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(Citation)
Trees,35(6):1793-1806

(Issue Date)
2021-12

(Resource Type)
journal article

(Version)
Accepted Manuscript

Tolerance and acclimation of photosynthesis of nine urban tree species to warmer growing conditions

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Abstract (250)

To prepare and manage urban greenspace for a warmer future, we must select trees that can tolerate or acclimate to warmer growing conditions. Here, we compared tolerance and acclimation of photosynthesis to warmer growing conditions among urban trees species in Japan. Two paired experiments were installed where saplings of nine species were grown outside at two locations (warm- and cool-temperate climates) and in a greenhouse with and without passive warming. We compared the temperature where quantum yield declined to 50% of maximum value (T_{50}) due to excess heat (50-60ºC) and the thermal optimum for photosynthesis (T_{opt}) among species. For two deciduous and three evergreen species, T_{50} was higher for saplings grown in warm- than cool-temperate climate. T_{50} was also higher under passive warming for three species, of which two evergreen species (*Morella rubra*, *Quercus myrsinifolia*) showed marked increases (5-7ºC). T_{opt} was higher under passive warming in three of six species examined, but the acclimation response of photosynthesis and stomatal conductance to warming was highly species-specific. We inferred that *M. rubra* and *Q. myrsinifolia*, which acclimated consistently to warmer growing conditions in both experiments, are heat-hardy species. Our results also suggest warm-temperate evergreen species are not necessarily more tolerant of warmer growing conditions than cool-temperate deciduous species. For example, despite its warm-temperate origin, *Machilus thumbergii* showed no acclimation response and photosynthetic rates were lower under passive warming. Our results indicate species need to be screened individually to assess their physiological tolerance and acclimation potential to warmer climate.

Keywords: climate change, global warming, photosynthetic acclimation, urban trees

Declarations

Funding: This research was funded by a grant from Sumitomo Forestry Inc. to Kobe University.

Conflicts of interest/Competing interests (include appropriate disclosures): none declared.

Availability of data and material (data transparency): Data will be made available in a database at Kobe University.

Code availability (software application or custom code): NA

Authors' contributions:

HI and SI conceived and designed the study. SI prepared the plant material and CH, SI, and HI made the measurements with assistance from MN and HK. MO helped with statistical analyses. HI wrote the paper and all co-authors have approved of the draft.

Ethics approval (include appropriate approvals or waivers): NA

Consent to participate (include appropriate statements): NA

Consent for publication (include appropriate statements): NA

Availability of data and material (data transparency):

Key Message

Tolerance and acclimation of photosynthesis to warmer growing conditions among nine urban tree species was species-specific indicating that individual screening is needed to prepare urban greenspace for a warmer future.

Introduction

Climate change is already affecting the global environment (Pachauri et al. 2014). Impacts on trees include, reductions in growth and increasing mortality due to drought (Carnicer et al. 2011; McDowell and Allen 2015; Williams et al.), changes in leafing and flowering phenology due to warming (Cleland et al. 2007; Menzel et al. 2006), latitudinal and altitudinal range shifts and local decline/extinction of species (Jump et al. 2009; Lenoir et al. 2008; Thomas et al. 2004). Global climate change is progressing at rates faster than any previous climate shift in Earth's history (Visser 2008; Zachos et al. 2001). Because of their slow regeneration rates, most tree species will not be able to migrate or adapt quickly enough in response to climate change (Jump and Penuelas 2005). Extant trees, therefore, must acclimate in situ in order to survive.

Social adaptation to climate change includes redesigning and managing urban greenspace for a warmer future (Demuzere et al. 2014; Gill et al. 2007). Urban greenspace plays an important role in mitigating negative effects of climate change on our society, including buffering heat island effects and controlling stormwater runoff. (Caplan et al. 2019; Emmanuel and Loconsole 2015). These functions could be lost if tree health is not maintained and urban greenspace managed sustainably (Chen et al. 2017). For example, to adapt urban greenspace to future climate, the city of Melbourne is moving away from planting European species, which are susceptible to heat and drought, to using more tolerant native species (Nitschke et al. 2017; Norton et al. 2013). Selecting trees for adaptation of urban greenspace to climate change, however, is not a straightforward task (Roy et al. 2017). Planting species originating in warmer climates may not necessarily be the solution, because tropical and sub-tropical species are not adapted to temperature fluctuation and have low acclimation potential to changes in temperature (Cunningham and Read 2002; Perez et al. 2016). Therefore, to prepare for a warmer future, we must develop methods to assess species' tolerance and acclimation potential to warmer climate.

In urban areas of the warm-temperate zone, summer surface temperatures near the

pavement may exceed 50ºC (Chen et al. 2017; Emmanuel and Loconsole 2015). When exposed to high temperatures, plants maintain leaf temperature by increasing transpiration (Pallardy 2008). This could lead to water deficit for urban trees, which have limited access to ground water (Pataki et al. 2011). Stomatal closure to maintain leaf water balance, on the other hand, could lead to overheating and ultimately to carbon starvation (McDowell et al. 2008; Sevanto et al. 2014). Physiological acclimation to high temperature can be achieved by either up-regulating photosynthesis or down-regulating respiration to maintain positive carbon balance (Dusenge et al. 2019; Lombardozzi et al. 2015; Slot and Kitajima 2015). At the leaf level, photosynthetic rate generally shows a unimodal response to temperature, defining a thermal optimum for photosynthesis (T_{opt}). Photosynthetic rate decreases at higher temperatures not only due to stomatal closure, but also slower rates of enzymatic reactions, and extreme temperatures can cause biochemical damage to photosynthetic proteins and membranes (Hikosaka et al. 2006; Kumarathunge et al. 2019; Sage and Kubien 2007; Yamori et al. 2014). Leaves may acclimate to high temperature through an upward shift in T_{opt} and/or increasing photosynthetic rates at higher temperature (Berry and Bjorkman 1980; Kumarathunge et al. 2019; Way and Yamori 2014). The thermal optimum for photosynthesis varies among species as a result of adaptation to climatic conditions in their native habitat, as well as among individuals due to photosynthetic acclimation to specific growing conditions (Cheesman and Winte 2013; O'Sullivan et al. 2017; Sendall et al. 2015). Previous studies, which examined photosynthetic thermal acclimation of leaves, present mixed results. In tropical trees, experimental warming of leaves produced no or negative (down-regulation) photosynthetic acclimation responses (Doughty 2011; Slot et al. 2014). In cool-temperate trees, photosynthetic rates did not acclimate (up-regulate) in response to experimental warming, but rather decreased (Carter and Cavaleri 2018). These results suggest, photosynthetic response to warming can be highly variable among species and regions.

Here, we compared tolerance and acclimation of leaf photosynthetic properties to

warmer growing conditions among nine urban tree species commonly planted across Japan. Two paired experiments were installed. The same set of saplings were grown under ambient conditions in warm- and cool-temperate climates at two different locations. Another set of saplings were grown under controlled conditions in a greenhouse with and without passive warming. To compare thermal tolerance and thermal optimum among species, we measured threshold temperatures for loss of leaf photosynthetic function and the response of light-saturated photosynthetic rate to temperature. We inferred that species with greater thermal tolerance are those which maintain leaf photosynthetic function at higher temperatures. Species with greater thermal acclimation are those which exhibit significant responses to differences in climate and to the warming treatment.

Materials and Methods

Four-year-old, potted saplings of three deciduous: *Cornus florida* L., *Liquidambar styraciflua* L., and *Zelkova serrata* (Thunb.) Makino, and six evergreen trees: *Fraxinus griffithii* C.B.Clarke, *Ligustrum lucidum* Aiton, *Ligustrum japonicum* Thunb., *Machilus thunbergii* Sieb. et Zucc., *Morella rubra* Lour., *Quercus myrsinifolia* Blume, were used in the common garden experiment (Table 1). We installed two paired experiments in April 2019. In the “regional experiment”, four replicate pots of each species were grown outside at two locations in Japan. One set was grown in cool-temperate climate at the Monbetsu Station, Sumitomo Forestry Co. Ltd. in Monbetsu City, Hokkaido (44.36ºN, 143.30ºE) and another in warm-temperate climate at the Tsukuba Research Institute, Sumitomo Forestry Co. Ltd. in Tsukuba City, Ibaraki Prefecture (36.11ºN, 140.02ºE). We chose these two locations because they have contrasting temperatures (5.2-8.8ºC difference in mean monthly temperature during the study period), while relative humidity and solar radiation were similar (Table S1). To control for differences in precipitation, the pots were watered regularly. All saplings were planted in pots (height x diameter = 186 x 205 mm) filled with 5:3:2 mixtures

of red ball earth, Kanuma pumice, and manure. Plant sizes are shown in Table 1. All saplings were watered for 15 min at 5:00 am and 7:00 pm each day. According to the Japan Meteorological Agency database, mean monthly temperature and total precipitation at the two locations during Jan-Nov 2019 were 8.7ºC, 708.5 mm and 16.2ºC, 1265.0 mm, respectively.

In the "greenhouse experiment", the saplings were grown under controlled conditions in a greenhouse in Tsukuba. We placed one set (four saplings of each species) inside a 3x3 m mini-greenhouse constructed using transparent plastic sheeting to passively increase the temperature (hereafter: "passive warming", Fig. 1). A sheet of transparent plastic was placed over the saplings outside of the mini-greenhouse (ambient/control) to maintain similar irradiance levels. We confirmed that maximum irradiance levels were similar and sufficient (> 1400 µmol m^{-2} on sunny days) for both treatment and control plants.

Temperatures varied with season (Fig. 2). The mean temperature difference between passive warming and ambient condition was 1.7ºC and the mean difference in daily maximum temperature was 4.5ºC. Although we did not measure air humidity in the two treatments, we acknowledge that it may have been higher inside the mini-greenhouse. We presumed, however, that higher humidity would allow the saplings to maintain higher stomatal conductance and better control of leaf temperature. Thus, we inferred that any differences found between passive warming and ambient conditions would be a conservative result.

Thermal tolerance

To assess thermal tolerance, we measured quantum yield (QY) of dark-adapted leaves at various temperatures (20-60ºC) using a FluoroPen FP110 (Photo System Instruments, Drásov, Czech Republic). Before measurement, we watered the pots and allowed the saplings to rehydrate in darkness in the lab overnight. Under complete darkness, we cut out leaf discs (ca. 1.5 cm diameter) using a hole-puncher from intact current-year leaves of each sapling. For each species, four leaf

discs (one from each sapling) were sealed in plastic bags with moist cloth to keep humidity within the bag at equilibrium with leaf moisture. The bags were then sealed and immersed for 30 min in water heated to a set temperature (*T*) using a make-shift water bath consisting of a sous vide cooker (Felio F9575, Fujisho Co., Tokyo, Japan) and a 3L molybdenum pot. Then, the bags were removed from the water and allowed to cool to room temperature for 15 min before measuring QY with the FluorPen. Here, QY is a fluorometric measurement of maximum quantum yield of photosystem II, also referred to as Fv/Fm (maximum – minimum chlorophyll fluorescence relative to maximum fluorescence). The amount of time for heating and cooling were determined in a pilot study as necessary for leaves to equilibrate to heat and to room temperature so that we could determine if irreversible change had occurred. This procedure was repeated for each temperature setting. Temperature settings were varied and customized for each species to obtain good regression estimates (see below for statistical analyses). To observe seasonal change in thermal tolerance, measurements were made twice during the growing season, during and after the hottest season: Aug 6 and Sept 19 in cool-temperate climate (Monbetsu), Jul 29-Aug 1 and Sept 24-26 in warm-temperate climate (Tsukuba).

Temperature-photosynthesis relationship

We measured the temperature response of light-saturated photosynthetic rate (A_{net}) on one leaf from one representative sapling of six of the nine species (*C. florida, Z. serrata, L. lucidum, L. japonicum, M. thumbergii*, and *M. rubura*) in the greenhouse experiment from Sep 1-6 using a portable photosynthesis measurement system (LI-6400-XT, LI-COR Biosciences, Lincoln, NE, USA) with LED light source (LI-6400-02B). The CO_2 concentration in the chamber was set to 400 ppm and light intensity was initially set at 600 μmol m^{-2} s^{-1} and then increased until photosynthetic rate reached light-saturation (1200 – 1400 μmol m^{-2} s^{-1}, depending on species). Initially, room temperature was set to 20ºC and the block temperature of the LI-6400 was

increased from 15 to 20ºC. Then, room temperature was increased to 25ºC and block temperature was increased from 25 to 40ºC. As we increased the temperature, relative humidity was adjusted by running a commercially available humidifier (SH-OR30 WT, Topland Co., Tokyo, Japan) near the inlet of the LI-6400 to prevent vapor pressure deficit (VPD) from increasing too rapidly. At each temperature setting, leaf gas exchange was allowed to acclimate to cuvette conditions before logging ten measurements of A_{net}. Temperature settings were varied and customized for each species to obtain good regression estimates (see below for statistical analyses). From these measurements, we obtained the relationship between leaf temperature (T_{leaf}) and A_{net}, as well as between VPD and stomatal conductance (G_S).

Statistical analyses

To assess leaf thermal tolerance of each species, measurements of QY from the four leaf disks were plotted in relation to T. We fit a logistic curve to the relationship using non-linear least-squares regression to obtain the heat tolerance curve for each species:

$$\mathrm{QY} = \frac{a}{1+\exp\{b(T-T_{50})\}} \qquad \text{(eq. 1)}$$

Where T_{50} is the temperature and b is the slope at the inflection point where QY is 50% of the initial, maximum value, a. The 95% confidence intervals for the parameter estimates were obtained using the drc package in R (ver. 3.5.3, R Development Core Team).

The relationship between T_{leaf} and A_{net} was analyzed using quadratic regression:

$$A_{net} = c(T_{leaf}-T_{opt})^2+d \qquad \text{(eq. 2)}$$

Where, T_{opt} is the optimum temperature when A_{net} is highest and c is a coefficient determining the concavity of the unimodal curve. Regression analyses were conducted using JMP ver. 15J (SAS Institute Japan, Tokyo) to calculate 95% confidence intervals for each parameter estimate. The relationship between VPD and G_S was analyzed using log-linear regression:

$$G_S = \alpha + \beta \ln\mathrm{VPD} \qquad \text{(eq. 3)}$$

For each species the regression estimates were compared between treatments using analysis of covariance (ANCOVA), where treatment (ambient/warming) is the main effect and VPD is the covariate. A significant interaction term would indicate difference between treatments in the response of G_S to VPD.

Parameter estimates for equations 1 and 2 were considered significantly different between species and treatments if confidence intervals did not overlap. We chose this test because our sample sizes are limited and it is a more conservative test than comparing non-linear regressions between pooled vs. individual regressions using dummy variables. For a given species, significant difference in parameter estimates between climates/treatments was interpreted as photosynthetic acclimation. We also compared T_{50} of the same species between seasons to infer whether the acclimation response was reversible.

Results

Thermal tolerance

In the Jul-Aug measurement of the regional experiment (ca. four months after the experiment was initiated), T_{50} of current-year leaves was 2.7-3.9ºC higher in warm-temperate climate for three evergreen (*M. rubra, F. griffithii, Q. myrsinifolia*) and two deciduous (*C. florida*, *L. styraciflua*) species (Table 2). The T_{50} of other species did not vary with climate, while for *Z. serrata*, the slope of the logistic curve was less steep in warm-temperate climate, reflecting slower decrease rate of QY in response to increasing temperature (Fig. 3). Seasonal change in T_{50} was observed only in warm-temperate climate where T_{50} was 1.7-3.5ºC lower in Sep for *M. thumbergii C. florida*, and *F. griffithii*.

In the Jul-Aug measurement of the greenhouse experiment, T_{50} of current-year leaves was 1.6-7.6ºC higher under passive warming for *M. rubra*, *Q. myrsinifolia* and *C. florida* (Table

3). The effect of warming on T_{50} was especially marked for *M. rubra* and *Q. myrsinifolia* (7.6 and 5.3ºC difference, respectively). Seasonal change in T_{50} was observed mostly under passive warming. Under ambient condition, T_{50} was 1.7ºC lower in Sep for *C. florida*. Under passive warming, T_{50} was 1.8-5.5ºC lower in Sep for *M. rubra*, *M. thumbergii* and *C. florida*. The seasonal response of *M. rubra* was especially marked (5.5ºC difference).

As a result of acclimation, species rank in T_{50} varied between climates and treatments (Fig. 5). In cool-temperate climate, *M. thumbergii* and *Z. serrata* had the highest T_{50}. In warm-temperate climate, there was no significant difference among the top five species, *Z. serrata* retreated from second to seventh in rank, and *L. japonicum* and *L. lucidum* had the lowest T_{50} among the nine species. Of the five species whose T_{50} was higher in warm- than cool-temperate climate, *M. rubra*, *F. griffithii* and *Q. myrsinifolia* advanced markedly in rank. In the greenhouse experiment, there was very little difference in T_{50} among the nine species under ambient condition. Under passive warming, however, the T_{50} values of *M. rubra* and *Q. myrsinifolia* were significantly higher than the other species. Here again, *L. japonicum* and *L. lucidum* had the lowest T_{50} among the nine species.

Temperature-photosynthesis relationship

In the greenhouse experiment, patterns of photosynthetic acclimation to passive warming varied among species (Fig. 6). For *L. lucidum*, *L. japonicum* and *Z. serrata*, T_{opt} was higher under passive warming (Table 4), although for *Z serrata*, the T_{opt} estimate under ambient condition was lower than the measured temperature range. *L. lucidum* and *L. japonicum* had the highest T_{opt} under passive warming. For *L. japonicum*, A_{net} did not change and only T_{opt} shifted upward. For *L. lucidum* and *M. rubra*, the concavity of the T_{leaf}-A_{net} relationship (c) was less negative under passive warming, i.e., A_{net} decreased less with increasing temperature. For *Z. serrata*, an overall increase in A_{net} was observed under passive warming, whereas for *M.*

thumbergii A_{net} decreased. For *C. florida*, A_{net} decreased with increasing T_{leaf} under ambient condition ($P < 0.01$), while it remained constant under passive warming.

During our measurement of A_{net}, VPD increased gradually with increasing temperature for all six species (Fig. S1). The pattern of VPD increase in relation to air temperature was similar among the four evergreen species. For the two deciduous species, *Z. serrata* and *C. florida*, VPD increased more rapidly for saplings grown under passive warming. The response of G_S to VPD varied among species. For *L. lucidum*, *L. japonicum* and *M. rubra*, G_S increased with increasing VPD and the response was more marked under passive warming than ambient condition (Fig. 7). This indicated that higher A_{net} of *L. lucidum* and *M. rubra* at high temperatures under passive warming was coupled with higher G_S. In contrast, for *Z. serrata*, *M. thumbergii* ad *C. florida* G_S decreased with increasing VPD, reflecting stomatal control of transpiration rate. For *Z. serrata*, and overall increase in G_S was observed under passive warming, indicating that higher overall A_{net} under passive warming was coupled with higher G_S. For *M. thumbergii* and *C florida*, G_S was less responsive to VPD under passive warming, suggesting reduced stomatal control of transpiration rate.

Discussion

Thermal tolerance

Our results indicated that species' thermal tolerance can vary widely in response to differences in regional climate, as well as to experimental warming. We expected that the evergreen species, which originate in warm-temperate to sub-tropical climates, would be more tolerant of warmer climate than the cool-temperate deciduous species. Indeed, *M rubra* and *M. thumbergii*, both evergreen species of warm-temperate origin, had the highest T_{50} among the nine species when grown in warm-temperate climate. In addition, three of the six evergreen species showed acclimation response of T_{50} to differences in climate, although *M. thumbergii* did not. However,

in both experiments, *L. japonicum* and *L. lucidum*, both warm-temperate evergreen species, consistently ranked lowest in T_{50} and showed no acclimation responses. On the other hand, *C. florida*, a deciduous species, whose T_{50} was 3.4ºC higher in warm-temperate than cool-temperate climate, ranked third in T_{50} under warm-temperate climate. This species also showed acclimation response of T_{50} in both experiments.

In a reciprocal transplanting experiment, Cunningham and Reed (2002) found that when grown in temperate climate, tropical species showed greater reductions in maximum net photosynthesis than temperate species grown under tropical climate. Tropical species also had narrower temperature ranges for maximum photosynthesis, suggesting lower thermal acclimation potential. These results suggest that temperate species, which are more adapted to temperature fluctuation, may have high thermal tolerance and acclimation potential than tropical and sub-tropical species. Our results indicate that species originating from warm regions may not necessarily be more tolerant or show greater acclimation potential to warmer growing conditions than those originating from cool regions.

Although some plants can maintain photosynthetic activity at temperatures as high as 40ºC (Colombo and Timmer 1992), irreversible biochemical damage occurs in many plants above 55ºC (Sharkey 2005). The T_{50} values of the nine street-tree species in this study were mostly around 50ºC. However, for two warm-temperate evergreen species in our study, *M. rubra* and *Q. myrsinifolia*, T_{50} was higher than 55ºC under passive warming suggesting these two species may be the most tolerant of extreme temperature among the nine species examined. *M. rubra* and *Q. myrsinifolia* also showed the greatest acclimation response, where T_{50} of current-year leaves was 5-7ºC higher under passive warming. In our experiment, warming increased mean temperature difference by 1.7ºC. Maximum temperatures under warming, however, were 4-5ºC higher than ambient condition, exceeding 45ºC in late July (Fig. 2). Our results indicate *M. rubra* and *Q. myrsinifolia* are able to acclimate to such high temperatures. Several other species also showed

acclimation of thermal tolerance in response to different climates as well as to warming, but for many species these responses were dampened when temperatures decreased in Sep, suggesting that acclimation of thermal tolerance may be a short-term response. This may be because increasing thermal tolerance involves metabolic costs, such as production of isoprenes, heat-stress proteins, etc., strengthening of thylakoid membranes, and regeneration of rubisco (Law and S.J. 1999; Sharkey 2005).

Temperature-photosynthesis relationship

Each of the six species examined showed unique acclimation response of the temperature-photosynthesis relationship to warming, suggesting that photosynthetic acclimation is species-specific. This could explain why previous studies of leaf warming produced such mixed results (Carter and Cavaleri 2018; Doughty 2011; Slot et al. 2014). We found that upward shifts in T_{opt} may or may not involve changes in overall photosynthetic rate. Up-regulation of photosynthetic rates, observed along with higher stomatal conductance for *Z. serrata* in this study, may reflect higher overall metabolism in response to warming (Dusenge et al. 2019). On the other hand, species showing down-regulation, such as *M. thumbergii*, which also showed lower stomatal control of transpiration under warming, could still maintain positive carbon balance if leaf respiration is also down-regulated (Araki et al. 2017; Atkin and Tjoelker 2003; Way and Yamori 2014). For *L. lucidum* and *M. rubra*, high photosynthetic rates in response to increasing temperature under passive warming were coupled with high stomatal conductance, i.e., increasing transpiration. Such species may not be able to maintain photosynthetic rate if high temperatures co-occur with drought conditions. Variable responses to higher temperature has also been found among tropical tree species (Cheesman and Winte 2013), suggesting species-specific physiological responses, including measurements of leaf photosynthesis and respiration, as well as stomatal control in response to increasing temperature and water stress, need to be examined

in order to predict acclimation potential of each species to warmer climate.

Conclusion

In the face of global climate change, we must manage forests and trees to prepare for uncertain future climate conditions (Millar et al. 2007). Urban trees and greenspace must also be managed and sustained to adapt to climate change (Roy et al. 2017). This is no easy task, and involves long-term planning at various spatial scales from replanting individual trees to redesigning cities. Our results provide a scientific basis for assessing physiological tolerance and acclimation potential of urban tree species to warmer growing conditions. Further investigation is needed to test specific responses to increasing temperature, because in our regional experiment, unknown factors other than temperature may have been confounded and in our greenhouse experiment we could not control for air humidity. Similar tests comparing urban tree species' tolerance and acclimation to changes in temperature, as well as co-varying effects of precipitation/humidity, are needed to prepare urban greenspace for a warmer future.

Acknowledgements

We thank Ms. H. Ishii, Ms. M. Hioki, Dr. K. Ohshiman and the staff of Sumitomo Forestry Co. Ltd. for assistance with the experiments, and K. Kuroda, W. Azuma and members of the Laboratory of Forest Resources, Kobe Univ. for guidance and advice during research.

References cited

Araki MG, Gyokusen K, Kajimoto T (2017) Vertical and seasonal variations in temperature responses of leaf respiration in a Chamaecyparis obtusa canopy Tree Physiology 37:1269-1284

Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature Trends in Plant Science 8:343-351

Berry J, Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants Annual Review of Plant Physiology 31:491-543

Caplan JS, Galanti RC, Olshevski S, Eisenman SW (2019) Water relations of street trees in green infrastructure tree trench systems Urban Forestry & Urban Greening 41:170-178 doi:https://doi.org/10.1016/j.ufug.2019.03.016

Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought Proceedings of the National Academy of Sciences 108:1474-1478

Carter KR, Cavaleri MA (2018) Within-canopy experimental leaf warming induces photosynthetic decline instead of acclimation in two northern hardwood species Frontiers in Forests and Global Change 1:11

Cheesman AW, Winte rK (2013) Growth response and acclimation of CO_2 exchange characteristics to elevated temperatures in tropical tree seedlings Journal of Experimental Botany 64:3817–3828

Chen Y, Wang X, Jiang B, Wen Z, Yang N, Li L (2017) Tree survival and growth are impacted by increased surface temperature on paved land Landscape and Urban Planning 162:68-79 doi:https://doi.org/10.1016/j.landurbplan.2017.02.001

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change 22:357-365

Colombo S, Timmer R (1992) Limits of tolerance to high temperatures causing direct and indirect damage to black spruce Tree Physiology 11

Cunningham S, Read J (2002) Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature Oecologia 133:112–119

Demuzere M et al. (2014) Mitigating and adapting to climate change: Multi-functional and multi-scale assessment of green urban infrastructure Journal of Environmental Management 146:107-115 doi:https://doi.org/10.1016/j.jenvman.2014.07.025

Doughty CE (2011) An in situ leaf and branch warming experiment in the Amazon Biotropica 43:658-665

Dusenge ME, Duarte AG, Way DA (2019) Plant carbon metabolism and climate change: elevated

CO_2 and temperature impacts on photosynthesis, photorespiration and respiration New Phytologist 221:32-49

Emmanuel R, Loconsole A (2015) Green infrastructure as an adaptation approach to tackling urban overheating in the Glasgow Clyde Valley Region, UK Landscape and Urban Planning 138:71-86 doi:https://doi.org/10.1016/j.landurbplan.2015.02.012

Gill SE, Handley JF, Ennos AR, Pauleit S (2007) Adapting cities for climate change: The role of the green infrastructure Built Environment 33:115-133 doi:10.2148/benv.33.1.115

Hikosaka K, Ishikawa K, Borjigidai A, Muller O, Onoda Y (2006) Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate Journal of Experimental Botany 57:291–302

Jump AS, Matyas C, Penuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species Trends in Ecology and Evolution 24:694-701

Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change Ecology Letters 8:1010-1020

Kozlowski T, Pallardy S (2002) Acclimation and adaptive responses of woody plants to environmental stresses Botanical Review 68:270-334

Kumarathunge DP, Medlyn BE, Drake JE, Tjoelker MG (2019) Acclimation and adaptation components of the temperature dependence of plant photosynthesis at the global scale New Phytologist 222:768-784

Law R, S.J. C-B (1999) Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase Plant Physiology 120:173-182

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century Science 320:1768-1771

Lombardozzi DL, Bonan GB, Smith NG, Dukes JS, Fisher RA (2015) Temperature acclimation of photosynthesis and respiration: a key uncertainty in the carbon cycle–climate feedback Geophysical Research Letters 42:8624–8631.

McDowell N, Allen CD (2015) Darcy's law predicts widespread forest mortality under climate warming Nature Climate Change 5:669-672

McDowell N et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologist 178:719

Menzel A, Sparks TH, Estrella N, Roy DB (2006) Altered geographic and temporal variability in phenology in response to climate change Global Ecology and Biogeography 15:498-504

Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: Managing in the face of uncertainty Ecological Applications 17:2145-2151

Nitschke CR, Nichols S, Allen K, Dobbs C, Livesley SJ, Baker PJ, Lynch Y (2017) The influence of climate and drought on urban tree growth in southeast Australia and the implications

for future growth under climate change Landscape and Urban Planning 167:275-287 doi:https://doi.org/10.1016/j.landurbplan.2017.06.012

Norton B et al. (2013) Planning for a cooler future: green infrastructure to reduce urban heat. Victorian Centre for Climate Change Adaptation Research, Melbourne

O'Sullivan OS et al. (2017) Thermal limits of leaf metabolism across biomes Global Change Biology 23:209-223 doi:10.1111/gcb.13477

Pachauri RK et al. (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland

Pallardy SG (2008) Physiology of woody plants, third edition. Academic Press, San Diego

Pataki DE, McCarthy HR, Litvak E, Pincetl S (2011) Transpiration of urban forests in the Los Angeles metropolitan area Ecological Applications 21:661-677

Perez TM, Stroud JT, Feeley KJ (2016) Themal trouble in the tropics Science 351:1392-1393

Roy S, Davison A, Östberg J (2017) Pragmatic factors outweigh ecosystem service goals in street tree selection and planting in South-East Queensland cities Urban Forestry & Urban Greening 21:166-174 doi:https://doi.org/10.1016/j.ufug.2016.12.003

Sage RF, Kubien DS (2007) The temperature response of C3 and C4 photosynthesis. Plant, Cell & Environment Plant, Cell & Environment 30:1086–1106

Sendall KM et al. (2015) Acclimation of photosynthetic temperature optima of temperate and boreal tree species in response to experimental forest warming Global Change Biology 21

Sevanto S, McDowell N, Dickman LT, Pangle R, Pockman W (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses Plant, Cell & Environment 37:153-161

Sharkey TD (2005) Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene Plant, Cell & Environment 28:269-277

Slot M, Kitajima K (2015) General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types Oecologia 177:885–900

Slot M, Rey-Sánchez C, Gerber S, Lichstein JW, Winter K, Kitajima K (2014) Thermal acclimation of leaf respiration of tropical trees and lianas: Response to experimental canopy warming, and consequences for tropical forest carbon balance Global Change Biology 20:2915-2926

Thomas CD et al. (2004) Extinction risk from climate change Nature 427:145-148

Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change Proceedings of the Royal Society B: Biological Sciences 275:649-659

Way DA, Yamori W (2014) Thermal acclimation of photosynthesis: On the importance of

adjusting our definitions and accounting for thermal acclimation of respiration Photosynthesis Research 119:89-100

Williams AP et al. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality Nature 3:292-297

Yamori W, Hikosaka K, Way DA (2014) Temperature response of photosynthesis in C3, C4, and CAM plants: temperature acclimation and temperature adaptation Photosynthesis Research 119:101-117

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present Science 292:686-693

Table 1. Sizes of the potted saplings of each species used in the study. Mean ± one s.d. of all saplings are shown (n = 16 for each species). These were then equally distributed: three each among the two sites and two treatments.

Species	Basal diameter (mm)	Height (cm)
C. florida	8.1±1.0	80.9±14.4
L. styraciflua	9.8±0.8	98.1±5.0
Z. serrata	7.7±0.8	78.1±15.5
F. griffithii	6.8±0.9	94.4±18.6
L. lucidum	8.0±0.6	83.3±11.1
L. japonicum	8.9±1.2	65.2±8.3
M. thumbergii	7.5±1.0	70.2±12.9
M. rubra	13.8±2.0	81.9±13.5
Q. myrsinifolia	8.2±0.7	70.9±9.5

Species names with underline indicate evergreen trees.

Table 2. T_{50} (temperature at 50% of maximum quantum yield, ºC, mean ± one s.e.) for current-year-old leaves of the nine tree species grown in cool- and warm-temperate climates. Species are listed in order of decreasing T_{50} in warm-temperate climate during Jul-Aug. Asterisk (*) indicates significantly higher value for warm- than cool-temperate climate and bold indicates significantly lower value for Sep than Jul-Aug ($P < 0.05$).

Rank	Species	Season	0-yr		
			cool	warm	
1	*M. rubra*	Jul-Aug	47.24±1.0	50.62±1.2	*
		Sep	48.87±0.8	48.87±1.4	
2	*M. thumbergii*	Jul-Aug	49.17±1.1	50.52±1.5	
		Sep	48.85±1.0	**48.85**±0.5	
3	*C. florida*	Jul-Aug	47.03±1.1	50.43±0.4	*
		Sep	47.53±0.6	**48.74**±0.3	*
4	*F. griffithii*	Jul-Aug	46.38±1.0	50.28±0.4	*
		Sep	46.74±0.9	**46.74**±0.5	*
5	*Q. myrsinifolia*	Jul-Aug	46.09±1.4	50.00±0.4	*
		Sep	47.84±0.7	47.84±0.7	*
6	*L. styraciflua*	Jul-Aug	46.83±0.8	49.55±0.5	*
		Sep	47.59±0.6	47.59±1.2	*
7	*Z. serrata*	Jul-Aug	48.74±0.3	48.98±1.5	
		Sep	48.12±0.6	48.12±1.3	
8	*L. japonicum*	Jul-Aug	47.86±0.5	48.68±0.8	
		Sep	48.45±1.0	46.97±0.4	
9	*L. lucidum*	Jul-Aug	47.42±0.5	48.36±0.5	
		Sep	46.97±0.7	46.97±0.4	

Species names with underline indicate evergreen trees.

Table 3. T_{50} (temperature at 50% of maximum quantum yield, ºC, mean ± one s.e.) for current- and one-year-old leaves of the nine tree species grown in ambient and passive warming conditions in a greenhouse. Species are listed in order of decreasing T_{50} under passive warming during Jul-Aug. Asterisk (*) indicates significantly higher value for warming than ambient condition and bold indicates significantly lower value for Sep than Jul-Aug ($P < 0.05$).

Rank	Species	Season	0-yr		
			Ambient	warming	
1	*M. rubra*	Jul-Aug	50.02±1.5	57.63±1.3	*
		Sep	50.25±0.7	**52.10**±1.0	*
2	*Q. myrsinifolia*	Jul-Aug	50.34±0.9	55.68±0.3	*
		Sep	50.35±0.2	53.78±0.5	*
3	*M. thumbergii*	Jul-Aug	50.70±1.4	52.95±1.4	
		Sep	49.00±0.6	**49.58**±1.2	
4	*L. styraciflua*	Jul-Aug	51.04±1.0	52.41±0.8	
		Sep	49.62±0.4	50.95±1.1	
5	*F. griffithii*	Jul-Aug	50.03±1.2	52.00±1.2	
		Sep	50.75±0.4	53.01±0.4	*
6	*C. florida*	Jul-Aug	50.33±0.3	51.95±1.0	*
		Sep	**48.59**±1.3	**50.13**±0.3	
7	*Z. serrata*	Jul-Aug	50.11±1.9	50.53±1.3	
		Sep	49.20±0.7	50.03±1.5	
8	*L. lucidum*	Jul-Aug	50.01±1.2	50.09±1.6	
		Sep	48.95±0.8	50.92±1.2	
9	*L. japonicum*	Jul-Aug	48.33±0.4	48.76±1.2	
		Sep	48.37±0.9	47.71±0.5	

Species names with underline indicate evergreen trees.

Table 4. Regression coefficients (estimate ± one s.e.) of the relationship between leaf temperature and maximum photosynthetic rate (A_{net}) for current-year leaves of the six tree species grown in ambient and passive warming conditions in a greenhouse shown in Fig. 6. Species are listed in order of decreasing thermal optimum for photosynthesis (T_{opt}) under passive warming. Quadratic regression of the form $A_{net} = c\,(T + T_{opt})^2 + d$ was used. Values in bold indicate significantly higher T_{opt} and smaller c for warming than ambient condition ($P < 0.05$).

	Species	*Treatment*	T_{opt} (°C)	c	d	r^2	P
1	*L. lucidum*	Ambient	25.86 ± 0.13	-0.034 ± 0.0011	5.63 ± 0.03	0.936	<0.01
		Warming	**28.63** ± 0.12	**-0.017** ± 0.0009	5.65 ± 0.03	0.937	<0.01
2	*L. japonicum*	Ambient	25.23 ± 0.76	-0.001 ± 0.0006	5.46 ± 0.02	0.813	<0.05
		Warming	**27.63** ± 0.10	-0.010 ± 0.0004	5.50 ± 0.01	0.884	<0.01
3	*M. rubra*	Ambient	25.35 ± 0.11	-0.015 ± 0.0007	5.75 ± 0.01	0.877	<0.01
		Warming	26.25 ± 0.21	**-0.005** ± 0.0004	6.11 ± 0.01	0.861	<0.01
4	*Z. serrata*	Ambient	17.70 ± 0.67	-0.009 ± 0.0006	6.90 ± 0.04	0.860	<0.01
		Warming	**22.40** ± 0.20	-0.009 ± 0.0003	8.33 ± 0.01	0.845	<0.01
5	*M. thumbergii*	Ambient	22.35 ± 0.36	-0.008 ± 0.0007	8.87 ± 0.04	0.920	<0.01
		Warming	21.37 ± 0.52	-0.008 ± 0.0006	5.90 ± 0.02	0.902	<0.01
6	*C. florida*	Ambient	ns	-0.055 ± 0.002*	6.73± 0.06	0.889	<0.01
		Warming	ns	ns	ns	ns	ns

Species names with underline indicate evergreen trees.

*For *C. florida*, linear regression ($A_{net} = c\,T + d$) was used.

Figure captions

Fig. 1. Potted saplings in the greenhouse (ambient) and double-green house (passive warming). The dimensions of the double greenhouse are 3 x 3 m.

Fig. 2. Mean hourly temperatures during the experiment for Monbetsu City, Hokkaido (cool-temperate climate) and Tsukuba City, Ibaraki (warm-temperate climate), and for ambient and passive warming conditions in a greenhouse in Tsukuba. All data were taken by thermometers set up beside the potted trees. Some data are missing for the greenhouse during July due to mechanical failure.

Fig. 3. Quantum yield (QY) of current-year leaves in relation to leaf temperature for the nine tree species grown in cool- and warm-temperate climates. Temperature and slope at the inflection point of the logistic regression curve is T_{50} and b, respectively, in Table 2. Asterisks next to species names indicate significant difference in T_{50} between climates and thick lines indicate significant difference in b ($P < 0.05$). Species are listed in the same order as Table 2. Species names with underline indicate evergreen trees.

Fig. 4. Quantum yield (QY) of current-year leaves in relation to leaf temperature for the nine tree species grown in ambient and passive warming conditions in a greenhouse. Temperature and slope at the inflection point of the logistic regression curve is T_{50} and b, respectively, in Table 3. Asterisks next to species names indicate significant difference in T_{50} between treatments and thick lines indicate significant difference in b ($P < 0.05$). Species are listed in the same order as Table 3. Species names with underline indicate evergreen trees.

Fig 5. Nine urban tree species in Japan ranked in order of decreasing T_{50} (regression estimate ± one standard error) in the two experiments, where saplings were grown in cool- and warm-temperate climates, and under ambient and passive warming conditions in a greenhouse. Species names with underline indicate evergreen trees.

Fig. 6. Maximum photosynthetic rate of current-year leaves (A_{net}) in relation to leaf temperature for six tree species grown in ambient and passive warming conditions in a greenhouse. Each point is the mean of ten measurements taken at each temperature setting on one leaf from a representative sapling for each species (standard error = 0.009~0.095 μmol m^{-2} s^{-1}). Lines indicate significant quadratic regressions (drawn using all ten observations for each temperature setting) whose peak is T_{opt} (values are shown in each graph). Values in bold are significantly higher for warming than ambient condition ($P < 0.05$). Thick lines indicate significant difference in concavity of the quadratic regression curve ($P < 0.05$, Table 4).

Species are listed in the same order as Table 4. Species names with underline indicate evergreen trees.

Fig. 7. Stomatal conductance of current-year leaves (G_S) in relation to vapor pressure deficit (VPD) for six tree species grown in ambient and passive warming conditions in a greenhouse. Data are from the same measurement as Fig. 5. Lines indicate significant log-linear regressions of the form $G_S = \alpha + \beta \ln\mathrm{VPD}$ ($P < 0.05$). For all six species, the slope and intercept were significantly different between warming and ambient conditions ($P < 0.05$). Species names with underline indicate evergreen trees.

Fig. S1. Vapor pressure deficit (VPD) in relation to air temperature (T_{air}) for six tree species grown in ambient and passive warming conditions in a greenhouse. Data are from the same measurement as Fig. 5. Lines indicate significant linear regressions ($P < 0.05$). This relationship was similar for the four evergreen species whose names are underlined ($P < 0.05$). For *Z. serrata* and *C. florida*, the relationship was significantly different between warming than ambient conditions ($P < 0.05$).

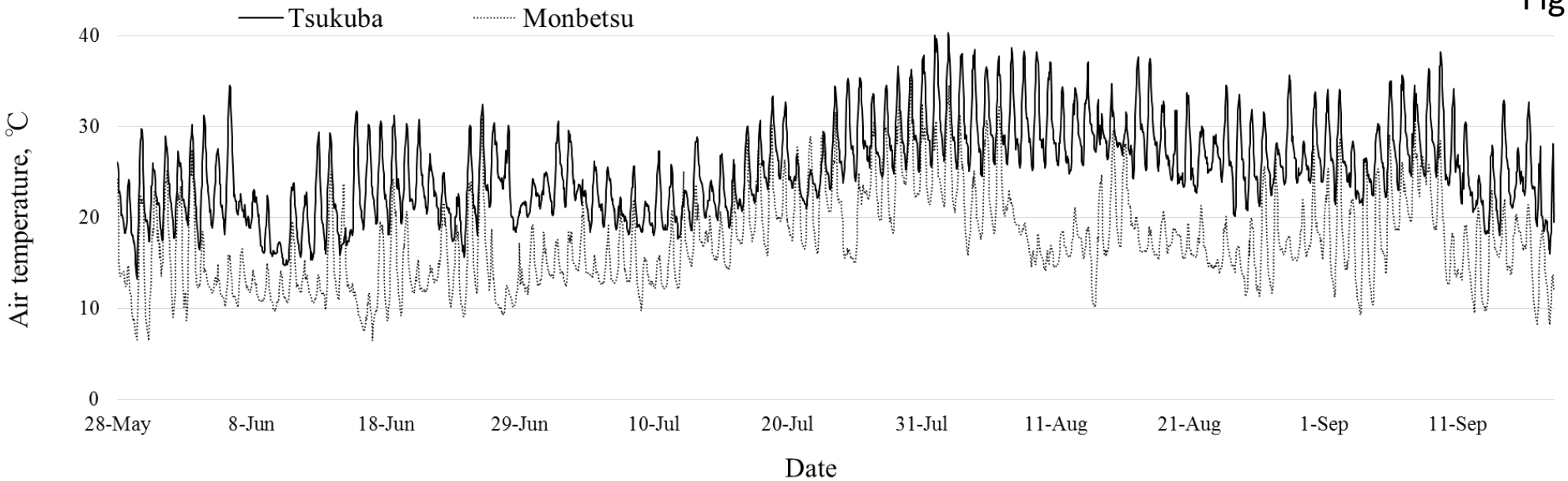
Table S1. Monthly mean temperature, total precipitation, relative humidity and solar radiation during the study period for the two sites in the regional experiment (Apr-Sep, 2019). Data are from the Japan Meteorological Agency database.

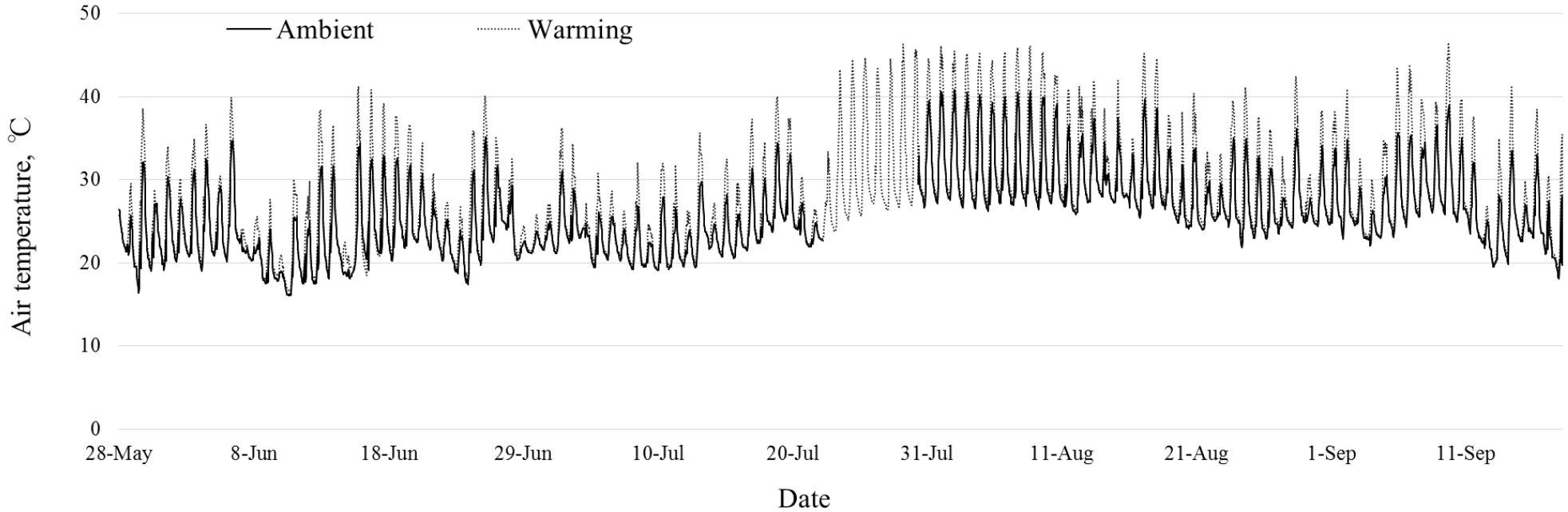
Month	Temperature(°C)		Precipitation (mm)		Humidity (%)		Solar radiation (MJ m^{-2})	
	Monbetsu	Tsukuba	Monbetsu	Tsukuba	Monbetsu	Tsukuba	Monbetsu	Tsukuba
Apr	5.4	12.3	15.0	82.0	63	67	18.8	18.3
May	13.5	18.7	21.5	95.5	66	70	20.1	21.2
Jun	13.5	20.9	58.5	141.5	85	82	19.2	15.9
Jul	18.1	23.5	59.0	160.0	90	88	18.6	13.5
Aug	18.6	27.4	239.5	57.5	91	83	13.8	17.3
Sep	17.4	23.8	98.5	172.5	77	82	14.1	14.6
Total			492.0	709.0			104.6	100.8

Figure

Fig 1

Fig 2


Tsukuba
Monbetsu
Air temperature, ℃
40
30
20
10
0
28-May
8-Jun
18-Jun
29-Jun
10-Jul
20-Jul
31-Jul
11-Aug
21-Aug
1-Sep
11-Sep
Date


Ambient
Warming
Air temperature, ℃
50
40
30
20
10
0
28-May
8-Jun
18-Jun
29-Jun
10-Jul
20-Jul
31-Jul
11-Aug
21-Aug
1-Sep
11-Sep
Date

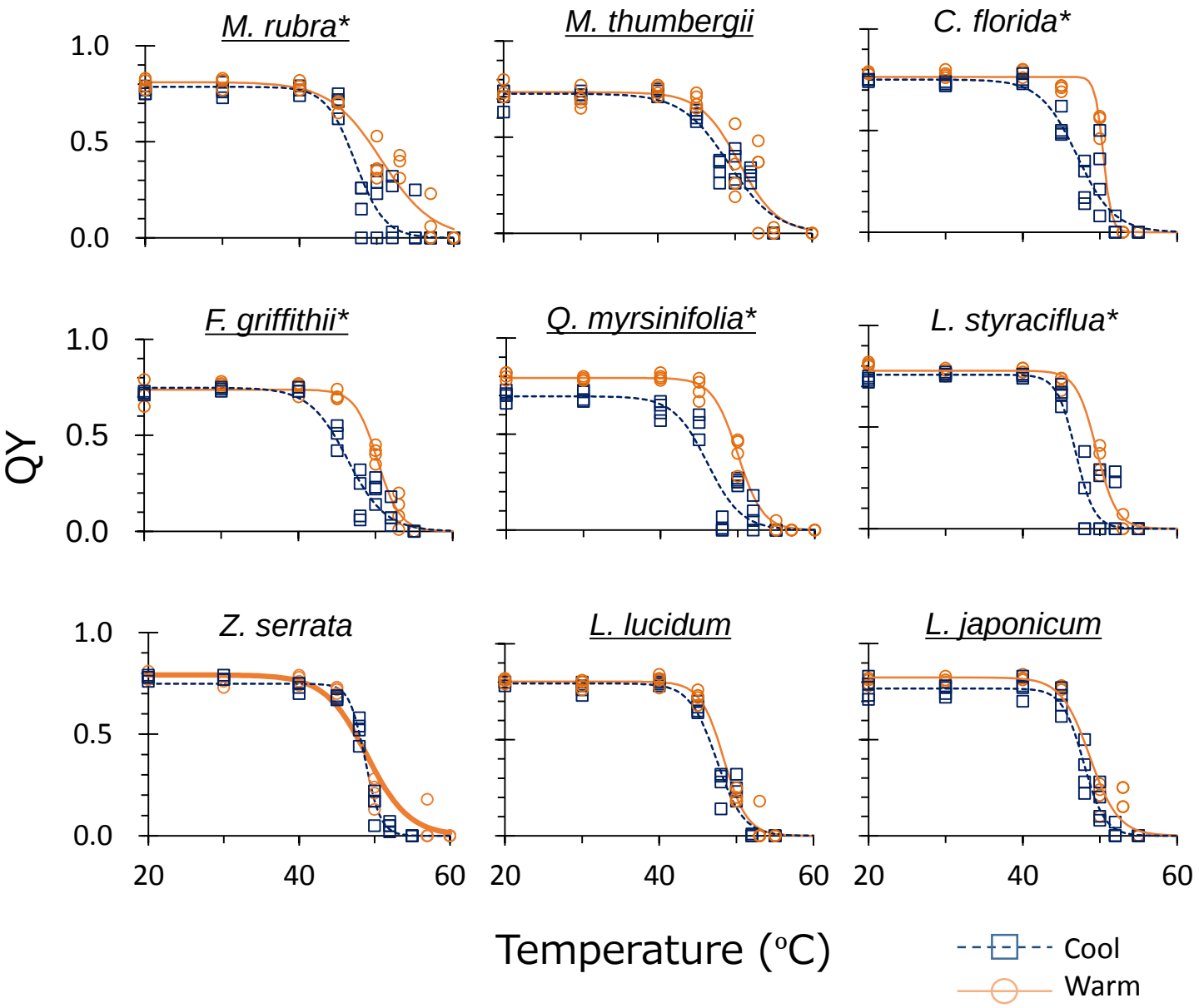

M. rubra*
M. thumbergii
C. florida*
F. griffithii*
Q. myrsinifolia*
L. styraciflua*
Z. serrata
L. lucidum
L. japonicum
QY
1.0
0.5
0.0
20
40
60
Temperature (°C)
Cool
Warm

Fig 3

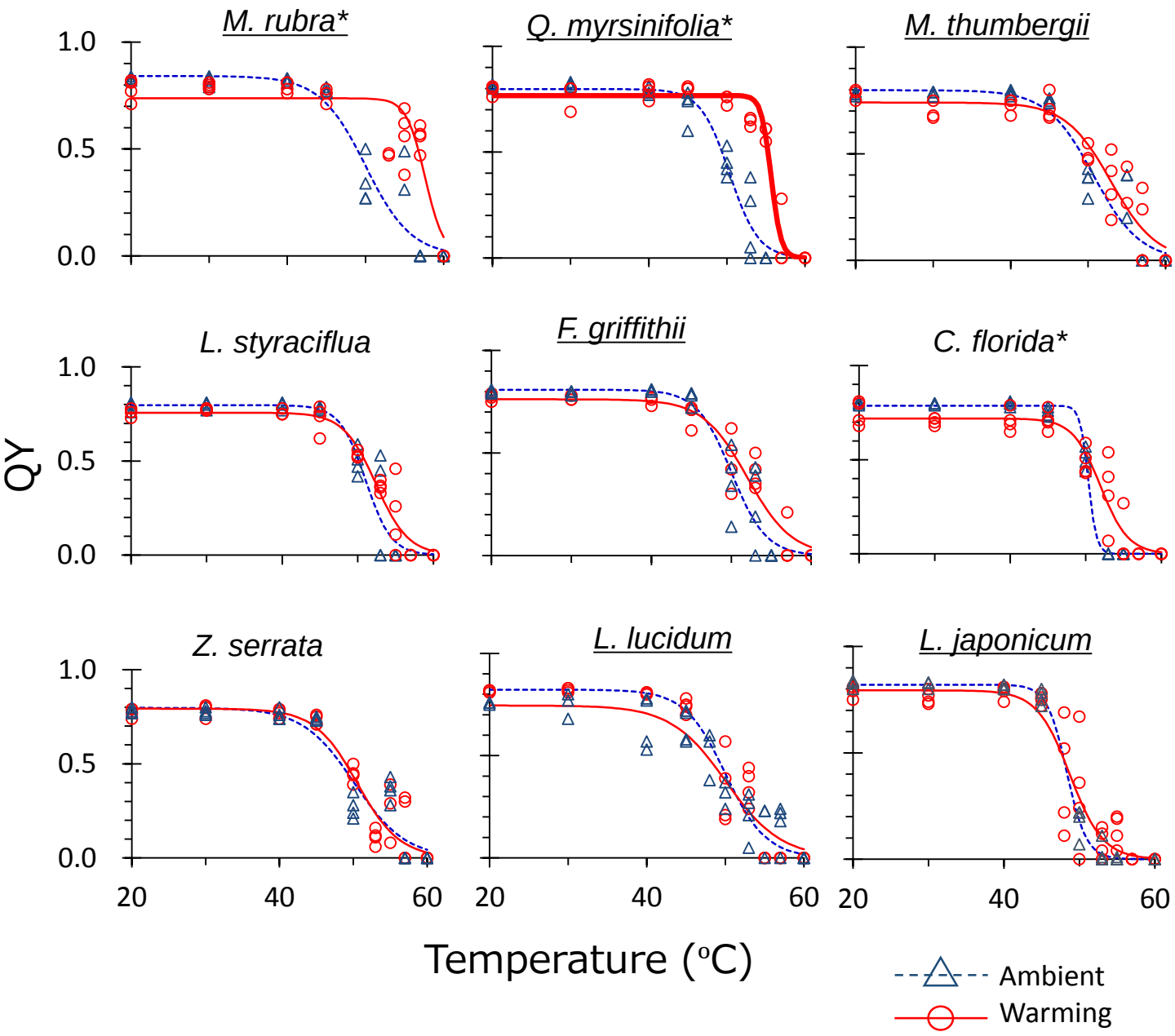

M. rubra*
Q. myrsinifolia*
M. thumbergii
L. styraciflua
F. griffithii
C. florida*
Z. serrata
L. lucidum
L. japonicum
QY
1.0
0.5
0.0
20
40
60
Temperature (°C)
Ambient
Warming

Fig 4

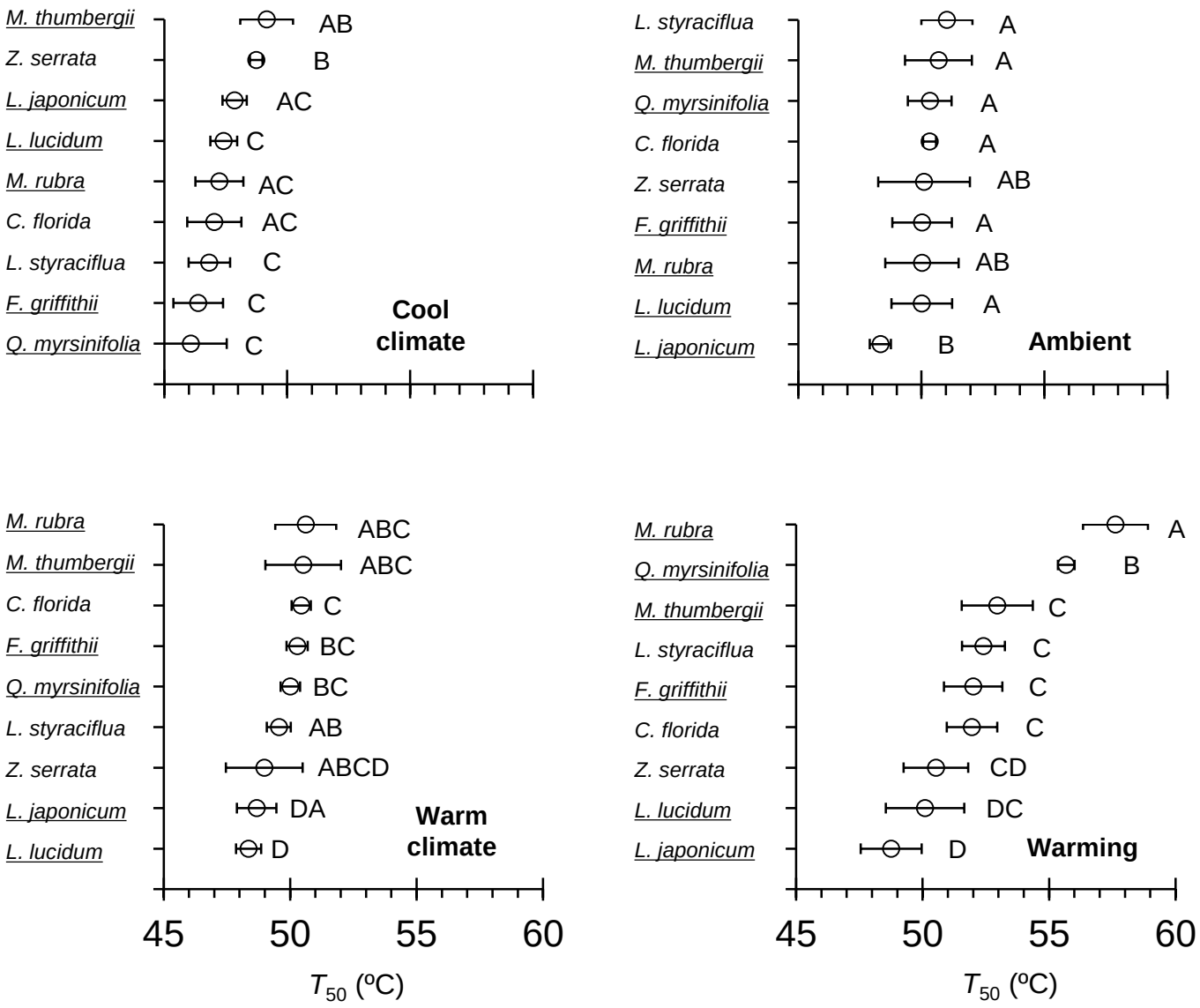

M. thumbergii
Z. serrata
L. japonicum
L. lucidum
M. rubra
C. florida
L. styraciflua
F. griffithii
Q. myrsinifolia
AB
B
AC
C
AC
AC
C
C
C
Cool climate
L. styraciflua
M. thumbergii
Q. myrsinifolia
C. florida
Z. serrata
F. griffithii
M. rubra
L. lucidum
L. japonicum
A
A
A
A
AB
A
AB
A
B
Ambient
M. rubra
M. thumbergii
C. florida
F. griffithii
Q. myrsinifolia
L. styraciflua
Z. serrata
L. japonicum
L. lucidum
ABC
ABC
C
BC
BC
AB
ABCD
DA
D
Warm climate
M. rubra
Q. myrsinifolia
M. thumbergii
L. styraciflua
F. griffithii
C. florida
Z. serrata
L. lucidum
L. japonicum
A
B
C
C
C
C
CD
DC
D
Warming
45
50
55
60
T50 (ºC)
45
50
55
60
T50 (ºC)

Fig 5

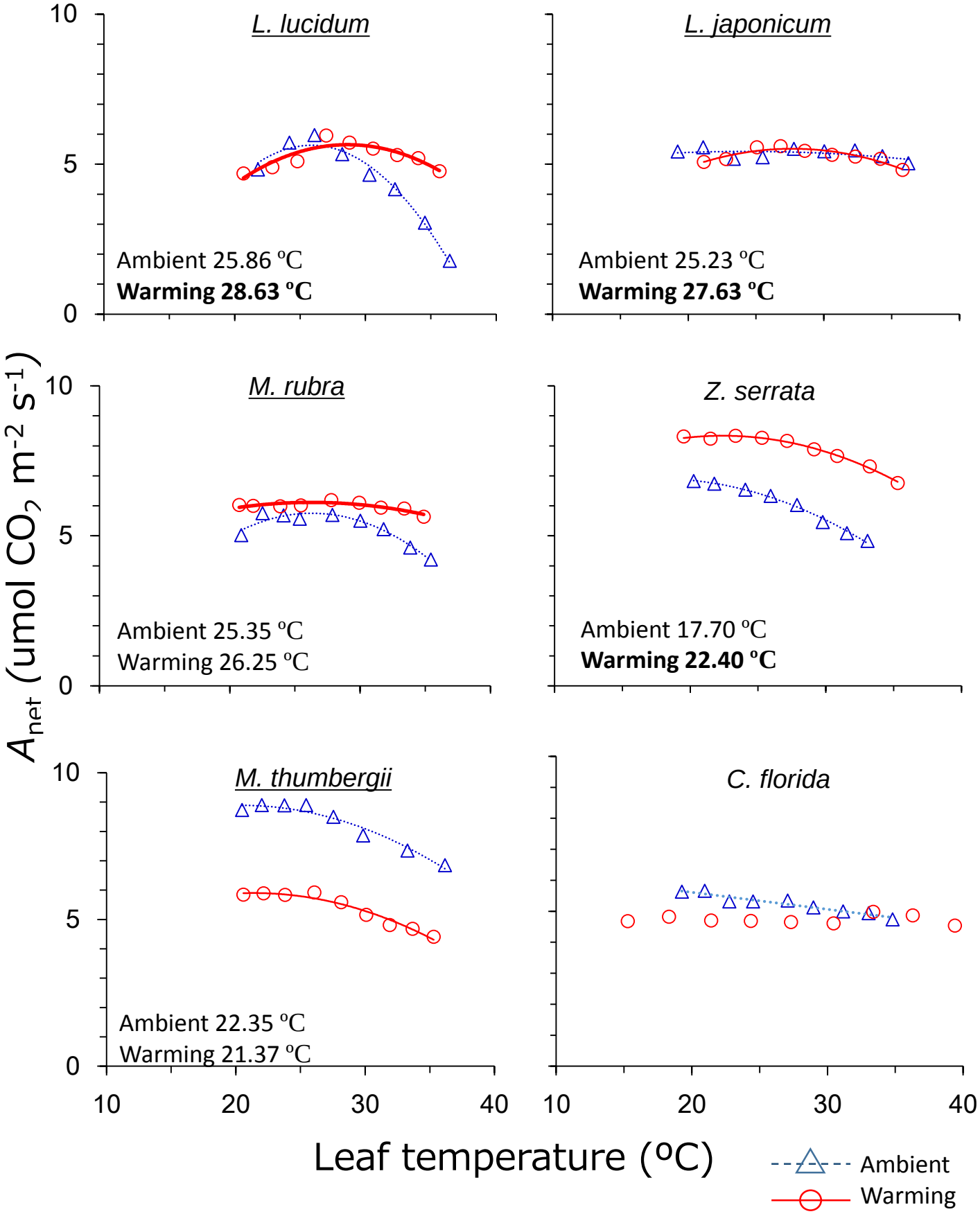

L. lucidum
Ambient 25.86 °C
Warming 28.63 °C
L. japonicum
Ambient 25.23 °C
Warming 27.63 °C
M. rubra
Ambient 25.35 °C
Warming 26.25 °C
Z. serrata
Ambient 17.70 °C
Warming 22.40 °C
M. thumbergii
Ambient 22.35 °C
Warming 21.37 °C
C. florida
A_{net} (umol CO_2 m^{-2} s^{-1})
Leaf temperature (°C)
Ambient
Warming

Fig 6

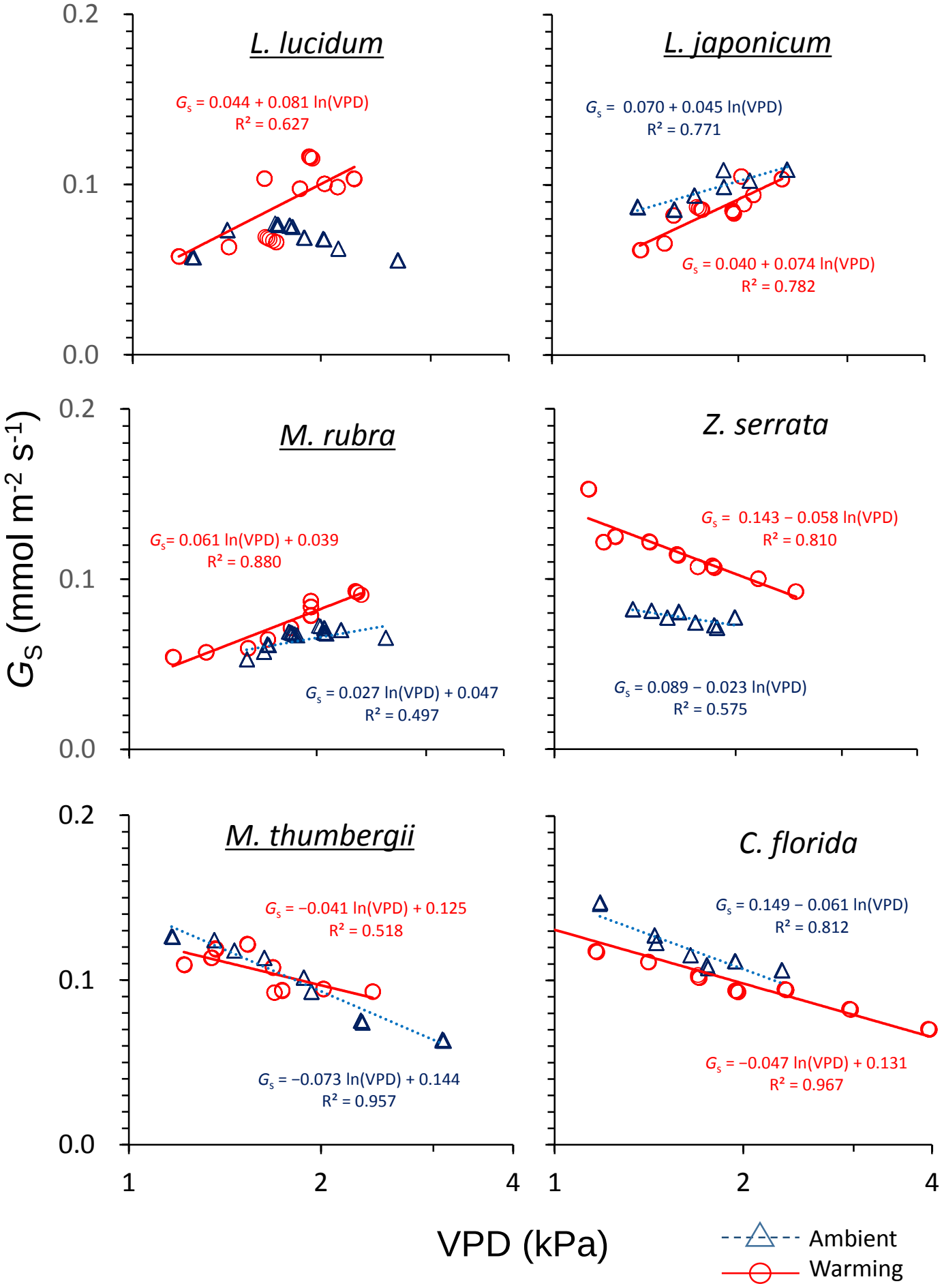

L. lucidum
Gs = 0.044 + 0.081 ln(VPD)
R² = 0.627
L. japonicum
Gs = 0.070 + 0.045 ln(VPD)
R² = 0.771
Gs = 0.040 + 0.074 ln(VPD)
R² = 0.782
M. rubra
Gs= 0.061 ln(VPD) + 0.039
R² = 0.880
Gs = 0.027 ln(VPD) + 0.047
R² = 0.497
Z. serrata
Gs = 0.143 − 0.058 ln(VPD)
R² = 0.810
Gs = 0.089 − 0.023 ln(VPD)
R² = 0.575
M. thumbergii
Gs = −0.041 ln(VPD) + 0.125
R² = 0.518
Gs = −0.073 ln(VPD) + 0.144
R² = 0.957
C. florida
Gs = 0.149 − 0.061 ln(VPD)
R² = 0.812
Gs = −0.047 ln(VPD) + 0.131
R² = 0.967
Gs (mmol m-2 s-1)
0.0
0.1
0.2
1
2
4
VPD (kPa)
Ambient
Warming

Fig 7

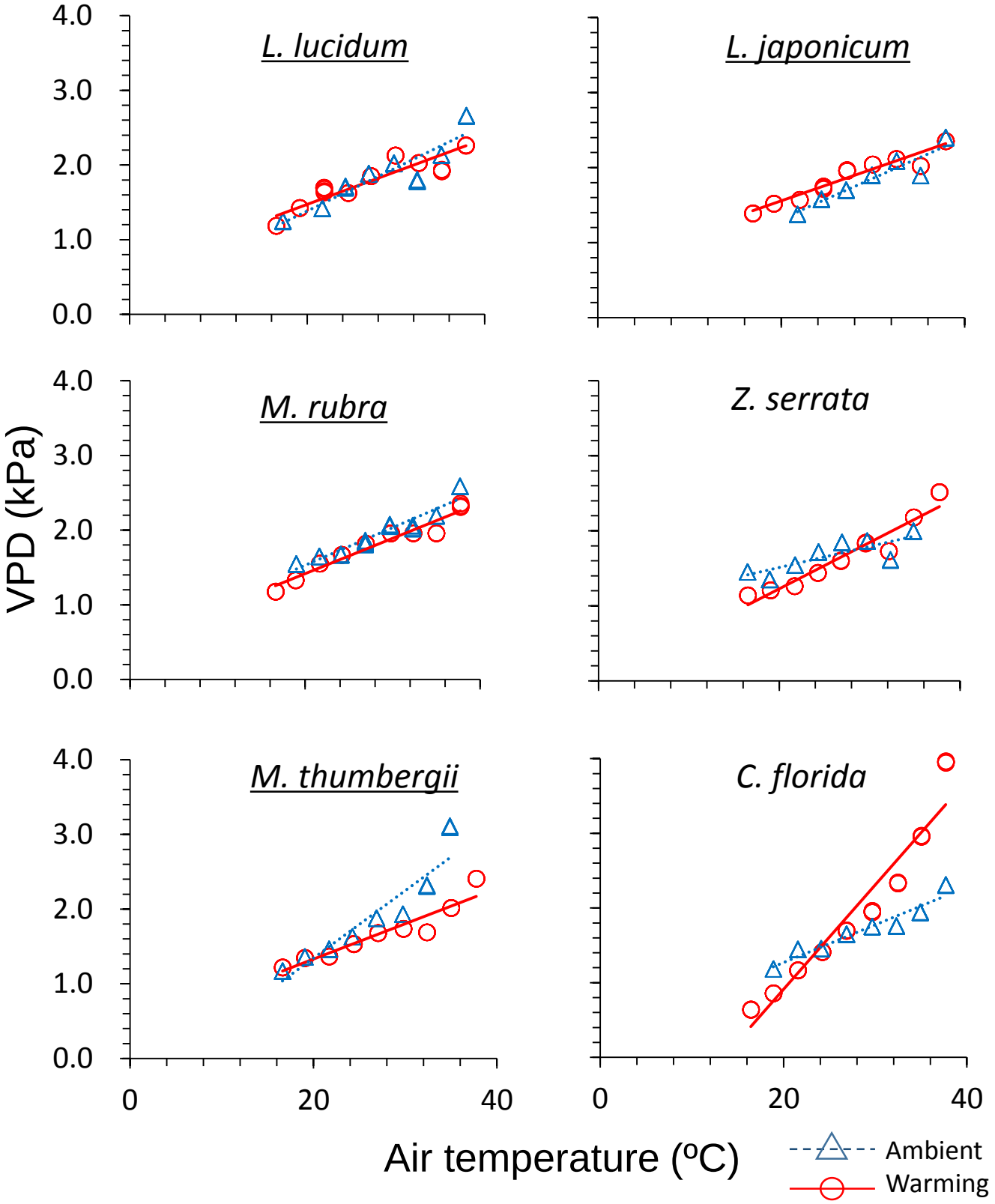

L. lucidum
L. japonicum
M. rubra
Z. serrata
M. thumbergii
C. florida
VPD (kPa)
4.0
3.0
2.0
1.0
0.0
0
20
40
Air temperature (ºC)
Ambient
Warming

Fig S1