Tree Transpiration and Urban Temperatures: Current Understanding, Implications, and Future Research Directions

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The expansion of an urban tree canopy is a commonly proposed nature-based solution to combat excess urban heat. The influence trees have on urban climates via shading is driven by the morphological characteristics of trees, whereas tree transpiration is predominantly a physiological process dependent on environmental conditions and the built environment. The heterogeneous nature of urban landscapes, unique tree species assemblages, and land management decisions make it difficult to predict the magnitude and direction of cooling by transpiration. In the present article, we synthesize the emerging literature on the mechanistic controls on urban tree transpiration. We present a case study that illustrates the relationship between transpiration (using sap flow data) and urban temperatures. We examine the potential feedbacks among urban canopy, the built environment, and climate with a focus on extreme heat events. Finally, we present modeled data demonstrating the influence of transpiration on temperatures with shifts in canopy extent and irrigation during a heat wave.

Keywords: urban temperatures, urban tree canopies, climate change, transpiration, sap flow, heat waves

Cities across the world are pledging to uphold the Paris Agreement goals to reduce greenhouse gas emissions (Rosenzweig et al. 2010) with the creation of climate action plans, many of which include efforts to increase tree canopy cover as a nature-based solution (Anderson et al. 2019, Lamb et al. 2019). Trees provide a suite of essential ecosystem services; their ability to cool local air temperatures improves human health and reduces building energy demands (Pataki et al. 2011a), both of which are key to cities in the era of climate change. Most cities experience the urban heat island (UHI) effect, wherein the air temperatures of the urban core are warmer (approximately 1–3 degrees Celsius [°C]) than the surrounding areas (Oke et al. 2017). The impacts of increased frequency, intensity, and duration of heat waves under a warming urban climate presents a major public health concern (Field et al. 2012, Li and Bou-Zeid 2013, Krayenhoff et al. 2018). Extreme heat events are currently the number one cause of weather-related deaths in the United States (Weinberger et al. 2017). As urban air temperatures rise there is an urgent need for an improved mechanistic understanding of the mitigation potential of urban tree canopy on air and surface temperatures to help inform local governments establishing climate action plans (Zhou et al. 2019).

The cooling effects of tree canopies have been widely recognized (Bowler et al. 2010, Rahman et al. 2020). Trees cool the environment directly via two primary mechanisms. First, trees reduce surface temperatures by blocking incoming daytime solar radiation from reaching the ground, such as pavement, which have high-heat absorption capacity (or surface storage; figure 1). In turn, this shading results in less absorption and storage of incoming short-wave radiation by surfaces and the reemission of long-wave radiation from surfaces to the atmosphere, thereby lowering local air temperatures. Studies show that tree shade can result in reductions of short-wave radiation reaching the surface by 60%–90% with upward of 20°C differences in surface temperatures between shaded areas and sunny asphalt areas (Bowler et al. 2010, Rahman et al. 2020). The impact shading can have on surface temperatures is shown to vary with the underlying surface type. For example, for every unit of canopy leaf area index (LAI) a grass surface was cooled by 1.2°–3°C, whereas an asphalt surface was cooled by 5°–6°C (Harden and Jensen 2007, Gillner et al. 2015). Collectively, studies show that the influence of tree shading is strongly controlled by tree morphological characteristics such as canopy size, shape, and structure (Rahman et al. 2015, 2020,

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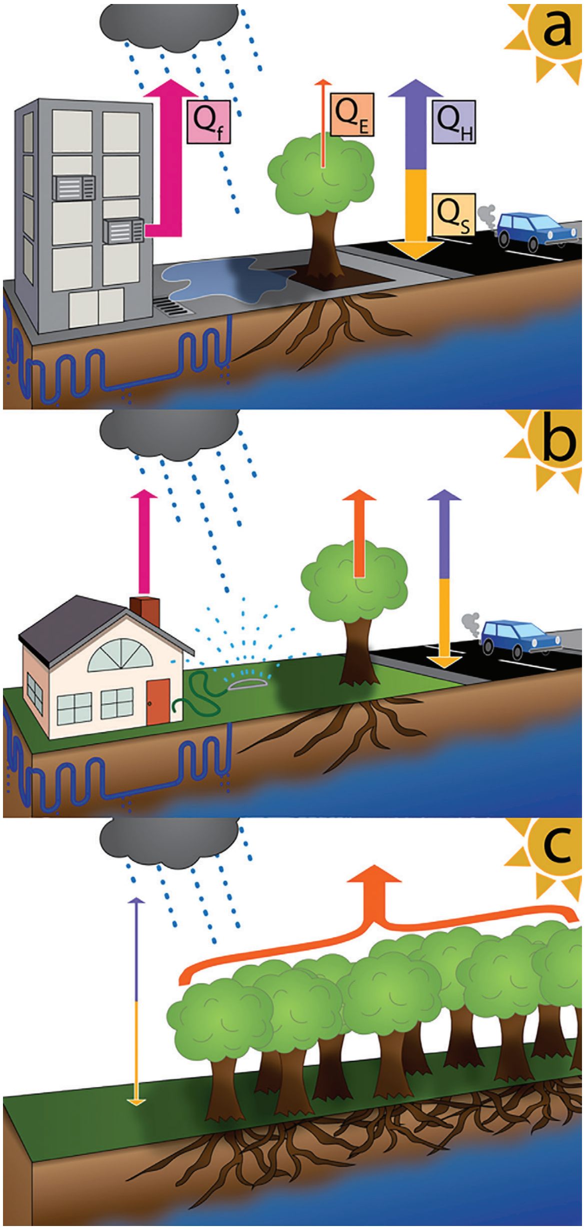

Figure 1. Conceptual diagram of the surface energy budget and water resources found across different urban areas, including (a) a densely built urban form, (b) a residential neighborhood, and (c) an urban forest patch. The surface energy budget is a result of energy exchanges (in watts per square meter) due to incoming radiation, convection, and conduction between components of the land surface and the atmosphere. The net radiation fluxes (Q^*) are composed of the sensible heat flux (Q_H), the latent heat flux (Q_E), changes in the storage of heat at the surface (ΔQ_S). In addition, there is heat energy produced from anthropogenic sources (Q_F) such as vehicles and building heating and cooling systems. The sensible heat flux (Q_H) is driven by temperature differences between the surface and the atmosphere. The latent heat flux (Q_E) is driven by the energy used to evaporate water from surfaces, especially those of tree canopies due to tree transpiration. The storage of heat (ΔQ_S) varies across different urban surfaces. In each panel the major energy fluxes are shown with the size of the arrows demonstrating the variability in the magnitude of the different energy fluxes. The direction of the arrows represents positive fluxes. The size of the Q_E flux is strongly influenced by the availability of water in each urban locale and density of canopies. (a) Street trees experience harsher environmental conditions, with potential for high heat loads and increased atmospheric aridity. In absence of irrigation, street trees have restricted water availability because of the small soil pits size and the restricted capacity to intercept storm water; however, in some cases urban trees can access leaky infrastructure (Randrup et al. 2001). (b) In residential areas trees are often actively irrigated in addition to intercepting storm water runoff. (c) Trees in forest fragments and sometimes nonirrigated parks, are dependent on the interception of rainfall and soil moisture retention, and in some cases, they can access groundwater supplies or leaky infrastructure. Illustration: Sarah Garvey.

McPherson et al. 2018, Smithers et al. 2018). However, tree canopy can also raise nighttime air temperatures compared with identical areas without them because tree canopy can trap long-wave radiation in the atmosphere under the canopy (Ziter et al. 2019). The relationship between air temperature and the temperature of the canopy itself is also species dependent (Leuzinger et at. 2009). Data sets exist that report morphological characteristics that influence shading influence for popular urban tree species (McPherson et al. 2018, Rahman et al. 2020), and some urban climate models have introduced parameterization to include such effects (Grimmond et al. 2010).

Second, trees cool the environment by the process of transpiration, wherein water is taken up by tree roots and moved through the stem and then evaporates through leaf stomates. The term evapotranspiration includes both transpiration and the evaporation of water from all urban surfaces (e.g., leaf surfaces, lakes, and soil surfaces). The energy (i.e., latent heat) used to evaporate water transpired by trees consumes heat energy (i.e., sensible heat) in the local environment that would otherwise raise air temperature and, instead, cools leaf surfaces and nearby air temperatures by advection. In Los Angeles, irrigated street trees collectively moved to the atmosphere upward of 30 million gallons of water per day (Pataki et al. 2011b), shifting the local energy balance toward greater latent than sensible heat fluxes (or conductive heat flux), cooling the local and regional air temperatures (see figure 1 for more details). The impact of transpiration on air temperatures has been shown to vary between 1° and 8°C (Georgi and Zafiriadis 2006, Rahman et al. 2017). Similar to shading, the extent of cooling provided by transpiration is strongly influenced by morphological characteristics of trees; however, transpiration is also influenced by physiological characteristics such as species level differences in wood anatomy, water use efficiency (WUE, the ratio of carbon uptake via photosynthesis relative to the amount of water lost via transpiration), and the regulation of stomatal conductance in response to environmental conditions and the built environment. The suite of physiological responses of transpiration in urban environments is more difficult to quantify than morphological characteristics, and until recently, there has been a paucity of data examining the ecophysiological controls on urban tree transpiration.

In addition, trees can cool local air temperatures indirectly by reducing human dependence on and use of cooling services. Air conditioners emit waste heat to the outdoor environment in the short term (Salamanca et al. 2014, Stratópoulos et al. 2018) and increase temperatures in the long term through emissions of carbon dioxide (CO_2) and other greenhouse gases (Pataki et al. 2011a, de Munck et al. 2012). Globally, cities consume over 75% of the world's energy, accounting for more than 70% of the global CO_2 emissions, and energy consumption by cities is expected to increase 25%–58% by 2050 because of the projected rapid increases in urban populations and climate warming (van Ruijven et al. 2019). Rarely, however, have the dynamic feedbacks between cooling services, urban trees, and local meteorological conditions been examined jointly, especially during extreme heat events when it matters the most for human health.

Investigations on the cooling influence of urban trees have focused primarily on the joint influence of shading and transpiration (Shashua-Bar et al. 2009, Bowler et al. 2010, Tan et al. 2018, Rahman et al. 2019). This focus is in part because of the difficulties in disentangling empirically the effects of shading and transpiration on urban temperatures without direct measures of tree transpiration, which are rare (Rahman et al. 2020). In heterogenous urban areas where the assumptions of tower-based approaches for quantifying evapotranspiration are often violated, tree-based sensors can be used to track the movement of water by individual trees (known as sap flow sensors) and used to quantify tree transpiration. Until recently, there has been a paucity of data on urban transpiration using ground-based sensors. Consequently, studies attempting to quantify the role of transpiration in urban environments have assumed similar ecophysiological responses as those observed in rural areas (Litvak et al. 2017), preventing our full understanding of the mechanistic drivers that influence the cooling influence trees can have across different urban environments.

The extent to which urban trees can mitigate excess urban heat is largely influenced by how tree growth effects on shading and transpiration respond to unique urban environments and the feedbacks between trees and urban form (the physical characteristics that make up the built environment). Our understanding of urban forest structure and function, however, has been largely based on the translation of observations from well-studied rural, intact forests to urban areas with similar climatic and tree species composition (Pataki et al. 2011a). This approach may be inappropriate because of the unique environments created by urban areas, influencing the ability of different patches of urban vegetation to perform ecosystem functions, particularly the transpiration of water (Pataki et al. 2011b). For example, urban areas are often a patchwork of impervious surfaces and buildings that vary in their heat capacity, waste heat production, and influence on the channeling of air flow. The urban form and the corresponding local management decisions on trees (i.e., pruning, irrigation, fertilization, and soil structure) result in variable spatial extents of urban tree canopies that often tightly overlap and interact with the built environment. Furthermore, there are often unique species assemblages in urban areas that lack nonurban analogs. Consequently, these unique urban features make it difficult to predict the response of urban trees on the basis of the functioning of trees in nearby rural counterparts (Jenerette et al. 2016, Ziter et al. 2019, Trlica et al. 2020).

In the present article, we synthesize the published literature on the influence of urban trees to cool local temperatures via transpiration. In particular, we compiled the existing literature using ground-based approaches to quantify urban tree transpiration rates and identify the key mechanistic drivers influencing the magnitude and direction of the cooling effect of transpiration in urban environments. We present new empirical sap flow data that demonstrates the relationship between tree transpiration and urban temperatures. We demonstrate how these tree-level measurements can be related to changes in local climate conditions by using urban canopy models that parameterize the unique aerodynamic features and full energy balance of the urban system. In doing so, we discuss the improvements needed in urban canopy models to more realistically incorporate the drivers of urban tree transpiration. Finally, we examine the potential feedbacks between urban tree canopies, the built environment, and climate with a focus on extreme heat events. In doing so, we identify key areas of future research needed to help optimize climate actions plans that incorporate tree canopies and transpiration to mitigate urban heat effects.

Quantification of urban tree transpiration

Quantifying rates of urban transpiration can help to inform our understanding of the role this process has on urban temperatures and the mechanistic drivers. By identifying the ecophysiological response of transpiration rates to different urban environments we can help guide the selection of tree species during planting initiatives and conservation efforts that aim to maximize the cooling influence trees have in cities. Classically, evapotranspiration is quantified using tower-based approaches (e.g., eddy covariance); however, these approaches are often challenging to deploy in urban areas because the heterogeneous terrain of urban areas often violates the methodological assumptions. Ground-based estimates of tree transpiration use sap flow sensors that estimate in real-time the movement of water in an individual tree stem. Measurements of sap flow can act as a proxy for transpiration or can be used in conjunction with estimates of sapwood area (the total area of hydraulically conductive tissue in a tree stem) to estimate rates of transpiration (Pataki et al. 2011b). Sap flow sensors allow for both fine spatial and temporal resolution of transpiration measurements and the study of the dynamic response of trees to their unique urban environments. In order to translate measures of transpiration into corresponding cooling effect, one of two approaches can be used. First, the total water loss determined by measures of transpiration can be multiplied by the latent heat of evaporation to compute the energy loss (in watts per square meter) due to latent heat exchange and corresponding reductions in convection. Second, urban canopy models that couple the mechanistic understandings of transpiration with the unique aerodynamic features and full energy balance of the urban system can be used to quantify shifts in the energy budget and impacts on surface or air temperatures.

In the past decade, there has been a growth in the number of studies examining transpiration in urban trees using sap flow sensors. As of 2010, there had only been five studies to conduct tree-level estimates of urban transpiration (see supplemental table 1 for references). Using a Web of Science search on 3 March 2020 and the keywords *sap flow*, *sap flux*, *transpiration*, and *urban*, we found a total of 40 studies to date in urban or suburban locales that examine urban tree transpiration using sap flow sensors. Of these studies, the most commonly cited motivation for these studies was to examine the cooling influence of trees (30% of studies) followed by the examination of water use by urban trees (32.5% of studies). The remaining studies cited a general understanding of ecosystem services (20% of studies), pollution uptake (7.5% of studies), storm water mitigation (7.5% of studies) or carbon uptake (2.5% of studies) as the studies motivation. The most commonly studied forest type was park trees, which represented 47.5% of the studies. Forest patches and street trees received similar attention among the 40 studies (each representing 27.5% of the studies), with a smaller number of studies conducted on roof top gardens (5% of studies) or at local urban nurseries (5% of studies). The majority of studies occurred in temperate climates (n = 31), followed by subtropical (n = 7), tropical ($\underline{n}$ = 1), and boreal (n = 1) climates. Studies in mesic environments represented 72% of the studies and occurred in Europe (n = 12), Asia (n = 9), United States (n = 5), and Australia (n = 1). The studies in arid or semiarid environments occurred in the United States (n = 7), Mexico (n = 1), and Asia (n = 4). There is a lack of studies in Africa and South America. Below we first present empirical lines of evidence on the cooling influence trees can have on urban climates, and then synthesize the literature on the influence of urban environments on tree transpiration.

Empirical evidence for the cooling influence of trees

Classically, the cooling influence of trees has been characterized by the comparison of urban temperatures with those in nearby rural ones. Urban temperatures are most commonly quantified as the surface or skin of the urban landscape using remote sensing products that often have a resolution of more than 30 meters. In contrast, air temperatures are measured by the deployment of metrological instruments that tend to have less continuous coverage across the landscape. The finer spatial resolution of ground-based approaches better captures the heterogeneity in local temperatures, which are more relevant to human thermal comfort, than remote sensing data products. Air temperature of cities is on average approximately 1°–3°C hotter than surrounding rural areas during the daytime, and upward of 12°C hotter at night, with even larger differences in surface temperatures (Oke et al. 2017). This UHI effect is driven primarily by differences in the evaporation of water between urban and rural areas. These differences in evaporation are due to the decrease in vegetation, as well as the increase in impervious area of cities that reduce water availability by lowering water infiltration rates and increasing water runoff (Li et al. 2019). Cities in arid climates show stronger correlations between transpiration and the magnitude of the heat island effect compared with cities in tropical regions (Manoli et al. 2019). The UHI is also driven by the increase in anthropogenic sources of waste heat in cities, the increased surface storage of heat in

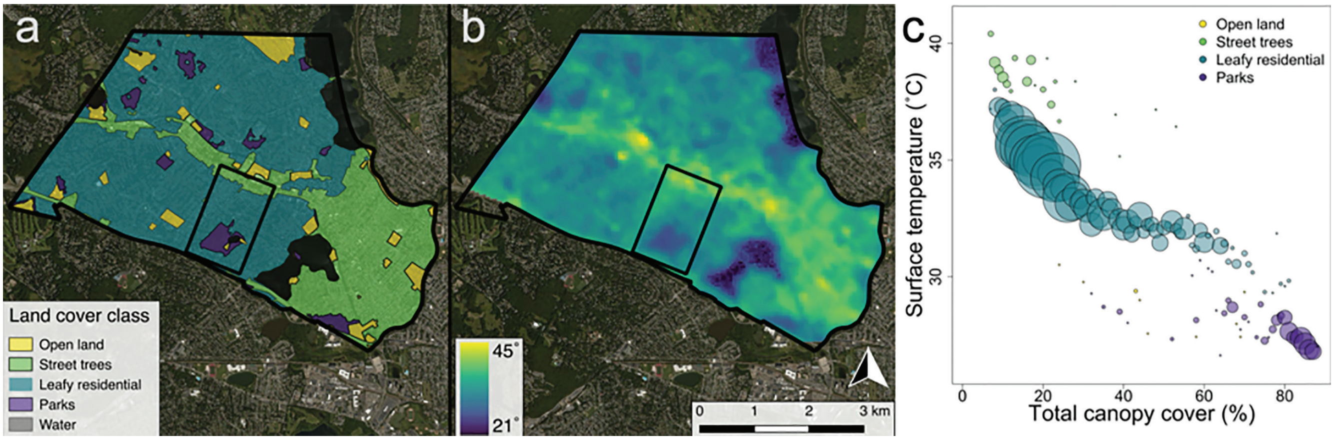

Figure 2. Example of the relationships between land cover classes (a) and land surface (or skin) temperature (b) for Arlington, Massachusetts, United States. In panel (c) the relationship between land surface temperature and total canopy cover is shown for the Menotomy Rocks Park in Arlington, Massachusetts, which is the area indicated in panels (a) and (b) by a black rectangle. Canopy cover is aggregated in 1% bins with the dot size representing the number of pixels within that bin. The color of the points corresponds to the different land cover classes. Surface temperature (in degrees Celsius) and canopy cover data (30-meter resolution) were obtained from Wang and colleagues (2017). Land cover classifications combine MassGIS Land Use data and manual classification with aerial photography (30-meter resolution).

impervious surfaces that have lower albedos (i.e., pavement, concrete, etc.), and reradiation of heat from these high-heat-capacity surfaces. The UHI effect intensifies with the occurrence of heat waves (Li and Bou-Zeid 2013, Schatz and Kucharik 2015), which are predicted to increase in magnitude and duration as the climate continues to warm (Field et al. 2012).

Within city boundaries, the negative correlation between tree canopy extent and urban air or land surface (i.e., ground or pavement) temperatures is often shown empirically on small scales with studies comparing urban parks with nearby nongreen areas. These studies are still rare (fewer than 40 studies; Bowler et al. 2010) and tend to have low replication both in space and time, meaning that often a single park is examined, predominantly in temperate regions, and over the course of a single day. On larger scales (with a resolution of lower than 30 meters), satellite data have been used to examine the relationship between urban surface temperatures and canopy extent, using either metrics of greenness or land use classifications (Wang et al. 2017). In figure 2, an example of this type of analysis is shown for Arlington, Massachusetts, illustrating the strong negative correlation between canopy extent and urban surface temperatures at a resolution of 30 meters. Collectively, these studies demonstrate the significant cooling influence of vegetation in cities showing a reduction in air temperatures by 0.5°–9°C (Turner-Skoff and Cavender 2019) and upward of 20°C for surface temperatures (Bowler et al. 2010).

Although the UHI effect is well documented (Oke et al. 2017), there are far fewer studies on the heterogeneity of temperatures (either air or surface) within cities at the small spatial scales experienced by humans and that are needed to address public health concerns for climate change adaptation. Furthermore, few studies collect the necessary data to disentangle the effects of shading versus transpiration on local air and surface temperatures (except see Tan et al. 2018, Rahman et al. 2019). The few studies that exist at small spatial scales, however, are informative. Using a mounting sensor system on a bicycle that quantified air temperatures and humidity, Ziter and colleagues (2019) mapped variations on small spatial scales (10–100 meters) along regular transects in the city throughout the summer of 2016 in Madison, Wisconsin. Although they found a negative relationship between ground level air temperatures and canopy extent, this relationship was nonlinear. Substantially greater cooling impacts were observed when canopy cover exceeded 40% for a given examined area that ranged from 10 to 100 meters. Furthermore, Ziter and colleagues (2019) and others (figure 2; Wang et al. 2017) have shown that cities are more of a heat archipelago than a heat island, especially during extreme heat events, meaning intraurban air temperature variations are often of comparable or greater magnitude than the air temperature differences observed between adjacent urban and rural locales (Ziter et al. 2019).

Biophysical drivers of urban transpiration rates

Under average climatic conditions, the drivers that influence transpiration are similar to those that influence photosynthesis because of the strong coupling between these two plant processes. At the leaf level, transpiration rates are controlled by stomatal conductance, or gas exchange between leaves and the surrounding air. Plants regulate their stomatal conductance in response to light levels, atmospheric demand for water (i.e., vapor pressure deficit), water and nutrient availability, wind, and atmospheric CO_2 concentrations (McCarthy et al. 2011, Teskey et al. 2014, Drake et al. 2018).

The biophysical factors that affect rates of transpiration vary between rural and urban environments, as well as across the urban landscape. For example, the combination of higher ambient CO_2 (street level typically more than 500 parts per million of CO_2; Brondfield et al. 2012), greater nutrient availability (via atmospheric deposition or fertilizer application; Rao et al. 2014, Decina et al. 2017), greater water availability (via intentional irrigation or unintentional leaking water pipes; Stål 1998, Randrup et al. 2001), warmer air temperatures (Zipper et al. 2017), longer growing seasons, and higher light availability (because of reduced competition) can together make urban areas an oasis for trees (Melaas et al. 2016). Conversely, urban areas can also contain stressful environments that reduce rates of growth and transpiration and therefore the cooling effects of urban trees. Higher light availability, air temperatures that exceed optimal range for photosynthesis, exposure to invasive pests, limited water availability (soil desiccation or lack of irrigation) and rooting depth restrictions can act to reduce tree growth and transpiration rates (Rahman et al. 2011, Roman and Scatena 2011,Wang et al. 2017). Furthermore, larger trees can encounter unique risk because of their size, including excessive pruning, limited root space, and direct removal because of hazard risk (Stål 1998, Roman and Scatena 2011).

As a result of the urban oasis, some urban trees grow faster and store more carbon than nearby rural forests (McCarthy et al. 2011, Smith et al. 2019, Trlica et al. 2020). Smith and colleagues (2019) observed that growth rates of street trees in Boston, Massachusetts, were nearly four times higher than their rural counterparts. Higher growth rates in urban forests can affect rates of transpiration, but this is modulated by the tree's WUE. Although there is a positive correlation between growth and transpiration rates of urban trees, it is weaker than expected with significant variation because of differences among species or cultivars and conditions of different planting locations (McCarthy et al. 2011, Lahr et al. 2018, Stratópoulos et al. 2018). For example, although many tree species examined by McCarthy and colleagues (2011) had corresponding increases in growth rates and water use, some species either had high growth rates but low water use, or low growth rates with high water use, illustrating the importance of understanding species level differences in strategies deployed to maintain WUE by trees (McCarthy et al. 2011).

Conversely, higher urban air temperatures and sun exposure can stress trees with negative impacts on their growth and transpiration rates. Reinmann and Hutyra (2017) found that although nonirrigated temperate urban forest edges had an enhanced rate of forest growth compared with urban forest interiors (89% increase within 10 meters of forest edge), the magnitude of this edge growth enhancement declined strongly with heat stress. Heat stress alone explained over 30% of the interannual variability in forest growth rate over a two-decade period.

In addition to higher heat loads, urban environments experience additional stressors that affect plant functions including higher soil salinity from the addition of road salts, acidic soil conditions, and heavy metal toxicity (Pickett and Cadenasso 2009). The maximal growth of urban trees can be limited by the soil space available for them to grow, especially trees in densely developed areas (Quigley 2004). These stressors can be particularly harsh for young trees without well-developed root systems and resource reserves. Young urban trees have high mortality with an average lifespan of a street tree being 13–20 years, compared with more than 100 years in many rural forest trees (Roman and Scatena 2011). This high mortality rate of young urban trees is not well understood, but is likely a consequence of urban stressors described above as well as a variety of urban activities that directly damage trees. Despite recent initiatives to increase canopy cover in cities across the United States, 44 states have had a net loss in tree cover in urban areas between 2009 and 2014 (Nowak and Greenfield 2018). Although the exact reasons for these declines in canopy cover are still under investigation, studies suggest that this loss is due to direct removal of trees with changes in land use and the numerous stressors described above that lead to mortality of young and old trees in urban environments (Nowak and Greenfield 2012, Nowak and Greenfield 2018, Ossola and Hopton 2018, Smith et al. 2019).

Hydraulic strategies of urban trees

In cities, human amendments of nutrients, water, and other unique urban conditions allow for a wide variety of native and nonnative tree species to exist with a diverse array of hydraulic strategies. This pattern is especially true in cities that have warmer climates (Jenerette et al. 2016). In many cases, urban tree species experience environmental conditions for which there is no analog in their native range or in rural environments. This difference between urban and rural ecosystems makes it difficult to estimate rates of transpiration in urban trees without direct studies of trees in urban environments (Litvak et al. 2017, McCarthy and Pataki 2010). For example, tree species from arid climates typically have higher WUE, maintained by lower overall rates of transpiration than temperate or riparian species; however, in well-irrigated urban landscapes for the same set of species, the opposite has been observed (Goedhart and Pataki 2012).

Despite the unique conditions that urban trees experience, we are aware of only one study that examined how biophysical factors influence transpiration rates of different urban tree species compared with rural conditions. In Los Angeles, California, McCarthy and Pataki (2010) compared rates of transpiration for the native tree species American sycamore (*Platanus racemose)* and nonnative canary pine (*Pinus canariensis*), each growing in various urban environments and in nearby rural locales. They found considerable site to site and seasonal variability in transpiration rates, with urban street trees having the highest rates of transpiration, in

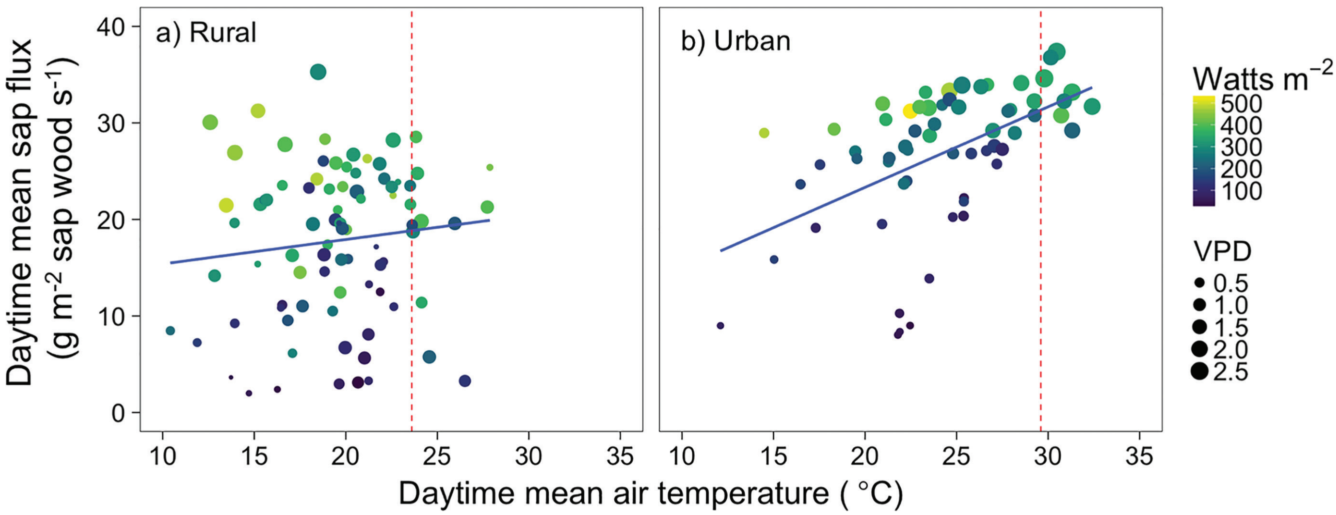

Figure 3. Panels (a) and (b) show a case study on the relationship between daytime average sap flow, a proxy for transpiration, and average daytime air temperatures and mean vapor pressure deficit (VPD, a metric of atmospheric aridity) for a sample of sugar maple trees (Acer saccharum) growing in either a rural (a) or urban (b) environment. In the rural site, this relationship is shown as the average of ten trees growing in a rural forest at the Hubbard Brook Experimental Forest (HBEF) located in North Woodstock, New Hampshire (approximately 100 miles outside of Boston) in the 2010 growing season (r^2 = .02, p = .02 for temperature; r^2 = .04, p < .001 for VPD; Harrison et al. 2020). In the urban site this relationship is shown for a Sugar Maple tree growing in a well-irrigated, well-lit urban backyard located in Boston, Massachusetts in the 2018 growing season (r^2 = .25, p < .0001 for temperature; r^2 = .63, p < .0001 for VPD). At the rural site sap flow data were collected using 20-millimeter thermal dissipation probes (Harrison et al. 2020), whereas, at the urban site, data were collected using the compensation heat pulse method with 20-millimeter sensors (Jones et al. 2020). The differences in the probe methodology between sites, however, does not significantly influence rates for the observed range (Forster 2017). In each panel, points represent daytime values, defined as the hours of 06:00 to 21:00 for the peak growing season (June 1 to September 1), and colors represent the median of hourly daytime solar radiation. The size of the points represents the corresponding median hourly daytime VPD. The blue line shows the linear regression through all data points. In panels (a) and (b), the red dashed line is the mean of the daily max air temperature observed in July for each site (2001–2007). Air temperature, VPD, and solar radiation was obtained for the rural site from nearby HBEF headquarters (USDA Forest Service, Northern Research Station 2019) and for the urban site from nearby weather underground station no.KMABOSTO269.

particular the riparian species, *P. racemose*. The difference in transpiration rates by planting location was driven by water stress in the case of *P. canariensis* and by both water and nutrient availability in the case of the riparian tree species *P. racemose*.

We compared rates of sap flow for sugar maple (*Acer saccharum)* trees growing in the city of Boston, Massachusetts with those in a rural forest in Woodstock, New Hampshire (Hubbard Brook, a distance of approximately 125 miles from Boston; figure 3). The urban tree (*n* = 1 tree) grew in a well lit and well irrigated backyard, whereas the rural trees (*n* = 10 trees) were canopy trees in an intact forest stand. In the city of Boston the majority of trees are grown in the open with high light conditions, approximately 85% of the cities' canopy area located within 10 meters of a forest edge (Trlica et al. 2020). The urban sap flow data are only illustrative as a single tree was measured every 15 minutes for a full growing season, but the data show clear correlations between sap flow and atmospheric drivers. The urban tree had a stronger relationship between sap flow rates and both air temperatures or atmospheric aridity (shown by the metric vapor pressure deficit or VPD; r^2 = .25, p < .0001 for temperature; r^2 = .63, p < .0001 for VPD) compared with the rural trees (r^2 = .02, p = .02 for temperature; r^2 = .04, p < .001 for VPD). The corresponding radiation data showed that the weak relationships at the rural site between sap flow and atmospheric conditions (either temperature or VPD) were not explained by differences in cloud coverage between the two sites. We hypothesize that the differences in trends between sap flow and atmospheric conditions between urban and rural environments are likely driven by the lower water availability, nutrient resources, and lower air temperatures observed at the rural site (Harrison et al. 2020) compared with the urban site (Jones et al. 2020). Collectively, our case study and the one by McCarthy and Pataki (2010) raise doubt as to the validity of assumption that at a given atmospheric aridity (i.e., VPD), temperature, and solar radiation, urban trees have similar transpiration rates as rural trees.

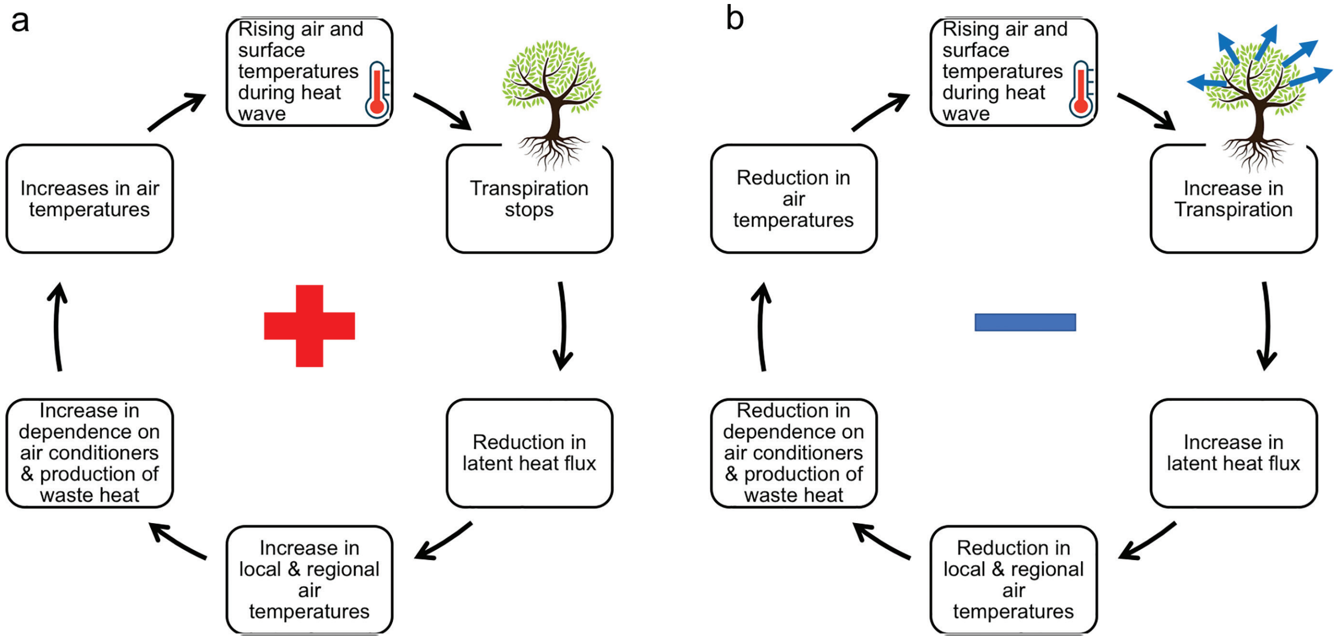

Figure 4. Conceptual diagram illustrating the negative and positive feedbacks on land–atmosphere interactions that either diminish or amplify the intensity of heat waves. The backbone of coupled plant–climate models is the assumption that carbon capture via photosynthesis and water uptake (i.e., transpiration) by trees declines or stops during heat waves. Panel (a) illustrates the steps in a negative feedback loop that acts to diminish the intensity of heat waves. As air temperatures increase during a heat wave event, if trees maintain water uptake and loss via transpiration, then latent heat fluxes will remain high. The latent heat of evaporation removes heat from the atmosphere resulting in lower air temperatures. A reduction in air temperatures during a heat wave can result in reduction in building cooling needs and the associated waste energy emitted from cooling services. Conversely, panel (b) illustrates the steps in a positive feedback loop that acts to amplify the intensity of heat waves. As air temperatures rise during a heat wave, with all things otherwise held constant, if trees respond to these rising air temperatures by closing their stomates and stopping to transpire water, then this would result in lower latent heat fluxes from the evaporation of water and greater dominance by positive sensible heat fluxes that act to increase air temperatures. These positive feedbacks amplify urban heat, increasing building cooling demand, electricity use, and carbon dioxide emissions.

Rather, the unique conditions and responses of different tree species to urban environments can result in large differences in anticipated transpiration rates.

Hydraulic strategies deployed by different tree species or genotypes (Lahr et al. 2018) influence rates of transpiration, WUE, and responses to environmental conditions (Bush et al. 2008, McCarthy et al. 2011, Rahman et al. 2019). In particular, the woody architecture of sapwood influences a tree's hydraulic strategies. The size and location of of water-carrying vessels within the sapwood varies by species. The architecture of sapwood in most angiosperms can be categorized as either ring porous, where sapwood has a bimodal distribution of small and large vessels that carry water, or diffuse porous, where sapwood has a uniform distribution of vessels that carry water. Rahman and colleagues (2019) found through a common garden experiment of two commonly planted urban tree species, rates of transpiration were higher in the diffuse-porous species Linden (*Tilia*) than in the more water use efficient and ring-porous species Black Locust (*Robinia*). Similarly, in the arid cities of Los Angeles, California and Salt Lake City, Utah, it was found that for well-irrigated urban trees, the response of transpiration rates to changes in the aridity of the atmosphere (vapor pressure deficit ranged from 0–5 kilopascals) varied on the basis of the type of hydraulic architecture of the sapwood (Bush et al. 2008, Litvak et al. 2012). For example, transpiration rates of diffuse-porous species varied linearly with increases in atmospheric aridity, as theory would expect under well-irrigated conditions. In contrast, tree species with ring-porous sapwood had a nonlinear response of transpiration rates to increases in atmospheric aridity. This pattern, however, is in contrast to observations of ring- versus diffuse-porous species studied in rural forests under drought conditions (Roman et al. 2015), illustrating the need for similar studies in urban environments.

Responses of transpiration rates to heat waves

Tree responses to heat waves are poorly studied especially in cities, but can have significant impacts on urban climatic conditions (figure 4). Trees can acclimate to gradual increases in air temperature with increases in the optimal temperature of photosynthesis and WUE. It is unknown whether this acclimation can occur on time scales of days that are associated with heat waves. Evidence suggests that in some cases observations of how trees acclimate to normal seasonal temperature changes can be used to predict their responses to climate change (Aspinwall et al. 2016). Other models assume that photosynthesis and transpiration decline or stop at extreme temperatures experienced during heat waves (Teskey et al. 2014) and anticipated with climate change (Field et al. 2012). Studies in rural forests show that rates of transpiration are greater on extreme heat than average days (Kauwe et al. 2018, Harrison et al. 2020), but the response in urban areas is unknown. Observational data in Los Angeles, California suggests that vegetation may continue to transpire during heat waves, as was indicated by a stronger relationship between vegetation extent (as determined by satellite data) and surface air temperatures during heat waves (Shiflett et al. 2017). If transpiration declines or stops in response to extreme temperatures this can act to amplify temperatures during heat waves (figure 4).

The first empirical experiment to induce a simulated extreme heat wave on field grown and relatively large trees (43°C for four consecutive days on Eucalyptus trees in Australia) found that rates of transpiration by trees were maintained during heat wave conditions (Drake et al. 2018). The trees, which were not irrigated, were able to obtain sufficient water from the soil profile during the heat wave to sustain transpiration. However, there was a strong decoupling between transpiration and photosynthesis during the heat wave that was not observed with chronic warming alone. Instead of keeping stomata open to maintain photosynthesis as theory predicts, the trees instead kept their stomata open to sweat, or to cool their internal leaf temperatures. A recent analysis of eddy covariance studies in Australia (OzFlux) found evidence for this phenomenon as well, however, similar analysis in temperate forests of the United States (FLUXNET) found mixed responses (Kauwe et al. 2018). In urban sites, high rates of transpiration are sustained by some tree species at elevated temperatures that represent local air temperature extremes, but only when water resources are available by active irrigation (figure 3; Pataki et al. 2011b). It remains to be examined whether sustained transpiration rates, or the decoupling of transpiration and photosynthesis, is widespread, species specific, or sensitive to temperature thresholds rather than locally defined heat extremes. The answer to this key knowledge gap has significant impacts on predictions of urban climatic conditions and carbon storage with climate change.

Access to water resources

A key control on urban rates of transpiration and growth rates is access to water, which varies substantially between cities and within city boundaries because of differences in planting locations, infrastructure, and management decisions (figure 1). Across a large evapotranspiration gradient in the United States ranging from 400 to 1000 millimeters per year, climate was found to strongly differentiate forest structure (height and size distribution of vegetation) and forest areal extent in urban areas—more so than socioeconomic factors—with forest cover doubling along the evapotranspiration gradient (Ossola and Hopton 2018). Water stress can interact with other urban stressors to exacerbate their negative effects. For example, Meineke and Frank (2016) found that for the common street tree species, *Quercus phellos* (willow oak), that the combination of water stress and warming made this species more susceptible to herbivory damage from an insect pest.

The sources of water used by urban trees remains highly uncertain, making it difficult for cities to manage municipal water resources and to predict transpiration rates and their associated cooling effects (Litvak et al. 2017). Stable isotope analyses are often used to determine water resources accessed by trees; however, these analyses have rarely been conducted in urban environments. Bijoor and colleagues (2011) used oxygen and hydrogen isotopes to determine the sources of water used by urban trees in Los Angeles, California. They found that the majority of urban trees in this arid city had very shallow root systems (less than 30 centimeters) and were dependent on water found in the top soil. However, despite frequent irrigation maintaining high soil moisture availability in surface soils, some trees obtained significant amounts of water from deeper groundwater sources. In some cases, there were also unexplained sources of water thought to be from runoff, storm drains, or leaking infrastructure.

In arid cities, where forests do not naturally occur, the survival of trees and cooling influence they provide are dependent on irrigation (Pataki et al. 2011a, 2011b, Wheeler et al. 2019). The irrigation of urban vegetation can use more than 50% of municipal residential water consumption in many arid cities throughout the United States (Litvak et al. 2017). Consequently, municipalities face trade-offs between the ecosystem services provided by trees, such as cooling via transpiration and carbon storage, and ecosystem disservices, such as the costs of irrigation and maintenance. McCarthy and colleagues (2011) showed that urban forest planners can maximize growth of trees while conserving water by selecting tree species with both high WUE and high growth rates. More studies are needed, however, to understand the differences in WUE among tree species and across urban forms and climates to inform urban planners and to model estimates of transpiration in urban environments (Litvak et al. 2017).

From tree transpiration to temperature reductions

Weather, climate, and Earth system models focused on urban areas are essential tools for translating observed drivers of evapotranspiration into the implications it has on urban climatic conditions (Chen et al. 2011, Li et al. 2016a, 2016b). These urban weather, climate, and Earth system models often employ the so-called urban canopy models to simulate

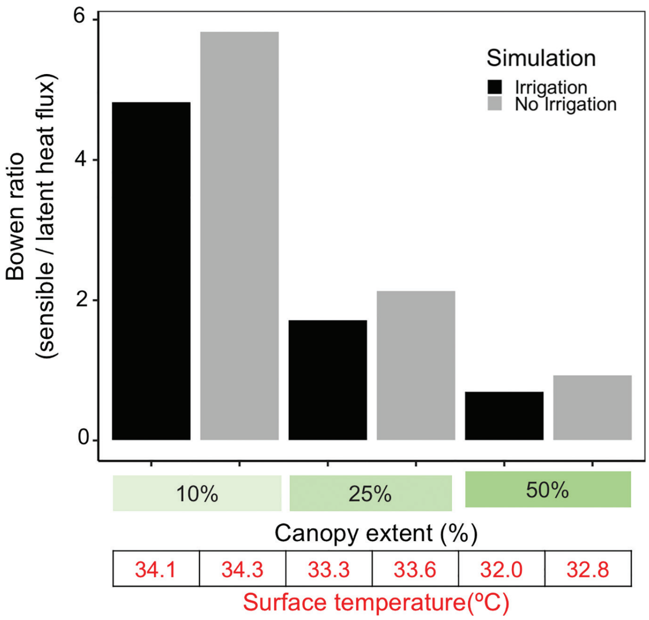

Figure 5. Model simulation results for a summer heat wave with different levels of canopy extent and irrigation. We used the WRF model to test the influence of irrigation and canopy coverage on surface temperatures and the Bowen ratio (sensible or latent heat flux) during a summer heat wave in Boston, Massachusetts. The Bowen ratio indicates the extent to which the atmosphere is warming (because of higher sensible heat fluxes) versus cooling (because of higher latent heat flux). Model parameterization is specified in supplemental methods.

the impacts of the built environment, urban vegetation, and anthropogenic energy consumption on the surface energy budget under changing atmospheric conditions, management decisions, and policy implementations (Grimmond et al. 2010, 2011, Best and Grimmond 2015). Using these urban canopy models, studies have demonstrated the important role vegetation can have on urban climatic conditions. For example, observational data and modeling results show that increases in canopy cover result in a reduction in the sensible heat flux and an increase in the latent heat flux. The ratio of sensible to latent heat flux is known as the Bowen ratio and a higher Bowen ratio indicates a stronger heating of the atmosphere (figure 5; Loridan and Grimmond 2012, Best and Grimmond 2016). These cooling effects of canopies are amplified by increases in irrigation and other anthropogenic sources of water (figure 5; Best and Grimmond 2016).

In the present article, we demonstrate this effect and the ability of models to translate empirical findings into climate implications in figure 5 where we have simulated the urban surface energy budget for a neighborhood in Boston, Massachusetts, during a summer heat wave in 2018. We show the Bowen ratios and surface temperatures for six different scenarios, including a factorial design that includes variable assumptions about vegetation coverage (10%, 25%, or 50% coverage) and water availability (irrigation versus no irrigation). As vegetation coverage increases so does the latent heat flux as was indicated by a decline in the Bowen ratio. This corresponds to a 1.5°C decrease in surface temperatures between the high (50%) and low (10%) canopy scenarios that were not irrigated. When vegetation was irrigated, there was an additional 0.6°C of cooling or 2.1°C decrease in surface temperatures. Differences in surface temperatures were driven by an increase of approximately 35% in latent heat fluxes. These results are broadly consistent with previous modeling studies (Loridan and Grimmond 2012, Best and Grimmond 2016), which together illustrate the cooling benefits provided by the combination of increased canopy cover and water availability.

Future research directions

Our synthesis of the literature highlights several key areas of future research directions on urban tree transpiration and how it influences urban climates. First, there is a need for more studies on urban transpiration rates across the different types of urban areas (such as some of those shown in figure 1) as they relate to variability in water resources. Urban trees experience unique conditions compared with their rural counterparts that hinder our abilities to extrapolate rural forest function to urban areas. Second, future studies should explore how transpiration rates vary among different urban planting locations for different plant hydraulic strategies. Our current climate models do not resolve critical ecophysiological attributes or capture human amendments in the urban environment. Finally, there are few studies examining the interaction and feedbacks between urban transpiration rates and the built environment during heat wave conditions when the cooling effect of trees is needed the most. As is illustrated in figure 4, the response of urban tree transpiration to heat wave conditions can either help to reduce temperatures during heat waves or can act to exacerbate already dangerously hot conditions. Existing literature suggests that the type of feedback that occurs during heat waves between trees and the built environment will depend on how plant hydraulic strategies respond to heat waves and the type of water resources available.

Our current understanding of the mechanisms driving the observed negative and nonlinear relationships between the extent of canopy and urban temperatures (air or surface) requires further investigation. Ziter and colleagues (2019) postulated that this relationship could be a consequence of the higher LAI with higher levels of canopy cover resulting in greater shading, especially of impervious surfaces that have higher heat capacity. Alternatively, Ziter and colleagues (2019) suggest that the high canopy cover may be associated with land use types that provide synergistic cooling benefits. For example, higher canopy cover could be more often associated with large green spaces or parks that have a grass layer below the canopy, or areas with higher water and nutrient availability that favor tree species with higher growth rates, transpiration, or leaf area. Rahman and colleagues (2020) suggested that the underlying surface characteristics (e.g., lawn versus pavement) determine potential evapotranspirational cooling more than LAI. Furthermore, research is needed to test these alternative hypotheses explicitly.

Our improved understanding of urban tree ecophysiology needs to go hand in hand with efforts to better represent trees in urban canopy models. Current modeling approaches, although they are insightful, do not capture some of the key urban vegetation characteristics our synthesis identifies as key drivers of transpiration. For example, given the demonstrated higher transpiration capacity of trees in urban environments, models that use a grass-type parameterization of transpiration are likely dramatically underestimating the cooling from transpiration provided by urban vegetation. Furthermore, the big leaf approach of modeling the activity of vegetation in the urban environment does not account for differences in functional response of trees with different hydraulic strategies that could lead to under- or overestimates of transpiration, especially during heat waves (figure 4). Finally, many urban canopy models still do not represent interactions between urban vegetation and the built environment, meaning that the urban vegetation is treated as a separate entity. Although the effects on surface temperature and humidity are captured through simple area-averaging procedures, this approach prohibits the use of models to better inform our understanding of interactions between urban canopies and the built environment. There are ongoing efforts to address these deficiencies (Lemonsu et al. 2012), but the consideration of urban trees in urban canopy models remains limited and is an area in critical need of further model development and validation (Ryu et al. 2016).

Expanding urban vegetation, or *green space*, in cities is one of a suite of effective solutions for reducing the negative impacts of the UHI effect and extreme heat events in cities (Lamb et al. 2019). A more complete understanding of the limitations of tree ecophysiology in the urban environment can help identify when alternative cooling strategies, such as cool roofs or pavements (surfaces with high albedo), are better suited than tree canopy to combat excess urban heat. Some studies have shown that the combined use of green infrastructure and cool roofs help maximize cooling effects, and the most optimal strategy to do so varies spatially within and across cities (Li et al. 2014). Furthermore, research is needed on the type of configurations of green infrastructure and geoengineering solutions that provide optimal cooling. Any given type of nature-based solution may not be equally effective for all cities. Critically evaluating alternative strategies are especially important given the mismatch between the timelines of planetary warming and the time needed for a tree to grow to sufficient size to provide cooling through shade and evapotranspiration. For this reason, cities seeking to increase canopy cover and associated ecosystem services that canopy provide will need to consider not just planting small trees but also conserving large trees (Trlica et al. 2020) that often are removed during development or redevelopment projects (Morgenroth et al. 2017). Because, as the proverb goes, the best time to plant a tree is 20 years ago. The second best time is now.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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