10}(x+1)$  transformed *M. tenebricosa* abundance measured on both dates. As a measure of overall population growth on each tree, I calculated the ratio of September 2015 to April 2014 adult females. Population growth ratio data were log transformed to increase the normality of residuals.

To predict the effect of temperature and watering treatment beyond the period of our experiment I created a simple population growth curve of *M. tenebricosa* abundance over the next 15 years, which is less than the average lifespan of an urban tree (Roman and Scatena 2011). Using the regression equations of temperature predicting *M. tenebricosa* egg production, I calculated the predicted number of offspring that could establish on the tree of origin for each watering treatment in the absence of all other factors. Next, I calculated the ratio of observed 2015 *M. tenebricosa* abundance to the number of offspring predicted by fecundity as a metric of percent establishment. Percent establishment represents individuals that survive and establish on the region of branch that we sampled, encompassing the effect of emigration, predation, parasitism, and other dynamic factors. The product of initial population (POPULATION<sub>i</sub>), predicted egg count, and percent establishment predict the abundance of the following year's population:

$$(1) \text{PREDICTED ABUNDANCE} = \text{POPULATION}_i \times \text{PREDICTED EGG COUNT} \times \% \text{ESTABLISHMENT}$$

Using this equation, I calculated population growth on our study trees for each treatment as well as hypothetical growth assuming each *M. tenebricosa* population

began with 10 individuals. To illustrate the extremes of population change based on the effect of initial population abundance, temperature, and watering treatment, I calculated *M. tenebricosa* population growth on the warmest watered and unwatered trees, and the coolest watered and unwatered trees for each model.

## Statistical Analyses

Each measured variable was analyzed using ANCOVA, with watering treatment as a categorical predictor and tree canopy temperature as a covariate predicting the response. Analyses were conducted using PROC GLM and LSMEANS in SAS 9.4 (SAS Version 9.4, Cary, NC). Each ANCOVA was first run as the full model with each predictor and an interaction term. If the interaction was not significant it was removed, and the slopes of each regression line were assumed equal to test the hypothesis that each line's y-intercept was the same. Population growth models were analyzed as repeated measures ANOVA with year, watering treatment, and their interaction predicting *M. tenebricosa* abundance.

## Results

### Effect of temperature and water treatment on drought stress

Mean tree canopy temperature from May 2014 through August 2014 ranged from 23.64 to 25.90°C with a mean ( $\pm$ SEM) of 25.15 ( $\pm$ 0.13).

Water potential of the watered trees ranged from -2.28 to -3.39 MPa with a mean of -2.95 ( $\pm$ 0.11) and unwatered trees ranged from -2.80 to -3.96 MPa with a mean of -3.45 ( $\pm$ 0.12). There was no interaction between temperature and water

treatment. Therefore, I assumed the regression lines for each water treatment had equal slopes and tested the hypothesis that they had equal y-intercepts. Xylem water potential was significantly predicted by the full model with temperature and watering treatment ( $F_{2,19} = 10.49$ ,  $P = 0.0009$ ). As temperature increased, *A. rubrum* xylem water potential (MPa) decreased ( $F_{1,19} = 8.26$ ,  $P = 0.0097$ ), and was consistently more negative on unwatered than watered trees ( $F_{1,19} = 13.06$ ,  $P = 0.0019$ ) (Figure 2).

#### *Effect of temperature and water treatment on M. tenebricosa fitness and abundance*

The effect of temperature on adult female body size did not depend on watering treatment ( $F_{1,18} = 1.58$ ,  $P = 0.2449$ ). Therefore, I assumed equal slopes and tested the hypothesis that the regression lines had equal y-intercepts. Adult female *M. tenebricosa* body size was significantly associated with the full model of tree canopy temperature and water treatment ( $F_{2,19} = 6.21$ ,  $P = 0.0084$ ) (Figure 3a).

*Melanaspis tenebricosa* body size increased with the main effect of tree canopy temperature ( $F_{1,19} = 7.48$ ,  $P = 0.0131$ ), corroborating Dale and Frank (2014b). More importantly, *M. tenebricosa* on unwatered trees were 3% larger than those on watered trees ( $F_{1,19} = 5.14$ ,  $P = 0.0353$ ).

The effect of temperature predicting adult female embryo production was also not dependent on watering treatment ( $F_{1,18} = 0.44$ ,  $P = 0.5178$ ). *Melanaspis tenebricosa* embryo count was associated with the full model of temperature and water treatment ( $F_{2,19} = 5.74$ ,  $P = 0.0112$ ) (Figure 3b). Adult females produced significantly more offspring as tree canopy temperature increased ( $F_{1,19} = 5.05$ ,  $P =$

0.0367). More strikingly, *M. tenebricosa* on unwatered trees produced 17% more offspring per individual than those on watered trees ( $F_{1,19} = 6.62$ ,  $P = 0.0186$ ). Thus, the 577 *M. tenebricosa* on the warmest unwatered tree have the potential to produce over 27,000 offspring per 0.3 m of twig while the lone female on the coolest watered tree would only produce 28.

April 2014 *M. tenebricosa* abundance ranged from 0 to 577 live adult females per 0.3 m of twig with a mean ( $\pm$ SEM) of 160.73 ( $\pm$ 41.61). September 2015 *M. tenebricosa* abundance ranged from 0 to 1018 live adult females per 0.3 m of twig with a mean of 194.39 ( $\pm$ 59.32). At the beginning of the experiment (April 2014), tree canopy temperature and *M. tenebricosa* abundance were significantly, positively associated ( $R^2 = 0.41$ ,  $F_{1,19} = 13.14$ ,  $P = 0.0018$ ), but did not differ between treatments ( $F_{1,19} = 0.27$ ,  $P = 0.6092$ ). By the end of the experiment (September 2015), tree canopy temperature was still significantly associated with *M. tenebricosa* abundance ( $R^2 = 0.46$ ,  $F_{1,17} = 13.43$ ,  $P = 0.0019$ ), but showed no difference in abundance between watering treatments ( $F_{1,17} = 1.04$ ,  $P = 0.3216$ ) (Figure 3a). Population growth ratio was not significantly predicted by tree canopy temperature ( $R^2 = 0.06$ ,  $F_{1,17} = 0.70$ ,  $P = 0.4138$ ) and did not differ between watering treatments ( $F_{1,17} = 0.36$ ,  $P = 0.5579$ ) (Figure 3b).

Mean percent establishment was 0.052 for unwatered trees and 0.038 for watered trees and was not significantly different between treatments ( $t_{1,17} = 0.55$ ,  $P = 0.5932$ ). The final population growth equations for each treatment (W = watered, UW = unwatered) were as follows, where Population<sub>*i*</sub> represents *M. tenebricosa* abundance year one through fifteen and TEMP is tree canopy temperature:

$$(2) \text{ PREDICTED ABUNDANCE (UW)} = \text{POPULATION}_i \cdot ((3.465 \cdot \text{TEMP}) - 42.58) \cdot 0.052$$

$$(3) \text{ PREDICTED ABUNDANCE (W)} = \text{POPULATION}_i \cdot ((6.296 \cdot \text{TEMP}) - 120.30) \cdot 0.038$$

The full model of watering treatment, year, and their interaction predicting *M. tenebricosa* abundance on our study trees was significant ( $F_{29,269} = 30.99$ ,  $P < 0.0001$ ). My model suggests that a detectable difference in abundance, as indicated by non-overlapping error bars, between watered and unwatered trees would occur during the fourth year, or fourth generation of *M. tenebricosa* ( $F_{1,17} = 5.48$ ,  $P = 0.0325$ ), and become increasingly different over time (Figure 4a). Figure 4b illustrates *M. tenebricosa* population growth of the largest initial population on the warmest watered and unwatered trees, and the smallest initial population on the coolest watered and unwatered trees. These lines represent the extremes of population growth based on the effect of temperature, watering treatment, and initial population size.

When initial *M. tenebricosa* abundance is ten individuals on all trees, the full model of watering treatment, year, and their interaction predicting population growth was significant ( $F_{29,269} = 496.59$ ,  $P < 0.0001$ ). Treatment comparisons show a difference in abundance between treatments during year two, or the second generation of *M. tenebricosa* ( $F_{1,17} = 332.26$ ,  $P < 0.0001$ ). This population growth model suggests that regardless of temperature, *M. tenebricosa* abundance on unwatered trees would be greater than on watered trees after the first generation.

## Discussion

The rate and severity of global climate change and urbanization are increasing, yet we still have inconsistent predictions about how heat and drought will affect herbivorous insects (Bale et al. 2002, Jamieson et al. 2012, IPCC 2014). Inconsistencies are partly the result of single-factor and observational studies, which ignore the synergistic and additive relationships that affect ecological processes (Scherber et al. 2013). In fact, few studies have simultaneously examined the effect of temperature and drought on herbivorous pests, and none have manipulated drought on established urban trees, rather than young or potted trees (Koricheva et al. 1998, Raupp et al. 2010, Jamieson et al. 2012). Here I show that drought exacerbates the effect of warming such that *M. tenebricosa* produced over 17% more offspring on the warmest unwatered trees than the warmest watered trees, and over 65% more than the coolest watered trees. Understanding how multiple climatic factors like temperature and drought act together to affect insect pests and their host trees is essential for managing forests and ecosystem services under climate change (Leuzinger et al. 2011, Robinson et al. 2012).

There is mixed support in the literature about the effects of plant drought stress on herbivorous arthropods, but sap-feeding insect performance generally increases with plant stress (Mattson and Haack 1987, Koricheva et al. 1998, Zvereva and Kozlov 2006, Jamieson et al. 2012). On trees in particular, drought stress increases sugar and nitrogen concentrations, which herbivores are able to exploit (White 1984, Koricheva et al. 1998). Since herbivorous insects are primarily nitrogen-limited, greater plant nitrogen concentration can increase fecundity,

development rate, and abundance (Mattson 1980, Koricheva et al. 1998, Herms 2002). For example, McClure (1980) showed that the fecundity, survival, and abundance of an armored scale insect, *Fiorinia externa*, increased as percent total nitrogen content of eastern hemlock trees increased. Although I don't know how nutrient content differed among trees, my results corroborate this evidence and suggest that tree drought stress benefits pest fitness.

An important note about the effect of drought and temperature on *M. tenebricosa* and similar insect pests is the extended timeline by which things happen. On my study trees, *M. tenebricosa* abundance increased by three orders of magnitude across just over a 2°C increase in tree canopy temperature (Figure 3a). However, this occurred over many years of infestation and exposure to the urban environment. Just one year of watering alleviated drought stress and resulted in smaller insects with lower fecundity compared to individuals on unwatered trees. Although lower fecundity did not significantly reduce population growth after two years, my model suggests that we aren't likely to see a difference until the fourth year of watering. In addition, my model shows a remedial effect of reducing *A. rubrum* water stress on *M. tenebricosa* abundance such that fourteen years of reduced water stress would bring pest abundance on the warmest, most heavily infested watered tree below that of the coolest, least heavily infested unwatered tree (Figure 4b). However, if each tree started with equal, small populations, as when newly planted trees were colonized, *M. tenebricosa* abundance would differentiate between watering treatments during the second year, regardless of temperature (Supplemental 1a). This emphasizes the importance of reducing water stress

throughout the ontogeny of *A. rubrum* street trees, particularly early on, so that *M. tenebricosa* cannot grow to damaging populations.

Urban warming, drought stress, and *M. tenebricosa* abundance reduce *A. rubrum* tree condition and ecosystem services (Dale and Frank 2014a). Therefore, chronic pest infestations of *M. tenebricosa* and other scale insects pose an inconspicuous, yet serious threat to urban forests as cities expand and climatic conditions become warmer and drier (Schaffer and Mason 1990, Dale and Frank 2014a). Research has shown that organisms respond similarly to temperature in urban and natural forests (Jochner et al. 2013, Youngsteadt et al. 2014). Since abiotic conditions like temperature and drought resemble those projected in natural forests, results like mine may predict future pest pressures in natural forests (George et al. 2007, Grimm et al. 2008, Hahs and Evans 2015). In addition, cities may experience impending pest outbreaks associated with climate change before surrounding natural forests (Robinet et al. 2011). Future studies should take a similar approach of manipulating multiple urban environmental stress factors and measuring their effect on insects and plants under field conditions. Only then may we obtain a more complete understanding of the effects of future global change on urban and natural ecosystems.

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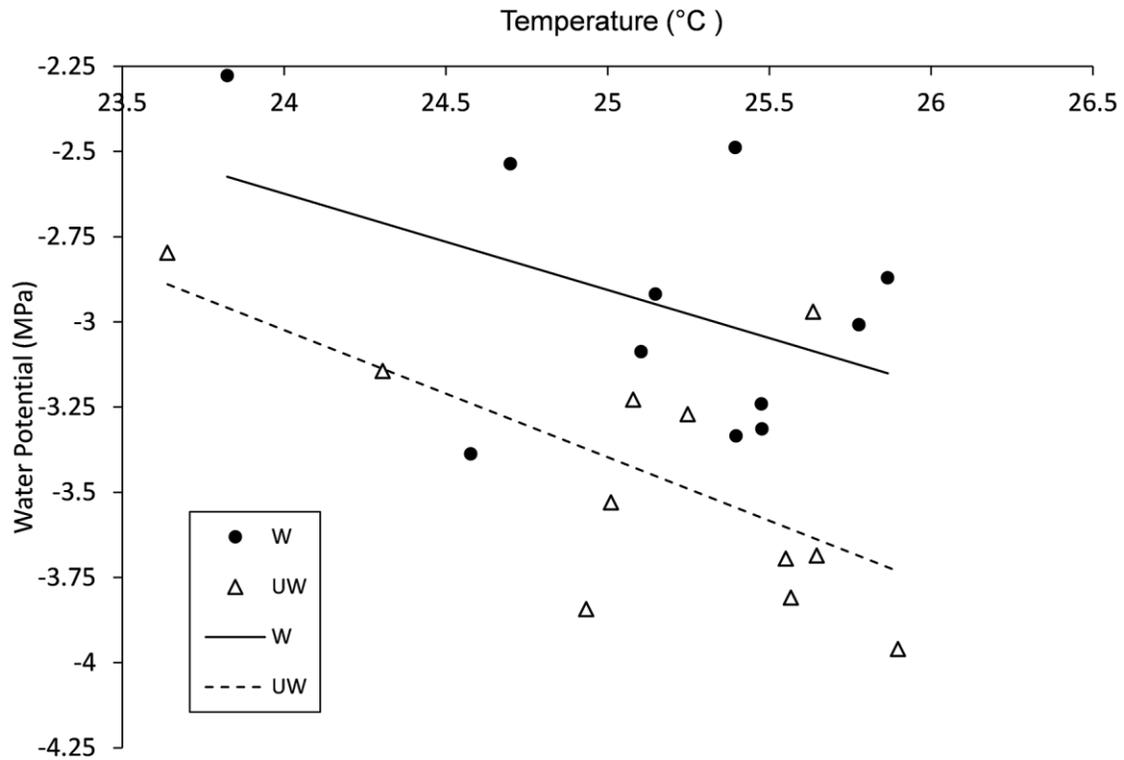


Figure 1. ANCOVA regression plot of tree canopy temperature and watering treatment (W=watered, UW=unwatered) predicting mean xylem water potential (MPa). Temperature and watering treatment significantly predict xylem water potential ( $P < 0.05$ ) (Watered  $R^2 = 0.18$ , Unwatered  $R^2 = 0.41$ )

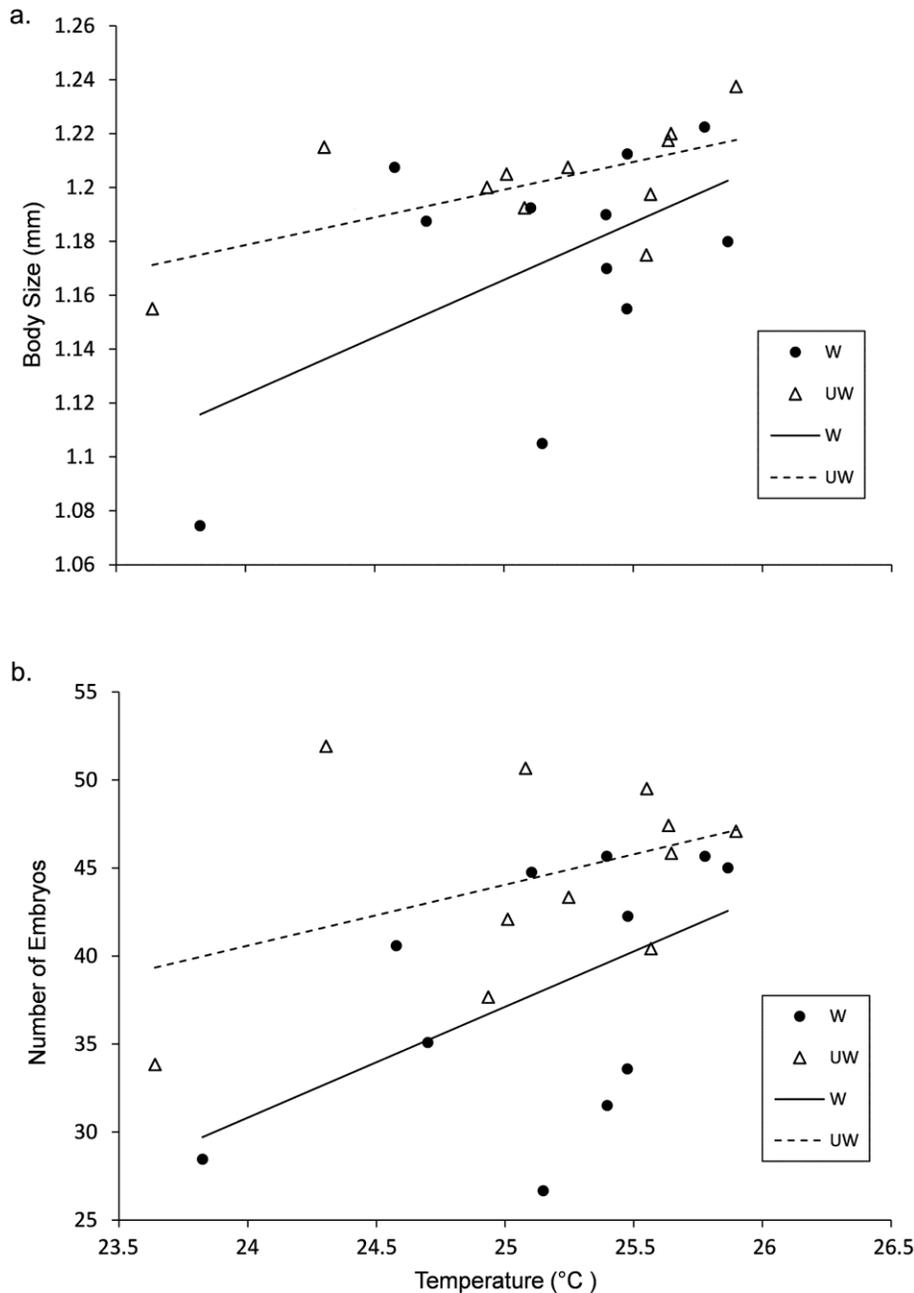


Figure 2. (a) ANCOVA regression plot of tree canopy temperature predicting mean *M. tenebricosa* adult female body size of individuals from each watering treatment (W=watered, UW=unwatered). Temperature and watering treatment significantly predict mean body size ( $P < 0.05$ ) (Watered  $R^2 = 0.31$ , Unwatered  $R^2 = 0.37$ ). (b) ANCOVA regression plot of tree canopy temperature predicting mean number of embryos per individual *M. tenebricosa* adult female on each watering treatment. Temperature and watering treatment significantly predict the mean number of embryos produced per individual ( $P < 0.05$ ) (Watered  $R^2 = 0.27$ , Unwatered  $R^2 = 0.17$ ).

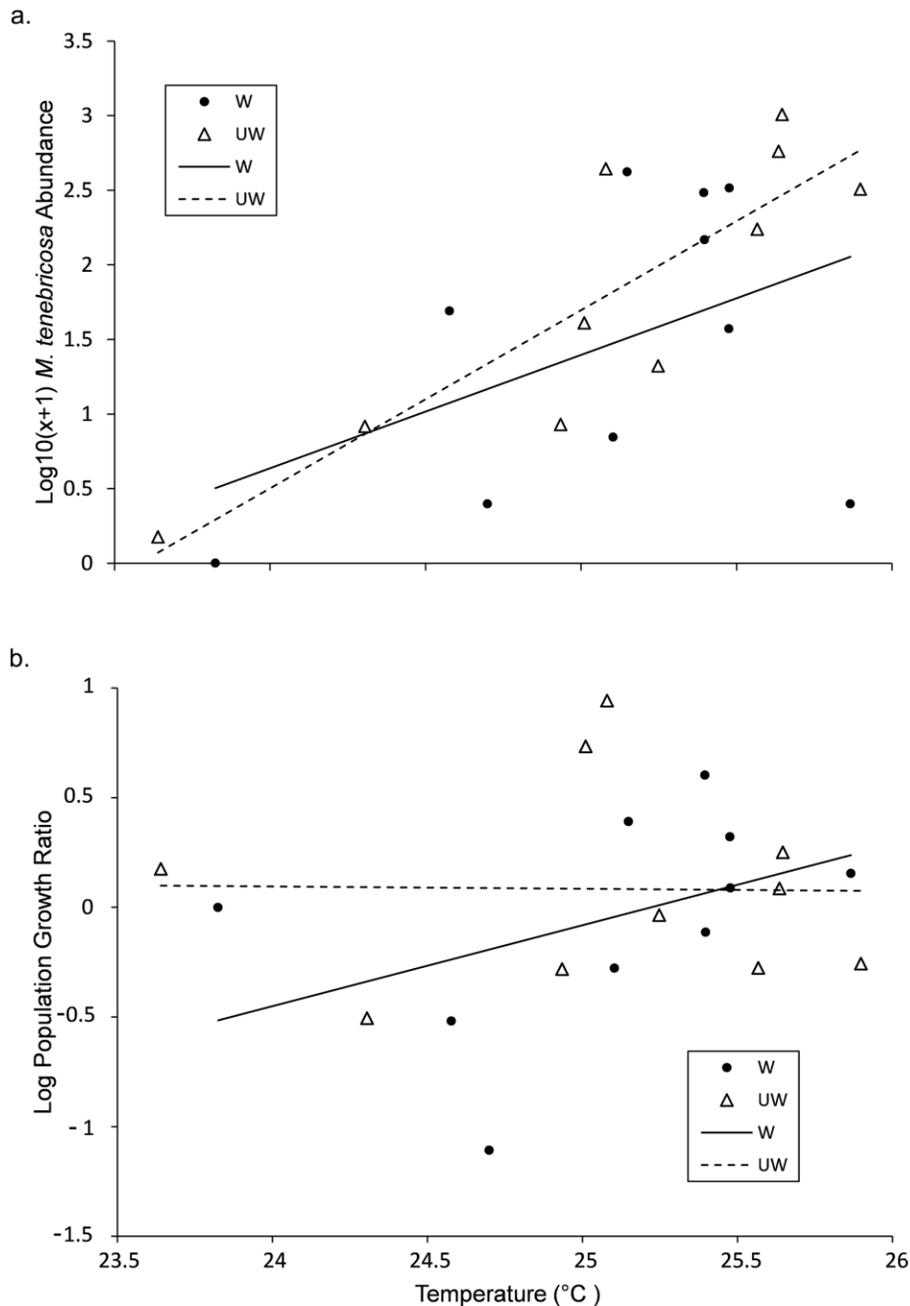


Figure 3. (a) ANCOVA regression plot of tree canopy temperature predicting 2015 *M. tenebricosa* abundance on trees from both watering treatments (W=watered, UW=unwatered). Mean temperature, but not watering treatment or their interaction, significantly predicted *M. tenebricosa* abundance ( $P < 0.05$ ) (Watered  $R^2 = 0.20$ , Unwatered  $R^2 = 0.74$ ). (b) ANCOVA regression plot of mean tree canopy temperature predicting the *M. tenebricosa* log<sub>10</sub> population growth ratio of individuals on watered and unwatered trees. There was no significant relationship between variables ( $P > 0.05$ ) (Watered  $R^2 = 0.19$ , Unwatered  $R^2 = 0.00$ ).

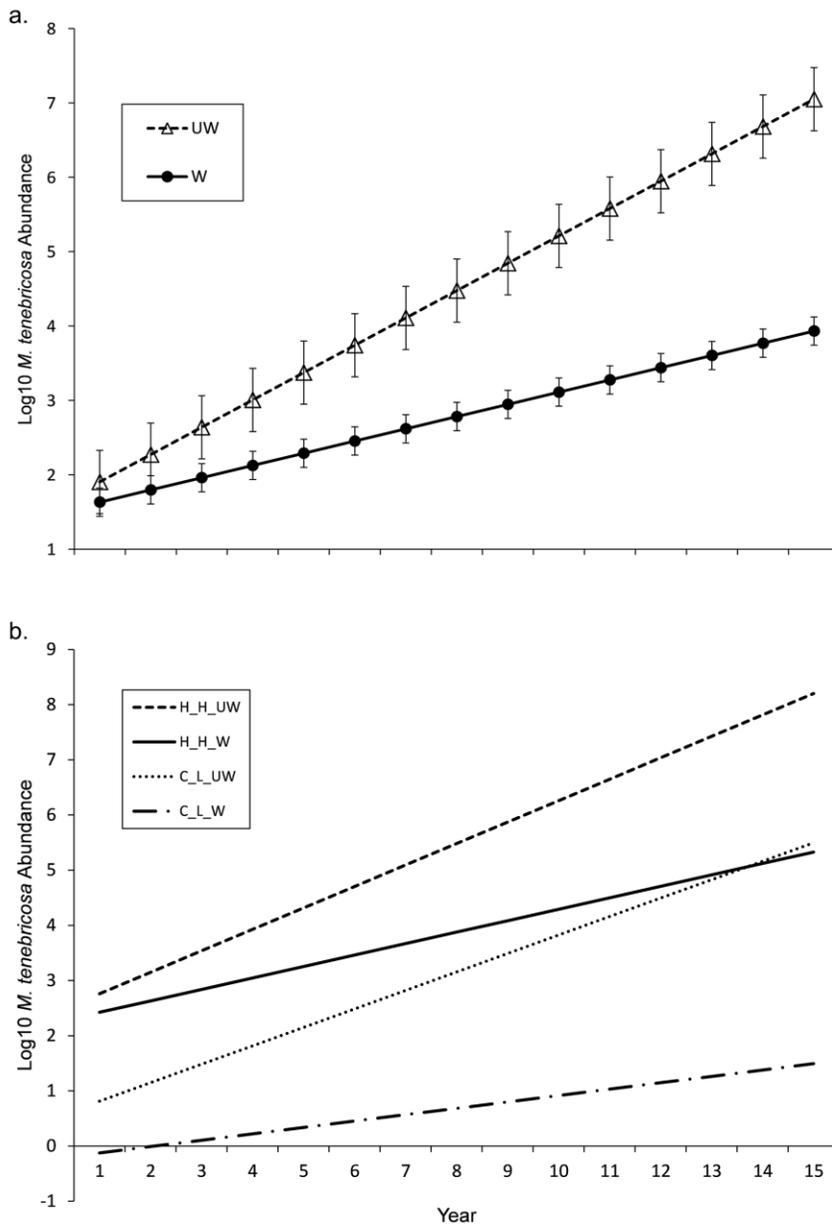


Figure 4. (a) Mean *M. tenebricosa* abundance on watered and unwatered study trees over the next 15 years. The effect of time, watering treatment, and their interaction was significant ( $P < 0.05$ ). Mean *M. tenebricosa* abundance was significantly different between watering treatments beginning in the fourth year ( $P < 0.05$ ). (b) *Melanaspis tenebricosa* abundance on watered and unwatered trees at different temperatures and levels of initial abundance. H\_H\_UW represents the warmest, unwatered tree with the greatest initial *M. tenebricosa* abundance. H\_H\_W is the warmest, watered tree with the greatest initial *M. tenebricosa* abundance. C\_L\_UW represents the coolest, unwatered tree with the lowest initial *M. tenebricosa* abundance. C\_L\_W is the coolest, watered tree with the lowest initial *M. tenebricosa* abundance.

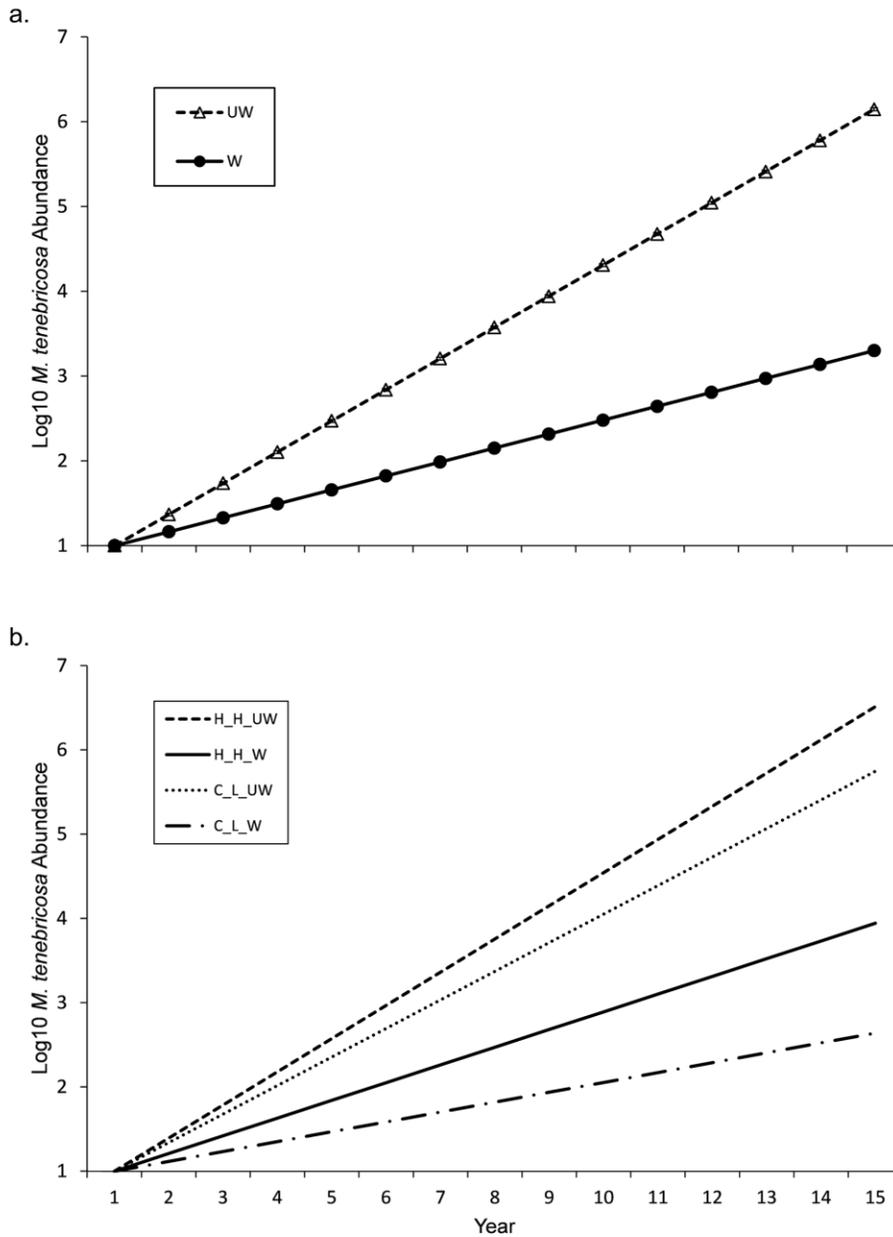


Figure 5. (a) Hypothetical time series of mean *M. tenebricosa* abundance on watered and unwatered trees over the next 15 years assuming an equal, low initial population size of 10 individuals. The effect of time, watering treatment, and their interaction is significant ( $P < 0.05$ ). Mean *M. tenebricosa* abundance is significantly different between watering treatments beginning in the second year ( $P < 0.05$ ). (b) *Melanaspis tenebricosa* abundance on watered and unwatered trees at different temperatures and levels of initial abundance. H\_H\_UW represents the warmest, unwatered tree with the greatest initial *M. tenebricosa* abundance. H\_H\_W is the warmest, watered tree with the greatest initial *M. tenebricosa* abundance. C\_L\_UW represents the coolest, unwatered tree with the lowest initial *M. tenebricosa* abundance. C\_L\_W is the coolest, watered tree with the lowest initial *M. tenebricosa* abundance.

## **Chapter 5: The effects of urban warming, drought, and an herbivore pest on street tree physiology and growth**

### Introduction

Trees provide services like cooling, air filtration, and carbon sequestration that benefit human and environmental health (Maas et al. 2006, Pataki et al. 2006, Lovasi et al. 2008, Donovan et al. 2013). The global climate is warming, which many predict will increase tree growth, and thus, the services they provide (Rustad et al. 2001, Way and Oren 2010, IPCC 2014). In support of this, research in urban habitats, often warmer than their surrounding rural areas, has shown that urban trees grow faster and sequester more carbon than trees in surrounding rural habitats (McPherson and Peper 2012, Searle et al. 2012). However, recent studies have shown that warming can also increase tree pests and reduce tree health (Kurz et al. 2008, Dale and Frank 2014a). In addition, many global change projections suggest a greater frequency and severity of drought, which can have direct and indirect negative effects on tree growth and services (Koricheva et al. 1998, Ryan 2011, Wu et al. 2011, Carter et al. 2014). However, few studies have included both pests and drought in predicting how warmer temperatures will affect tree health and services, particularly in cities. Thus, predictions of how climate change and urbanization will affect trees contradict recent findings in warm urban forests.

High temperatures and low water availability increase the atmospheric demand for water, which increases tree xylem negative pressure causing embolism and vessel cavitation (Sperry and Tyree 1988). Prolonged, drought-induced cavitation can reduce transpiration rates, cause branch dieback, and eventual tree death (Vilagrosa et al. 2003, Litvak et al. 2012). Under heat and drought, plants are

also less able to repair radical oxygen-induced damage to photosynthetic reaction centers, therefore, reducing their energy efficiency and photosynthetic capacity (Maxwell and Johnson 2000). Therefore, future periods of warming and reduced precipitation could cause large carbon losses in natural forests (West et al. 2008). Similarly, urban trees can exhibit drought and heat-associated reductions in gas exchange rates, which reduces carbon sequestration, air filtration, and cooling services (Sperry 2000, Litvak et al. 2012, Savi et al. 2014).

Herbivorous arthropod abundance and damage can increase with warming caused by climate change or urbanization (Raupp et al. 2010, Dale and Frank 2014a, Youngsteadt et al. 2014). Herbivore feeding can reduce woody plant services such as carbon sequestration by reducing photosynthesis and growth or causing plant death (Nykanen and Koricheva 2004, Zvereva et al. 2010). For example, Coffelt et al. (1993) found that caterpillar-induced leaf damage reduced oak tree growth and vigor, especially on trees in urban sites. Less conspicuous feeding by chronic herbivores such as sap-feeders can also reduce tree services (Bale et al. 2002, Zvereva et al. 2010, Boyd et al. 2013). Smith and Schowalter (2001) showed that *Cinara pseudotsugae*, an aphid pest of Douglas fir, drastically reduced root and shoot growth, which had lasting negative effects on carbohydrate storage. Additionally, feeding by the armored scale insect, *Unaspis euonymi*, reduced photosynthetic carbon assimilation by 63% compared to uninfested plants (Cockfield et al. 1987). Because of their small size and sedentary life history, herbivores like scale insects, often escape detection. Therefore, scale-infested urban trees may provide fewer ecosystem services than predicted by models (Cregg and Dix 2001).

Drought stress can increase pest feeding and fitness by increasing nitrogen concentration within vascular fluids (White 1984). This is particularly true for sap-feeding pests like scale insects (Koricheva et al. 1998). Previously, Dale (2015) found that both urban warming and drought stress increased the fitness of *Melanaspis tenebricosa*, a scale insect pest of urban trees. Few studies have investigated the combined effects of warming, drought, and pests on tree growth and services, particularly urban trees. Since climate models predict warming and drought to increase in tandem in many places, and these conditions are already present in cities, understanding their complex interactions is critical for managing forest resources.

*Acer rubrum* is among the most common landscape tree species in the southeastern United States and the most common genus of landscape tree in the eastern U.S. (Raupp et al. 2006). Despite its popularity, *A. rubrum* street trees commonly experience drought stress at or above damaging levels (Dale 2015). In addition, a large percentage of urban *A. rubrum* are infested with, *M. tenebricosa* (Hemiptera: Diaspididae), which become more abundant and damaging at higher temperatures (Dale and Frank 2014a, b). To determine the direct and indirect effects of warming and drought on tree function and ecosystem services, I manipulated drought stress of *A. rubrum* street trees across an existing gradient of urban warming. My prediction was that warming would increase photosynthetic carbon assimilation, but be limited by drought such that warming benefited tree carbon allocation only when sufficient water was available. My first objective was to quantify *A. rubrum* drought stress at my study sites and determine its association with

temperature and water availability. Second, I measured *A. rubrum* photosynthesis, stomatal conductance, transpiration, and leaf photosystem damage to determine the underlying mechanisms affecting tree services. My final objective was to determine the effect of temperature, pest abundance, and drought on tree carbon assimilation by measuring trunk diameter growth and stem elongation over two years.

## Materials and methods

### Study organisms

*Acer rubrum* is a widespread bottomland, softwood species native to eastern North America (Tirmenstein 1991). Because of its hardiness and aesthetic appeal, *A. rubrum* is commonly planted as a street tree in the southeastern U.S. Xylem vulnerability curves suggest that *A. rubrum* is moderately drought tolerant and can tolerate as low as -3.9 MPa of stem xylem negative pressure before embolism occurs in 50% of vessels (Johnson et al. 2011).

*Melanaspis tenebricosa* is a univoltine, armored scale insect herbivore that feeds on xylem parenchyma cells within woody tissue of primarily *A. rubrum* (Metcalf 1922, Beardsley and Gonzalez 1975). These sessile insects are drastically more abundant and damaging in urban than surrounding rural habitats (Metcalf 1922, Frank et al. 2013, Youngsteadt et al. 2014). Severe *M. tenebricosa* infestations can cause branch dieback, canopy thinning, and tree death (Metcalf 1922, Frank et al. 2013).

## Study system and design

For this study, I used *A. rubrum* street trees that ranged in size from 15 to 38 cm in diameter at breast height (DBH). All trees were located in the right-of-way and therefore property of the City of Raleigh, NC, USA. In Raleigh, NC, *A. rubrum* is the second most common street tree, comprising nearly 14% of street trees (Dale unpublished data). To select study sites, I used ArcMap 10.2 to overlay a geocoded street tree inventory map onto a Landsat thermal image of surface temperature acquired on 18 August 2007, prepared as described in Meineke et al. (2013). I used the fishnet selection function in ArcMap 10.2 to create a grid of 2x2 km squares, divided the city into equal quadrants, and randomly selected three grid squares per quadrant. From each selected grid square, I picked a pair of *A. rubrum* from the hottest and coldest sites, resulting in 48 trees at 24 randomly selected sites. Tree pairs at each site were at least 15 m and no more than 75 m apart. Four study sites were lost between survey years due to tree damage or removal, which reduced the total sample size to 40 trees in 2015.

### *Measuring tree canopy temperature and manipulating A. rubrum drought stress*

I determined tree canopy temperature by placing an iButton thermochron DS1921G (Dallas Semiconductor, Dallas, TX, USA) remote temperature logger 4.5 m above ground within each tree's canopy. iButtons were mounted on the underside of a lateral branch attached to an iButton wall mount within a 59-ml portion container (Dart Container Corporation, Mason, Michigan, USA) using a cable-tie. iButtons recorded temperature every two hours from May through August 2014 and 2015. All

analyses with temperature use the mean 2014, mean 2015, or mean two-year daily temperature for the period May through August.

At each site, one tree was watered and one tree was not. However, all trees received water from natural precipitation. Nineteen watered trees had diameters of 15 to 30 cm, which required two TreeGator® slow-release watering bags (Spectrum Products Inc., Youngsville, NC) around their base. The five remaining watered trees were 32 to 38 cm in diameter and required three watering bags around their base. Each bag held approximately 75 liters and was filled twice per week from May through August 2014 and 2015, resulting in 300 liters of water per tree per week for nineteen trees and 450 liters per week for five trees.

To determine if watering treatments reduced tree drought stress, I used a pressure chamber (PMS Instrument Company, Albany, OR) to measure midday xylem water potential of each tree once during June, July, and August 2014 and 2015 (McCutchan and Shackel 1992, Dale and Frank 2014a). Midday water potential measurements were made from 1100 to 1500. I removed one 15 cm terminal twig from sun-exposed locations approximately 5.5 m above ground on the north and south sides of each tree. Weather conditions during each measuring period were mostly sunny and between 32 and 37°C.

#### *The effect of temperature and drought stress on M. tenebricosa abundance*

*Melanaspis tenebricosa* abundance was determined on each *A. rubrum* street tree by pruning one 0.3 m live terminal twig, 5 m above ground, from each cardinal direction of the canopy as in Dale and Frank (2014a). Live adult female *M.*

*tenebricosa* were counted under a dissecting microscope to determine average abundance per 0.3 m of twig in April 2014 and September 2015. Since both temperature and pest abundance are predicted to affect tree ecosystem services, I used each as an independent variable predicting the measured tree responses. To ensure multicollinearity was not confounding my results, I conducted multiple regression analyses and determined that VIF values for each test were less than or equal to 2.

#### *The effect of temperature and drought stress on A. rubrum leaf-level processes*

Light response curves were conducted using a Li-COR 6400 portable photosynthesis system to determine the light intensity at which photosynthetically active radiation (PAR) completely saturated *A. rubrum* photosystems ( $A_{\text{sat}}$ ). A light curve describes the net CO<sub>2</sub> assimilation by a leaf as a function of an increase in PAR from total absence of light to a high intensity (Lobo et al. 2013). Light curves determined that PAR of 1700 was the saturating light intensity and was used for all light saturated photosynthesis field measurements. For each study tree, I selected three fully expanded, undamaged leaves from the terminal ends of southeast-facing branches. Each leaf was growing from a different first-order lateral branch to eliminate an effect of branch origin on leaf processes. I measured  $A_{\text{sat}}$  on 2 cm<sup>2</sup> for each leaf, controlling leaf environmental conditions at 1700 PAR, 400 ppm CO<sub>2</sub> concentration, 30°C block temperature, and 50-60% relative humidity. Each leaf was exposed to these set environmental conditions until photosynthesis and stomatal

conductance remained static for 3 minutes at which point leaf processes were recorded.

To determine the effect of temperature and drought stress on ecosystem services, I used a Li-COR 6400 portable photosynthesis system with a pulse amplitude modulated (PAM) leaf chamber fluorometer sensor head to measure photosynthetic rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), stomatal conductance rate ( $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ ), and transpiration rate ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) on *A. rubrum* street trees (LI6400, Li-COR Inc., Lincoln, NE, USA). Based on preliminary trials, leaves and branches had to remain attached to the tree to get accurate readings of leaf processes. Therefore, I took leaf measurements on 36 of 48 trees in 2014 and 30 of 40 trees in 2015 that had branches accessible to the portable photosynthesis system.

To capture the amount of drought-induced photosystem damage in my trees, I estimated the dark-adapted maximum quantum efficiency of photosystem II reaction centers ( $F_v/F_m$ ) (Maxwell and Johnson 2000). I collected three branches from each tree, wrapped three leaves per branch in aluminum foil, placed them in a closed cooler on ice, and kept them in the dark for at least 4 hours.  $F_v/F_m$  was determined in a darkroom on dark-adapted leaves using the Li-COR 6400 portable photosynthesis system PAM leaf chamber fluorometer. I measured  $F_v/F_m$  on 48 *A. rubrum* street trees in 2014 and 40 in 2015.

#### *The effect of temperature, drought, and M. tenebricosa on A. rubrum growth*

Tree growth is a measure of the amount of carbon trees have sequestered and allocated to biomass. Growth also directly relates to the amount of shade and

therefore cooling, that a tree is able to provide. To determine how temperature and drought affected tree growth, I measured annual change in diameter at breast height (DBH) and total stem elongation over two years. Stem elongation was determined on each tree by collecting five randomly selected branches from each cardinal direction and measuring the distance between bud scars for 2014 and 2015 growth. The average total stem elongation of 20 branches per tree was used for analysis.

### Statistical Analyses

All statistical analyses were conducted in SAS 9.4 statistical software (SAS Institute, Cary, NC, USA). The effect of temperature and watering treatment on xylem water potential, and *M. tenebricosa* abundance were each tested using ANCOVA and LSMEANS with the PROC MIXED procedure. I also tested the effect of tree canopy temperature, *M. tenebricosa* abundance, and watering treatment on tree ecosystem services using PROC MIXED ANCOVA and LSMEANS. Study site was included as a random effect in each PROC MIXED model since each site hosted a pair of watered and unwatered trees, although temperature and environmental conditions were not identical for each. If there was no significant interaction between predictors, the interaction terms were removed to test for a difference in y-intercepts between watering treatment regression equations assuming equal slopes. I used PROC GLM and LSMEANS to conduct repeated measures ANOVA to determine the effect of watering treatment and survey year on tree ecosystem services. All data and analyses from 2014 consist of 48 trees unless

otherwise noted. Because of lost study sites, all 2015 data and analyses include 40 trees unless otherwise specified.

## Results

### *Measuring tree canopy temperature and A. rubrum drought stress*

The 2015 field season was over 1 °C warmer and received 10 cm less precipitation than 2014 (SCONC 2015). Summer 2014 mean tree canopy temperature (N=48) ranged from 23.54 to 25.88 °C with a mean ( $\pm$ SEM) of 24.74 ( $\pm$ 0.09). Summer 2015 mean tree canopy temperature (N=40) ranged from 24.38 to 26.98 °C with a mean ( $\pm$ SEM) of 26.05 ( $\pm$ 0.11). The two-year average of summer tree canopy temperature (N=40) ranged from 24.04 to 26.32 °C with a mean ( $\pm$ SEM) of 25.40 ( $\pm$ 0.10). There was no difference in tree canopy temperature between watered and unwatered trees during either year.

Midday xylem water potential of watered trees in 2014 ranged from -3.46 to -2.27 Mpa with a mean ( $\pm$ SEM) of -2.84 ( $\pm$ 0.08). Unwatered tree xylem water potential in 2014 ranged from -3.96 to -1.85 Mpa with a mean ( $\pm$ SEM) of -3.11 ( $\pm$ 0.10). Water potential of watered trees in 2015 ranged from -3.71 to -2.66 Mpa with a mean ( $\pm$ SEM) of -3.25 ( $\pm$ 0.07). Unwatered tree water potential in 2015 ranged from -4.68 to -2.60 Mpa with a mean ( $\pm$ SEM) of -3.57 ( $\pm$ 0.11).

During the summer of each year, mean xylem water potential significantly decreased as tree canopy temperature increased (Table 1; Figure 1). More importantly, watered *A. rubrum* were consistently less drought stressed than the unwatered trees across the urban temperature gradient (Table 1; Figure 1). In

addition, drought stress increased over time for all trees, potentially the cumulative result of stress over the growing season (Figure 2). However, the difference in drought stress between watered and unwatered trees increased over time such that unwatered trees were most different from watered trees on the final two survey dates (Figure 2).

#### *The effect of temperature and drought stress on *M. tenebricosa* abundance*

*Melanaspis tenebricosa* abundance in 2014 ranged from 0 to 1188 adult females per 0.3 m with a mean ( $\pm$ SEM) of 126.66 ( $\pm$ 38.32) and was not different between watering treatments ( $F_{2,45}=1.25$ ,  $P=0.2696$ ). As 2014 tree canopy temperature increased, *M. tenebricosa* abundance also increased ( $R^2=0.52$ ,  $F_{2,45}=48.45$ ,  $P<0.0001$ ). In 2015, *M. tenebricosa* abundance per 0.3 m ranged from 0 to 1389 adult females with a mean of 171.79 ( $\pm$ 50.19). As in the previous year, 2015 *M. tenebricosa* abundance significantly increased with tree canopy temperature ( $R^2=0.51$ ,  $F_{2,45}=38.10$ ,  $P<0.0001$ ) but did not differ between watering treatments ( $F_{1,37}=0.7985$ ,  $P=0.3773$ ).

#### *The effect of temperature, drought stress, and *M. tenebricosa* on *A. rubrum* leaf-level processes*

Photosynthesis, stomatal conductance, and transpiration rate were measured on 36 *A. rubrum* in 2014 and 30 *A. rubrum* in 2015, each time with half of the trees represented by each watering treatment. I analysed each year individually, then tested the relationship between mean two-year photosynthesis and mean two-year

tree canopy temperature. The effect of temperature, *M. tenebricosa*, and watering treatment on photosynthesis varied by year (Table 2; Figure 3a,b). The effect of two-year mean temperature on two-year mean photosynthetic rate depended on watering treatment such that photosynthesis decreased as temperature increased on unwatered trees but did not change with temperature on watered trees (Table 2; Figure 3c). The main effects of watering treatment, *M. tenebricosa* abundance, and temperature were each nearly significant ( $0.0759 > P > 0.0515$ ), suggesting that as temperature and *M. tenebricosa* increase, carbon assimilation decreases, but more severely on unwatered trees (Figure 3c). Repeated measures ANOVA suggests that there was a significant difference in mean photosynthetic rate between survey years and watering treatments. On average, photosynthesis was greater in 2014 than 2015 ( $F_{1,163}=6.41$ ,  $P=0.0123$ ) and significantly higher on watered than unwatered trees ( $F_{1,163}=11.64$ ,  $P=0.0008$ ) (Figure 4a).

The effect of temperature, *M. tenebricosa* abundance, and watering treatment on stomatal conductance varied by year (Table 2; Figure 3d,e). As two-year temperature increased, stomatal conductance slightly decreased ( $R^2=0.187$ ), although not significantly ( $F_{1,12}=3.57$ ,  $P=0.0833$ ) and was no different between watering treatments (Table 2, Figure 3f). There was no effect of *M. tenebricosa* abundance on stomatal conductance ( $F_{1,12}=0.10$ ,  $P=0.7519$ ). Repeated measures ANOVA suggests that stomatal conductance was also significantly greater in 2014 than 2015 ( $F_{1,163}=52.10$ ,  $P<0.0001$ ), but was not different between watering treatments ( $F_{1,163}=2.18$ ,  $P=0.1417$ ) (Figure 4b).

Temperature and watering treatment affected transpiration rate differently each year (Table 2; Figure 2g,h). As two-year tree canopy temperature increased, mean transpiration rate nearly significantly decreased ( $R^2=0.24$ ,  $F_{1,12}=4.40$ ,  $P=0.0579$ ). Watering treatment and *M. tenebricosa* abundance had no effect on transpiration rate (Table 2). In contrast to photosynthesis and stomatal conductance, leaf transpiration rate was significantly greater in 2015 than 2014 ( $F_{1,163}=9.69$ ,  $P=0.0022$ ) (Figure 4c). However, transpiration rate was no different between watering treatments ( $F_{1,163}=0.94$ ,  $P=0.3344$ ).

As two-year temperature increased,  $F_v/F_m$  slightly, although significantly, decreased ( $R^2=0.053$ ,  $F_{1,16}=5.91$ ,  $P=0.0272$ ) but was not affected by watering treatment ( $F_{1,16}=0.63$ ,  $P=0.4373$ ). *Melanaspis tenebricosa* abundance was nearly significantly associated with  $F_v/F_m$  ( $F_{1,16}=4.12$ ,  $P=0.0594$ ). Repeated measures ANOVA showed a significant relationship between mean  $F_v/F_m$  and the full model of survey year, watering treatment, and their interaction ( $F_{3,797}=7.53$ ,  $P<0.0001$ ). The effect of watering treatment on  $F_v/F_m$  depended on which year I measured it ( $F_{1,734}=9.32$ ,  $P=0.0023$ ) such that unwatered trees in 2014 had  $F_v/F_m$  values much lower than watered trees but were no different in 2015 (Figure 4d). On average, watered trees had significantly higher  $F_v/F_m$  values than unwatered trees ( $F_{1,734}=14.79$ ,  $P<0.0001$ ). In addition, mean  $F_v/F_m$  was higher in 2015 than 2014 ( $F_{1,734}=7.38$ ,  $P<0.0067$ ).

### *The effect of temperature, drought, and M. tenebricosa on A. rubrum growth*

*Acer rubrum* DBH growth was measured on the 40 trees remaining at the end of the study. Two year diameter growth was low, ranging from 0 to 1.45 cm with a mean ( $\pm$ SEM) of 0.69 ( $\pm$ 0.09) on watered trees. Unwatered tree diameter growth ranged from 0.15 to 1.56 cm with a mean ( $\pm$ SEM) of 0.59 ( $\pm$ 0.08). Tree canopy temperature, *M. tenebricosa* abundance, and watering treatment had no effect on DBH growth (Table 3; Figure 5a) although, watered trees grew 17% more in diameter than unwatered trees.

Average total stem elongation from May 2014 through September 2015 ranged from 4.15 to 58.75 cm with a mean of 29.19 ( $\pm$ 3.65) on watered trees. On unwatered trees, total stem elongation ranged from 5.87 to 38.85 cm with a mean of 22.76 ( $\pm$ 2.11). Tree canopy temperature was not associated with total stem elongation, however, *M. tenebricosa* abundance was ( $F_{1,17}=10.93$ ,  $P=0.0042$ ). As *M. tenebricosa* abundance increased, total stem elongation also increased ( $R^2=0.30$ ) (Figure 5b). Additionally, stems grew consistently more on watered than unwatered trees ( $F_{1,17}=6.46$ ,  $P=0.0211$ ) (Table 3; Figure 5b). On average, branches of watered trees grew over 28% more than those of unwatered trees over two years.

### Discussion

Urban areas are characterized by impervious surfaces, which can make them much warmer and drier than surrounding rural areas (Kim 1992, Graves 1994, Nowak and Greenfield 2012). As predicted, I found that street tree drought stress increased with urban warming and watering reduced this stress. Temperature and

drought affected leaf-level processes by reducing photosystem II efficiency, stomatal conductance, and transpiration rates on trees at warmer sites. These heat-induced changes reduced photosynthetic carbon assimilation on unwatered but not watered trees, especially during 2014. Therefore, watering reduced drought stress and increased leaf-level services such that watered trees grew more than unwatered trees. Thus predictions about warming and tree growth hold true, but are dependent on drought.

Urban trees often face drought stress because temperatures are high and water infiltration is low (Kim 1992, Graves 1994, Nielsen et al. 2007). Drought stress causes xylem embolism and cavitation, which disrupts water movement through trees (Sperry and Tyree 1988). The water potential at which xylem cavitation becomes damaging in *A. rubrum* is -3.9 MPa (Johnson et al. 2011). Unwatered trees in my study, which represent normal urban street trees, were consistently below this threshold. This suggests that xylem cavitation may have played a role in reducing tree growth and photosynthesis on unwatered compared to watered trees. Under prolonged drought conditions cavitating vessels may not recover and cell division may be reduced (Ryan 2011). Thus drought-stressed trees become less efficient at water transport, and photosynthesis (McDowell 2011, Ryan 2011). In my study, this was evident as unwatered tree water potential became more negative over time but remained relatively constant on watered trees.

My results suggest that temperature and drought had a stronger effect than *M. tenebricosa* abundance on *A. rubrum* ecosystem services. This was tested with an existing urban temperature gradient but also by evaluating services in hotter and

cooler years. Reducing drought stress increased photosynthetic carbon allocation to biomass and was greatest on the warmest, watered *A. rubrum* street trees. Experimental warming studies suggest that future warmer temperatures will increase tree growth rates (Way and Oren 2010). For example, Hellmers et al. (1970) found that warming increased growth and bud development of spruce trees under controlled conditions. Across an urban-rural temperature gradient in New York, USA, *Quercus rubra* grew 23% more in warmer than cooler urban sites (Searle et al. 2012). Although these studies provide insight into the effects of warming on tree growth, they ignore important environmental factors like drought. Consistent with Wu et al. (2011), my results suggest that the effect of temperature on photosynthesis and growth is dependent on drought stress. Therefore, my results support previous findings but elucidate the importance of drought in forest services, which is projected to become more severe under future climate change (Carter et al. 2014, IPCC 2014).

Trees reduce temperatures by transpiring water and providing shade (Oke et al. 1989, Taha 1997). Transpiration is driven by the evaporation of water from stomates, which increases with temperature and pulls water through xylem tissue from the roots to leaves (Litvak et al. 2012). Under drought, plants may close stomates to conserve water and prevent xylem cavitation at the cost of reducing photosynthesis and using reserves of carbohydrates through respiration (Sperry 2000, Adams et al. 2009). This may reduce tree growth, which I found as unwatered trees grew less than watered trees. However, despite receiving over 300L of water each week, as temperatures warmed, drought stress increased and stomatal

conductance decreased on watered trees. This is concerning since the unwatered trees represent the urban street tree status quo and reduced conductance means less growth and carbon storage. Interestingly, transpiration rates were much higher during the warmer, drier 2015 growing season, although trees closed their stomates in response to warming across the urban temperature gradient. This suggests that warmer climatic temperatures associated with climate change and urbanization may increase *A. rubrum* water loss by shifting the point at which trees close their stomates, thereby increasing xylem cavitation rates and subsequent damage (West et al. 2008).

In this study, tree growth increased with urban warming and pest abundance regardless of drought. However, Dale and Frank (2014a) found that urban warming and *M. tenebricosa* abundance reduced tree condition by causing branch dieback and canopy thinning. Although my study trees grew more as temperature and *M. tenebricosa* abundance increased, I suspect that the canopies were also less dense and providing fewer overall services at warmer sites with more abundant *M. tenebricosa*. In addition, I did not measure root growth and nutrient storage, which is affected by herbivore feeding and warmer growing temperatures (Wargo et al. 1972, Coffelt et al. 1993, Way and Oren 2010). Therefore, *M. tenebricosa* feeding and drought stress may have reduced carbohydrate storage in tree roots, making trees less able to overcome future damage (Loescher et al. 1990). As urban areas expand, temperatures warm, and precipitation events become more extreme, the combined effects of warming and drought may reduce *A. rubrum* services in urban

and natural forests, which would affect humans and the environment (Maas et al. 2006, Pataki et al. 2006).

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Table 1. ANCOVA with mean tree canopy temperature and watering treatment predicting *A. rubrum* xylem water potential during the 2014 and 2015 growing seasons. Interactions were not significant so they were removed from the model. Bolded values are significant ( $P < 0.05$ ).

	N	F	P
2014	48		
Watering treatment		F <sub>1,22</sub> =17.70	<b>P=0.0004</b>
2014 Temperature		F <sub>1,22</sub> =12.16	<b>P=0.0021</b>
2015	40		
Watering treatment		F <sub>1,18</sub> =18.93	<b>P=0.0004</b>
2015 Temperature		F <sub>1,18</sub> =6.96	<b>P=0.0167</b>

Table 2. ANCOVA with tree canopy temperature, *M. tenebricosa* abundance, and watering treatment predicting leaf-level services during 2014, 2015, and the two year mean. Interactions were included if significant or nearly significant. Bolded values are significant and italicized values are nearly significant ( $P < 0.05$ ).

			N	F	P	
Photosynthesis	2014		36			
		Watering treatment		$F_{1,15}=14.85$	<b>P=0.0004</b>	
		2014 Temperature		$F_{1,15}=1.88$	P=0.9561	
		2014 <i>M. tenebricosa</i>		$F_{1,15}=2.8$	P=0.1167	
			Temp * Water Trt		$F_{1,18}=15.25$	<b>P=0.0019</b>
	2015			30		
		Watering treatment			$F_{1,12}=3.02$	P=0.1078
		2015 Temperature			$F_{1,12}=2.95$	P=0.1115
			2015 <i>M. tenebricosa</i>		$F_{1,12}=1.24$	P=0.2866
	2YR mean			30		
		Watering treatment			$F_{1,11}=4.77$	<i>P=0.0515</i>
		2yr Temperature			$F_{1,11}=3.84$	<i>P=0.0759</i>
2015 <i>M. tenebricosa</i>				$F_{1,11}=4.26$	<i>P=0.0634</i>	
		Temp * Water Trt		$F_{1,11}=5.21$	<b>P=0.0434</b>	
Conductance	2014		36			
		Watering treatment		$F_{1,15}=3.79$	<i>P=0.0706</i>	
		2014 Temperature		$F_{1,15}=0.084$	P=0.3726	
		2014 <i>M. tenebricosa</i>		$F_{1,15}=0.92$	P=0.3550	
			Temp * Water Trt		$F_{1,18}=3.79$	<i>P=0.0706</i>
	2015			30		
		Watering treatment			$F_{1,12}=2.23$	P=0.1608
		2015 Temperature			$F_{1,12}=1.73$	P=0.2129
			2015 <i>M. tenebricosa</i>		$F_{1,12}=0.29$	P=0.5995
	2YR mean			30		
		Watering treatment			$F_{1,12}=1.40$	P=0.2600
		2yr temperature			$F_{1,12}=3.57$	<i>P=0.0833</i>
2015 <i>M. tenebricosa</i>				$F_{1,12}=0.10$	P=0.7519	
Transpiration	2014		36			
		Watering treatment		$F_{1,15}=3.88$	<i>P=0.0690</i>	
		2014 Temperature		$F_{1,15}=1.72$	P=0.2103	
		2014 <i>M. tenebricosa</i>		$F_{1,15}=1.60$	P=0.2261	
			Temp * Water Trt		$F_{1,18}=3.92$	<i>P=0.0676</i>
	2015			30		
		Watering treatment			$F_{1,12}=0.05$	P=0.8350
		2015 Temperature			$F_{1,12}=3.10$	P=0.1035
2015 <i>M. tenebricosa</i>				$F_{1,12}=0.87$	P=0.3692	

Table 2 (continued).

	2YR mean		30		
		Watering treatment		$F_{1,12}=0.59$	$P=0.4560$
		2yr temperature		$F_{1,12}=4.40$	$P=0.0579$
		2015 <i>M. tenebricosa</i>		$F_{1,12}=0.06$	$P=0.8084$
Fv/Fm	2014		46		
		Watering treatment		$F_{1,20}=3.65$	$P=0.0704$
		2014 Temperature		$F_{1,20}=5.89$	<b><math>P=0.0248</math></b>
		2014 <i>M. tenebricosa</i>		$F_{1,20}=6.84$	<b><math>P=0.0165</math></b>
	2015		40		
		Watering treatment		$F_{1,17}=0.01$	$P=0.9188$
		2015 Temperature		$F_{1,17}=3.03$	$P=0.0999$
		2015 <i>M. tenebricosa</i>		$F_{1,17}=1.32$	$P=0.2668$
	2YR mean		40		
		Watering treatment		$F_{1,16}=0.63$	$P=0.4373$
		2yr temperature		$F_{1,16}=5.91$	<b><math>P=0.0272</math></b>
		2015 <i>M. tenebricosa</i>		$F_{1,16}=4.12$	$P=0.0594$

Table 3. ANCOVA with mean tree canopy temperature, *M. tenebricosa* abundance, and watering treatment predicting DBH growth and total stem elongation over two years. Interactions were not significant so they were removed. Bolded values are significant ( $P<0.05$ ).

		N	F	P
DBH Growth		48		
	Watering treatment		$F_{1,17}=1.08$	$P=0.3125$
	2YR Temperature		$F_{1,17}=0.05$	$P=0.8195$
	2015 <i>M. tenebricosa</i>		$F_{1,17}=0.75$	$P=0.3987$
Total Stem Elongation		40		
	Watering treatment		$F_{1,17}=6.46$	<b><math>P=0.0211</math></b>
	2YR Temperature		$F_{1,17}=0.41$	$P=0.5319$
	2015 <i>M. tenebricosa</i>		$F_{1,17}=10.93$	<b><math>P=0.0042</math></b>

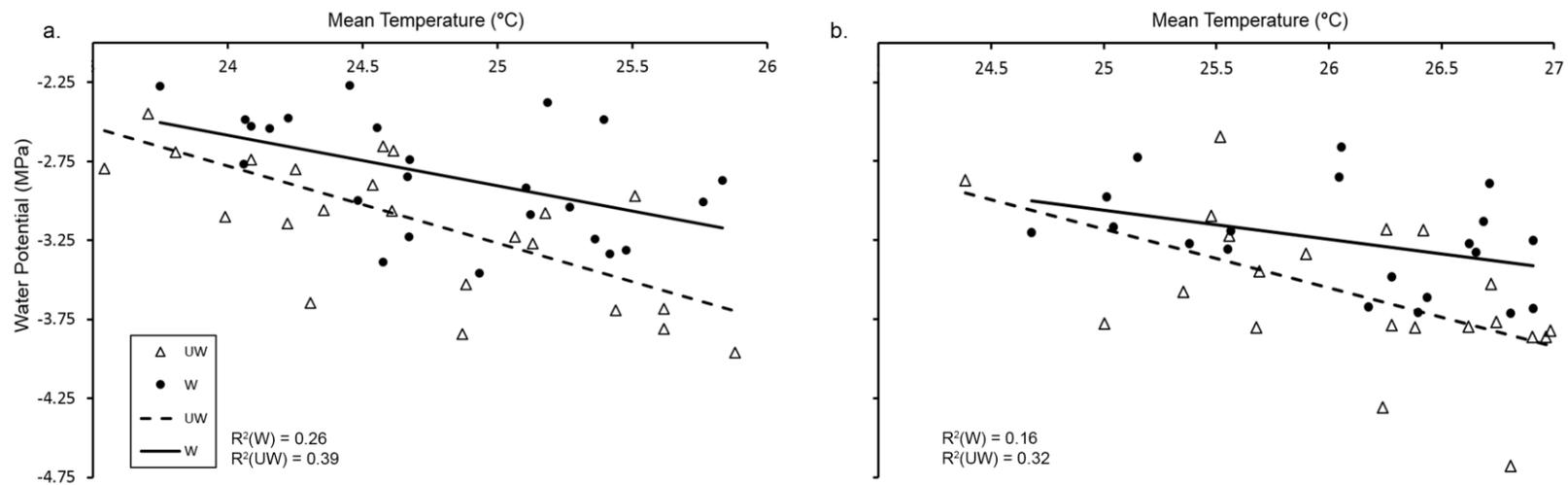


Figure 1. ANCOVA regression plots of tree canopy temperature regressed with mean xylem water potential for each watering treatment. (a) 2014 mean tree canopy temperature predicting 2014 mean water potential. (b) 2015 mean tree canopy temperature predicting 2015 mean water potential. W = watered and UW = unwatered trees.

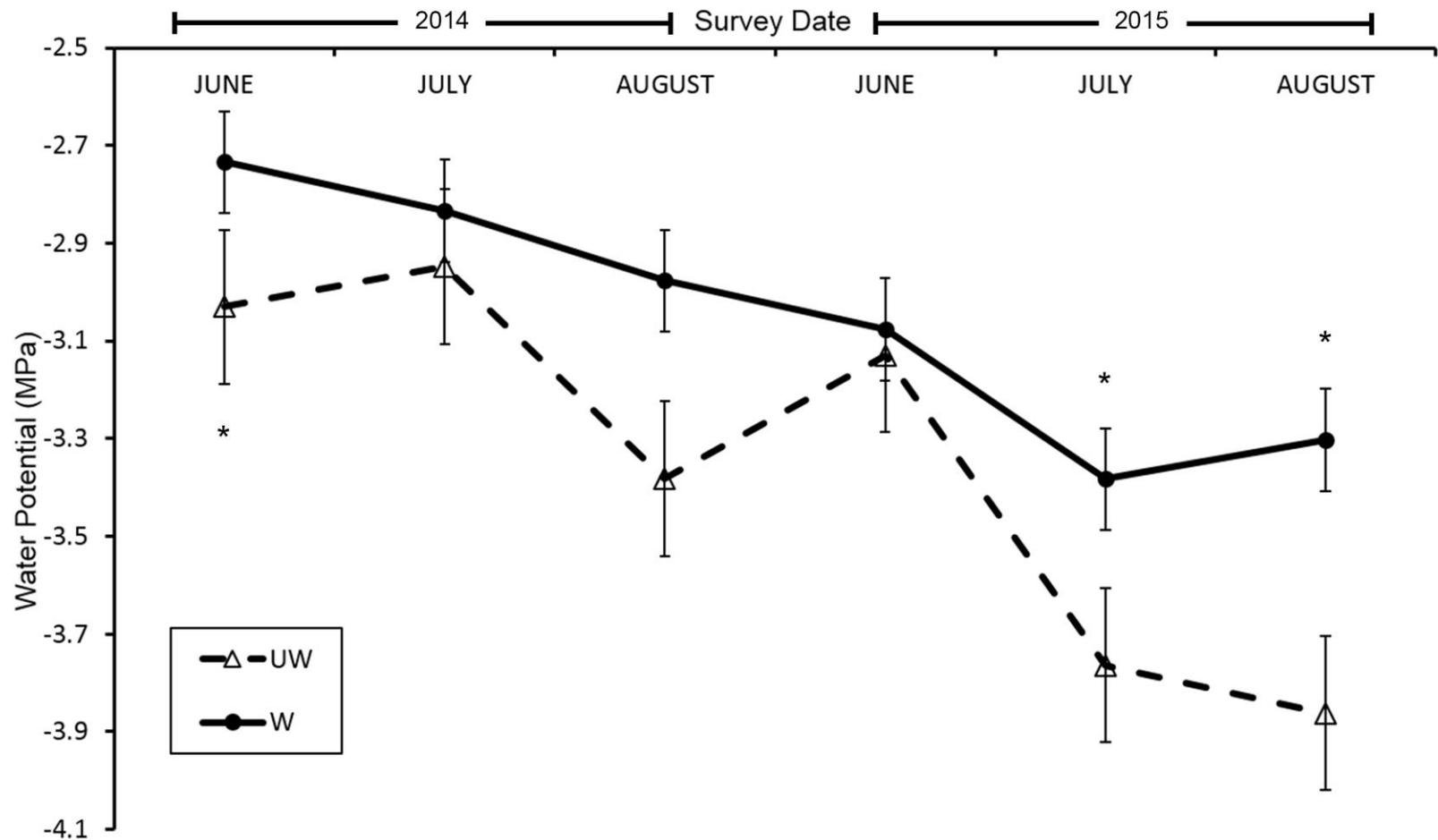


Figure 2. Mean xylem water potential time series during each summer month of the two-year study. W = watered and UW = unwatered trees. Asterisks indicate a significant difference between watering treatments ( $P < 0.05$ ). Error bars are standard error of mean values.

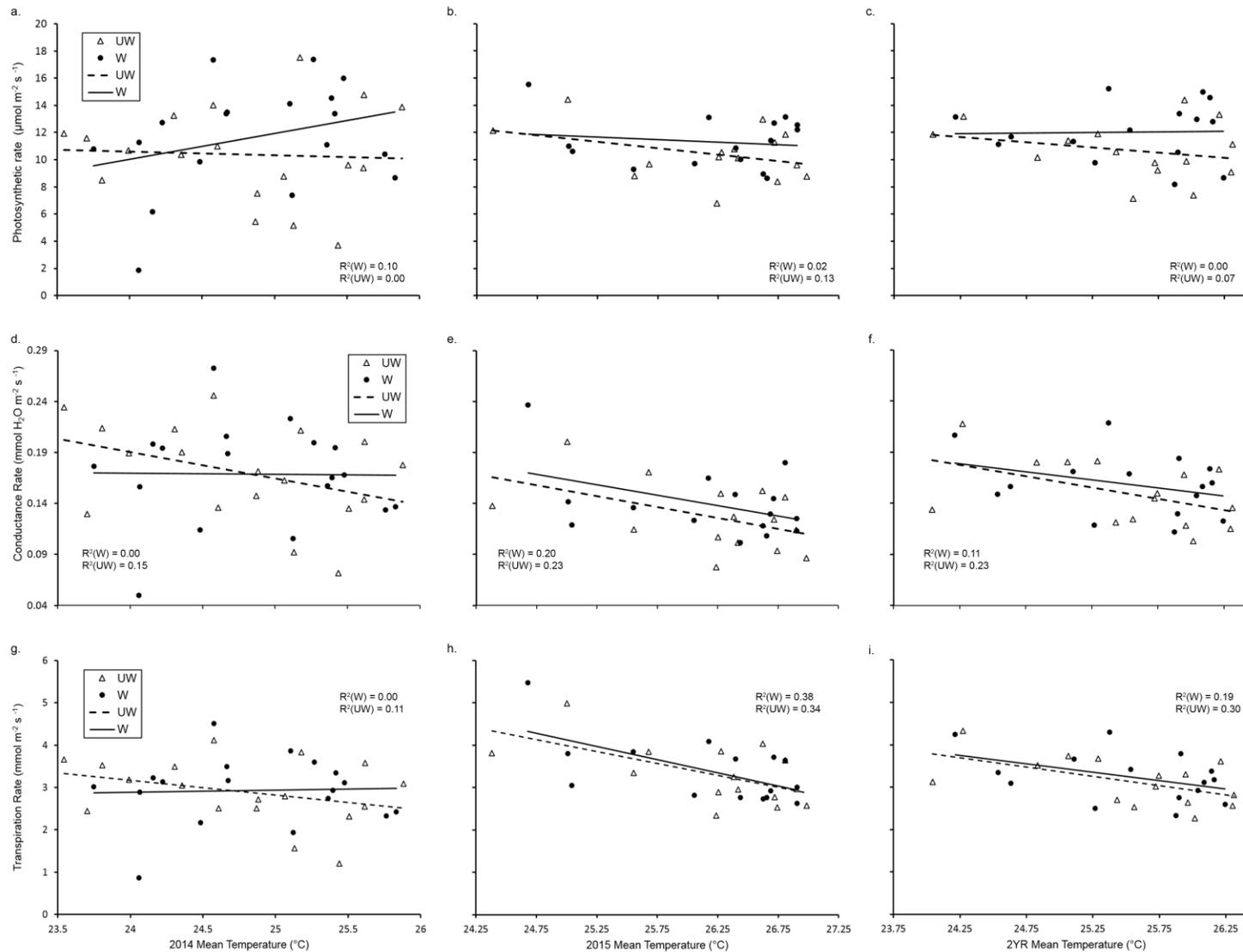


Figure 3. ANCOVA regression plots of tree canopy temperature predicting leaf-level services for 2014 (left column), 2015 (middle column), and the two-year means (right column). (a-c) photosynthesis rate, (d-f) stomatal conductance rate, and (g-i) transpiration rate.  $R^2$  values are embedded within each plot. W = watered and UW = unwatered trees.

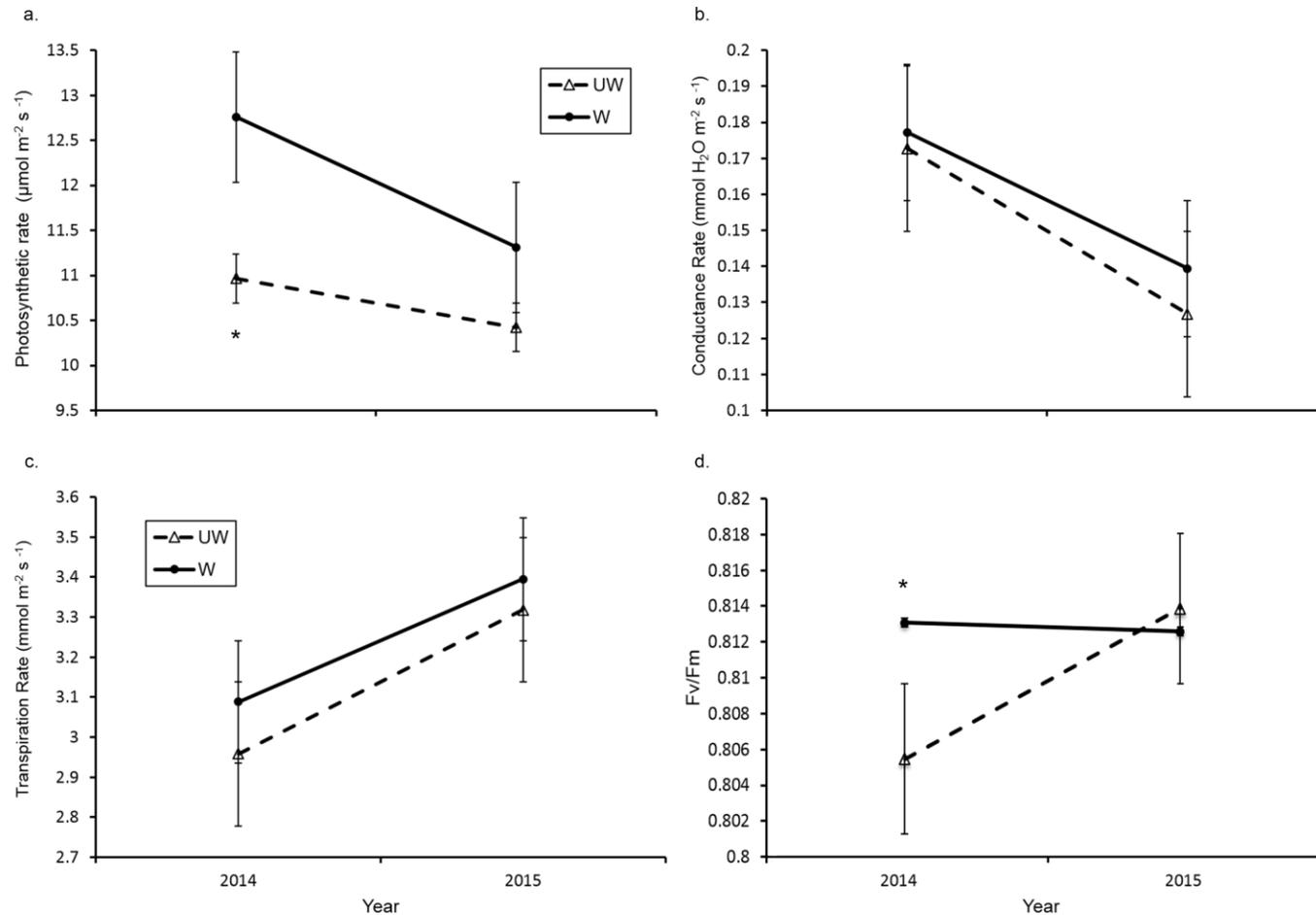


Figure 4. Repeated measures ANOVA of mean leaf-level services and photosystem damage during 2014 and 2015 per watering treatment. (a) photosynthesis rate, (b) stomatal conductance rate, (c) transpiration rate, and (d)  $F_v/F_m$  value. Asterisk indicates significant difference between treatments ( $P < 0.05$ ). Error bars are standard error of the mean. W = watered and UW = unwatered trees.

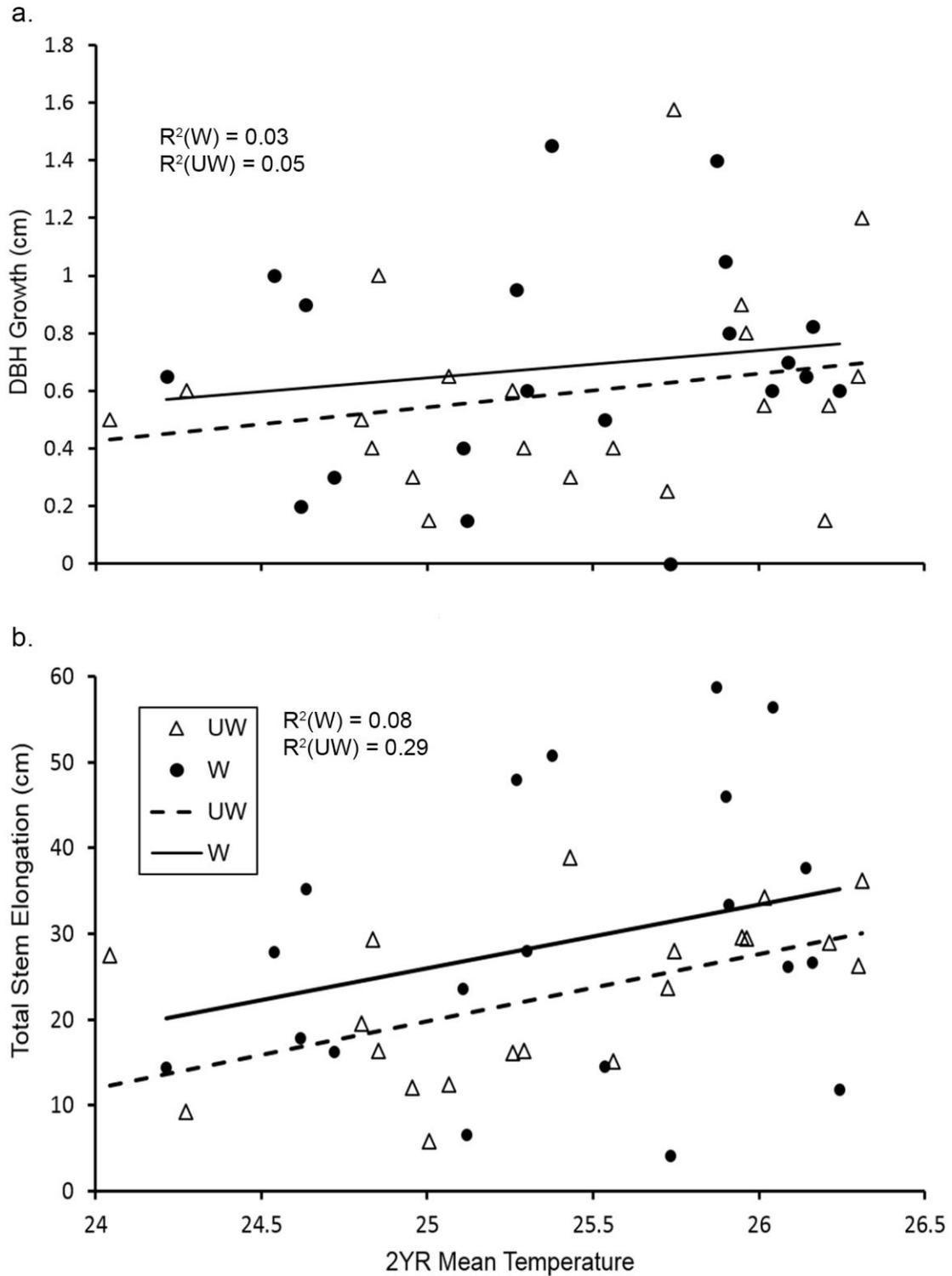


Figure 5. ANCOVA regression plots of two-year mean tree canopy temperature regressed with tree growth for each watering treatment. (a) Mean temperature predicting two-year DBH growth. (b) Mean temperature predicting two-year total stem elongation. W = watered and UW = unwatered trees.