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# Water availability drives urban tree growth responses to herbivory and warming

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## Abstract

1. Urban forests provide important ecosystem services to city residents, including pollution removal and carbon storage. Climate change and urbanization pose multiple threats to these services. However, how these threats combine to affect urban trees, and thus how to mitigate their effects, remains largely untested because multi-factorial experiments on mature trees are impractical.
2. We used a unique urban warming experiment paired with a laboratory chamber experiment to determine how three of the most potentially damaging factors associated with global change for urban and rural trees—warming, drought, and insect herbivory—affect growth of *Quercus phellos* (willow oak), the most commonly planted large shade tree in the southeastern US, which is known for its resilience to these potential stressors.
3. In a previous study, we found that the urban heat island effect was associated with reduced growth of *Q. phellos* and higher abundance of *Parthenolecanium* scale insects, key pests of oaks in cities. Here, we tested the hypothesis that tree water stress is the mechanism for these effects of warming. We found evidence that water stress is a major, interactive factor reducing urban tree growth, but found no evidence that water stress is associated with *Parthenolecanium* survival or abundance. Warming and *Parthenolecanium* only reduced growth in *Q. phellos* saplings that were simultaneously water stressed.
4. *Synthesis and applications.* Across many temperate cities worldwide, urban trees grow less than rural trees. Our results point to water stress as the most likely driver for this pattern. Importantly, we found that water stress both reduces tree growth on its own and exacerbates effects of warming and insect pests on tree growth. Therefore, management strategies targeted at increasing tree hydration in cities may reduce effects of these three key stressors that are expected to intensify with further urbanization and climate change.

## KEYWORDS

climate change, herbivory, trees, urban heat island effect, warming, water relations

## 1 | INTRODUCTION

Warming and water availability are two aspects of global change with profound potential to influence tree growth. At mid- to high

latitudes, where most tree carbon is stored (Pan et al., 2011), warming should increase photosynthesis and growth rates when trees have enough water and temperatures do not exceed their thermal limits (Chung et al., 2013; Way & Oren, 2010). If water is scarce,

warming should reduce tree growth by inducing water stress that causes xylem cavitation (Maherali, Pockman, & Jackson, 2004) and reduces photosynthesis (Penuelas et al., 2004). Though these predictions are clear in theory and supported by observations from mature trees (e.g. Brzostek et al., 2014) and small-scale experiments on seedlings and saplings (e.g. Kuster, Dobbertin, Guenthardt-Goerg, Schaub, & Arend, 2014), we still lack experimental evidence to determine how warming and drought will combine to affect mature trees and the amount of carbon they store. (But see Gaylord et al., 2013; Norby et al., 2016 for experiments on mature trees exploring single global change factors.)

Concurrently, warming and water stress can increase insect herbivore abundance (Creeden, Hicke, & Buotte, 2014; Dale & Frank, 2017; Jactel et al., 2012), a situation in which species interactions, which are often ignored in models of responses to global change (Zarnetske, Skelly, & Urban, 2012), may affect tree responses to changing climatic factors. For example, in the mountain regions of North America, warming induces water stress in ponderosa pines and increases the geographic range and voracity of mountain pine beetles (Creeden et al., 2014). Extensive climate-induced outbreaks of these and other herbivores have turned many forests from carbon sinks into sources as trees die and decompose or burn (Creeden et al., 2014; Kurz et al., 2008). Though not well studied, non-outbreak species that typically do not kill trees (here, we call them “chronic herbivores”) can also become more abundant in response to warming and drought. This is due in some cases to direct benefits of warming. As temperatures increase, insect metabolic rates increase, driving higher survival and egg production, until insect thermal maxima are reached and fitness declines (Angilletta, 2009). In other cases, herbivores benefit indirectly because drought increases nitrogen availability (Huberty & Denno, 2004) and/or reduces host plant defenses, increasing herbivore survival (Jactel et al., 2012). In most cases, though, warming and drought probably both affect insect herbivores, and all three factors thereafter interact to affect trees. Disentangling these factors and, importantly, determining if they interact to exacerbate one another, is a challenge that is critical for understanding the long-term effects of climate change on forests.

Urban environments provide the unique opportunity to determine the effects of prolonged warming, water availability, and herbivores on mature trees. The urban heat island effect is caused by hard surfaces that absorb radiation from the sun and emit energy from that radiation as heat, increasing temperatures 1–12°C above rural temperatures (Oke, 1973). Urban warming is locally heterogeneous, creating a mosaic of thermal conditions to which urban plants and animals are exposed (Dale & Frank, 2014b; McCluney, Burdine, & Frank, 2017; Meineke, Dunn, Sexton, & Frank, 2013). Therefore, mature trees within cities have experienced a range of warmer temperatures (compared to nearby trees in natural areas) and potential consequences for decades. This situation is not easily replicated experimentally and, at least for some species, effects of urban warming are congruent with the effects of climate change (Youngsteadt, Dale, Terando, Dunn, & Frank, 2015; Ziska et al., 2003). In addition to serving as an experimental system for exploring effects of broader climate warming, urban forests provide

a suite of critical services to city residents that are contingent on tree function and growth (Willis & Petrokofsky, 2017). Trees reduce pollutants, electricity use (through cooling that reduces air conditioning use), and incidence of cardiovascular, lung and metabolic diseases (Akbari, Pomerantz, & Taha, 2001; Mullaney, Lucke, & Trueman, 2015; Willis & Petrokofsky, 2017). However, urban foresters and other resource managers do not have adequate tactics to improve or preserve tree services. This is in large part because the effects of multiple potential stressors associated with urbanization are difficult to disentangle.

Here, we disentangle effects of key stressors associated with climate change and urbanization focusing on *Quercus phellos* (willow oak), the second most common tree in cities across the southeastern US and the most common large shade tree (E.K. Meineke, unpubl. data). Because healthy large trees sequester 90 times more carbon per year than healthy small trees (Nowak, 1994), *Q. phellos* has vast potential to affect urban carbon dynamics. In addition, *Q. phellos* may provide a more conservative view into the effects of climate change than more susceptible or rare tree species. Species within *Quercus* are resilient to various stressors (e.g. Abrams, 1990) and *Q. phellos* is particularly resilient to herbivory (e.g. Coffelt, Schultz, & Wolf, 1993).

We previously found that, within the thermal mosaic in Raleigh, NC, USA, *Q. phellos* photosynthesis and growth were reduced at relatively hot urban sites (Meineke, Youngsteadt, Dunn, & Frank, 2016). Pest arthropod densities on *Q. phellos* were also higher at hotter urban sites (Meineke et al., 2013, 2016), though they did not reduce growth substantially (Meineke et al., 2016). Thus, the mechanism for reduced growth of this species in hotter urban areas remains unknown. In our study area, Raleigh, NC, USA, *Q. phellos* lives far from the southern edge of its range, where, in the absence of other stressors, warming should increase its growth (Way & Oren, 2010).

We paired field and laboratory experiments to determine how water deficits add to or interact with the effects of warming and key chronic herbivores of *Q. phellos*, phloem-feeding scale insects in the genus *Parthenolecanium*, on tree growth. In the field, we employed a factorial experiment within the urban temperature mosaic to determine if urban warming was associated with water deficits and if water deficits were associated with *Parthenolecanium* abundance and growth of mature trees. In the laboratory, we manipulated temperature, water availability and *Parthenolecanium* in a factorial experiment to determine if and how they interacted to affect growth of young trees. We also tested how laboratory temperature and water availability affected *Parthenolecanium* survival. Together, these manipulations allowed us to determine effects of three of the most imminent stressors associated with climate change and urbanization on growth of a highly resilient tree species.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

The focal tree in this study *Q. phellos* (Family: Fagaceae) is a member of the red oak group (*Erythrobalanus*). *Quercus phellos* is native to and distributed across the central and eastern United States.

It is widely planted, and wildlife species use its structure as habitat and its acorns as food (USDA, [https://plants.usda.gov/factsheet/pdf/fs\\_quph.pdf](https://plants.usda.gov/factsheet/pdf/fs_quph.pdf)). Our focal insect herbivore, *Parthenolecanium quercifex*, or the oak lecanium scale (Hemiptera: Coccidae), is the most common pest on *Q. phellos*. *Parthenolecanium quercifex* is univoltine. In spring, *P. quercifex* females live on branches and feed on the phloem. Nymphs move to leaves where they feed during summer. For more details about the life history of *P. quercifex*, see Meineke et al. (2016). *Parthenolecanium quercifex* co-occurs on branches with its congener *Parthenolecanium corni* (Camacho, Chong, Braman, Frank, & Schultz, 2017). *Parthenolecanium quercifex* and *P. corni* have similar life histories, and the phylogeny of this group is not well resolved. Furthermore, the morphological characters used to tell them apart require slide mounting. Therefore, we treat them as *Parthenolecanium* sp. *Parthenolecanium* reduces tree growth by feeding on sap and promoting sooty mold on tree leaves, which blocks leaf light interception (Wood, Tedders, & Reilly, 1988).

## 2.2 | Field experiment

### 2.2.1 | Study design

Raleigh, NC, USA is a humid, temperate city located at 35.77°N, 78.64°W. For detailed information on Raleigh climate, see Meineke et al. (2013). To choose study sites, we used a Landsat infrared layer of surface temperature in April 2011. The Raleigh Department of Parks, Recreation and Cultural Resources provided a map of Raleigh street trees that we overlaid with the thermal image. We chose 10 sites above and 10 sites below median temperature, each of which contained two *Q. phellos* less than 30 m apart. See Meineke et al. (2016) for more details and a map of these study sites. Trees were  $20.9 \pm 1.2$  cm (mean  $\pm$  SEM) in diameter at breast height. With a mist blower (model: 451; Solo, Newport News, VA, USA), we treated one tree per site with horticultural oil (SuffOil-X; BioWorks, Victor, NY, USA) to suppress small-bodied arthropods. For more details on how trees were treated, see Meineke et al. (2016). This created a split-plot design with temperature (hot/cold) as the whole plot factor and oil treatment (yes/no) as the split-plot factor.

To measure air temperature, we installed an iButton thermocron data logger (DS1921G, precision: 0.5°C, accuracy:  $\pm 1.0^\circ\text{C}$ , Dallas Semiconductor, Dallas, TX, USA) on the northern, bottom-most branch of one tree per site. We placed iButtons on shaded branches to reduce sun exposure associated with malfunctions in other studies (Meineke, Dunn, & Frank, 2014). To further prevent malfunctions due to solar radiation and precipitation, we placed iButtons in wall mounts (Dallas Semiconductor) within 2.54-cm deep plastic cups.

### 2.2.2 | Responses

To determine *Parthenolecanium* abundance, we collected 12 c. 30-cm branches from the lower, outer canopy of each study tree on

15 March 2015, using a pole pruner. *Parthenolecanium* sampling was limited to lower branches, because it was not possible to sample higher than five metres without a bucket truck. We also measured midday stem water potential, a measurement of peak water stress. We collected bottom, outer branches from the north side of each tree, using a pole pruner between 1,100 and 1,400 on 16 August 2013 (two branches per tree), from 29–30 July 2014 and from 29–30 August 2014 (during both 2014 dates, three branches per tree). Branches were placed in a pressure chamber (1505D; PMS Instrument Company, Albany, NY, USA). We recorded mid-day water potential as the amount of pressure required for the xylem to release water, as in other studies (Dale & Frank, 2014a). To determine tree radial growth, we measured diameter at breast height of each tree 1.4 m above the ground in October 2014 and June 2015. We used diameters to calculate basal area ( $\pi r^2$ ) and subtracted the starting basal area from the ending basal area to calculate basal area growth in early 2015.

### 2.2.3 | Statistical analyses

We performed all analyses in RStudio (R Core Team, 2015). Here iButtons recorded unreasonably high temperatures during mid-day (45°C+) that we believe were due to solar radiation heating iButtons (Hubbart, Link, Campbell, & Cobos, 2005). We avoided the biases introduced by these readings by extracting temperatures between 18:00 and 20:00 hr. We used these for all downstream analyses. We used the *plyr* package (Wickham, 2011) to calculate average temperatures for 15 July to 15 August 2013, 1–29 July 2014 and 1–29 August 2014, c. 1 month before each water potential measurement. In 2013, iButtons failed at two sites. These sites were excluded from analyses. In 2014, an additional site was removed from the study at the request of a homeowner.

To determine how temperature affected water potential, we used linear mixed-effects models (lme) in the *nlme* package (Pinheiro, Bates, DebRoy, & Sarkar, 2016) for each date on which water potential was measured. We specified water potential as the response (three values per tree, depending on year), temperature as a fixed effect, and tree nested within site as a random effect. We included interactions between temperature and oil treatment and removed them from models because they were not significant. To determine if water potential was associated with higher *Parthenolecanium* abundance and if oil treatments reduced *Parthenolecanium* abundance, we used linear mixed-effects models with average water potential per tree in July and August 2014 and oil treatment as fixed effects and *Parthenolecanium* average abundance per branch as the response in each model. We included an interaction between water potential and oil treatment. Because we detected a significant interaction, we tested for the effects of water potential on treated and untreated trees separately in simple linear models as post hoc tests of how water potential affected *Parthenolecanium* abundance. To determine how water stress and herbivore suppression with oil affected tree growth, we used linear mixed-effects models with average water potential per tree in

July and August 2014 as fixed effects (in separate models), original tree size as a covariate (da Silva et al., 2002), oil treatment as a fixed effect, and tree basal area growth as the response. We included an interaction between water potential and oil treatment in each model and removed interaction terms from the models if they were not significant.

## 2.3 | Laboratory chamber experiment

### 2.3.1 | Study design

To determine how temperature, drought and herbivory by *Parthenolecanium* affected *Q. phellos*, we conducted a laboratory chamber experiment with a three by two factorial design in the North Carolina State University phytotron facility (<https://www.ncsu.edu/phytotron/information.html>). We purchased 56 bare root *Q. phellos* saplings from Rennerwood, Inc (Tennessee Colony, USA; local wildtype) and grew them in 20.3-cm diameter pots in potting mix (2P; Fafard, Agawam, MA, USA) starting on 5 April 2013. When trees arrived, they were  $28.42 \pm 0.84$  cm tall (mean  $\pm$  SEM). We fertilized each tree on 11 April, 20 June and 20 July 2013 by placing 4 g of 14-14-14 (N-P-K) Osmocote Classic (Geldersmolen, The Netherlands) pellets in the soil. Directly after arrival, we treated saplings with Safer Brand Insecticidal Soap (Lititz, PA, USA) 185 ml/L H<sub>2</sub>O to remove any insects.

Trees were divided between two  $2.4 \times 3.7 \times 2.1$  m chambers with T-12, 1,500 ma, cool-white fluorescent and 100 W incandescent lamps for “hot” and “cold” treatments. To determine sunrise/sunset times in chambers, we used projected sunrise/sunset data for 2013 from the US Naval Observatory ([http://aa.usno.navy.mil/data/docs/RS\\_OneYear.php](http://aa.usno.navy.mil/data/docs/RS_OneYear.php)). For 1 hr at the onset of sunrise and sunset, only incandescent bulbs were lit to simulate twilight. Temperatures for the cold chamber were selected based on 1981–2010 Raleigh normal average temperatures measured at the NCSU weather station (<https://www.ncdc.noaa.gov/data-access/land-based-station-data/land-based-datasets/climate-normals/1981-2010-normals-data>). To represent temperature differences commonly observed within urban heat islands (Oke, 1973), the hot chamber was set 4°C higher than the cold chamber at all times. This represents differences in 6–8 p.m. temperatures measured by iButtons between relatively hot and cold sites within Raleigh, NC. We kept this temperature difference constant during day and night for feasibility. We raised temperatures in both chambers every month during spring and reduced them each month starting in August to induce dormancy and mimic natural conditions.

Slight deviations from actual Raleigh temperatures were necessary for this experiment. In April and May, we raised cold chamber temperatures by 3°C above normal to induce leaf expansion so that *Parthenolecanium* could establish on saplings in May (see below). From August to November, we lowered chamber temperatures more quickly to induce dormancy, because in a preliminary experiment laboratory saplings took longer than urban trees to become dormant. In November, after leaves began to fall, we set both chambers

to equal temperatures as outdoor temperatures reached the low-temperature limits for the environmental chambers. Temperature and sunrise/sunset times in chambers are detailed in Table S1.

To impose drought-like conditions, half of the trees in each temperature treatment received pulsed water inputs. The remaining trees were saturated. We used a pulsed rather than a consistently sparse watering regime, because pulsed water inputs can increase insect pest abundances (Huberty & Denno, 2004). We watered trees in the “saturated” treatment every 2 days with 2.6 L of water or until the soil was saturated, and measured soil moisture at these times, using a soil moisture sensor (SM150; Delta-T Devices, Cambridge, UK) in three haphazardly selected locations per pot for three pots per treatment. When average soil moisture of “pulsed” trees in either temperature treatment was below 5%, we watered trees in all treatments with 2.6 L of water or until the soil was saturated. We chose 5% soil moisture as a threshold because it is below the mean soil moisture for the city of Raleigh (McCluney et al., 2017) but not low enough to cause *Q. phellos* to shed its leaves (2%), as observed in a preliminary experiment (E.K. Meineke, unpubl. data). In many other studies, researchers use wilting as a benchmark for water stress rather than percent soil moisture (e.g. Grinnan, Carter, & Johnson, 2013), but *Q. phellos* does not readily wilt. To measure water potential, we clipped the highest, lateral branch from each tree at the stem base and pressurized it with the same methods used in our field study, on 22 July and 9 September 2013. On 22 July, one tree was watered before water potential measurements, and this data point was excluded from analyses.

When *Parthenolecanium* matured on field trees in May 2013, we collected egg sacs from three *Q. phellos* trees on the NCSU campus not included in our urban field study. We attached three egg sacs to half of the saplings in each laboratory treatment, using elastic ties. *Parthenolecanium* hatched in the laboratory from late May to early June 2013 and settled on leaves. In June 2013, when we observed no more *Parthenolecanium* hatching in the city or in the warming chambers, we removed the egg sacs.

### 2.3.2 | Responses

On 27 June 2013 and 10 September 2013, we counted *Parthenolecanium* on eight haphazardly selected leaves per tree. On each of these dates, we counted the number of leaves on each study tree that were infested with *Parthenolecanium*. On 27 June, we used random numbers to select five of the leaves we counted and labelled them with a permanent marker. We recounted *Parthenolecanium* on those leaves on 27 July and 9 September 2013 to determine how watering regimes and temperature affected *Parthenolecanium* survival. To estimate *Parthenolecanium* abundance per tree for analyses, we calculated the average *Parthenolecanium* density per leaf in June and September from the eight-leaf counts and multiplied these values by the number of infested leaves on each tree.

To estimate the total leaf area, we counted all leaves on each tree on 11 April, 27 June, 27 July and 10 September 2013. Five leaves per tree were collected and measured on an LI-COR Area Meter

(LI-3100, Lincoln, USA) on 28 August 2013. To estimate total leaf area per tree on each date, we multiplied average area per leaf by the number of leaves. We estimated leaf area acquired during the experiment by subtracting leaf area in April from leaf area in September. To determine the mechanisms for leaf area differences between treatments, we also calculated the number of leaves acquired over the course of the experiment (total leaves in September minus leaves in April) and the average leaf size per tree.

All trees were harvested on 11–12 December 2013. Root and shoot biomass were separated, dried and weighed. We clipped each tree with pruners at soil level to separate above-ground (shoot) from below-ground (root) biomass. We washed soil from roots using water and dried shoot and root biomass separately in paper bags in a drying room until late January 2014. We weighed dried shoot and root biomass of each tree and summed these to calculate total biomass.

Dry root and shoot biomass were ground in February 2014 (Model 4; Thomas Wiley, Swedesboro, NJ, USA) and carbon and nitrogen concentrations were determined, using an elemental analyser Perkin Elmer 2400 CHNS Analyser (2400 CHNS Analyser; PerkinElmer, Akron, OH, USA) by the NCSU Environmental and Agricultural Testing Service. To determine carbon to nitrogen ratios, we divided percent carbon by percent nitrogen. We calculated total carbon in root and shoot biomass and summed these to determine total carbon sequestered per tree. Data were missing from two shoot samples and one root sample.

### 2.3.3 | Statistical analyses

We analysed *Parthenolecanium* survival from June to July and from July to September, using logistic regressions (glm) in the *stats* package (R Core Team, 2015) with average survival per leaf as the response and temperature, water treatment and an interaction between these two variables as predictors. We included total leaves on which *Parthenolecanium* was counted as weights in the models so that *Parthenolecanium* survival estimates for trees on which more leaves were counted contributed more to parameter estimates. We used ANOVAs to determine how the same predictors affected estimated *Parthenolecanium* abundance, which was log transformed to meet linear regression assumptions.

To determine how our treatments affected the plants, we used ANOVAs for each response with temperature (cold/hot), *Parthenolecanium* (absence/presence) and water treatment (saturated/pulsed) as factors. Initially, we included a three-way interaction between all factors and progressively removed non-significant interactions. We modified this analysis for models that did not meet ANOVA assumptions, as specified below. Models for shoot biomass, root biomass and total biomass were square root transformed. Models for percent nitrogen, percent phosphorous and percent carbon were  $\text{asin}(\sqrt{x/100})$  transformed. All transformations resulted in models that met ANOVA assumptions.

Models of water potential from both dates that included all predictor variables did not meet ANOVA assumptions due to unequal variances between treatments. Therefore, we first used

non-parametric Kruskal–Wallis tests to determine if water treatments (saturated/pulsed) affected water potential. Then, we used two-way ANOVAs to test for the effects of temperature and *Parthenolecanium* on pulsed and saturated trees, separately. We included interactions between temperature and *Parthenolecanium* in final models if they were significant. To improve residuals, water potential of saturated trees on both dates was  $\log_{10}$  transformed.

In the full model for leaf area acquired by trees, two interactions were significant. We lacked the power to detect differences between all significant treatments using Tukey honest significant difference (HSD) tests ( $n = 7$  for each treatment). Therefore, we used separate two-way ANOVAs to test for the effects of temperature and *Parthenolecanium* on pulsed trees and saturated trees. We used these same methods to analyse total leaves (sqrt) acquired by trees. For analyses of total leaf area acquired, within the pulse-stressed treatment, we found a significant interaction between temperature and water treatment. Therefore, we used a Tukey HSD to test for differences between all treatments. We used a linear contrast to test the a priori hypothesis that *Parthenolecanium* only reduced leaf area on hot trees with pulsed water inputs. In all analyses, leaf area acquired was log transformed to improve residuals. One tree was excluded from analyses because it died during the experiment.

Because *Parthenolecanium* densities varied within treatments, we tested for the effects of *Parthenolecanium* as a continuous predictor on leaf area acquired, biomass, and carbon sequestration. We built separate, simple linear models for each treatment, response variable, and predictor. Predictors included average estimated *Parthenolecanium* per leaf, estimated *Parthenolecanium* abundance, and percent of leaves with *Parthenolecanium* in June, early in the experiment when *Parthenolecanium* was presumably feeding most.

## 3 | RESULTS

### 3.1 | Field experiment

All data for this project are deposited in a Dryad repository (Meineke & Frank, 2018). As reported in Meineke, Holmquist, Wimp, and Frank (2017), temperatures at sites in 2013 and 2014 were correlated ( $R^2 = .45$ ), indicating that sites that are relatively hot remain so across years. This is expected because impervious surface and coarse vegetation drive urban temperatures (Dale & Frank, 2014b), and these structural aspects of cities do not change from year to year. In August 2013, monthly average temperatures ranged from 24.7 to 27.3, in July 2014 27.2 to 30.7, and in August 2014 24.3 to 26.2.

Treating trees with horticultural oil for herbivorous arthropods did not affect water potential or basal area growth (see Table 1). In August 2013, water potential ranged from  $-3.0$  to  $-0.5$ , in July 2014  $-2.9$  to  $-0.9$ , and in August 2014  $-2.9$  to  $-0.9$ . Trees at sites with warmer air temperatures had lower water potentials (higher water stress) on both dates in 2014 but not in 2013. Slope estimates across years trended toward lower water potential with increasing urban temperatures (Table 1). There was a significant effect of the



Date	Predictor	Estimate ± SE	Statistic	p
<b>(a) Water potential</b>				
August 2013	Intercept	-0.82 ± 0.55	$F_{1,34} = 0.004$	.949
	Mean August temp.	-0.07 ± 0.11	$F_{1,15} = 0.36$	.559
	Oil treatment (sprayed)	0.09 ± 0.10	$F_{1,16} = 0.78$	.392
July 2014	Intercept	3.29 ± 2.26	$F_{1,75} = 2.11$	.15
	<b>Mean July temp.</b>	<b>-0.17 ± 0.07</b>	<b><math>F_{1,17} = 4.46</math></b>	<b>.049</b>
	Oil treatment (sprayed)	-0.06 ± 0.10	$F_{1,18} = 0.39$	.542
August 2014	Intercept	2.82 ± 0.23	$F_{1,76} = 155.40$	<.0001
	<b>Mean August temp.</b>	<b>-0.03 ± 0.01</b>	<b><math>F_{1,17} = 10.47</math></b>	<b>.005</b>
	Oil treatment (sprayed)	0.00 ± 0.01	$F_{1,18} = 0.02$	.899
<b>(b) <i>Parthenolecanium</i> abundance</b>				
July 2014	Intercept	0.58 ± 1.07	$F_{1,18} = 5.19$	.594
	<b>Water potential</b>	<b>-1.84 ± 0.67</b>	<b><math>F_{1,16} = 5.19</math></b>	<b>.017</b>
	Oil treatment (sprayed)	1.04 ± 1.25	$F_{1,16} = 5.19$	.414
	<b>Water potential × oil treatment</b>	<b>1.40 ± 0.80</b>	<b><math>F_{1,16} = 5.19</math></b>	<b>.038</b>
August 2014	Intercept	2.00 ± 1.19	$F_{1,17} = 2.83$	.110
	Water potential	-0.70 ± 0.61	$F_{1,16} = 2.47$	.136
	<b>Oil treatment (sprayed)</b>	<b>-1.01 ± 0.29</b>	<b><math>F_{1,16} = 12.20</math></b>	<b>.001</b>
	Water potential × oil treatment	-0.88 ± 1.05	$F_{1,15} = 0.69$	.417

**TABLE 1** Statistics from field experiment on effects of urban warming and herbivore removal on mature *Quercus phellos* tree water potential and growth. Significant associations are in bold

interaction between water potential in July and oil treatment on *Parthenolecanium* abundance. Untreated trees with lower water potential in July had more *Parthenolecanium* (July:  $F_{1,17} = 9.39$ ,  $p = .007$ , adjusted  $R^2 = .32$ ), such that the most water-stressed tree had 43 times more *Parthenolecanium* than the least stressed tree on which we detected individuals. In the model with August water potential, oil treatments reduced *Parthenolecanium* abundance, and we found a trend toward more *Parthenolecanium* on trees with lower water potentials. Trees with lower water potential in August grew less in early 2015 (Figure 1d, July:  $F_{1,33} = 0.56$ ,  $p = .460$ , adjusted  $R^2 = .20$ ; August:  $F_{1,32} = 10.71$ ,  $p = .003$ , adjusted  $R^2 = .36$ ). Overall, we found that urban warming was associated with increased water stress in late summer, and this water stress was associated with less tree growth and more *Parthenolecanium* early the following growing season.

## 3.2 | Laboratory chamber experiment

### 3.2.1 | Water potential

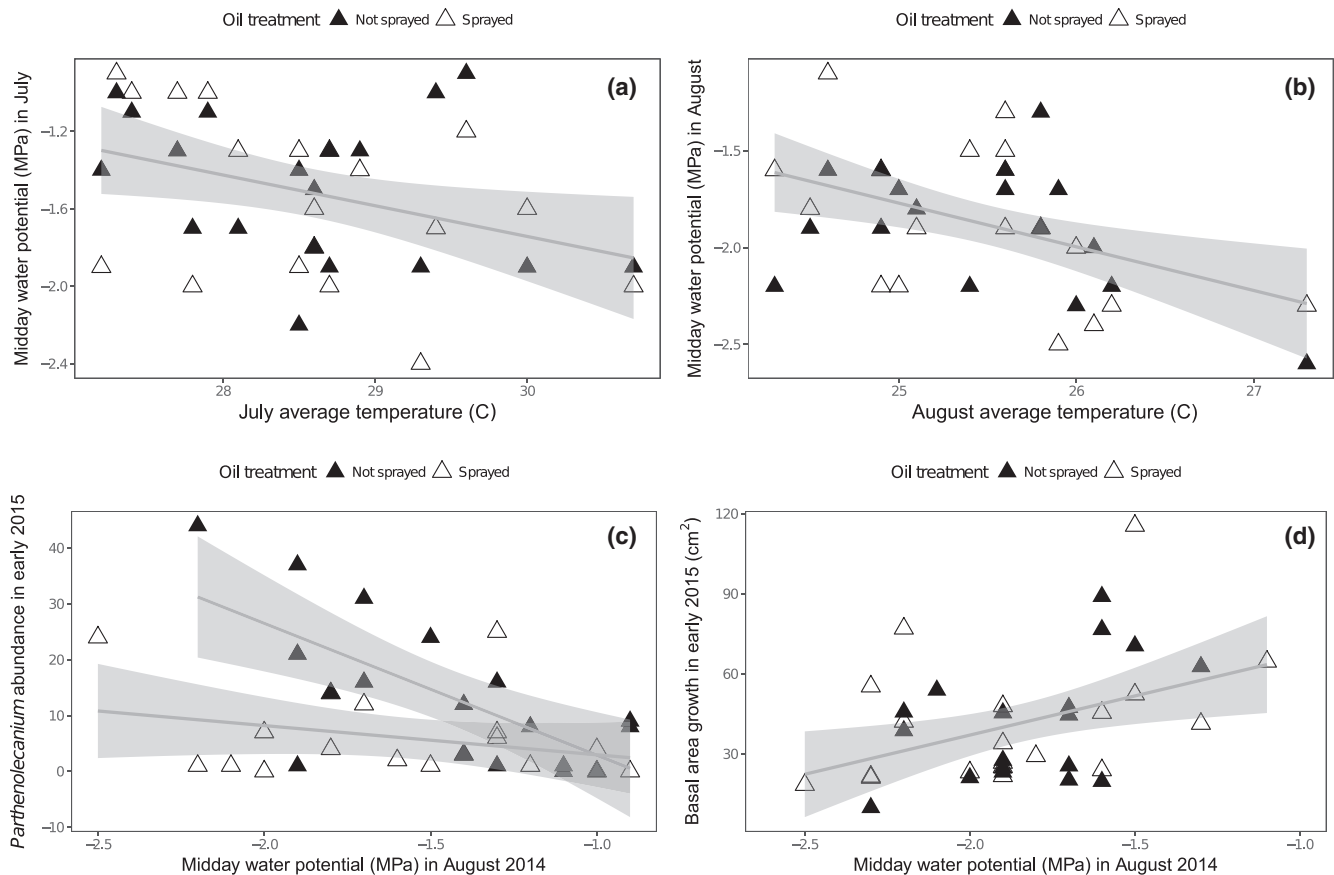
In July and September, trees with pulsed water inputs had significantly lower water potential (higher stress) than those in the saturated treatment (July: Figure 2a,  $X^2_1 = 34.13$ ,  $p < .0001$ ; September: Figure 2b,  $X^2_1 = 39.19$ ,  $p < .0001$ ), which indicates that water treatments were

implemented as intended. In July, within pulsed trees, the effects of temperature interacted with the effects of *Parthenolecanium*, such that cold trees with *Parthenolecanium* had lower water potentials than without *Parthenolecanium* (Tukey HSD:  $p = .028$ ). Neither *Parthenolecanium* nor temperature affected water potential of saturated trees (Table 2a). In September, water potential was uniform across trees within water treatments, such that neither *Parthenolecanium* nor temperature affected water potential of pulsed or saturated trees (Table 2b).

### 3.2.2 | *Parthenolecanium* survival

More *Parthenolecanium* survived in hot than cold chambers from June to July (Figure 3, temp.:  $X^2_1 = 4.3$ ,  $p = .038$ , water:  $X^2_1 = 0.90$ ,  $p = .34$ ) but not from July to September (temp.:  $X^2_1 = 0.14$ ,  $p = .24$ , water:  $X^2_1 = 0.51$ ,  $p = .47$ ), indicating that, at least in this life stage, temperature, not tree water stress, increases *Parthenolecanium* survival. There was no significant interaction between water availability and temperature. Neither water availability nor temperature affected total *Parthenolecanium* abundance (Table S2a).

Carbon and nitrogen concentrations of trees did not explain differences in *Parthenolecanium* survival across treatments. Trees with pulsed water inputs had significantly higher nitrogen concentrations and significantly lower C:N ratios of shoots (percent nitrogen:



**FIGURE 1** Correlations between warming, water potential *Parthenolecanium* scale insect abundance, and tree growth in the city. (a, b) Urban warming reduced tree water potential (increases water stress). (c) Trees with lower water potential had higher *Parthenolecanium* abundance and (d) grew less

Figure S1a; C:N: Figure S1b) and roots (percent nitrogen: Figure S1c, C:N: Figure S1d). There was a non-significant trend toward higher percent nitrogen of roots in plants with *Parthenolecanium*. All statistics associated with nutrients are located in Table S2b–g.

### 3.2.3 | Leaf area

*Parthenolecanium* had a marginally significant positive effect on leaf area acquired in the saturated treatment. In contrast, for trees that received pulsed water inputs, there was a significant interaction between *Parthenolecanium* and temperature (Figure 4a; Table 2c), such that hot trees with pulsed water inputs and *Parthenolecanium* acquired the least leaf area (Tukey HSD  $p = .081$ ; Linear contrast  $p = .010$ ). Less leaf area acquired in hot, pulsed trees with *Parthenolecanium* was due to smaller leaf size and number. Within the pulsed water treatment, hot trees acquired fewer leaves (Table S2h). In contrast, temperature did not affect leaves acquired in the saturated treatment. However, saturated trees with *Parthenolecanium* acquired more leaves than those without *Parthenolecanium* (Figure S2a) and trended toward higher total leaf area, which suggests that trees may compensate for *Parthenolecanium* when they are saturated. In the model for leaf size, there was a significant interaction between temperature and *Parthenolecanium* (Figure S2b; Table S2i), such that

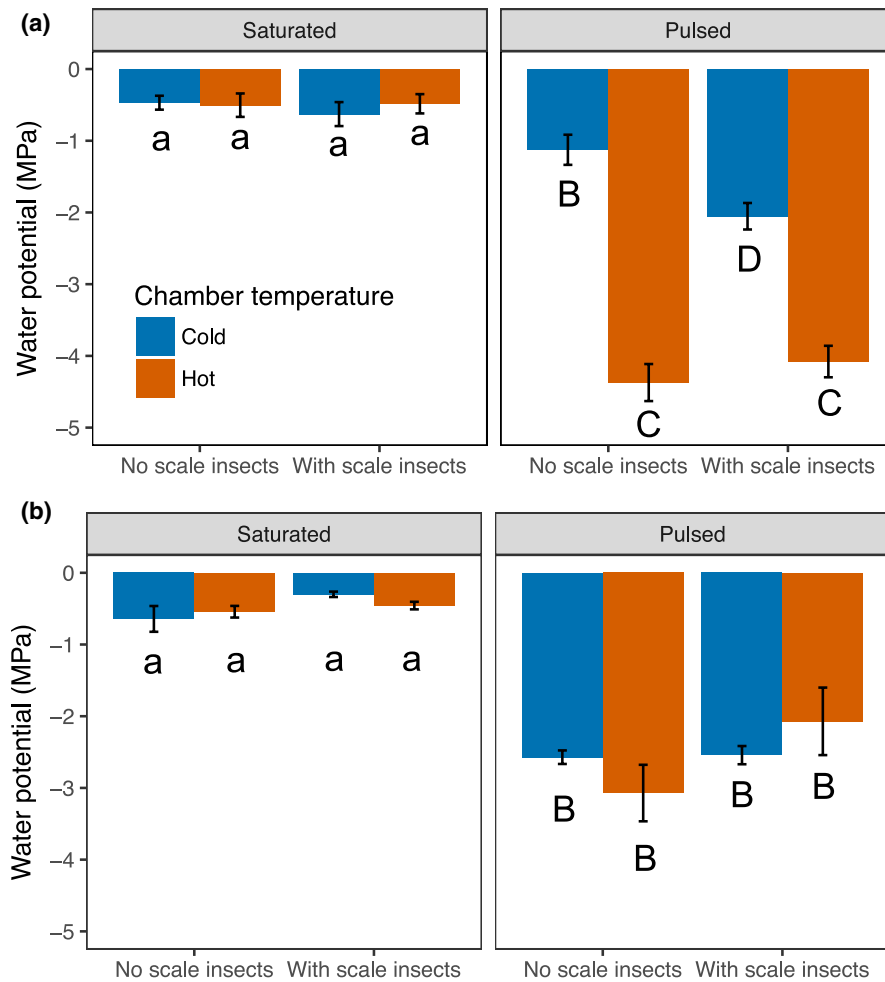
average leaf size was lowest on hot trees with *Parthenolecanium*. However, we did not detect significant differences between individual treatments using Tukey HSD.

### 3.2.4 | Root and shoot biomass

Treatment effects on woody biomass mirrored effects on leaf area, such that the effects of warming and *Parthenolecanium* on tree biomass depended on water availability. Hot trees with pulsed water inputs had less shoot biomass than any other treatment (Figure S3a; Table S2j). Hot, saturated trees had more root biomass than did trees from any other treatment (Figure S3b, Table S2k; Tukey HSD for all treatments:  $p < .0001$ ). In the model for total biomass, there was a marginally significant three-way interaction between *Parthenolecanium*, temperature, and water treatment (Figure 4b, Table 2d), such that, like leaf area acquired, mean biomass was lowest on hot trees with *Parthenolecanium* that were given pulsed water inputs. Carbon sequestration followed the same trend as total biomass, but only the interaction between temperature and water was significant (Figure S3c, Table S2l).

In analyses with *Parthenolecanium* as a continuous predictor, trees with a higher percentage of infested leaves had significantly lower total biomass, but only if they were in hot chambers





**FIGURE 2** Effects of water availability, warming and *Parthenolecanium* scale insects on water potential in the laboratory. (a) In July, *Parthenolecanium* reduced water potentials (increased water stress), but only for trees that were relatively cool and, therefore, not as water-stressed. (b) In September, pulsed trees were uniformly stressed. Letters refer to Tukey HSD tests within water treatments. Capital and lower-case letters indicate that pulsed and saturated trees were analysed separately (see statistics) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

and received pulsed water inputs (Figure 4d;  $F_{1,11} = 5.08$ ,  $p = .046$ , Adjusted  $R^2 = .32$ ). All other response variables followed this trend, notably shoot biomass (Figure S3d,e;  $F_{1,11} = 4.26$ ,  $p = .063$ , Adjusted  $R^2 = .28$ ). Neither *Parthenolecanium* per leaf (total biomass of saplings with pulsed water inputs and *Parthenolecanium*:  $F_{1,11} = 0.75$ ,  $p = .404$ , adjusted  $R^2 = .00$ ) nor estimated *Parthenolecanium* abundance (total biomass of saplings with pulsed water inputs and *Parthenolecanium*:  $F_{1,11} = 1.83$ ,  $p = .203$ , adjusted  $R^2 = .06$ ) was significantly associated with any of the response variables.

## 4 | DISCUSSION

Urban trees provide many services that improve human and environmental health. However, these services are driven by tree photosynthesis and growth, which are reduced by stressors within cities. Among these stressors, our research reveals that water stress is the critical factor determining tree growth. Importantly, water stress also acts as an interactive factor, in that urban warming and insect pests only reduced growth of water stressed trees. Management tactics for reducing urban tree water stress, such as providing greater soil quality and root volume, as well as watering during dry periods, could serve dividends by maximizing tree growth and services.

How warming and host plant water stress combine to affect insect herbivore abundance in cities remains unknown except for one other scale insect whose life history differs from pests associated with *Q. phellos* (Dale & Frank, 2017). Therefore, we tested how warming and water stress affected *Parthenolecanium*. In the city, we found that trees in warmer environments and trees with lower water potentials (higher stress) had more *Parthenolecanium*. However, water-stress and warming were correlated in the city and either of these factors could have increased *Parthenolecanium* abundance. Thus, we disentangled effects of warming and water stress on *Parthenolecanium* in the laboratory.

We expected that pulsed water inputs would increase nitrogen concentrations and that this, along with warming, would increase *Parthenolecanium* survival and abundance (Huberty & Denno, 2004). Contrary to this prediction, only warming and not water stress increased *Parthenolecanium* survival. However, we leave open the possibility that water stress increases herbivore abundance in urban heat islands. First, *Parthenolecanium* had limited opportunities to benefit from higher nitrogen concentrations observed in water-stressed trees in the laboratory. Many insects produce more eggs in response to higher nitrogen concentrations (e.g. Wang, Tsai, & Broschat, 2006), but in our study, *Parthenolecanium* remained nymphs, so we could not test for effects of higher nitrogen concentrations on eggs. Second,

**TABLE 2** Statistics from laboratory experiment on effects of warming, herbivores and water availability on *Quercus phellos* saplings. Significant effects are in bold. If no significant interactions were detected, main effects coefficients are from models without interactions

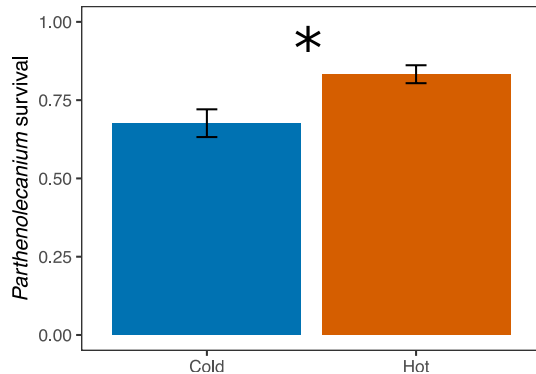
Treatment	Predictor	Estimate ± SE	Statistic	p
<b>(a) July water potential</b>				
Saturated	Temperature (hot)	0.05 ± 0.14	$F_{1,25} = 0.15$	.702
	<i>Parthenolecanium</i> (present)	-0.07 ± 0.14	$F_{1,25} = 0.24$	.627
	Temp. × <i>Parthenolecanium</i>	-0.18 ± 0.29	$F_{1,24} = 0.39$	.539
Pulsed	<b>Temperature (hot)</b>	<b>-2.03 ± 0.31</b>	<b><math>F_{1,23} = 145.29</math></b>	<b>&lt;.0001</b>
	<i>Parthenolecanium</i> (present)	-0.93 ± 0.31	$F_{1,23} = 1.17$	.290
	<b>Temp. × <i>Parthenolecanium</i></b>	<b>-1.22 ± 0.44</b>	<b><math>F_{1,23} = 7.62</math></b>	<b>.011</b>
<b>(b) September water potential</b>				
Saturated	Temperature (hot)	0.05 ± 0.14	$F_{1,25} = 0.15$	.702
	<i>Parthenolecanium</i> (present)	-0.07 ± 0.14	$F_{1,25} = 0.24$	.627
	Temp. × <i>Parthenolecanium</i>	-0.18 ± 0.29	$F_{1,24} = 0.39$	.539
Pulsed	Temperature (hot)	-0.01 ± 0.33	$F_{1,25} = 0.00$	.965
	<i>Parthenolecanium</i> (present)	0.51 ± 0.33	$F_{1,25} = 2.50$	.127
	Temp. × <i>Parthenolecanium</i>	-0.97 ± 0.63	$F_{1,24} = 2.35$	.139
<b>(c) Leaf area acquired</b>				
Saturated	Temperature (hot)	-0.06 ± 0.15	$F_{1,24} = 0.15$	.704
	<i>Parthenolecanium</i> (present)	0.31 ± 0.15	$F_{1,24} = 4.20$	.051
	Temp. × <i>Parthenolecanium</i>	-0.23 ± 0.30	$F_{1,23} = 0.58$	.454
Pulsed	<b>Temperature (hot)</b>	<b>-0.08 ± 0.10</b>	<b><math>F_{1,23} = 15.46</math></b>	<b>.001</b>
	<i>Parthenolecanium</i> (present)	-0.11 ± 0.09	$F_{1,23} = 0.79$	.383
	<b>Temp. × <i>Parthenolecanium</i></b>	<b>-0.35 ± 0.13</b>	<b><math>F_{1,23} = 6.84</math></b>	<b>.015</b>
Predictor	Estimate ± SE	Statistic	p	
<b>(d) Sapling biomass</b>				
<b>Temperature (hot)</b>	<b>-0.02 ± 0.40</b>	<b><math>F_{1,47} = 13.30</math></b>	<b>.001</b>	
<b>Water treatment (saturated)</b>	<b>0.22 ± 0.39</b>	<b><math>F_{1,47} = 41.87</math></b>	<b>&lt;.0001</b>	
<i>Parthenolecanium</i> (present)	-0.13 ± 0.39	$F_{1,47} = 0.18$	.678	
<b>Temp. × water</b>	<b>1.15 ± 0.56</b>	<b><math>F_{1,47} = 25.00</math></b>	<b>&lt;.0001</b>	
Temp. × <i>Parthenolecanium</i>	-0.47 ± 0.56	$F_{1,47} = 0.65$	.425	
Water × <i>Parthenolecanium</i>	<b>0.14 ± 0.55</b>	<b><math>F_{1,47} = 5.35</math></b>	<b>.025</b>	
Temp. × water × <i>Parthenolecanium</i>	1.55 ± 0.78	$F_{1,47} = 3.91$	.054	

*Parthenolecanium* feeds most as second instars on branches (E.K. Meineke, pers. obs.), and this life stage was not included in our laboratory study. Other *Parthenolecanium* life stages and other arthropod species may benefit from higher nitrogen concentrations in water-stressed plants in urban heat islands. It is also possible that the frequency or severity of stress we induced was not optimal for increased *Parthenolecanium* survival (Banfield-Zanin & Leather, 2015; Huberty & Denno, 2004; Mody, Eichenberger, & Dorn, 2009). Though, warming and water stress may also affect herbivores via plant defenses, we focus on nutrition here because sap-feeders are generally less susceptible to plant defenses than other herbivore feeding guilds (Walling, 2008). *Parthenolecanium* survived better in hotter conditions in the laboratory, contributing to mounting evidence that heat is a key driver of insect fitness

in temperate cities. However, effects of urban warming on arthropods may vary across latitudes, because insect responses to warming are nonlinear (Omkar, 2004; Ponsonby & Copland, 2000; Wang & Tsai, 2000). If *Parthenolecanium* thermal limits are reached at more southern latitudes (Youngsteadt, Ernst, Dunn, & Frank, 2017), urban warming should reduce fitness.

Detrimental effects of phloem-feeding herbivores on trees are generally to be expected (e.g. Zvereva, Lanta, & Kozlov, 2010). However, our study uncovers a complex relationship between a phloem-feeder and its host plant, wherein *Parthenolecanium* only reduced growth of water-stressed trees (Figure 4c,d). These results are consistent with theory (Hawkes & Sullivan, 2001) and empirical studies that identify photosynthesis as a mechanism by which trees compensate for herbivory. Phloem-feeders remove

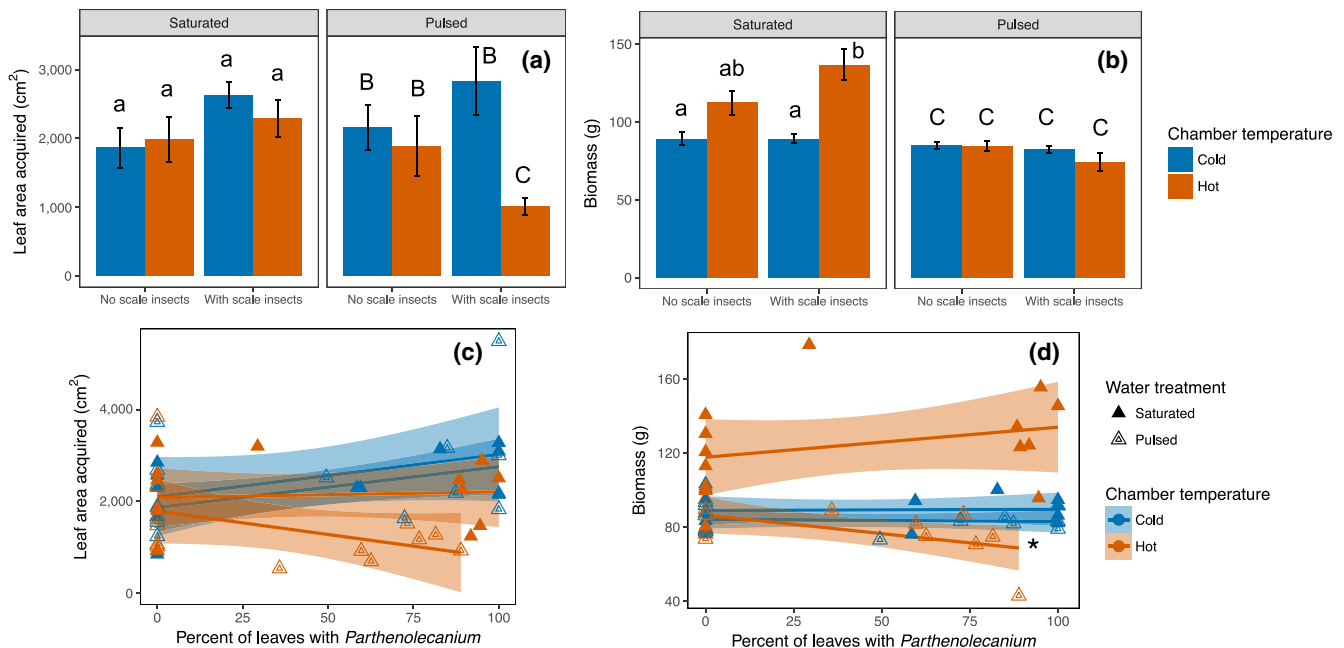
photosynthate, which stimulates photosynthesis (Schaffer & Mason, 1990). However, compensatory photosynthesis requires that plants open their stomata. Our results are consistent with a model in which water-stressed laboratory saplings could not increase photosynthesis in response to *Parthenolecanium* due to stomatal closure. In turn, *Parthenolecanium* reduced biomass accumulation in water-stressed trees. As the physiological functions involved in this response—i.e. photosynthesis, stomatal conductance—are universal, our results may generalize to other tree species.



**FIGURE 3** *Parthenolecanium* scale insect survival. *Parthenolecanium* survived better in hot than in cold laboratory chambers. The red bar refers to hot chambers, and the blue bar refers to cold chambers. The \* indicates a significant difference in survival between hot and cold chambers [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

*Parthenolecanium* reduced water potentials in cold but not hot laboratory chambers, showing that these pests may exacerbate urban tree water-stress. We believe *Parthenolecanium* did not affect water potential in the hot laboratory chamber because trees were so water-stressed that *Parthenolecanium* had negligible effects. Trees in the hot chamber had water potentials below  $-1.42$  MPa, where *Q. phellos* loses 50% hydraulic conductivity (Maherali, Moura, Caldeira, Willson, & Jackson, 2006). In September, we believe all trees in the pulsed water input treatment approached maximum water stress and thus neither temperature nor *Parthenolecanium* affected water potential. In the field, urban warming was associated with higher water stress in 2014 but not 2013. Conditions and water potentials were similar across years (see Figure 1). We suggest that we may not have detected significant effects of temperature on water potential in 2013 because it was measured on two rather than three branches per tree.

The interactive effects of herbivores, water stress and warming, we observed yield to be a key prediction: If host trees become water-stressed due to climate change (Brzostek et al., 2014), forest fragmentation (Bennett et al., 2013) or urbanization (Dale & Frank, 2014a), innocuous herbivores may reduce tree growth even if they remain at current densities. This is concerning because trees worldwide are close to their hydraulic limits, and drought intensities and frequencies are expected to increase in many areas with climate change (Choat et al., 2012; Dai, 2013).



**FIGURE 4** Effects of warming and *Parthenolecanium* scale insects on tree growth depended on water availability. (a) *Parthenolecanium* only reduced leaf area of trees that were in hot conditions with low water availability, and (b) tree biomass followed this same trend. (d) *Parthenolecanium* only reduced total biomass in trees that were in hot conditions with low water availability and (c) leaf area followed this same trend. Letters refer to Tukey HSD tests except within water treatments in (a), in which bars that were significantly different in linear contrasts were also given different letters. Capital and lower-case letters indicate that pulsed and saturated trees were analysed separately (see statistics). Only significant categorical predictors are shown, except in (b), where all treatments are shown due to a marginally significant three-way interaction [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Within cities, local-scale changes driven by urban warming and herbivory combine at larger spatial scales to reduce ecosystem services, such as carbon storage (Meineke et al., 2016). To the extent that cities can predict the biotic effects of climate change in more natural systems (Youngsteadt et al., 2015), we provide evidence that warming and herbivory may reduce tree growth, and therefore above-ground carbon storage, in rural forests when they co-occur with drought. However, one limitation of our study is that effects of global change factors on saplings in the laboratory may not represent effects on mature trees. For example, tree responses to drought vary with ontogeny. In *Quercus rubra* (red oak), saplings close their stomata to avoid water loss, whereas mature trees access deeper sources of water and increase water use efficiency (Cavender-Bares & Bazzaz, 2000). Therefore, mature *Q. phellos* in the city may require more severe water stress than laboratory saplings to induce stomatal closure, a likely mechanism for the interactive effects of warming, insect herbivores and water availability we observed. However, we suggest that mature trees in cities experience more severe water stress than those in natural habitats (Mullaney et al., 2015) and that mature urban trees may respond more similarly to laboratory saplings than mature trees in forests. This is supported by a previous experiment showing that trees in hotter areas within Raleigh, NC have lower rates of light saturated photosynthesis associated with stomatal closure (Meineke et al., 2016). Importantly, other factors, such as pollution, may covary with urban temperatures and account for some variation in our analyses. While we could not control these factors, our study design allowed us to determine tree water stress across a range of thermal environments. This study, combined with previous measurements of tree physiology (Meineke et al., 2016), strongly implicate water stress as a mechanism for reduced tree growth in urban heat islands.

Temperatures are projected to continue increasing globally through climate change and locally via development, but urban forestry programmes have limited budgets to address challenges posed by global change (Roman, McPherson, Scharenbroch, & Bartens, 2013). This study provides evidence that alleviating water stress could be a high-impact management strategy to mitigate effects of drought, warming, and increasing pest pressure. Cities have traditionally been designed to expel stormwater to avoid flash floods (Coutts, Tapper, Beringer, Loughnan, & Demuzere, 2013). However, accumulating evidence shows that this creates drought-like conditions that are exacerbated by urban heat (e.g. Dale & Frank, 2017). Therefore, a key priority for urban planners could be to design urban landscapes that retain stormwater in vegetation. The most commonly used tool for estimating services provided by urban trees iTree (<https://www.itreetools.org/>) does not incorporate urban heat or other stressors. Our results suggest that, at least within the temperate zone, ecosystem service estimates for urban forests may be improved by incorporating a proxy for urban heat, such as impervious surface cover. To maximize ecosystem services in the face of multiple, increasing stressors, urban foresters could invest in hydration strategies such as appropriate soil quality and soil volume, and hydrogels (Kargar et al., 2017).

For long-term urban forest health, management strategies could include planting drought-tolerant tree species (Percival, Keary, & Sulaiman, 2006) and genotypes (Zwack, Graves, & Townsend, 1998) in the hottest areas within cities.

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## AUTHORS' CONTRIBUTIONS

E.K.M. and S.D.F. conceived of experiments and designed methodology; E.K.M. collected and analysed data. Both authors contributed to drafts and gave approval for publication.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.pb50v53/1> Meineke and Frank (2018).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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