Sap flow and leaf gas exchange response to drought and heatwave in urban green spaces in a Nordic city

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Abstract. Urban vegetation plays a role in offsetting urban CO_2 emissions, mitigating heat through tree transpiration and shading, and acting as deposition surfaces for pollutants. The frequent occurrence of heatwaves and concurrent drought conditions significantly disrupt the operational processes of urban trees, particularly their photosynthesis and transpiration rates. Despite the pivotal role of urban tree functioning in delivering essential ecosystem services, the precise nature of their response remains uncertain.With frequent heatwave events and the accompanying drought, the functioning of urban trees is severely affected in terms of photosynthesis and transpiration rate. The detailed response is, however, still unknown despite tree functioning having crucial effects on the ecosystem services they provide. We conducted sap flux density (J_s) and leaf gas exchange measurements of fourthree trees per species (*Tilia cordata*, *Tilia × europaea*, *Betula pendula*, *Malus spp.*) located in differentat four types of urban green areas (Park, Street, Forest, Orchard) in Helsinki, Finland. Measurements were made, over two contrasting summers 2020 and 2021. Summer 2021 had a strong local heatwave and drought, whilehereas summer 2020 was more typical for Helsinki. In this study, we aimed to understand the responses of urban tree transpiration (measured with sap flux density) and leaf gas exchange to heatwave and drought, and examine the main environmental drivers controlling the tree transpiration rate during these periods in urban green areas. We observed varying responses of sap flux density (J_s) during the heatwave period at the four urban sites. When comparing the heatwave and non-heatwave periods, a 35-67% increase in J_s was observed at the Park, Forest, and Orchard locations, while no significant change was seen at the Street site which exhibited comparable values.J_s was found to be 35-67% higher during the heatwave as compared to the non-heatwave period at the Park, Forest, and Orchard sites but similar J_s was observed at the Street site during the heatwave as compared to the non-heatwave period. Our results also showed that J_s was higher (31-63%) at all sites during drought compared to non-dry periods. The higher J_s during the heatwave and dry periods were mainly driven by the high atmospheric demand for evapotranspiration represented by the high vapor pressure deficit (VPD), suggesting that the trees were not experiencing severe enough heat or drought stress that stomatal control would have decreased transpiration. Accordingly, photosynthetic potential (A_{max}), stomatal conductance (g_s), and transpiration (E) at the leaf level did not change at the four sites during heatwave and drought periods, excluding

the Park site where significant reduction in g_s was seen. Only g_s was significantly reduced during the drought period at the Park site. VPD explained 55-69% of the variations in the daily mean J_s during heatwave and drought periods at all sites. At the Forest site while at the Forest site, the increase of J_s with the rise in VPD saturatedds after a certain VPD level likely of VPD, which might be evident due to low soil water availability at the Forest site during these hot and dry periods. Overall, the heat and drought conditions were untypically harsh for the region but not excessive enough to restrict stomatal control and the increased transpiration, indicating that ecosystem services such as cooling were not at risk.

Keywords: climate extreme, drought, sap flux, transpiration, urban trees

1 Introduction

Ongoing uUrbanization is increasing rapidly and transformsing the natural environment, land cover, and ecological functions. Urbanization enhances CO_2 emissions and the local urban heat island (UHI) effect, leading to harsher conditions in cities and a decrease in human thermal comfort when compared to more natural surroundings (Oke et al., 1989; Roth et al., 1989). These challenges highlight the need for adequate urban planning in the long-term development of urban areas. Urban green spaces have a role in offsetting anthropogenic CO_2 emissions and alleviating UHI effect, given their potential for carbon sequestration and storage, and water regulation to cool their surroundings (Lindén et al., 2016; Bowler et al., 2010; Havu et al., 2022; Hardiman et al., 20 Urban green areas play a vital role in compensating urban CO_2 emissions and mitigating the UHI effect as they have the potential for carbon sequestration and storage, and regulation of water for cooling the surrounding (Lindén et al., 2016; Bowler et al., 2010) Several studies have highlighted the CO_2 sequestration potential ofand annual carbon storage in urban vegetation (Nowak and Crane, 2002; Davies et al., 2011; Muñoz-Vallés et al., 2013; Nowak et al., 2013), and addressed urban green areas as a way of mitigating the cities' GHG emissions in cities (Dhakal, 2010; Paloheimo and Salmi, 2013; Pataki et al., 2021). The role of urban trees in mitigating UHI is also well-reported in many urban studies (Rahman et al., 2019; Pataki et al., 2011). Particularly, under extremely high temperatures, the potential of urban trees in heat mitigation has been shown to be significant (Gillner et al., 2015; Schwaab et al., 2021). Trees provide cooling effect through two main primary mechanisms. Firstly, urban trees reduce surface temperature by shading, resulting in less absorption and storage of incoming short-wave radiation by surfaces, lowering the local air temperature. Secondly, trees cool the environment through transpiration when water taken up by roots is released through leaf stomataes. The energy consumed to evaporate the water released from leaf stomata provides a cooling effect on the leaf surface and lowers nearby air temperature by advection. Urban trees also provide other ecosystem services such as pollutant deposition, aesthetics, recreation, soil conservation, and buffer for noise and wind (Brack, 2002; Jo, 2002; Jim and Chen, 2009; Pataki et al., 2009).

In urban conditions, trees are subjected to harsh environmental conditions, such as elevated air temperature, lower air humidity, limited soil water and nutrient availability, compared with surrounding areas (Nielsen et al., 2007). Climate extremes such as heatwaves and drought affect the physiologyprocesses and functioning of urban trees and thus also their potential of trees to mitigate the effect of climate extreme and to adapt to climate change. Hence, it is important to understand the response of the physiological processes regulating urban trees' functioning during extreme climate events.

In urban environmentcondition, trees are subjected to human disturbances such as construction activities, dense building and vandalism (Czaja et al., 2020) and climate change impacts including extreme weather such as heatwaves and drought. All these affect the potential of trees to mitigate and adapt to climate change, and thus it is important to understand the response and functions of urban trees during extreme climate events. In general, environmental conditions for urban trees are often more harshextreme than those in a natural forest stand, having e.g. higher air temperature, lower air humidity, and more limited soil water and nutrient availability (Nielsen et al., 2007). All these differences in local microclimate, growing conditions, species type, disturbances and management activities affected the processes andfunctioning of urban trees.

The rise in temperature during summer heatwaves has effects on tree function both directly with increasingaffects leaf temperature potentially leading to leaf damages (Kunert et al., 2022; Atkin and Tjoelker, 2003; Ghannoum and Way, 2011), and indirectly by increasing the vapor-pressure deficit (VPD) with consequences for transpiration and photosynthesis through stomatal control (Lloyd and Farquhar, 2008). TIn urban areas, tree responsesreactions to heatwaves in urban areas haveare rarely been studied, but trees in natural forests can adapt to the rising temperatures by enhancing growth and utilising water more efficiently if provided with enough moisture in the soil (Winbourne et al., 2020). However, such acclimation may not be possible for trees in urban settings as shown by their often higher The foliar temperatures, of urban trees are often higher, which further limits photosynthesis and transpiration through enzyme activity and stomatal regulation (Bussotti et al., 2014), hence such acclimation may not be apparent in urban settings. Droughts have been occurring more frequently in recent times causing severe symptoms for trees even in areas that are usually considered to be rather moist such as high latitude areas (Hartmann et al., 2022). A tree usually responds to drought in one of two ways: either by avoiding a significant decrease in water potential and relative water content through stomatal closure at the cost of reduced photosynthesis, i.e. the isohydric strategy, or by maintaining photosynthesis by keeping the stomata open at the cost of letting the water potential decrease, i.e. the anisohydric strategy (Villar-Salvador et al., 2004; De Micco and Aronne, 2012). Moreover, summer droughts are usually associatedco-occurs with high air temperature during summer furtherseverely severely reducing carbon assimilation, and transpiration through lowered stomatal conductance and increasing potential leaf damages affecting the functioning of trees and potentially resulting in leaf damage, reduced carbon assimilation and transpiration through lowered stomatal conductance (Bussotti et al., 2014; Winbourne et al., 2020).

However, the specific effects of an urban environment on the trees' response to stresses such as drought and heat are not yet fully known. A few studies have investigated the potential cooling effect of urban trees during heatwaves and droughts (Gillner et al., 2015), and their impact on urban tree functions (Rötzer et al., 2021) where the urban tree functions depend on the species type, growing con ditions, local climate and water availability. Nonetheless, because of the complex urban stressors and the spatial heterogeneity of urban landscapes, further studies are needed to quantify the impact of extreme events on urban trees' function. This information is especially needed for high-latitude cities because global warming is more prominent at high latitudes making their urban ecosystems particularly vulnerable. A tree usually responds to drought in two ways, by either avoiding the large decrease in water potential and relative water content or tolerating via maintaining the physiological processes during drought (Villar-Salvador et al., 2004; De Micco and Aronne, 2012). However, the effect of an urban environment on the tree's response to stress such as drought and heatwaves is not known, particularly in the

~~boreal urban environment. A few studies have investigated the potential cooling effect of urban trees during heat and drought (Gillner et al., 2015), and the impact of drought on urban tree functions (Rötzer et al., 2021). The urban tree functions were found to be affected by species type, growing conditions, local climate and water availability, particularly during heatwave and drought periods. Nonetheless, urban tree responses to extreme heat and drought are poorly addressed and with complex urban stressors and heterogeneity, need further study. Especially information on the impact of heat and drought on urban trees in high-latitude cities is lacking. Global warming is more prominent at high latitudes making urban ecosystems in high latitudes particularly vulnerable. Thus, it is important to understand the responses of trees to heat and drought in various urban environments in the boreal region.~~

In this study, we measured a set of typical processes regulating the functions of urban trees, specifically transpiration and leaf gas exchange, during local heatwave and drought in the boreal urban environment of Helsinki, Finland.~~In this study, we measured the functions of a set of typical urban tree species, particularly their transpiration and leaf gas exchanges, during heatwave and drought periods in a boreal urban environment in Helsinki, Finland.~~ We used sap flow as a proxy for whole tree transpiration and studied its response to hot~~In particular, our focus was on the response of sap flow rate patterns during heat~~ and dry periods in different urban green areas. From these measurements, we further quantified how much the different environmental factors control the sap flow rate. We addressed the following research questions:

1. How does local heatwave affect the transpiration and leaf gas exchange rates of boreal urban trees ~~of urban trees~~?
2. How does drought affect boreal urban tree transpiration and leaf gas exchange rates ~~of urban trees~~?
3. What are the main environmental drivers affecting transpiration rates during local heatwave and drought in high lattitude urban green areas?

We hypothesize that: H1) While increasing VPD during heatwaves increases the driving force for transpiration and thus sap flow, it also triggers stomatal closure, ultimately leading to a decrease in photosynthetic rates and a decoupling of VPD and leaf gas exchange rates.~~H1) even though a heatwave increases sap flux density due to increased VPD in the short term, it decreases the photosynthesisphotosynthetic potential due to lower stomatal conductance and also decreasing the role of VPD as a driver,~~ H2) A drought event decreases both sap flux density and the rate of photosynthesis~~photosynthetic potentialtic potential~~. To answer the questions and test the hypotheses, we conducted continuous sap flux and manual leaf-gas exchange measurements at four diverse urban green areas ~~(Park, Street, Forest and Orchard)~~ in Helsinki during the summers of 2020 and 2021.

2 Methods

2.1 Sites description

The study was conducted near the University of Helsinki Kumpula campus, located 4 km northeast of the Helsinki city center. The Kumpula area is characterized by heterogeneous land-use cover (Figure 1a), particularly by diverse urban vegetation. Within the study area, four sites were selected to be studied: a park with sparse trees ('Park'), a single line of roadside trees ('Street'), an urban forest ('Forest'), and an apple orchard ('Orchard'). These sites are located close to a micrometeorological eddy covariance station (FI-Kmp, 60°12'11.3"N 24°57'40.4" E), which is also an Associated Ecosystem Station of ICOS (Integrated Carbon Observation System) and part of the SMEAR (Station for Measuring Ecosystem Atmosphere Relations) III station (Vesala et al., 2008; Järvi et al., 2009). Overall, Helsinki is a humid continental region (according to Köppen climate classification), with annual precipitation of 652 mm yr^{-1} and yearly mean temperature of 6.5 °C during the 30-year climatic reference period 1991-2020 (FMI, 2021). The summer of 2021 experienced elevated temperatures at 21.6°C, which were 21% higher, along with minimal rainfall at 86 mm, showing a 51% deficit compared to the reference period.~~The summer of 2021 was hot and dry as the mean air temperature in July 2021 was 21.6°C, being 21% higher than in July 2020 (16.7°C) and 19% higher than the average mean temperature in July (18.1 °C) during a climatic reference period (1991 to 2020). The total precipitation for the months of June and July 2021 (86 mm) was 51% lower than during June and July 2020 (177 mm) and 27% lower than the average total precipitation in June and July during the climatic reference period (117 mm).~~

The urban park (Park; Figure 1b) is located in the Kumpula botanical garden, southwest of the FI-Kmp measurement tower. The study site is characterized by ~~a mixture of~~ *Tilia cordata* ~~*species*~~ trees and a ground layer of short vegetation comprised mainly of lawn species, clovers (*Trifolium repens*), and mosses. The ground vegetation was mowed daily using an automatic mowing device, leaving the clippings on-site and irrigation was activated on dry and warm days within the wider park area. The daily~~However, the~~ mowing and irrigation were restricted in the area around~~between~~ the studied trees (0.25 ha area) during the measurement period but the tree roots reached the irrigated area.

The roadside plantation (Street; Figure 1 c) is located on the road called Hermannin rantatie, 0.8 km east of the FI-Kmp measurement tower. It consists of a row of *Tilia* × *europaea*, a hybrid of *T. cordata* and *T. platyphyllos*. It~~The species~~ is the most commonly planted urban tree in Helsinki and Nordic countries in general, comprising 44% of Helsinki's Street trees (Sjöman et al., 2012). The street trees grow over a patch of soil spreading 60 m long and 2.7 m wide, with an average tree spacing of 8.2 m. Normally, the trees are regularly trimmed and maintained by the city gardening company, but they were non-managed during our study.

The urban forest (Forest; Figure 1d) is a small forest patch (25x30 m^2) located between the FI-Kmp measurement tower in the north and the Kumpula botanical garden in the south. This site is dominated by mature *Betula pendula* trees, but other deciduous trees such as *Betula pubescens, Alnus glutinosa, Acer platanoids*, and *Ulmus glabra* were also growing at the site. The sparse ground vegetation layer consisted mainly of *Aegopodium podagraria* and bare spots. This site was the only non-managed study site and was regenerated naturally. ~~Other deciduous trees such as *Betula pubescens, Alnus glutinosa, Acer platanoids*, and *Ulmus glabra* were also found in this urban forest as a species mixture. The ground layer was sparse consisting mainly of *Aegopodium podagrariaa* and bare spots.~~

The apple orchard (Orchard; Figure 1e) is located in the Kumpula school garden 0.9 km west of the FI-Kmp measurement tower. The site is characterized by scattered apple trees (20 trees per 30 m x 30 m area) planted over a managed lawn. There was no irrigation. The lawn in our measurement area was manually mown a few times during the summers.

More detailed descriptions of all four sites are given in Table 1 and soil properties, particularly soil water retention properties, are presented in Appendix A1. All sites were equipped with continuous measurements of sap flux and meteorological variables from June 2020 to September 2021, except the Orchard site, where data were recorded only from June to September

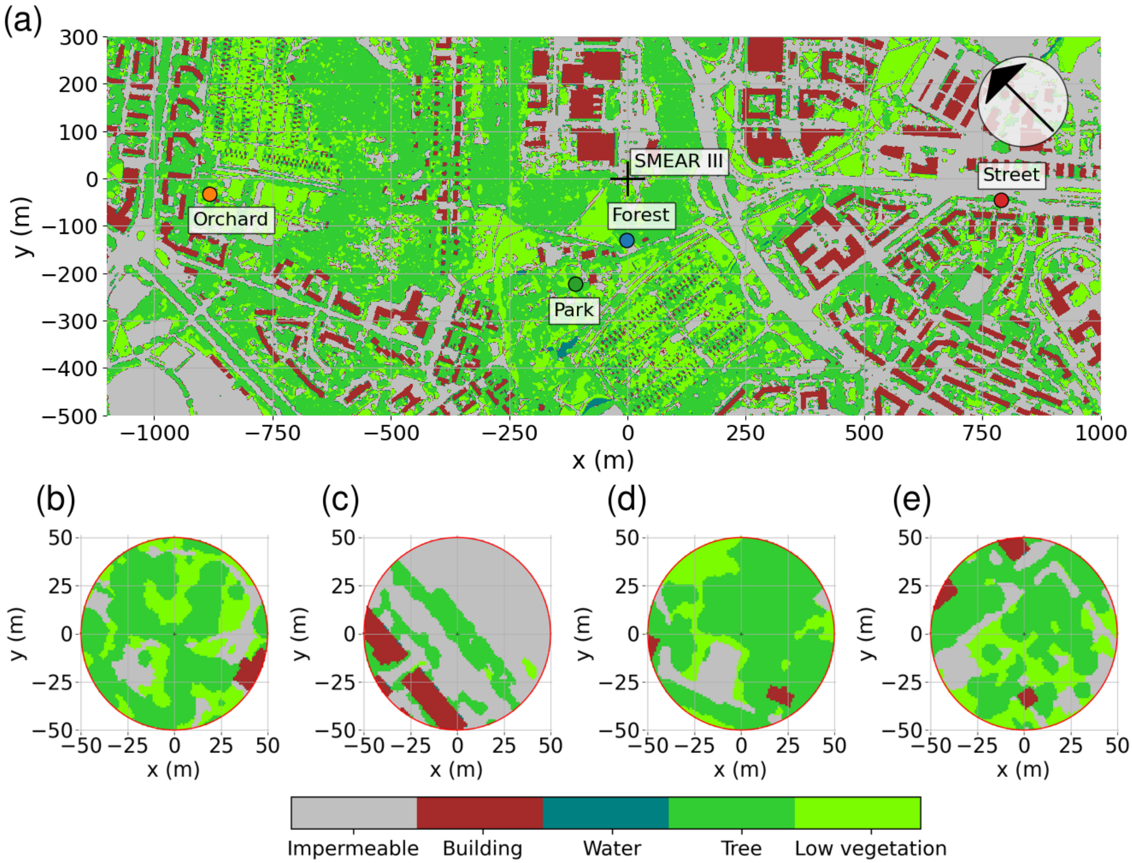

Figure 1. (a) Surface cover of the study area in Helsinki (StromJan, 2020) with the location of the FI-Kmp station at SMEAR III and the monitoring sites as well as the local surface covers at the (b) Park, (c) Street, (d) Forest, and (e) Orchard measurement sites.

2021. Manual leaf gas exchange measurements accompanied the continuous measurements~~The continuous measurements were accompanied by manual measurements of leaf gas exchange~~ during the summer months (June-August).

Table 1. The four study sites with information on their location, the dominating tree species, the mean diameter at breast height (DBH), sapwood area, and height of the selected three individuals, years since plantation (age), and soil particle type.

	Park	**Street**	**Forest**	**Orchard**
Latitude	60°12’08.4"N	60°11’51.6"N	60°12’07.7"N	60°12’30.17"N
Longitude	24°57’21.4"E	24°58’13.2"E	24°57’33.0"E	24°56’57.77"E
Tree species	*Tilia cordata*	*Tilia × europaea*	*Betula pendula*	*Malus spp.*
Drought strategies	Fairly Isohydric[1] ~~Drought tolerant~~	Isohydric[2] ~~Drought tolerant~~	Isohydric[3] ~~Drought tolerant~~	Isohydric[4] ~~Drought tolerant~~
DBH (cm)	26.3	19.5	23.6	30
Sapwood area (cm^2)	433.8	271.9	349.7	397.0
Height (m)	12.5	10	22	6.5
Age (years)	26	34	35	72 (approx.)
Soil type	Sand moraine	Fine sand moraine	Sand moraine	Sand clay

[1]Leuschner et al. (2019) [2]Liu et al. (2022); Kunert and Tomaskova (2020) [3]Zapater et al. (2013) [4]Lauri et al. (2011)

2.2 Sap flux measurements

Sap flux measurements were conducted using the Thermal Dissipation Probe (TDP; Granier, 1985). TDP sensors consist of ~~two thermocouple~~ needles (20-30 mm long) equipped with thermocouples, where the downstream ~~one~~ needle acts as a heating probe and the upstream needle~~other~~ as a reference probe. The thermocouples measure the temperature difference between the heated probe and the reference probe, which is used to calculate the sap flux density. Sap flux density can be scaled up to estimate the whole-tree water use. In our study, we selected three ~~sample~~ trees at each site (for a total of 12 trees) based on high sun exposure and dominant position~~ at the site~~. In each tree, a TDP sensor was inserted into the stem xylem at a height of 1.3 m.~~, where a~~ A vertical distance of 10 cm was kept between the heated and the reference probe. In the Street and Forest sites, the sensors were installed ~~higher,~~ at 2 m height to avoid damage or disturbance from pedestrians. The sensors were installed on the northern side of the stem. The installed sensors were insulated with reflective aluminum foil ~~after installation~~ to protect them and minimize the thermal gradient’s effect. ~~The upper probe was heated, and~~ The temperature difference (dT) was recorded every 1 min using a datalogger (Datataker DT80M). The sap flux density (J_s, g $\mathrm{cm}^{-2}\mathrm{h}^{-1}$) was calculated at 1 min interval based on Granier’s equation (eqn 1):

$$J_s = 42.84 * ((dT_{max} - dT)/dT)^{1.231}, \tag{1}$$

where dT_{max} is the maximum dT where zero J_s was observed. Zero flux condition was based on Lu et al. (2004), which was derived as the average local daily maximum dT of seven consecutive nights. Processing of raw sap flux data was conducted in R (RStudio Team, 2020). Further, daily tree water use was calculated by multiplying the daily sap flux density with the sapwood area. For *Tilia cordata*, *Tilia × europaea* and *Betula pendula*, the sapwood area was derived from the literature using species-specific allometric equations based on trunk diameter ~~relationship~~ (Gebauer et al., 2008; Hernandez-Santana et al., 2015) and for Orchard, we calculated the sapwood area by coring the stem of the apple trees. For further analysis, the sap flux density data were selected only for the growing season (June to September) for~~both~~ 2020 and 2021. Only sunny days data were considered to compare the sap flux density of the four sites~~, only sunny days data were considered~~. Sunny days were selected based on the following criteria: the daily total R_g was greater than 200 W m^{-2}, there was no precipitation, and the mean daytime vapor pressure deficit (VPD) was greater than 0.33 kPa (Riikonen et al., 2016). Sap flux data were averaged to half-hourly, daily, and monthly values for each measured tree~~site~~. In addition, we normalized the sap flux density using VPD by dividing the half-hourly J_s by the corresponding half-hourly VPD data. This was done to remove~~assess~~ the effect of VPD and also to examine the dependency of J_s on other environmental variables during these heatwave and drought periods.

2.3 Leaf gas exchange

Leaf gas exchange rates were~~was~~ measured using a portable gas exchange system (Walz GFS-3000, Heinz Walz, GmbH, Germany) with a standard measuring head (8 cm^2 cuvette, 2x4 cm). At each site, ~~leaf gas exchange was~~ measurements were done during the summers of 2020 and 2021 at approximately four-week intervals from the trees equipped with TDP sensors~~as the sap flux was measured~~. However, at the Park site, one different tree was selected for leaf gas exchange measurements to replace one of the sap flow-equipped trees as it was difficult to reach its canopy with a man lift. The measurements were recorded on the southern or southwestern side of the trees and conducted mainly during local morning time (8 AM-12 PM). ~~The measurements were performed on a healthy single leaf.~~ At the Park site, measurements were made at three canopy heights~~heights of the canopy~~ (top, middle, and bottom), whereas at the Street and Forest sites, only two heights (the top and bottom) were monitored. At the Orchard site, only one measurement was made in the middle of the canopy of each tree. The measurements were performed on one healthy leaf per tree and canopy height.

During each measurement, the CO_2 level was set to ~~ambient conditions, i.e.~~ 415 ppm. The temperature was left to~~not set to any value~~ and follow the ambient conditions. To screen out any potentially damaged leaves, a different leaf was selected from the same branch if ~~In case~~ the assimilation rate during the first 10 min of the measurement was very low (under 1.5 μmol m^{-2} s^{-1})~~, a different leaf from the branch was selected and the same measurement steps were repeated~~. The measurement steps involved setting photosynthetically active radiation (PAR) at 1200 μmol m^{-2} s^{-1} for 12 minutes and then increasing to a level of 1500 μmol m^{-2} s^{-1}. After reaching the maximum level, PAR was gradually decreased down to <1 μmol m^{-2} s^{-1} over ~~a period of~~ 43 minutes. Altogether, ~~once set,~~ 15 different PAR intensities were included. A simple light response curve was fitted to the net CO_2 exchange (*NE*(PAR), μmol m^{-2} s^{-1}), as follows:

$$NE(\mathrm{PAR}) = (A_{max} * \mathrm{PAR})/(\beta + \mathrm{PAR}) - R, \quad (2)$$

where R is the leaf~~plant~~ respiration i.e., NE measured at PAR = 0 (μmol m $^{-2}$ s^{-1}), A_{max} (μmol m^{-2} s^{-1}) is the maximum rate of photosynthesis and β (μmol m^{-2} s^{-1}) is the half-saturation constant describing the light intensity where photosynthesis rate is half of ~~the rate of~~ A_{max}.

From the above fitting, only A_{max} is considered in our analysis. Other variables of leaf gas exchange, namely stomatal conductance (g_s, mmol m^{-2} s^{-1}) and transpiration (E, mmol m^{-2} s^{-1}) were also recorded during the measurements. Maximum stomatal conductance and transpiration were calculated based on momentary g_s and E at PAR = 1100 μmol m^{-2} s^{-1}.

During the manual measurement campaigns in the summer of 2021, three leaf samples per site were also monthly collected in order to measure their relative water content (RWC). The samples were collected during the late afternoon (4 PM) and the fresh weight (FW) was measured. After that, the leaf samples were soaked overnight and turgid weight (TW) was measured. Later on, the samples were oven-dried at 60 °C for 24h, and the dry weight (DW) was measured. The RWC was calculated based on the equation below:

$$\mathrm{RWC}(\%) = ((\mathrm{FW} - \mathrm{DW})/(\mathrm{TW} - \mathrm{DW})) * 100, \quad (3)$$

2.4 Meteorological and soil data

At all four sites, meteorological variables, including air temperature (Air T, °C) and relative humidity (RH, %) were measured at a height of 1.5-1.8 m with a weather sensor (HMP110, Vaisala, Vantaa, Finland, at Park, Street and Forest sites; HC2A, Rotronic, Bassersdorf, Germany, at Orchard site). Soil sensors (Hydra-probe 2 SDI-12, Stevens, Oregon, USA, except ML3 ThetaProbe, Delta-T, Cambridge, UK, sensors in the Orchard) were installed at 10 and 30 cm depth to measure soil temperature (Soil T, °C) and soil moisture (SM m^3 m^{-3}). Data were recorded continuously at 1-minute intervals and then converted into half-hourly averaged data. Furthermore, the vapor pressure deficit (VPD, kPa) was calculated using Air T and RH based on saturated vapor pressure. Photosynthetically active radiation (PAR, W m^{-2}) and precipitation data were collected from the SMEAR III station FI-Kmp measurement tower and roof of a nearby building, respectively (Vesala et al., 2008; Järvi et al., 2009).

2.5 Detection of local heatwave and drought period

According to Fischer and Schär (2010), a heatwave is defined as a spell of at least six consecutive days with maximum temperatures exceeding the local 90th percentile of the control period. Accordingly, in our study, heatwave (Appendix A1) was defined against a control period spanning from 1991 to 2020. Further, our study period was categorized into four periods: heatwave (17 June 2021 to 18 July 2021), pre-heatwave (1 June 2021 to 16 June 2021), post-heatwave (19 July 2021 to 31 August 2021) and no heatwave (1 July 2020 to 31 July 2020) periods with mean daily maximum air temperatures of 26.4 °C, 21.5 °C, 20.4 °C and 19.6 °C respectively. The daily maximum air temperature during the heat period ranged from 20.5 to 30.2 °C, with a mean daily difference of 6 °C (ranging from 1.8 to 10.8 °C) above the average temperature in the control period.

To determine the drought period, a monthly Standardised Precipitation-Evapotranspiration Index (SPEI, (Vicente-Serrano et al., 2010) was calculated, indicating that June (SPEI = -1.4) and July 2021 (SPEI = -0.8) had moderate drought conditions. Here, we considered days with precipitation less than 1 mm and mean relative extractable soil water (REW) at the depth of 10 cm less than 0.45 as a dry period for all sites. As a result, the dry period was from 22 June 2021 to 27 July 2021 and wet period from 28 July 2021 to 31 August 2021. We calculated the REW from the soil moisture data, field capacity and wilting point of the site according to Granier et al. (1999), where the wilting point and field capacity of sandy loam (Park, Street and Forest) are 10 % and 22.9 %, respectively and those of clay (Orchard) are 25 % and 38.4 %, respectively based on Hagemann and Stacke (2015).

Taking into account the partial overlap between the heatwave and dry periods, we also identified three stress periods: only heat (17 June 2021 - 22 June 2021), both heat-dry (23 June 2021 - 18 July 2021) and only dry (19 July 2021 - 27 July 2021).

2.6 ~~Data and s~~Statistical analysis

To test the hypotheses, Kruskal Wallis test followed by Dunn's posthoc test was performed to examine differences in J_s and leaf gas exchange variables (A_{max}, g_s and E) between the different climatic periods (dry/wet/heatwave/post-heatwave/no heatwave). First, polynomial regression with 2^nd order degree was fitted between daytime mean J_s and daytime mean~~daily~~ VPD. Second, multiple linear regression analysis was performed to determine the effect of the meteorological variables on J_s. The tested variables were ~~between the J_s and different meteorological variables such as~~ VPD, PAR, soil moisture, and soil temperature at 30 cm. ~~to determine the effect of the meteorological variables and t~~The relative importance of each~~these~~ meteorological variable in controlling the daily J_s was assessed using ~~Student's t-test~~ the *t* statistic form the multiple linear regression summary ~~between the individual meteorological and daily J_s~~. Data processing (post-processing of sap flux, meteorological and gas exchange data) statistical analysis and visualization were conducted in Python (Python version 3).

3 Results

3.1 Weather conditions

The summer of 2021 (particularly July) was warm and dry, as compared to the summer of 2020, and the climatic reference period (1991–2020). The mean air temperature in July 2021 was 21.6°C, being 21% higher than that in July 2020 (16.7°C) and 19% higher than the average July temperature during the climatic reference period (18.1°C) (Figure 2a). At the four urban sites, high air temperature (20.2–21.6°C), high soil temperature (15.7–18.5°C), high VPD (0.9–1.1 kPa), and low soil moisture (0.1–0.4 m^3 m^{-3}) were observed during July 2021 (Figure 3 for the Park site, Appendices A2, **??** and A4 for the other sites). The total precipitation for June and July 2021 (86 mm) was 51% lower than for~~during~~ June and July 2020 (177 mm) and 27% lower than precipitation on average for the climatic reference period (117 mm) (Figure 2b).

The climatic conditions differred between~~varied across~~ the four sites during the summer of 2021. The mean of the meteorological variables (air temperature, VPD, soil temperature, and soil moisture) during the summer months (June, July, and August) 2021 were considered for comparison. Higher mean air temperature was observed at both Orchard (19.2 °C) and Street sites (19.3 °C) as compared to Forest (17.9 °C) and Park (17.8 °C) sites (Table 2). Similar mean VPD was found at the Orchard (0.78 kPa), Park (0.75 kPa), and Forest sites (0.75 kPa), but VPD was 11% higher ~~mean VPD~~ at the Street site (0.84 kPa). Also, the mean soil temperature at the Street site (19.9°C) was 24–34% higher than at the Park (16.1°C), Orchard (15.2°C) and Forest sites (14.8°C). The soil water availablity varied from 12.9% to 25% (Appendix A1). Mean soil moisture ~~content~~ differed between sites, the Orchard site having the highest values (0.37 m^3 m^{-3}), and the Forest site the lowest (0.09 m^3 m^{-3}) while

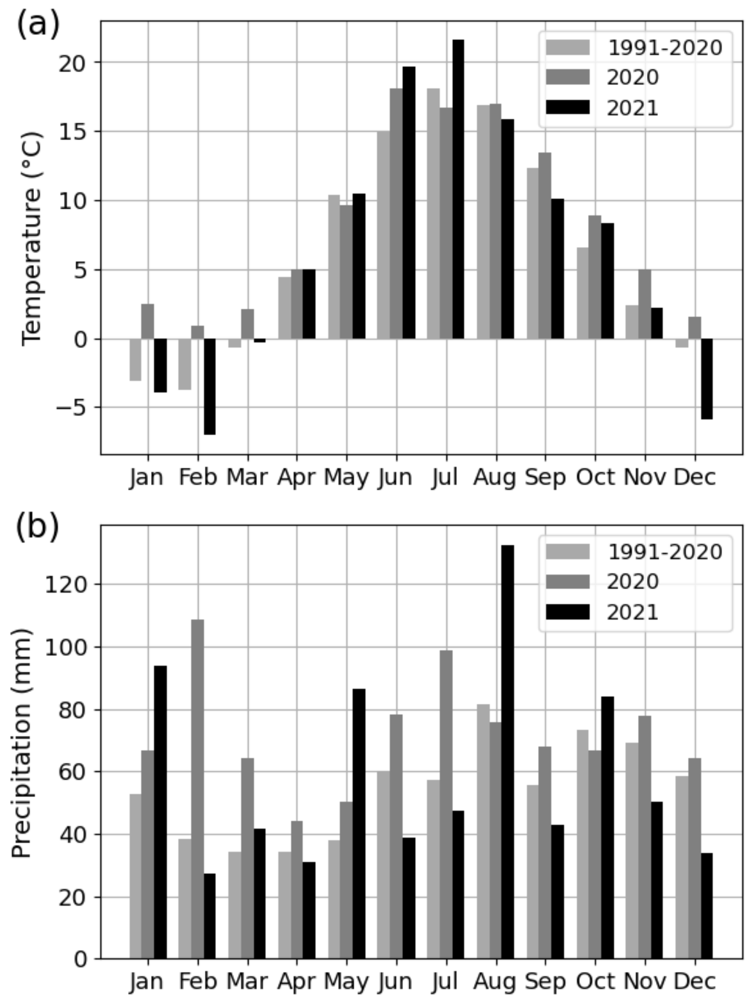

Figure 2. (a) Monthly mean air temperature and (b) monthly total precipitation for the years 2020 and 2021, and the climatic reference period of 30 years (1991-2020).

the Park and Street sites had intermediate values at 0.13 and 0.22 $m^3\ m^{-3}$, respectively. Soil moisture increased after rainfall events at all the sites except the Forest site, where soil moisture remained low throughout the late summer after the hot and dry July 2021 (Appendix **??**). The climatic conditions differred betweenvaried across the four sites during the summer of 2021. The mean of the meteorological variables (air temperature, VPD, soil temperature, and soil moisture) during the summer months (June, July, and August) 2021 were considered for comparison. Higher mean air temperature was observed at both Orchard (19.2 °C) and Street sites (19.3 °C) as compared to Forest (17.9 °C) and Park (17.8 °C) sites (Table 2). Similar mean VPD was found at the Orchard (0.78 kPa), Park (0.75 kPa), and Forest sites (0.75 kPa), but VPD was 11% higher mean VPD at the Street site (0.84 kPa). Also, the mean soil temperature at the Street site (19.9°C) was 24–34% higher than at the Park (16.1°C),

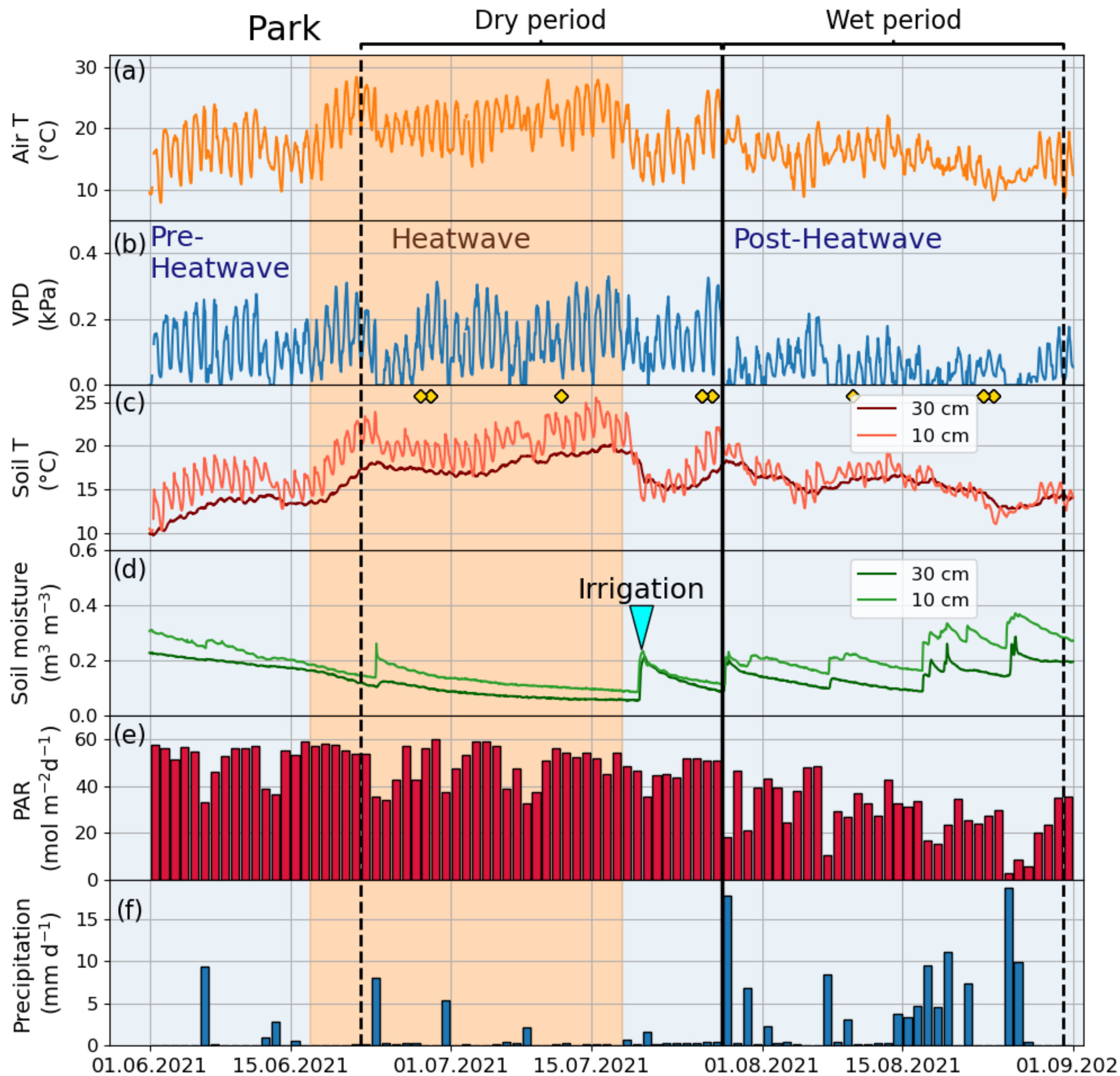

Figure 3. Meteorological and soil data from 2021 showing hourly a) air temperature (Air T), b) water vapor deficit (VPD), c) soil temperature (Soil T) and d) soil moisture measured at the Park site, and e) daily mean Photosynthetically active radiation (PAR) and daily sum precipitation data measured at the SMEARIII station. The orange shading indicates the heatwave period during the summer of 2021 and the black vertical line indicates the onset of the wet period. The yellow markers in panel (c) denote the manual leaf gas measurement dates.

Orchard (15.2°C) and Forest sites (14.8°C). The soil water availablity varied from 12.9% to 25% (Appendix A1). Mean soil moisture content differed between sites,varied largely as the Orchard site having the highest values (0.37 m^3 m^{-3}), and the Forest site the lowest (0.09 m^3 m^{-3}) while thewheareas Park and Street sites had intermediate values at 0.13 and 0.22 m^3 m^{-3}, respectively. Soil moisture increased~~conditions were recovered~~ after ~~the~~ rainfall events at all the sites except the Forest site, where soil moisture remained low throughout the late summer after the hot and dry July 2021 (Appendix A3).

Table 2. Monthly mean air temperature (Air T, °C), mean vapor pressure deficit (VPD, kPa), mean soil temperature (Soil T, °C) and mean soil moisture content (m^3 m^{-3}) for the four study sites in 2021.

		Air T	**VPD**	**Soil T**	**Soil moisture**
Park	**June**	18.4	0.84	14.4	0.16
	July	20.2	0.96	17.5	0.09
	August	14.8	0.45	14.7	0.15
	September	8.7	0.40	11.0	0.19
Street	**June**	19.8	0.93	18.5	0.23
	July	21.6	1.07	22.8	0.25
	August	16.1	0.51	18.5	0.25
	September	10.0	0.40	12.7	0.29
Forest	**June**	18.0	0.77	13.1	0.16
	July	20.7	1.01	16.9	0.07
	August	15.2	0.48	14.5	0.06
	September	8.7	0.34	11.2	0.06
Orchard	**June**	21.1	0.81	15.5	0.44
	July	21.1	1.05	15.7	0.28
	August	15.7	0.49	14.6	0.40
	September	9.4	0.35	12.9	0.49

3.2 Variability in sap flow rate in 2021

On~~Based on~~ sunny days, the mean daily water use~~sap flow rate~~ of the trees in the Park, Street, Forest and Orchard were 0.32 ± 0.01 kg cm^{-2} day^{-1}, 0.42 ± 0.01 kg cm^{-2} day^{-1}, 0.20 ± 0.01 kg cm^{-2} day^{-1} and 0.46 ± 0.01 kg cm^{-2} day^{-1}, respectively (Figure 4a), differing significantly from each other ($P<0.05$)~~$P<0.05$~~. The mean daytime sap flux density (J_s) for the summer period (June-August) was the highest at the Orchard site with 20.6 ± 0.3 g cm^{-2} h^{-1}, the lowest with 8.1 ± 0.1 g cm^{-2} h^{-1} at the Forest site, and 14.4 ± 0.2 g cm^{-2} h^{-1} and 17.7 ± 0.3 g cm^{-2} h^{-1} at the Park and Street sites, respectively. The monthly mean J_s differed significantly especially between July and September at the four sites ($P<0.05$) (Figure 4b).~~The monthly mean J_s differed significantly at the four sites ($P<0.05$) (Figure 4b).~~

3.3 The effect of heatwave on sap flux density

During the heatwave period, the mean sap flow rates of the trees at the Park, Street, Forest and Orchard sites were 0.38 ± 0.02 kg cm^{-2} day^{-1}, 0.42 ± 0.02 kg cm^{-2} day^{-1}, 0.24 ± 0.01 kg cm^{-2} day^{-1} and 0.52 ± 0.02 kg cm^{-2} day^{-1}, respectively. At

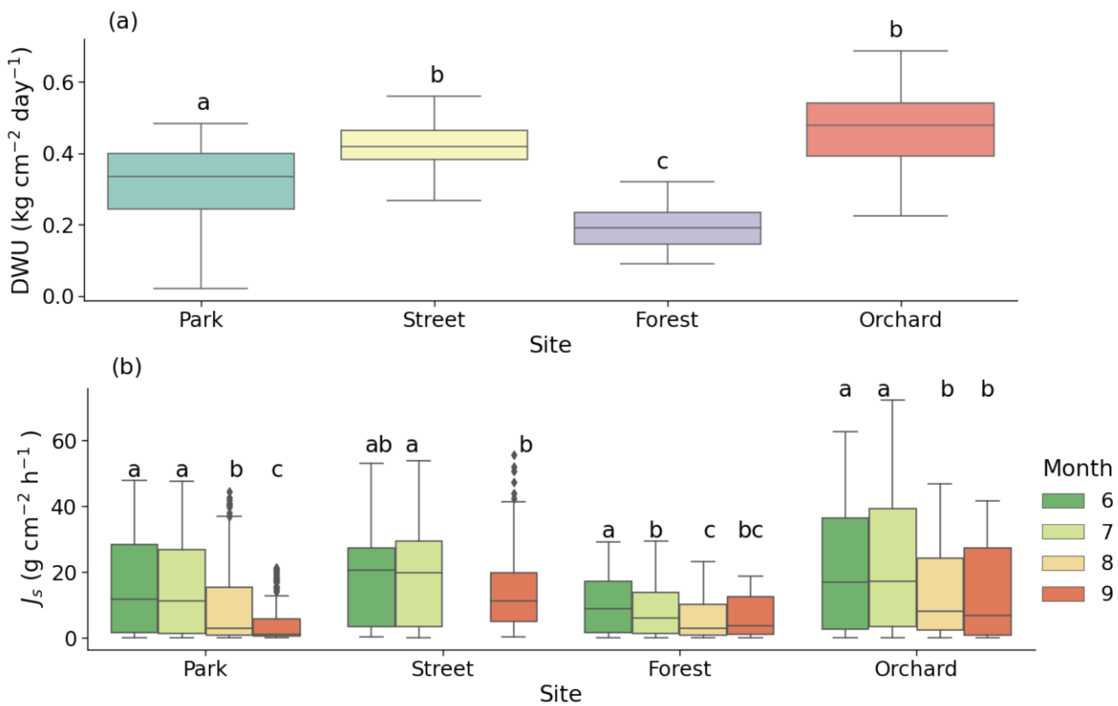

Figure 4. (a) Daily water use (DWU) of the trees and (b) monthly mean sap flux density (J_s) at the four urban vegetation sites: Park (*Tilia cordata*), Street (*Tilia* × *europaea*), Forest (*Betula pendula*) and Orchard (*Malus spp.*). The letters indicate the significant differences between the (a) sites and (b) monthly mean J_s at each site (P<0.05). Note: data was non-available for August at the Street site due to technical problems.

the Park site, the mean J_s during the heatwave period was 59% higher than during the no heatwave period and 39% higher than during the post-heatwave period but there was no significant difference with the pre-heatwave period. At the Street site, there was no significant difference in the mean J_s between the heatwave, no heatwave, pre-heatwave and post-heatwave periods. At the Forest site, the mean J_s during the heatwave period was 13% higher than during the pre-heatwave and 67% higher than during the post-heatwave periods. At the Orchard site, the mean J_s during the heatwave period was 35% higher than during the post-heatwave period but there was no significant difference with the pre-heatwave period (Figure 5a, P<0.05). At the Forest and Orchard sites, no data were recorded during the ~~from~~ no heatwave period ~~were not available~~.

When normalized with VPD, there were no significant differences in J_s between the heatwave, no heatwave, pre-heatwave and post-heatwave periods in the Park, Forest or Orchard (Figure 5b). At the Street site, normalized J_s during the heatwave period was 33% lower than during the no heatwave period and 7% lower than during the pre-heatwave period, but no difference were observed with the ~~but it did not differ from that of~~ post-heatwave period.

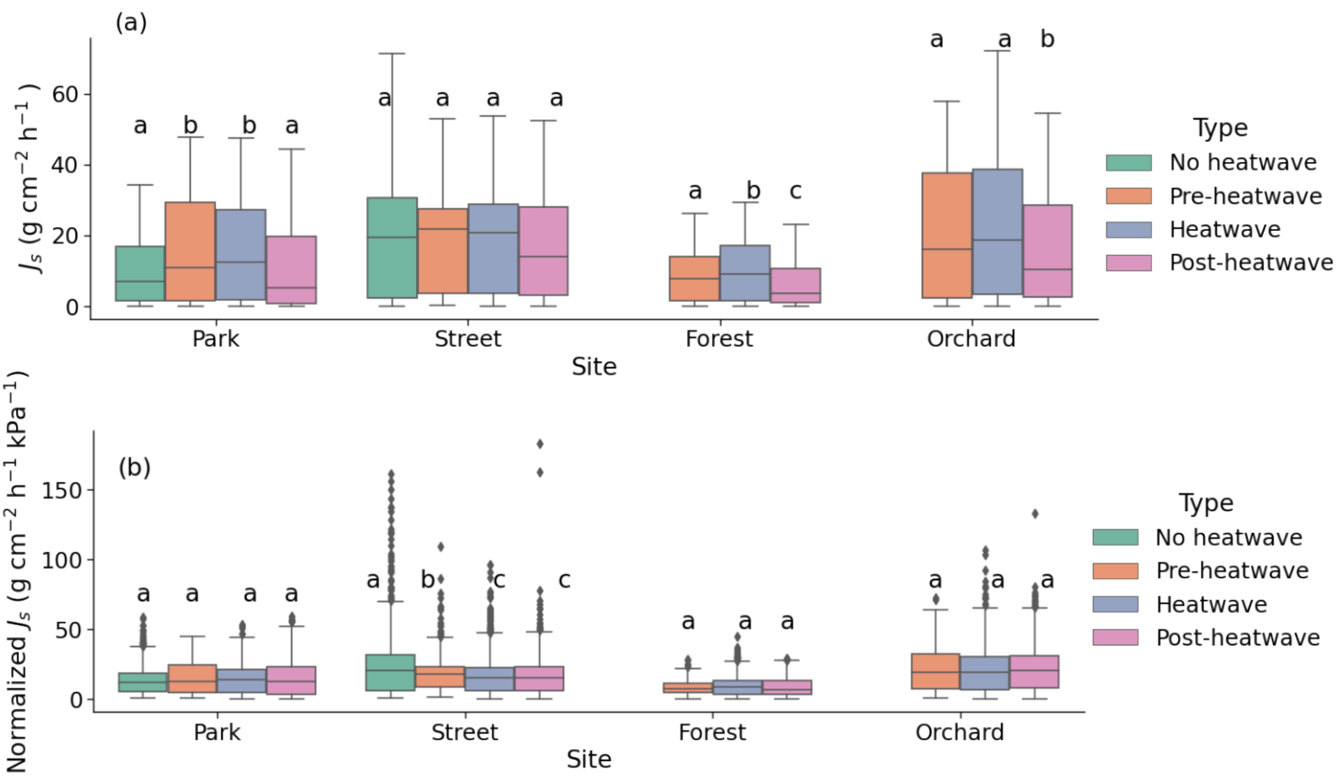

Figure 5. Sap flux densities at the four urban vegetation sites during different periods regarding a heatwave: a) mean J_s of the whole day and (b) mean normalized J_s by VPD on sunny days. The letters indicate the significant differences between the different periods within each site (P<0.05).

3.4 The effect of drought on sap flux density

During the dry period, the mean sap flow rates at the Park, Street, Forest and Orchard sites were ~~was~~ 0.36 ± 0.02 kg cm^{-2} day^{-1}, 0.42 ± 0.01 kg cm^{-2} day^{-1}, 0.20 ± 0.01 kg cm^{-2} day^{-1} and 0.50 ± 0.02 kg cm^{-2} day^{-1}, respectively. ~~The m~~ Mean J_s was significantly higher during the dry period than during the wet period at all sites (Figure 6a, P<0.05). At the Park, Street, Forest and Orchard sites, mean J_s were~~was~~ 66%, 31%, 43% and 53% higher ~~, respectively, higher~~ during dry period than wet period, respectively.

~~The~~ Normalized J_s was significantly lower during dry than wet period at all sites, with a reduction of ~~with~~ 16%, ~~lower at the Park site,~~ 48% ~~lower at the Street site~~, 28% ~~lower at the Forest site~~ and 26% in normalized J_s during the dry period at the Park, Street, Forest and Orchard sites, respectively~~lower at the Orchard site~~ (Figure 6b).

Considering the partial overlap of the heatwave and dry period, we identified ~~separated the period into~~ three stress periods: only heat (17 June 2021 - 22 June 2021), both heat-dry (23 June 2021 - 18 July 2021) and only dry (19 July 2021 - 27 July 2021) ~~by intersection of the heatwave and dry days which were defined earlier (as describe in section 2.5)~~ and analysed the

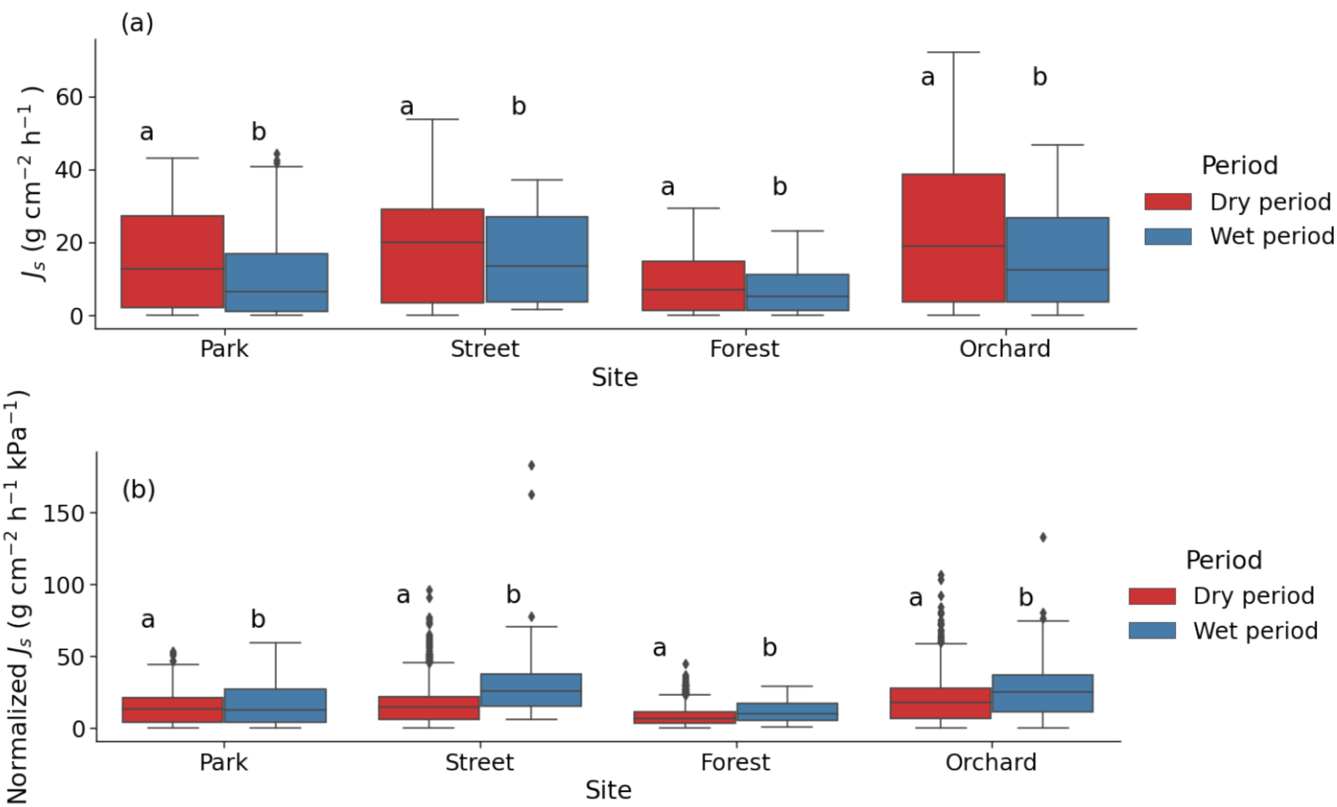

Figure 6. Sap flux density (J_s) during dry and wet periods at the four study sites. Based on sunny days, (a) data represented mean J_s of the whole day and (b) normalized J_s by VPD. The letters indicate significant differences in J_s between the dry and wet periods at each site (P<0.05)

effect of only heat, only dry and both heat-dry on sap flux density. This analysis revealed found out that the effect of heat was relatively strongerhigher than the effect of dry and drought or both heat and drought at the Park, Forest and Orchard sites, while at the Street site, the effect of heat, dry and drought and both wereare similar (Appendix A6).

3.5 Leaf gas exchange during the heatwave and drought periods

We compared leaf gas exchange variables, namely A_{max}, g_s and E, between the different heatwave periods and between dry and wet periods (Table 3). No significant differences in these three variables were found at the Park, Forest and Orchard sites between the different heatwave periods; however, at the Street site, A_{max} and E were significantly (P<0.05) higher during heatwave than post-heatwave periods but there was no significant difference as compared to the no heatwave period. Also, g_s showed no difference between the different heatwave periods at the Street site.

Comparing leaf gas exchange variables between dry and wet periods, we found that at the Street site, A_{max} was significantly higher (P<0.05) during dry period than wet period but no significant differences in g_s and E between dry and wet periods were

Table 3. Averages of leaf gas exchange variables: Maximum assimilation (A_{max}, μmol m^{-2} s^{-1}), Stomatal Conductance (g_s, mmol m^{-2} s^{-1}), and Transpiration (E, mmol m^{-2} s^{-1}) during heatwave, no heatwave, pre-heatwave and post-heatwave periods and during dry and wet periods at the four sites. The letters indicate ~~the~~ significant differences between the various heatwave periods or drought periods. No data available at the Street site during pre-heatwave and at the Orchard site during no heatwave period.

Site	**Type / Period**	A_{max}	g_s	**E**
Park	heatwave	13.6 ± 1.3	112.1 ± 14.1	1.5 ± 0.1
	pre-heatwave	13.6 ± 1.3	123.5 ± 0	1.9 ± 0
	post-heatwave	15.3 ± 1.1	141.3 ± 11	1.1 ± 0.1
	no heatwave	17.2 ± 1.4	147.8 ± 15.5	1.5 ± 0.1
	dry	15.0 ± 0.8	114.5 ± 7.7^{a}	1.5 ± 0.1
	wet	14.3 ± 2.0	163.3 ± 17.5^{b}	1.7 ± 0.2
Street	heatwave	10.9 ± 1.0^{a}	91.4 ± 7.3	1.2 ± 0.1^{a}
	pre-heatwave	-	-	-
	post-heatwave	6.6 ± 0.8^{b}	64.2 ± 12.0	0.8 ± 0.1^{b}
	no heatwave	8.7 ± 1.2^{a}	73.0 ± 11.1	0.8 ± 0.1^{a}
	dry	10.9 ± 1.0^{a}	91.4 ± 7.3	1.2 ± 0.1
	wet	6.6 ± 0.8^{b}	64.2 ± 12.0	0.8 ± 0.1
Forest	heatwave	16.4 ± 1.0	105.7 ± 17.8	1.3 ± 0.2
	pre-heatwave	16.3 ± 0	128.4 ± 0	1.5 ± 0
	post-heatwave	10.7 ± 2.9	104.2 ± 31.2	1.1 ± 0.3
	no heatwave	17.4 ± 2.3	133.5 ± 12.1	1.4 ± 0.1
	dry	16.4 ± 1.0	105.7 ± 17.8	1.3 ± 0.2
	wet	10.7 ± 2.9	104.2 ± 31.2	1.1 ± 0.3
Orchard	heatwave	14.1 ± 0.7	126.8 ± 5.4	0.7 ± 0.2
	pre-heatwave	13.3 ± 0	125.3 ± 0	2.0 ± 0
	post-heatwave	13.6 ± 1.0	157.3 ± 12.9	1.8 ± 0.1
	no heatwave	-	-	-
	dry	13.1 ± 1.4	135.4 ± 13.6	1.6 ± 0.1
	wet	14.0 ± 0.9	170.9 ± 20.4	1.9 ± 0.2

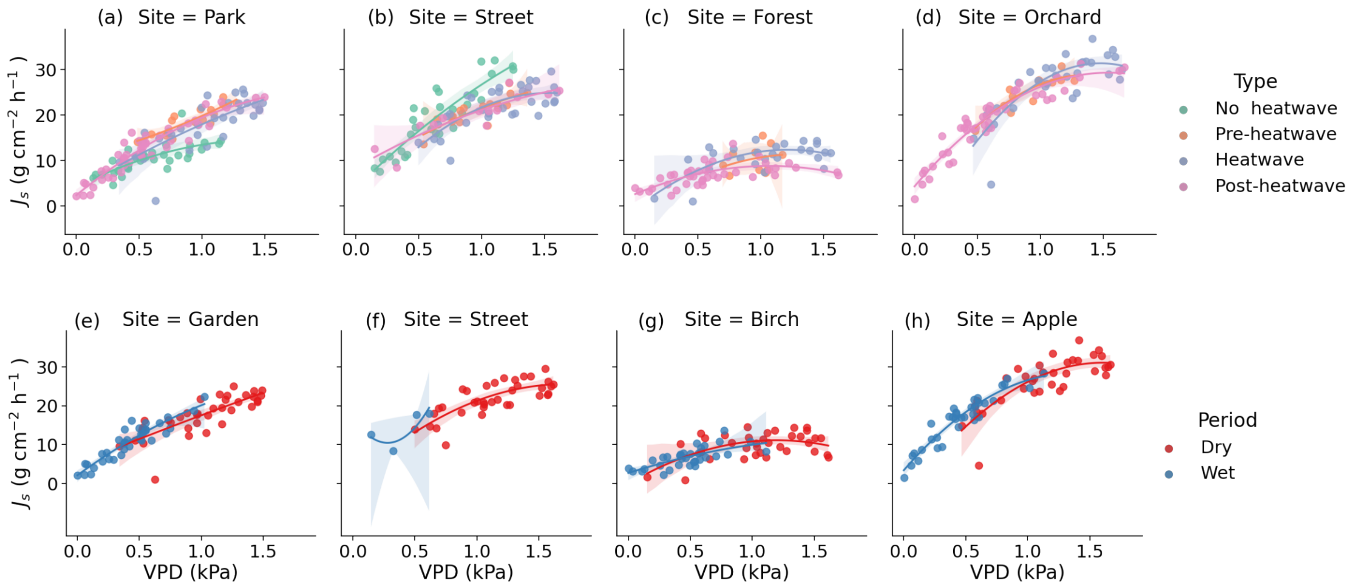

Figure 7. Observed (dots) and modeled (lines) relationship between the daytime mean daily VPD and J_s during the different heatwave periods as well as~~and both~~ dry and wet periods. Panels (a),(b),(c), and (d) show the relationship between VPD and J_s at the Park, Street, Forest and Orchard site, respectively, during the different~~various~~ heatwave periods. Panels (e),(f),(g),and (h) show the relationship between VPD and J_s at the Park, Street, Forest and Orchard site, respectively, during the dry and wet periods. The model is 2nd order polynomial fit (see Table 4).

found. Also, at the Park site, g_s was found to be significantly lower (P<0.05) during dry period than wet period. At the Forest and Orchard sites, no significant differences were found in A_{max}, g_s and E between dry and wet periods.

The monthly relative leaf water content (RWC) as a proxy of leaf water potential ~~showed that RWC~~ was found to be lower (4-35 %) during July as compared to June and August at the Forest and Orchard sites. However, RWC was found to be higher (5-8 %) during July than the other summer months at Park and Street sites (Appendix A5).

3.6 Environmental control on sap flux density

We tested the relationship between the daily daytime mean VPD and J_s using 2^{nd} order polynomial regression (Figure 7, Table 4). VPD explained the variation in J_s less during the heatwave than during post-heatwave and pre-heatwave except for Forest where the VPD was not a significant driver at all during pre-heatwave. During wet period, VPD explained a higher share of the variation of J_s at Park, Forest and Orchard sites. At~~while at~~ Street site, the ~~there was low~~ data availability was low and thus, the relationship could not~~cannot~~ be tested during wet period ~~except for Street where the wet data coverage is very low~~ (Fig. 7).

Multiple linear regression between J_s and a ~~higher~~ number of environmental variables (VPD, PAR, Soil T and SM) showed that PAR and VPD were the significant drivers for J_s at the Park, Street and Orchard sites but PAR was the only significant driver at the Forest site (Table 5). In addition, soil moisture was a significant variable in certain circumstances at certain sites, such as, in Park during heatwave and dry periods and in Forest during post-heatwave, dry and wet periods i.e. in the latter part of the growing season in general.

Table 4. Relationship between vapor pressure deficit and daily mean sap flux density using 2^{nd} order polynomial fit (see Fig. 7). The values indicate~~are showing~~ the squared coefficient of correlation (adj R^2) between the two variables. Relationships statistically significant at 0.05, 0.01 and 0.001 levels are marked with *, ** and *** respectively and non-significant as ns.

	no heatwave	**pre-heatwave**	**heatwave**	**post-heatwave**	**dry**	**wet**
Park	0.53^{***}	0.73^{***}	0.57^{***}	0.90^{***}	0.60^{***}	0.85^{***}
Street	0.80^{***}	0.62^{***}	0.55^{***}	0.75^{***}	0.58^{***}	0.22^{ns}
Forest	-	0.16^{ns}	0.43^{***}	0.44^{***}	0.25^{**}	0.48^{***}
Orchard	-	0.77^{***}	0.69^{***}	0.91^{***}	0.67^{***}	0.90^{***}

4 Discussion

In this study, we assessed the response of urban tree water use and leaf gas exchange during hot and dry summer 2021, across four urban green areas in Helsinki. Results indicated increased sap flux density in trees during the hot and dry periods, whereas carbon assimilation, stomatal conductance, and leaf-level transpiration remained largely unaffected. Sap flux density increase in such periods varied among the studied urban sites with distinct tree species and growth conditions. VPD emerged as the primary factor influencing tree water use in the heatwave and dry conditions. In summary, the urban trees in our study exhibited typical functioning during the summer of 2021, suggesting that the hot and dry conditions did not induce significant physiological changes or adjustments. However, we found some interesting insights that we will discuss further in this chapter. ~~In this study, we assessed the response of urban tree water use and leaf gas exchange to heat and drought during two contrasting summers 2020 and 2021, the latter being hot and dry, across four urban green areas in Helsinki. The results showed that tree water use, measured with sap flux density increased during the heatwave and the dry period but carbon assimilation, stomatal conductance and transpiration at leaf level did not generally change during these various periods. The increase in sap flux density during hot and dry periods varied across the urban sites that had different tree species and growing conditions. VPD was the main driver of tree water use during the heatwave and dry. Overall, it seems that the hot and dry conditions were not severe enough to trigger notable physiological adaptation as the urban trees in our study continued to function typically during the summer of 2021. Even though the air temperature was notably higher and precipitation notably lower than during previous summers, we did not get full support for the hypotheses H1 and H2 and conclude that the severe weather events did not alter the stomatal action and therefore the observed photosynthetic potential. However, we found some interesting insights that we will discuss further in this chapter.~~

Table 5. Multiple linear regression between daily mean sap flux density and various environmental drivers (VPD, PAR, Soil temperature and Soil moisture) as independent variables. t stat value indicates the relative importance of the variables in controlling the daily sap flux variations. Relationships statistically significant at 0.05, 0.01 and 0.001 levels are marked with *, ** and *** respectively and non-significant as ns.

Site		All data	no heatwave	pre-heatwave	heatwave	post-heatwave	dry period	wet period
Park	R^2	0.63	0.59	0.75	0.74	0.93	0.74	0.92
	Intercept	5 (1.4)^{ns}	-1.6 (-0.2)^{ns}	-16.6 (-0.9)^{ns}	-25.15 (-1.6)^{ns}	4.1 (1.1)^{ns}	-13.9(-1.1)^{ns}	3.0 (0.7)^{ns}
	VPD	9 (7.6)***	6.2 (3.1)***	9.1 (3.5)***	10.4 (5.1)***	9.3 (8.0)***	9.5 (5.2)***	11.0 (5.7)^{ns}
	PAR	0.01 (3.5)***	0.01 (1.14)^{ns}	0.01 (1.4)^{ns}	0.03 (3.1)***	0.02 (5.4)***	0.02 (3.6)***	0.01 (4.1)**
	Soil T	-0.1 (-0.3)^{ns}	0.5 (1.1)^{ns}	1 (1.4)^{ns}	0.8 (1.32)^{ns}	-0.1 (-0.6)^{ns}	0.4 (0.7)^{ns}	0.03 (0.1)^{ns}
	SM	-9.4 (-1.0)^{ns}	-10.5 (-0.4)^{ns}	45.6 (1.0)^{ns}	79.6 (2.3)***	-8.0 (-1.0)^{ns}	48.1 (2.1)***	-15.9 (-2.2)^{ns}
Street	R^2	0.73	0.84	0.65	0.71	0.75	0.71	-
	Intercept	5.9 (2.27)*	6.2 (0.3)^{ns}	7.0 (1.0)^{ns}	10.6 (1.1)^{ns}	40.7 (1.3)^{ns}	22.5 (2.0)^{ns}	-
	VPD	9.3 (7.8)**	17.5 (6.4)***	7.6 (2.5)*	4.6 (2.6)*	6.1 (1.4)^{ns}	5.9 (3.4)***	-
	PAR	0.03 (7.1)**	0.02 (2.5)*	0.02 (1.7)^{ns}	0.03 (4.4)***	0.01 (1.0)^{ns}	0.03 (4.0)***	-
	Soil T	-0.3 (-3.3)**	-0.5 (-0.9)^{ns}	0.07 (0.2)^{ns}	-0.1 (-0.5)^{ns}	-1.1 (-1.2)^{ns}	-0.7 (-1.6)^{ns}	-
	SM	12.6 (2.4)*	12.0 (0.2)^{ns}	-9.7 (-0.7)^{ns}	-13.9 (-1.0)^{ns}	-34.5(-0.5)^{ns}	-8.3 (-0.8)^{ns}	-
Forest	R^2	0.56	-	0.93	0.67	0.68	0.63	0.72
	Intercept	2.4 (1.4)^{ns}	-	91.0 (2.4)^{ns}	-2.3 (-0.1)^{ns}	-16.2(-1.8)^{ns}	-17.7(-2.1)*	-17.3(-1.5)^{ns}
	VPD	2.1 (2.0)^{ns}	-	2.9 (1.5)^{ns}	3.5 (1.7)^{ns}	-0.3 (-0.3)^{ns}	2.9(1.9)^{ns}	0.1(0.03)^{ns}
	PAR	0.02 (5.1)***	-	0.01 (1.3)^{ns}	0.02 (3.4)***	0.02(4.99)***	0.02(3.6)***	0.02(3.5)***
	Soil T	-0.1 (-1.1)^{ns}	-	-1.0 (-0.9)^{ns}	-0.6 (-0.8)^{ns}	-0.8 (-4.4)***	0.01(0.03)^{ns}	-0.8(-3.4)**
	SM	-1.4 (-0.2)^{ns}	-	-345.0 (-3.1)*	137.7 (1.1)^{ns}	515.0(3.6)***	222.1(5.0)***	515.2(2.8)**
Orchard	R^2	0.89	-	0.86	0.77	0.93	0.74	0.92
	Intercept	9.8 (1.7)^{ns}	-	-88.2 (-2.3)^{ns}	57.9 (0.8)^{ns}	27.0 (2.2)*	-31.2(-1.4)^{ns}	3.1 (0.8)^{ns}
	VPD	9.2 (8.0)***	-	5.9 (1.9)^{ns}	5.4 (2.1)^{ns}	7.8 (5.4)***	7.1 (3.4)**	11 (5.8)***
	PAR	0.04 (8.2)***	-	0.03 (2.9)*	0.05 (4.5)***	0.04 (7.6)***	0.05 (4.9)***	0.02 (4.07)***
	Soil T	-0.5 (-1.5)^{ns}	-	0.6 (0.5)^{ns}	-2.8 (-0.7)^{ns}	-1.6 (-2.1)*	2.1 (1.6)^{ns}	0.03 (0.1)^{ns}
	SM	1.5 (0.4)^{ns}	-	160.3 (3.2)*	-32.3 (-1.5)^{ns}	-2.9 (-0.8)^{ns}	-1.6 (-0.2)^{ns}	-15.9(-2.2)***

Values indicate coefficient $(t)^{sig}$

4.1 Site variability

Our study observed that the four urban vegetation sites in Helsinki exhibit variable climatic conditions where air temperature under the canopy, soil temperature, and soil moisture content were different. The highest air and soil temperatures were measured at the Street site, where impervious surfaces increase the temperatures due to heat storage. The high air temperature at the Orchard site is due to exposure of the site to direct sunlight throughout the day, heating the garden. Also, the high soil moisture at the Orchard site is mainly due to the difference in soil type, where the sand clay in the Orchard has higher water holding capacity than the sand moraine soil type at the other three sites. At the Street site, VPD was higher than at the other three sites because of the higher air temperature likely due to the larger cover of impervious surface at the Street site where the air temperature is marginally increased. Similar variability of meteorological conditions between different urban forests was found in Los Angeles metropolitan city, where the urban forests located near the city were warmer with higher VPD and lower photosynthetically active radiation as compared to the urban forests situated closer to the coast (Pataki et al., 2011). Among 10 different tree species in the city of Basel (Switzerland), the tree crown temperature was lower in the park than in the street although the study reported ; reporting that it is species-specific differences infor the cooling effect of urban trees (Leuzinger et al., 2010). Indeed, the difference in microclimatic conditions has been observed to vary depending on the type of vegetation, the composition of the species, the amount of green cover and the impervious surface in urban vegetation (Perini and Magliocco, 2014; Kjelgren and Clark, 1992). Also, many other studies have shown high variability in transpiration across different urban green areas (Pataki et al., 2011; McCarthy and Pataki, 2010; Sushko et al., 2021). For example, in the high-latitude city of Gothenburg (Sweden), *T. europaea* had two times higher daytime transpiration rates in a park compared to a street site (Konarska et al., 2016). Although the asymmetric measurement setup in our study limits us from comparingto compare the sites statistically we observed that Street sites had the highest sap flow rate during the summer of 2021 and the lowest at the Forest site, and we speculate that the differences might be related to growing conditions such as high soil moisture content and tree species. The sap flow rate of *Tilia cordata* at the Park was lower than that of *Malus spp* at the Orchard and *Tilia* × *europaea* at the Street but higher than that of *Betula pendula* at the Forest site. The low sap flow rate of *Betula pendula* at the Forest site could be explained byreduced due to the rather strong stomatal control typical for *Betula pendula*, i.e. it closes the stomata easily during dry conditions (Zapater et al., 2013), whereas *Tilia cordata* found at the Park site has less sensitive stomatal control (Leuschner et al., 2019), i.e. it keeps stomata open even in mild drought as it can tolerate drought better than *Betula Pendula*. Other studies in the streets of Munich and Helsinki have reported variability of transpiration rates, mainly due to the differences in tree species. In Munich, the water use transpiration of *Tilia cordata* Mill. waswere three times higher than water use of *Robinia pseudoacacia* L. tree in the (Rahman et al., 2019) and in the street trees of Helsinki, *Alnus glutinosa* have four times higher tree water use than *Tilia* × *vulgaris* (Riikonen et al., 2016).

4.2 Transpiration rate and leaf gas exchange during drought and heatwave

We observed varying responses of sap flux density during heatwave and drought periods at the studied sites. At the Park, Forest, and Orchard sites, J_s increased by 35-67% during the heatwave compared to periods of no heatwave and post-heatwave, whereas the heatwave did not affect J_s in the Street site. The pre-heatwave period did not differ from the heatwave period in terms of J_s in the Park and Orchard sites, but there was a slight increase (13%) at the Forest site during the heatwave period. ~~During the dry period,~~ J_s was significantly higher during the dry period than wet period at all sites. The leaf gas exchanges such as A_{max}, g_s, and E did not change during the heatwave and dry period, thus, indicating no changes in the photosynthetic potential during these periods. Hence, we conclude that the weather was not yet severe enough to give support to our study ~~the~~ hypotheses H1 and H2. ~~in our study.~~

VPD is the driving force for transpiration, so an increase in VPD leads to an increase in J_s ~~in transpiration~~ unless stomata in the leaves close to limit transpiration. The ~~ratio between J_s and~~ VPD was a significantdriver for J_s~~ly reduced~~ during all periods and at all sites, which indicates the substantial role of VPD; however, the relative importance of VPD over daily sap flow variation differed at the four sites and during different periods of heatwave and drought. The response of sap flow to changes in~~with~~ VPD was less sensitive during heatwave and drought periods than during the other ~~heatwave periods and wet~~ periods (Table 4). In theory, these results could indicate that the trees limited their water transport via stomatal control in harsh conditions. However, that was not captured by the leaf-level measurements, which on the other hand, may not represent the conditions over the different periods as well as these automatic measurements. Moreover, the leaf-level values~~measurements~~ were based on single-day measurements, which might not fully represent~~cover~~ our study's heatwave or drought periods. ~~in our study~~ Together, these results indicate that the observed increase in transpiration at the studied sites was caused by an increase in the driving force for transpiration, VPD.

Stomatal control limits plant transpiration during drought. For example, Rötzer et al. (2021) found a substantial reduction of 63% in the transpiration rate in urban *Tilia cordata* and *Robinia pseudoacacia* trees in the city of Würzburg, Germany during the European drought in 2018. During the dry period of this study, soil moisture content was notably reduced, ranging from 18% to 62% less compared to the wet period across all four locations. Similarly, during the heatwave period, the soil moisture content dropped significantly, ranging from 30% to 58% lower than the pre-heatwave period at all sites, except for the Street site. The availability of soil moisture at the Street site allowed an increase in A_{max} and E during the heatwave period. However, the observed reductions in soil moisture did not seem to be enough to cause strong stomatal regulation of transpiration (i.e., no change in g_s except for the Park site). At the Park site, the relative decrease in g_s ~~during the dry period~~ might be due to the influence of soil moisture reduction during the dry period and also due to the isohydric behavior typical for *Tilia cordata* growing in the Park. ~~Interestingly, it was previously reported that The non-stomatal limitation was earlier reported for reductions of photosynthesis in the temperate forest during European drought 2018 (Gourlez de la Motte et al., 2020) and these non-stomatal effects might play some role in our urban site, but this needsyet to be studied further. It may be also due to tree species' behaviors (isohydryl or anisohydryl) towards the drought response.~~ Also, previous studies ~~have also~~ reported that transpiration during the local extreme high temperature was maintained when there was sufficient water availability in the soil in different urban green sites in Los Angeles Metropolitan, the US (Pataki et al., 2011). Similarly, previous studies have shown that VPD is a significant driver for sap flow in *Tilia × vulgaris* street trees in Helsinki (Riikonen et al., 2016), and VPD and solar radiation for daytime transpiration rates in seven different tree species, including *Betula pendula*, studied in Gothenburg, Sweden (Konarska et al., 2016). Similarly to our results regarding the Park site, Konarska et al. (2016) also found that the maximum stomatal conductance was reduced by 50% in the studied species in Gothenburg even though transpiration rate remained high during dry conditions compared to wet conditions.

During the heatwave and the dry period, VPD explained most of the variation in the daily mean J_s at the Park (57-60%), Street (55-58%) and Orchard sites (62-69%). Similarly, previous studies in high latitude cities have reported that VPD correlates well with J_s in street trees (adj. R^2 = 0.74) in Helsinki, Finland (Riikonen et al., 2016), and in urban trees (R^2=0.44-0.75) in Gothenburg, Sweden (Konarska et al., 2016). Also, in Boston, Massachusetts, VPD has been shown to correlate with J_s (R^2 = 0.63, (Winbourne et al., 2020)). However, VPD did not explain daily variation in J_s at the forest site of our study. Also, J_s saturated after reaching certain VPD levels, especially at Forest and Orchard sites, and the saturation took place already in relatively~~rather~~ low VPD levels in the case of the Forest site. ~~compared to the Orchard site.~~ The difference in saturation levels may be species-specific or caused by differences in soil moisture availability as the Orchard site had higher soil moisture than the Forest site during the heatwave and dry period. J_s in *Tilia* at the Park and Street sites seemed to be more linearly correlated with VPD, i.e., transpiration continued to increase with increasing VPD during the stressful periods. With sufficient water supply by irrigation, less saturation with VPD was observed in urban trees previously (Winbourne et al., 2020; Marchin et al., 2022). Similarly, the non-saturation of J_s with high VPD observed at the Park site may be due to irrigation during the dry period. Several previous studies on~~in~~ urban trees have shown that the relationship between VPD and transpiration is species-specific and it is more typical that VPD increases linearly in diffuse-porous trees but saturates in ring-porous trees (Bush et al., 2008; Rahman et al., 2019). All the species studied here are diffuse-porous.

In addition to VPD, J_s was also influenced~~explained~~ by other environmental variables. The relative importance of soil moisture, soil temperature and solar radiation in influencing~~explaining~~ J_s differed significantly between the four studied urban sites. ~~In addition to VPD,~~ PAR was among the main environmental drivers of J_s at Park, Orchard and Street sites, whereas PAR alone influenced~~explained~~ J_s at the Forest site (Table 5). Soil temperature was significantly related with J_s only at the Street site. When the different climatic periods were analyzed separately, soil conditions (moisture and/or temperature) affected J_s during heatwave (t stat = 2.3, P <0.05) and dry periods ((t stat = 2.1, P <0.05) at the Park site, but not at the Street, Forest and Orchard sites. This can be explained by the irrigation provided at the Park site during the dry period. Overall, VPD and PAR were the main environmental variables influencing the urban tree transpiration during hot and dry conditions ~~the environmental variables that best explained urban tree transpiration during hot and dry conditions were VPD and PAR,~~ and the relative importance of these two varied depending on the tree species, growing conditions and irrigation practices.

The elevated levels of transpiration (represented by high J_s) observed in the studied green areas during the heatwave indicate the presence of transpirational cooling. This phenomenon could hold substantial promise for alleviating extreme heat conditions caused by exceedingly high temperatures.~~The high J_s during the heatwave in the studied green areas suggests transpirational cooling.~~ Trees at the Orchard and Street sites had the highest transpiration rates, and trees in the Forest had the lowest transpiration rates during the dry and heatwave periods. These differences were mainly due to tree species, their drought strategies (Gillner et al., 2017) and growing conditions of the sites, particularly soil moisture availability. Lower transpiration in *Betula pendula* at the Forest site indicates that *Betula pendula* trees growing in an urban forest do not cool the environment as much as *Tilia* or *Malus*. Several previous studies have reported that the transpirational cooling effect of urban trees during hot and dry days increases or sustains the transpiration rates to prevent excessive heat accumulation (Gillner et al., 2015; Duarte et al., 2016; Drake et al., 2018; Urban et al., 2017; Ibsen et al., 2021). Keeping the stomata open in hot and dry conditions cools down the internal leaf temperatures, enabling maintaining photosynthesis (De Kauwe et al., 2019; Urban et al., 2017; Drake et al., 2018). The response depends on the species tolerance to drought, water use efficiency, microclimatic conditions, and site heterogeneity (Bussotti et al., 2014; Winbourne et al., 2020; Rennenberg et al., 2006). Especially *Tilia cordata* is known for its fairly isohydric behavior (i.e., stomatal control is not strong) during heat and drought and an associated increase in transpiration rates causing a cooling effect in different urban conditions (Moser et al., 2017). However, also *Betula pendula*, which typically shows isohydric behavior (i.e., strong stomatal control), increased J_s during the heatwave and dry periods in the present study. Contrasting and species-specific responses of trees to heat and drought have been observed in several urban trees (Gillner et al., 2017; Osone et al., 2014) whereas, in our study,~~however here,~~ a relatively constant ~~pattern of heat and drought~~ responses was observed between the studied species.

Our study was limited~~In our study, we observed these responses of urban tree transpiration and leaf gas exchange patterns during heatwave and dry periods; however, there were challenges and~~ regarding~~limitations to~~ detailed comparison of tree species-specific responses or the effect of urban site type on the responses ~~at the four urban sites~~ as the studied tree species were ~~are~~ different in different site types ~~conditions~~. Also, the limited measurements of leaf gas exchange (i.e. point measurements) did not allow us to study in detail the leaf-level water~~could not be addressed more about water use efficiency~~ during the local extreme periods. Further study ~~with a complex model~~ capturing the effect of site conditions and tree species behavior separately would be helpful~~useful~~ in addressing the main factors affecting the different responses of urban vegetation during heatwaves and dry periods.

5 Conclusions

We conclude that the heat and drought ~~that occurred~~ in Helsinki in 2021 were still not extreme enough to damage or dampen the gas exchange functioning of urban trees. Against our hypotheses, photosynthetic potential was~~did~~ not reduced due to lowered stomatal conductance during heatwave and drought conditions. The transpiration and photosynthetic potential during these periods remained~~stayed~~ high, suggesting stable ecosystem services such as cooling and carbon sequestration during relatively rough conditions. However, the significant role of VPD in tree water use during heatwave and drought periods was evident~~well supported~~ in our study, but its overall significance decreased during drought periods. The observed responses in~~of varying~~ tree transpiration during hot and dry periods across the four urban green areas are mainly due to VPD, and further investigations would be needed to differentiate the role of other factors such as growing conditions (soil water availability), tree species and tree size with dedicated~~proper~~ sampling design~~strageties~~ and with the help of more complex modelling. As urbanization and the occurrence of extreme climate~~climate extreme~~ events are increasing~~rising, particularly in high-latitude regions,~~ the role of urban green areas in mitigating climate change and cooling local microclimate is becoming even more significant. ~~in cities.~~ Further studies on~~of~~ the cooling potential of urban trees will provide a better understanding and support mitigation strategies and city planning in the future.

Data availability. Datasets of sap flux density, meteorological and leaf gas exchange measurements at the four urban sites in Helsinki is stored in https://doi.org/10.5281/zenodo.7525319

Appendix A

Table A1. The soil properties of the four urban vegetation sites. Soil sample analyzed from the top 30 cm of soil.

	Park	**Street**	**Forest**	**Orchard**
Soil type	Sand moraine	Fine sand moraine	Sand moraine	Sandy clay
Bulk density (kg/l)	1.15	1.07	1.14	1.02
Main particle size distribution	66% sand 21% silt 8% clay	48% sand, 26% silt, 11% clay	71% sand 15% silt 11% clay	27% sand, 31% silt, 42% clay
Carbon content (%)	3.7	3.3	3.9	3.9
Nitrogen content (%)	0.252	0.168	0.329	0.32
C:N ratio	14.8	21.8	11.9	12.3
pH	5.6	7.2	6.5	5.9
Soil porosity	41.6 %	41.6 %	41.6 %	46.1 %
Field capacity	22.9 %	22.9 %	22.9 %	38.4 %
Wilting point	10 %	10 %	10 %	13.4 %
Available water capacity	12.9 %	12.9 %	12.9 %	25.0 %

*Available water capacity = Field capacity - Wilting point

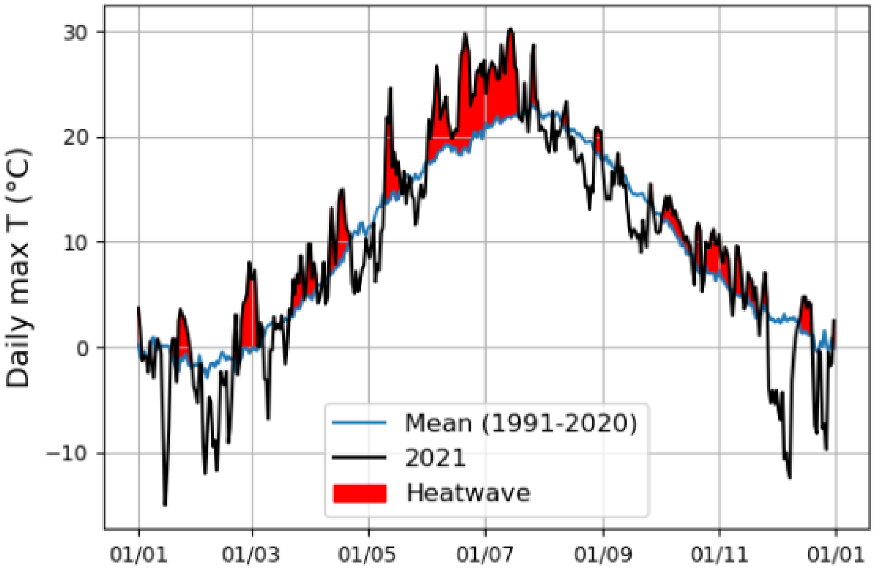

Figure A1. Heatwave detection using the daily maximum air temperature summer 2021 and the control period (1991-2020). The red color indicates the period where the daily maximum air temperature in the summer of 2021 exceeded the control period.

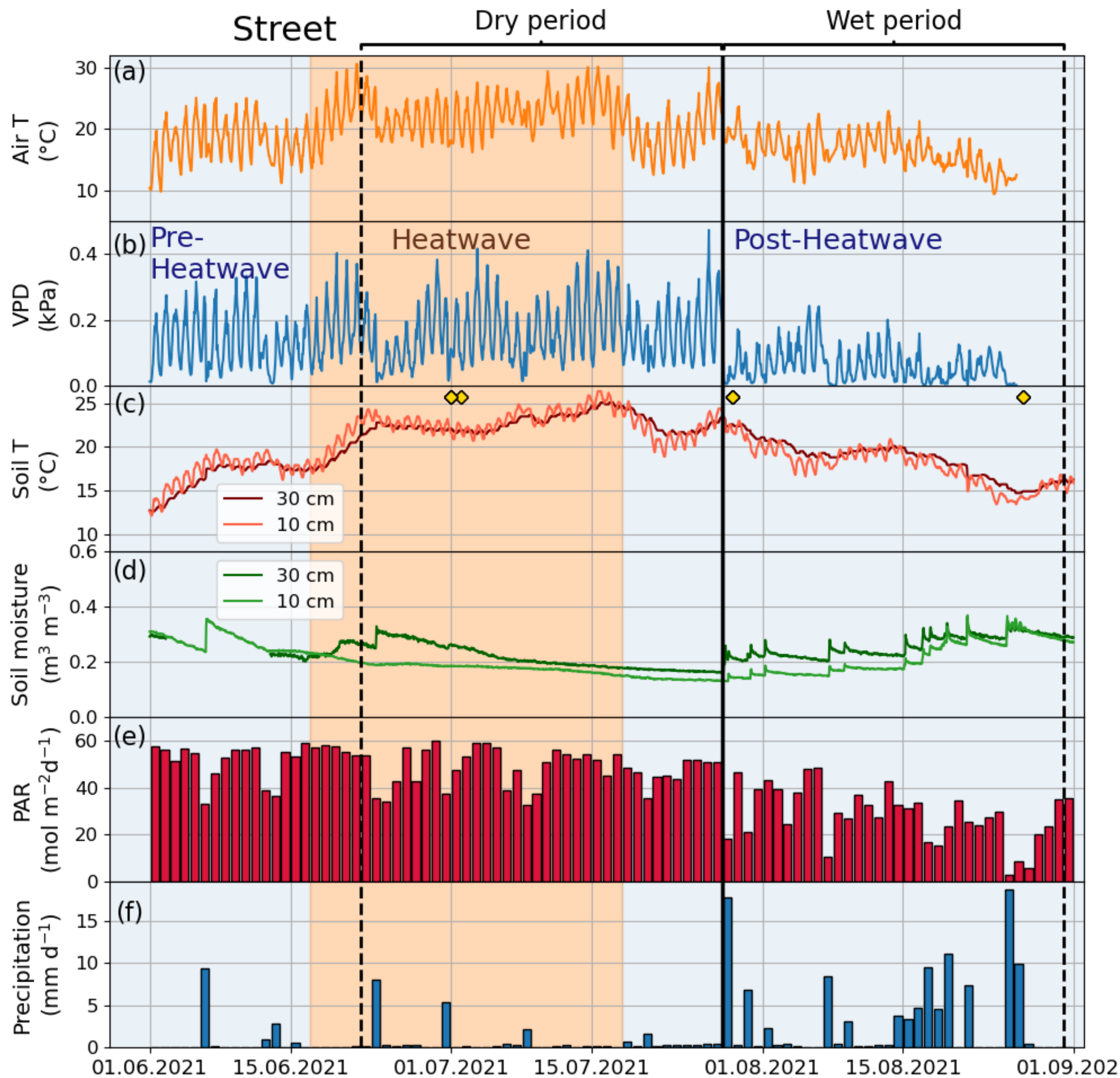

Figure A2. Meteorological condition at the Street site showing hourly a) air temperature (Air T), b) water vapor deficit (VPD), c) soil temperature (Soil T) and d) soil moisture measured and e) daily mean photosynthetically active radiation (PAR) and daily sum precipitation data measured at the SMEARIII station. The yellow markers in panel (c) denote the dates of manual leaf gas measurements.

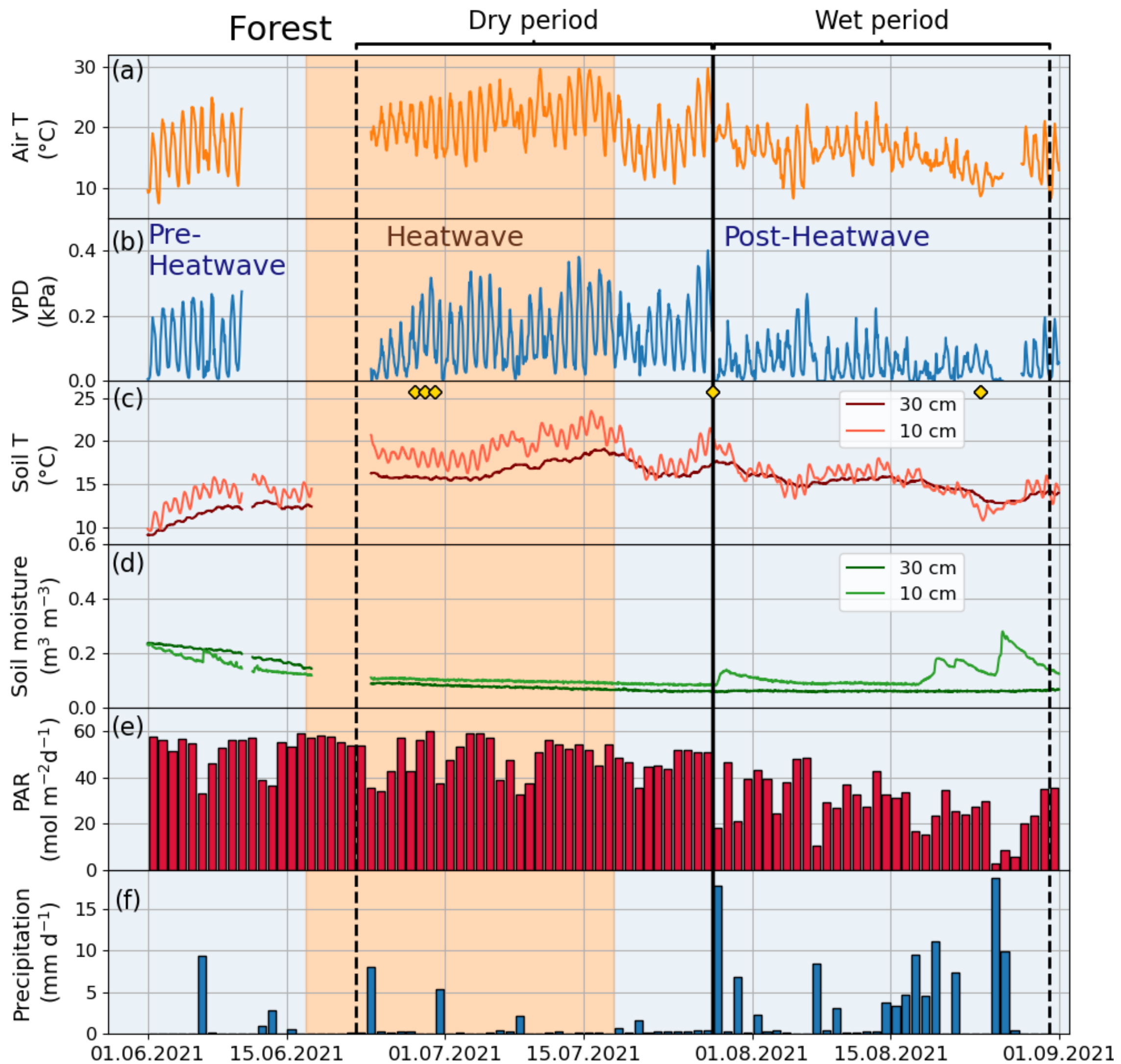

Figure A3. Meteorological condition at the Forest site showing hourly a) air temperature (Air T), b) water vapor deficit (VPD), c) soil temperature (Soil T) and d) soil moisture measured and e) daily mean photosynthetically active radiation (PAR) and daily sum precipitation data measured at the SMEARIII station. The yellow markers in panel (c) denote the dates of manual leaf gas measurements.

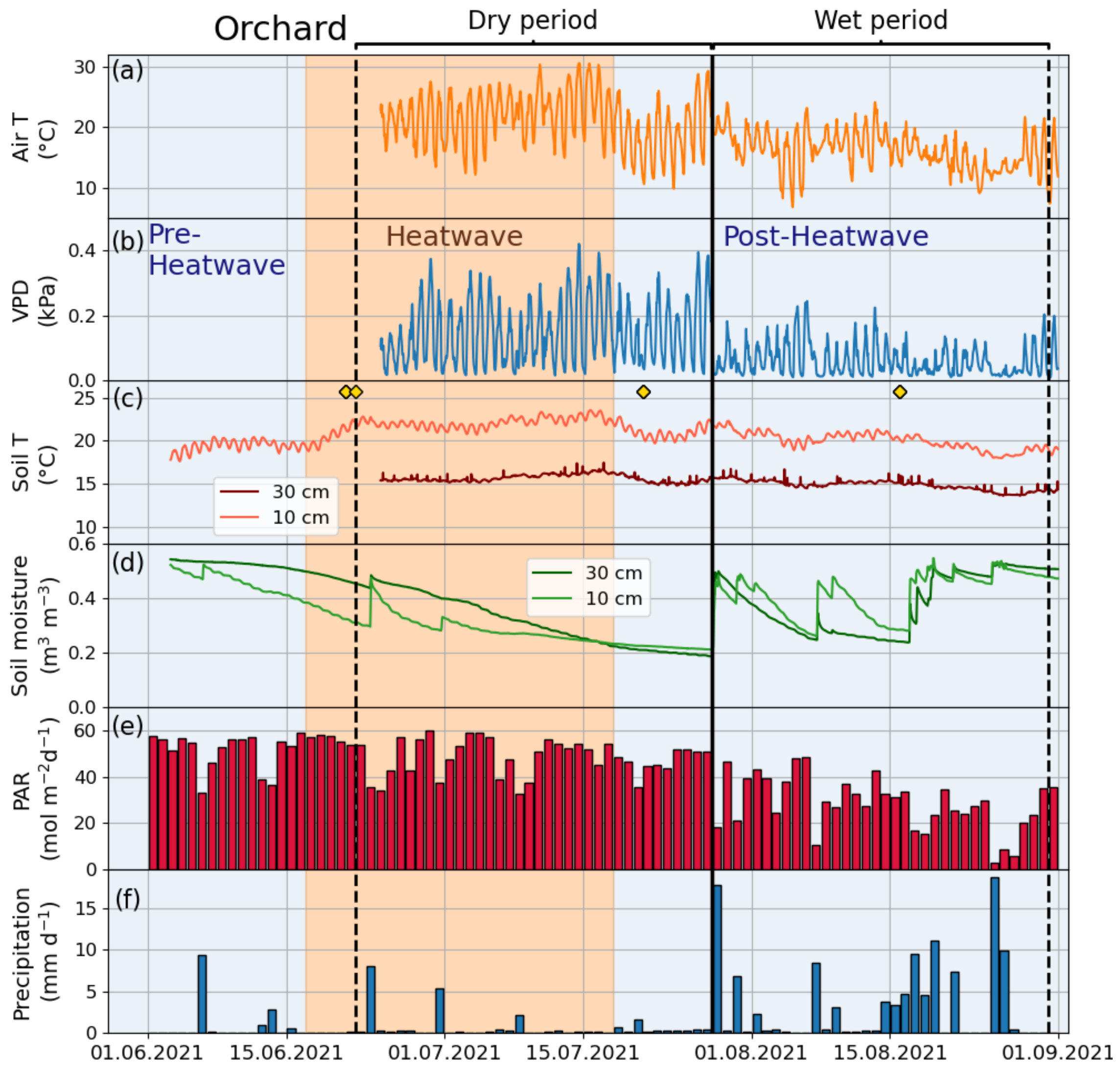

Figure A4. Meteorological condition at the Orchard site showing hourly a) air temperature (Air T), b) water vapor deficit (VPD), c) soil temperature (Soil T) and d) soil moisture measured and e) daily mean photosynthetically active radiation (PAR) and daily sum precipitation data measured at the SMEARIII station. The yellow markers in panel (c) denote the dates of manual leaf gas measurements.

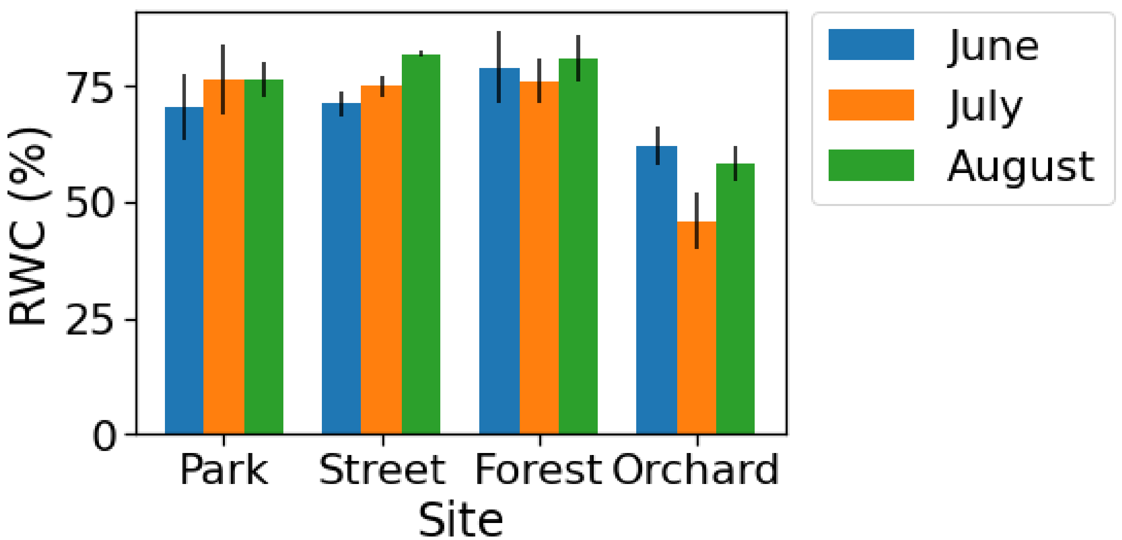

Figure A5. Monthly values of relative water content (RWC %) at the four urban sites.

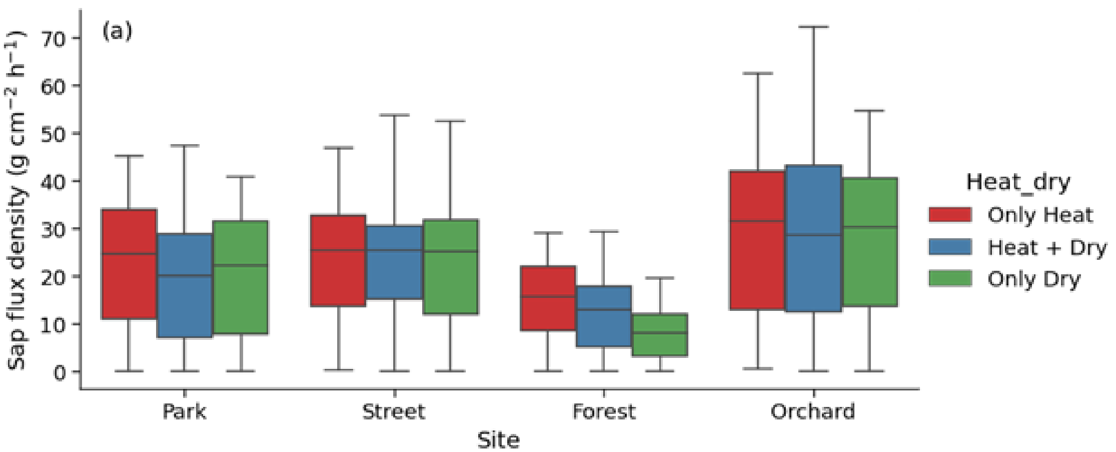

Figure A6. Pattern of sap flux density during heat and dry period at the four urban sites.

Author contributions. Conceptualization: JA, LK, LJ; Data collection: JA, JS, YF, AK, EK, EV; Formal analysis: JA, JS, AK; Funding acquisition: LK, LJ; Supervision: LK, LJ; Visualization: JA, JS; Writing—original draft preparation: JA; Writing—review and editing: JA, LK, LJ, YS, AL, EK. All authors have read and agreed to the article.

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