urban science

Review

The Morpho-Physio-Biochemical Attributes of Urban Trees for Resilience in Regional Ecosystems in Cities: A Mini-Review

Jihwi Jang and David W. M. Leung *

School of Biological Sciences, University of Canterbury, Christchurch 8041, New Zealand; jihwi.jang@pg.canterbury.ac.nz
* Correspondence: david.leung@canterbury.ac.nz; Tel.: +64-3369-5184

Abstract: Increased urbanization means human beings become the dominant species and reduction in canopy cover. Globally, urban trees grow under challenging and complex circumstances with urbanization trends of increasing anthropogenic carbon dioxide (CO_2) emissions, high temperature and drought stress. This study aims to provide a better understanding of urban trees' morpho-physio-biochemical attributes that can support sustainable urban greening programs and urban climate change mitigation policies. Globally, urban dwellers' population is on the rise and spreading to suburban areas over time with an increase in domestic CO_2 emissions. Uncertainty and less information on urban tree diversification and resistance to abiotic stress may create deterioration of ecosystem resilience over time. This review uses general parameters for urban tree physiology studies and employs three approaches for evaluating ecosystem resilience based on urban stress resistance in relation to trees' morphological, physiological and biochemical attributes. Due to the lack of a research model of ecosystem resilience and urban stress resistance of trees, this review demonstrates that the model concept supports future urban tree physiology research needs. In particular, it is necessary to develop integral methodologies and an urban tree research concept to assess how main and combined effects of drought and/or climate changes affect indigenous and exotic trees that are commonly grown in cities.

Keywords: urban ecosystem; urban tree physiology; climate change; ecosystem resilience; urbanization

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1. Introduction

1.1. Current Snapshot of Urban Vegetation

Under increasingly challenging conditions in urban environments (i.e., prolonged drought, elevated air temperature, carbon dioxide concentration, and combined effects of them), there is little evidence that indigenous (historically known) tree species in urban areas can acclimatize and prosper to compete with exotic species already commonly established in the cities. Urban ecosystem resilience depends on the diversity and vitality of urban trees. Current urban forests seem to lack in diversity, with high reliance on specific small numbers of species. The potential environmental threats to them include pathogens and diseases, biotic disturbance, and adverse effects of allelopathy [1,2]. Transpiration rates and levels of water-use efficiency (WUE) during long-term droughts may be modified by different trees along with varying cooling effects [3,4]. Differing foliar morphological traits and phenological patterns can affect biotic/abiotic resistance [5,6]. Diversity contributes to the increase of resistance to environmental stressors through competition and allelopathy among different species [7]. This may mean that high species diversity with indigenous trees might contribute to resistance to biotic/abiotic extremes and physiological acclimation in urban area over time.

There is much scientific evidence that exotic trees in cities have physiological (i.e., climate change mitigation and air pollutant removal) and phenological functions in trees on a leaf, canopy and cluster scale [8–10]. Nevertheless, there is still little known about the effect of indigenous tree species diversity on urban ecosystem services and their resistance to abiotic extremes.

Although some research has provided evidence of cooling effects [3], increase of stormwater absorption rates, resistance to soil pavement [11] and soil compaction [12] in exotic species, there has been little research conducted on the potential of indigenous trees acclimatizing to urban environments. Due to the lack of research on the topic, urban forest managers will continue the trend of preference toward planting small numbers of exotic species, leading to fewer indigenous trees in cities. With low biodiversity of indigenous trees in cities, urban forests will be less resilient, and the urban ecosystem service provided to urban citizens will be threatened. This is because native trees' diversity and individual function may provide ecosystem services that exotics do not.

1.2. Ecosystem Resilience

Ecosystem resilience generally can be defined as the ability to cope with disturbance and make a stable condition of the ecosystem without loss of ecological function and services in the ecosystem [13,14]. During the past few decades, ecosystem resilience has been a key concept in ecosystem ecology and ecosystem management [14]. Thus, ecological robustness is likely to have a crucial role in ecosystem service over time. This is because it is strongly connected to stabilization on environmental stress over a while [15]. The ecosystem resilience usually underpins the research concept that unstressed ecosystems and communities are resilient to anthropogenic impact and climate changes [14,16]. For instance, this concept in current research consists of diverse components with localized interaction and a selection process [17]. Therefore, resistance and resilience measurements are important for sustainable ecosystem health [16,17].

1.3. Definition and Importance of Urban Ecosystems

An urban ecosystem comprises biotic communities (including microbes, plants, animals, and humans), physical complexes, social elements, re-structurally built complexes by human activities meshed with the different components in spatially/temporally and heterogeneous interactions [18]. An urban ecosystem can be viewed as a conceptual framework for assessing ecological success in the urban setting to understand plant biodiversity, conservation, and ecological function in the urban environment [19]. Man-made habitats such as urban ecosystems can be considered an important biodiversity hotspot since there are entailed concepts and coexistence between indigenous and exotic species in the same environmental settings [20]. For these reasons, an urban ecosystem is usually accompanied by the concern of human impact and urbanization [21]. Therefore, urban ecosystems are important for understanding the ecological function and ecosystem resilience in cities because of increasing rapid urbanization, domestically and globally [22,23].

1.4. Role of Urban Forests in Ecosystem Services

Urban forests are likely to be a key component of urban ecosystems, because they provide various ranges of ecosystem services, which benefit urban dwellers. Therefore, the importance of urban trees can be highlighted through their wide range of functions. For instance, roadside trees can provide integral ecosystem service by improving urban wellbeing and aesthetic value [24]. Furthermore, urban forests/trees have many social and environmental functions, such as the purification of air and water quality improvement, the mitigation of urban heat island by its cooling effects [3,4,25], providing a place for recreational activities [26], and positively affecting the physical and mental health of urban dwellers [24,27] due to noise reduction [28]. Urban vegetation plays a role as a climate controller in cities, by reducing overheating [29] through shading during the summer season and by providing shelter in the winter months [10].

Compared with the urban ecosystem services of exotic tree species, those of indigenous trees are likely to provide contrasted or similar ecological functions [30]. It has been reported that various indigenous tree species that have a regional provenance have a high possibility for better environmental adaptability and also potential to handle challenging local climate conditions in urban environments. In addition to this, indigenous trees growing in cities can provide more cultural values and spiritual ecosystem service than exotic trees to urban dwellers. For instance, indigenous trees in urban settings attract more native birds and fauna [31,32] as well as provide a space for social, ritual, religious celebrations/ceremonies [31], and constitute a cultural heritage site. They are of cultural importance as an 'ecological integrity' [33] for citizens. However, whether indigenous trees in urban environments can prove equally resilient to abiotic stresses as commonly planted exotics is less studied.

1.5. Effects of Climate Change on Urban Trees

The environmental challenges faced by urban trees are likely to be exacerbated by climate change over time. As explained before, climate changes are linked to an increase in atmospheric temperature and a decline in annual precipitation with climatic variability among cities as a hotter and drier environment can be expected as time goes by [34]. Human impacts have led to a drastic increase in the levels of greenhouse gases (GHGs) such as atmospheric carbon dioxide (CO_2) and methane (CH_4) concentrations [35]. Global climate change (GCC) has been recognized as a warning sign to ecosystem health [36]. Climate change is expected to impact the world on a global scale as well as on a local scale. As a consequence of increased GHGs, including CO_2, the global average atmospheric temperature is expected to increase over time (by 1.5–6.0 °C till 2100 with an elevated CO_2 concentration 790 ppm (μmol mol^{-1})) [35,37–39]. In addition to this, increased global average surface and atmospheric temperature, evaporation and plant transpiration will be affected [40,41]. This would inevitably lead to variations in humidity and rainfall [42]. In some areas, this would lead to extreme rainfall events [34], while in other areas seasonal droughts are likely to be more severe [40,43,44]. Hence, GCC is a serious risk as well as a threat to plant growth and development, because forest ecosystems are highly sensitive to changes in environmental characteristics, which directly affect tree mortality and health condition [36,45]. Therefore, urban trees are more vulnerable to climate change with challenging abiotic extremes in cities, and finally can affect ecosystem services to urban dwellers [46].

High temperature and long-term drought conditions can affect tree growth, tree health condition, mortality, and restriction of carbon uptake [46,47]. This is because these abiotic stressors could result in carbon starvation of trees through reduced carbon assimilation and stomatal closure and a decrease in intercellular CO_2 concentrations [48]. As a defense mechanism, tree species also avoid reduction of transpiration by controlling water-use efficiency through species-specific response to abiotic stressors [49,50].

Warmer and higher temperatures can be the main factor leading to a reduction in trees' growth rates under drier conditions and soil water deficit [51]. Moreover, higher air temperature can accelerate urban heat island effect, increase surface's thermal impact and affect urban tree health [52]. Higher temperature and elevated CO_2 are regarded as pivotal determinants of tree species distribution. Drought due to a lack of precipitation can also limit tree species distribution in the urban area [53]. Temperature variations could largely affect plant's photosynthesis and respiration [54]. Regarding the higher temperature impact, it has been reported that tree species can adapt physiological adjustments to thermal conditions over time ('thermal acclimation') [54–56]. Berry and Bjorkman [57] and Crous et al. [58] noted that net photosynthesis can be shifted by 0.3–0.5 °C for each 1 °C shift in growth temperature. This is because photosynthesis is a key contributor to plant carbon (C) uptake and use. Therefore, thermal acclimation for C assimilation can be a tree's physiological adaptation strategy under GCC acceleration in cities [37,55]. There have been studies conducted on the reactions of introduced (exotic) tree species to degraded environments, but those of indigenous trees have yet to be researched. As having a biologically diverse habitat is necessary for health in a forest, it is important to conduct a study on the interactive effects of air temperature and elevated CO_2 levels on indigenous trees as well as on other exotic tree species in cities.

In this review, we compiled 162 publications (95 research publications/case studies and 67 publications of related reviews or background information about the issues at the global scale) in the recent decades. These publications reported data on ecophysiological and biochemical responses of trees grown in biotrons/phytotrons (i.e., under growth chamber/glasshouse conditions with urban environmental settings for tree growth dependent on different cities, countries and urban climate zones such as arid, tropical and temperate zones).

Several case studies in urban areas have been used in the past to improve our understanding of the morphological, physiological and biochemical responses of urban trees and to assess their relationships to trees' abilities to adapt to urban settings, sequester and store carbon. Most of the studies have been based in the US, followed by Australia, New Zealand and Korea as well as European countries, such as France and Germany (Figure 1).

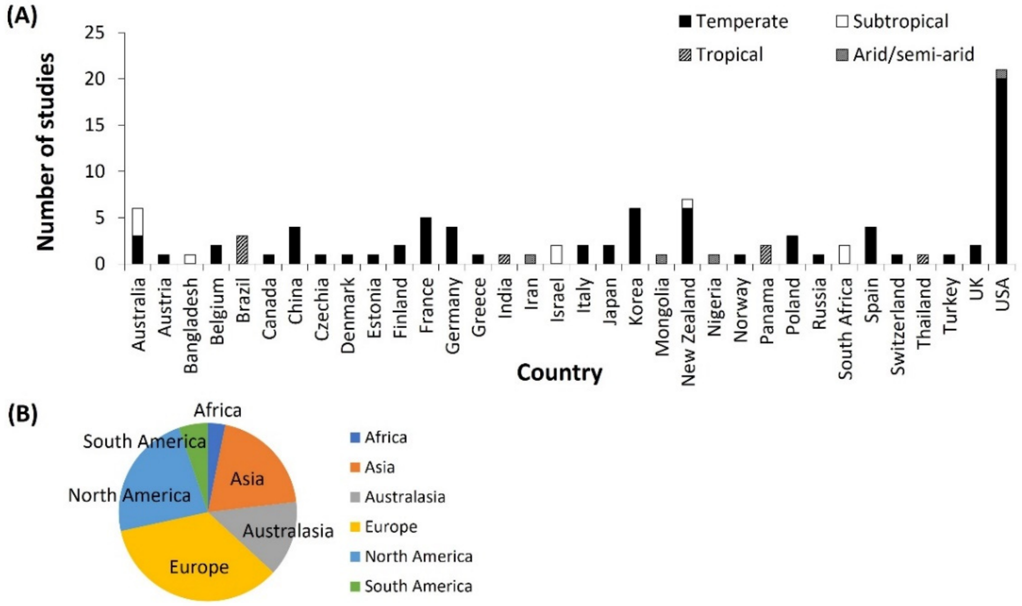

Figure 1. Summary of published studies investigating the morpho-physio-biochemical attributes of urban trees. (**A**) The number of studies and climate zone per country (excluding the following types of papers that covered global scale, commentary, opinion, forum, letters, communications, and articles focused only on environmentally controlled growth chamber/greenhouse conditions different from local climates), and (**B**) the total number of studies in our survey that are available from each continent.

This review explored and quantified how the general assumption about the growth and environmental defense mechanism of urban trees is supported by the existing data and literature in order to: (1) describe the basic concept of urban tree physiology study based on many case studies, and (2) lend support to the idea that we need to conduct more case studies and explore more compiled data to update the currently available information on the physiology of urban trees as a part of urban science in relation to the trends of global climate change.

2. Urban Tree Growth and Physiology: Synthesis and Discussion

2.1. General Tree Growth Condition in Cities

The urban environment is likely to strongly influence tree growth and physiological responses and vice versa since most of the urban areas have woody vegetation with uptake of CO_2 for photosynthesis [28]. Trees in the streets of many cities throughout the world belong to the component of urban infrastructure [59]. Therefore, these street trees that are public resources planted by municipalities provide numerous functional services that benefit urban residents [60]. However, the drastic changes in the urban landscape and environment have negatively impacted on urban trees and ecosystem health because many resources have been moved from other parts to cities [61]. For instance, soil moisture, atmospheric temperature, relative humidity (RH), and vapour pressure deficit (VPD) are often less favourable for street trees than for their rural environmental counterparts. This is because they result in slower or faster tree growth rate, lower density root systems and, higher leaf temperature, showing different relative tree growth rates till final tree development [6,62]. Another environmental feature for an urban area is a specific air chemical composition due to emissions from traffic, households, and industries, resulting in higher CO_2 concentration and more air pollution, increased atmospheric temperature by GHG. Hence, the urban trees growing on streets are subjected to a microenvironment characterized by higher pollution and GHG emission levels due to traffic volume, additional soil drought, and contamination by the input of heavy metals or high salinity [63], as well as a restricted area for root extension that in turn decreases water availability (i.e., cover plate of a tree base, tree pit covers, and road pavement) [11,64]. Although the physiological processes in urban trees are similar to those growing in natural forests, site conditions and regional characteristics (i.e., roadside trees and trees in a park) can induce different ecophysiological responses of trees and tree health at different site conditions. For instance, Olchowik et al. [65] reported that unhealthy (i.e., based on determination of chlorophyll fluorescence and level of foliar chlorophyll (Chl) content) street and park trees showed less diversity and abundance of *Cenococcum geophilum* fungi (the most common ectomycorrhizal fungal species encountered in forest ecosystems). This is because soil conditions under which street trees grow can contain much more Cl^- and Na^+ than those from the park trees [65]. Nevertheless, the ambient conditions under which these processes occur in cities are more variable and extreme than in natural forests and habitats [10]. Indeed, environmental conditions in urban areas are tremendously diverse because of differences in climate, building density and structure, road material, soil pavement. These factors lead to an increase in soil temperature, humidity and CO_2 concentration over time [66,67]. Generally, urban areas are warmer than their surroundings by up to 1–3 °C because of the dominating stone structures that absorb radiation more than vegetated surfaces and the lack of the cooling effect from evapotranspiration [10,68]. This is known as the urban heat island (UHI) effect, and urban areas are remarkably warmer at nighttime and during the winter season due to changes of evapotranspiration, infiltration and runoff by urban surface types [69].

2.2. General Parameters for Measurement to Abiotic Extremes in Cities

Based on these kinds of growth conditions and environmental characteristics, understanding and analyzing the trees' responses concerning the urban environment are required to scale up from individual tree levels to community and ecosystem levels [70]. In the urban environment, higher temperature and drought stress generally affect the plant's photosynthetic apparatus (i.e., photo-inhibitory and photo-oxidative damage) [71,72]. To determine physiological and biochemical indices of trees' abiotic stress, the parameters are generally used for measurements of the following: net photosynthetic rate (P_n), maximum photochemical efficiency of PSII (F_v/F_m), maximum electron transport rate (ETR), and PSII operating efficiency (F'_q/F'_m) [73]. Moreover, gas exchange measurements (i.e., photosynthetic rate, stomatal conductance, transpiration, and intercellular CO_2 contents) can provide important information about Rubisco activity (V_{max}) and maximum electron transport rate (ETR) for regenerating of ribulose-bisphosphate (J_{max}), which are both important for determining the limiting conditions for photosynthesis on the urban abiotic extremes [9,74–76].

Understanding tree growth in urban environments is likely to be vital for studying urban tree physiology and finding the reason how tree development is affected by the urban environment over time. To study urban tree physiology, it is required to use a combination of approaches (from molecular, biochemical, and morphological analysis to modelling approaches) and at different spatial scales (from a cell, leaf, and plant unit to forest and city unit) [45,77,78]. Measuring and studying tree physiological responses and morphological traits as well as growth development will be required for a better understanding of the capability on the impact of GCC on urban vegetation, and these can support strategies to optimize urban ecosystem management with resilience to environmental restraints (Figure 2).

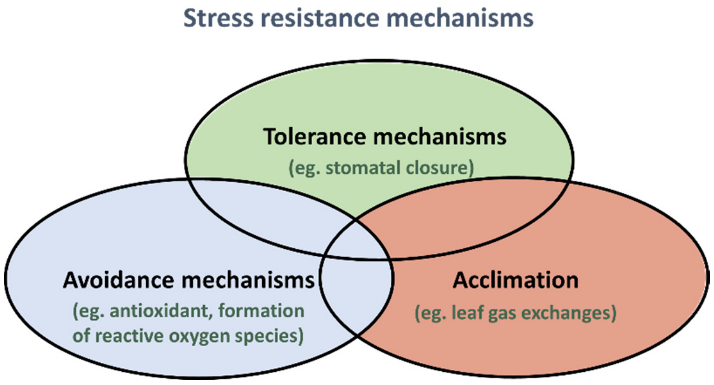

Figure 2. Conceptual framework of abiotic stress resistance mechanism in a tree.

3. Responses of Trees to Water Deficit: Synthesis and Discussion

Tree species show various adaptation strategies through their physiological responses and defence mechanisms. Drought is considered as a ‘complicated abiotic stress’ that affects various types of plants’ growth including woody plants with different levels of water deficits [79,80]. Moreover, drought and abiotic extremes can predispose trees to injuries by other biotic stresses such as pest insects and pathogens [81]. In this regard, trees have defence mechanisms and adaptation strategies to avoid or tolerate drought stress [82,83]. They can shorten their foliar life cycle and enhance the capacity of getting water through leaf or root [83,84]. Trees that have tolerance strategies for drought increase cell wall elasticity to maintain tissue turgidity through improving osmotic adjustment ability [72]. Altering metabolic paths and removing parts such as older leaves are other tolerance strategies for drought [85–87]. Even though different plants, including woody plants, have various responses according to their strategies and the severity of drought, all responses are related to getting rid of excess radiation and evaporation in the ends [79,82]. The responses of trees to drought stress can be divided into tree growth and morphological changes, tree physiological responses, and biochemical changes (Table 1).

Table 1. General parameters of measurement for effects of abiotic stressors on tree species.

Independent Variable	Rationale of Measurement	Reference
Leaf gas exchange (Auto-log; seasonal pattern)	Leaf gas exchange rate measurement can provide important information of abiotic stress extent through photosynthetic rate, stomatal conductance, transpiration rate, and intercellular CO_2 contents.	[72,88,89]
Light response curve (PN-photosynthetically active radiation (PAR) curve; A/*Q* curves; diurnal pattern)	Photosynthesis is influenced by physiological patterns over time and diurnal patterns are linked to tree growth, development, and environmental acclimation over time.	[72,89]
Estimation of derived parameters (V_{cmax} and J_{max}; A/*Ci* curves; indirect Rubisco activity measurement)	A/*Ci* curve also can be utilised for estimation of indirect Rubisco activity extent as an abiotic stress indicator. the plateau of the A/*Ci* curve related to the rate of maximum electron transport (μmol m^{-2} s^{-1}). As J_{max} (the rate of maximum electron transport (μmol m^{-2} s^{-1})) is related to the plateau of the A/*Ci* curve. The parameters from the A/*Ci* curves (i.e., V_{cmax} (maximum Rubisco activity) and R_d (the rate of dark respiration in μmol m^{-2} s^{-1})) can be calculated from the following equations: V_{cmax} (maximum Rubisco activity) = $\{k \times [Ci + Kc \times (1 + O/K_0)]2/[\Gamma^* + Kc \times (1 + O/K_0)]\}$; R_d (dark respiration rate) = $\{V_{cmax} \times (Ci - \Gamma^*)/[Ci + Kc \times (1 + O/Kc)] - (k \times Ci + i)\}$; J_{max} (election transport capacity) = $\{[4 \times (P'_{max} + Rd) \times (Ci + 2 \times \Gamma^*)]/(Ci - \Gamma^*)\}$. The rate of V_{cmax} can be used to estimate stress extent through the initial slope of the A/*Ci* curve using the linear equation ($A = k\, Ci + i$) within 50–200 μmol mol^{-1}. where Kc and K_0 are normally 404.9 μmol mol^{-1} and 278.4 mmol mol^{-1} at 25 °C, respectively, and O is 210 mmol mol^{-1}. *Ci*, where k, the initial slope of the A/*Ci* curve, can be described as CE (carboxylation efficiency), and –i/k is equal to Γ* (CO_2 compensation point in μmol mol^{-1}) in the absence of the mitochondrial respiration.	[90]

Table 1. *Cont.*

Independent Variable	Rationale of Measurement	Reference
Photopigment (chlorophyll and carotenoid contents)	Destructive photopigment measurement can be used as an accurate abiotic stress indicator for plant species. Chlorophyll a (Chl*a*) = 12.7 × A_{663} − 2.69 × A_{645}; Chlorophyll b (Chl*b*) = 22.9 × A_{645} − 4.68 × A_{663}; Total Chlorophyll (Chl_T) = 20.2 × A_{645} + 8.02 × A_{663}; Total Carotenoid (Car_T) = (1000 × A_{470} − 1.82 × Chl*a* − 85.02 × Chl*b*)/198. A_{XX} means the absorbance of the extract solution in a 1 cm path-length cuvette at a specific wavelength. The pigment concentration will be calculated as g kg^{-1} of FW from a 1 g m^{-3} (µg mL^{-1}) cuvette of extract.	[72]
Photosynthetic water use efficiency (WUE)	WUE is a key parameter related to photosynthetic activity during the drought and water deficit. WUE = A_{net}/Tr; WUE: Water use efficiency (µmol CO_2 $mmol^{-1}$ H_2O); A_{net}: Photosynthetic rate (µmol CO_2 m^{-2} s^{-1}); Tr: Transpiration rate (mmol H_2O m^{-2} s^{-1})	[91]
Leaf water status (LWP, leaf water potential; RWC, relative water content)	In physiological aspects, RWC and LWP are important indicators to estimate and quantify the extent of net water loss and water stress for plant species. RWC (%) = [(fresh weight − dry weight)/(turgid weight − dry weight)] × 100	[92,93]
Growth measurement (HRGR, Height relative growth rate; DRGR, Root collar diameter relative growth rate)	The relative growth rate provides more accurate changes of plant growth during the experimental period. RGR (cm day^{-1}) = (ln M_f − ln M_i)/T, M_i and M_f are initial and final growth data (seedling height and diameter), respectively, and T is the time interval (number of days).	[94]
Specific leaf area (SLA)	This is because SLA measurement is highly connected to osmotic adjustment and leaf longevity under abiotic stresses such as drought. SLA (cm^2 g^{-1}) = leaf area (cm^2)/leaf dry weight (g)	[95,96]
Leaf mass per area (LMA; inversion value of SLA)	Leaf area is decreased while weight and leaf-thickness are increased during the drought. LMA (is increased in drought conditions) and *Rd* are positively correlated on the tree's drought resistance study. Namely, if trees are increased their LMA values as a drought stress response, their root collar diameter can be increased relatively, as a resistance.	[97,98]
Stomatal characteristics and density (scanning electron microscopy; SEM)	This way can demonstrate thermal and drought stress induce reduced stomatal size (i.e., length and width) to control stomatal conductance (*Gs*) through the visible method.	[99]
Drought resistance index by root collar diameter (*Rd*)	This aims to evaluate drought resistance among different species, *Rd* and comparison study of relative change in morpho-physio-biochemical attributes at the same page can be more accurate to choose superior species amid the abiotic extremes. Drought resistance index by root collar diameter (*Rd*) = $X_{Drought}/X_{Control}$	[100]
Determination of chlorophyll fluorescence	Chlorophyll fluorescence measurement is one of the easiest ways to measure plants' stress responses through a non-destructive way. Environmental favourable conditions of plant species can be evaluated by chlorophyll fluorescence and its transient measurement (PSII behaviour).	[72,101,102]
Determination of proline contents	Through osmoprotectants proline contents, trees' abiotic stress extent can be quantified as one of the defence mechanisms.	[72,103,104]
Determination of lipid peroxidation (malondialdehyde; MDA)	MDA is a key parameter to quantify abiotic stress extent of the plant. MDA (nmol g^{-1} FW) = ((A_{532} − A_{600})/155,000) × 106	[72,105,106]
Total leaf nitrogen content (T-N) assessment	Quantifying foliar nitrogen (N) budget is linked to tree health and environmental adaptation. As it is an important contributor to plant vigour, and key source of photosynthesis and photopigment.	[107]

3.1. Changes in Growth and Morphological Parameters in Response to Drought

Stomatal control in response to drought stress is likely to be the most important morphological change. First of all, drought tree growth and biomass yield were found to be inhibited in many case studies on fast and slow-growing tree species, such as poplar and olive trees [108,109], because trees have to control carbon assimilation to avoid getting dehydrated during a drought period [110]. Limited carbon assimilation could result in carbon allocation as high as a tree could to maintain leaf water potential (LWP; ψw) [72]. Trees maintain a high level of LWP (ψw) to maximize water uptake and/or minimize water loss as one of the adaptation strategies [82]. Plants generally can control moderate water stress. There are generally two physiological strategies for minimizing water loss in plant species. The first way is stomata closure of leaf during the daytime and the second way is to increase leaf thickness for higher LWP [89,92,111], maximizing water uptake [82]. Wilson et al. [112] and Paudel et al. [113] also reported that trees reduce stomatal sizes to control and optimize stomatal conductance (Gs) during drought. Furthermore, trees' leaf morphologies can be changed to minimize water loss through a thickened leaf layer (i.e., cuticle and trichome), leaf rolling, heliotropism that causes a leaf to grow towards the sun, and reduction in the density and length of stomata in response to drought [99,114,115]. Regarding maximizing water uptake, the root system can be developed by carbon allocation that increases the root/shoot ratio till it reaches the brink of the value due to a limitation of drought [86,116,117].

3.2. Changes in Physiological Parameters in Response to Drought (Stomata and Leaf Area)

Carbon assimilation (i.e., photosynthesis) is the most fundamental and complex physiological process and metabolism in plant development [73,78]. Thus, trees' physiological traits are adapted to minimize water loss and maintain water potential to facilitate carbon assimilation [89]. Trees minimize foliar water loss through stomatal closure while increasing water-use efficiency through transpiration rate control [82,86,88,101]). Reduction in photosynthesis could be classified into two responses: stomatal limitation and non-stomatal limitation. Plant metabolism is relatively receptive and/or vulnerable to many environmental factors, such as water supply, soil moisture, atmospheric temperature, CO_2 concentration, and air humidity [118]. As a way through non-stomatal limitation, specific leaf area (SLA) can be used as a drought indicator based on the ratio of leaf area to leaf dry mass because leaf thickness is increased when plant species encounter water deficit with a higher water potential [72,92,119]. With regards to stomatal limitation, a leaf plays an important role in controlling carbon assimilation at the beginning of a water deficit. To quickly gain control of gas exchange and water status, it could be controlled by abscisic acid (ABA) and cytosolic pH gradients under water deficit [82,120]. As drought is prolonged, non-stomatal limitation plays an important role in reduction of carbon fixation [77,121,122]. Feltrim et al. [123] reported that a tree closes the stomata to avoid 'embolism' leading to a nutrient handicap and reduced photosynthesis in the physiological study of *Eucalyptus*. This is because a tree's responses under drought stress induce an increase of water flow into the xylem through the water pathway against hydraulic resistance, leading to xylem tension. Schenk et al. [124] reported that this can be a lethal blow to trees because excess tension can affect embolism formation. Embolism interrupts the water column and the water transport above ground. During long-term monitoring, when obstruction of xylem sap transport is prolonged, embolism can induce a high rate of tree mortality [125]. Throughout a severe drought period, Rubisco activities are restricted, and the carboxylation rate is decreased for various reasons [121,126]. As a result of photosynthesis reduction, excess energy is produced and it induces harmful oxidative stress [79,127–129].

3.3. Changes in Physiological Parameters (Especially Photosynthetic Pigments) in Response to Drought

Photosynthetic pigments (i.e., chlorophyll (Chl) and carotenoid (Car)) are key parameters to quantifying photosynthetic response in individual trees and the amount of gross primary production (GPP) in the forest ecosystem [130]. This is because these pigments are playing an important role in light-harvesting, photosystem (PS) protection, and tree development and growth [131]. The Chl content is decreased to limit the amount of energy absorbed, and the dissipated energy is increased to protect its photosystem by non-photochemical quenching or photochemical quenching ways. It is also a key contributor to photosynthetic rate [104,122]. Based on the case study of exotic tree species that commonly grow in cities such as *Shorea robusta*, *Ginko biloba*, and *Platanus occidentalis*, Car content in leaves showed a decreasing tendency in urban trees with abiotic extremes such as soil water deficit, high air temperature, and air pollution [74,75]. Chl has a key role in the carbon assimilation process of capturing light energy from natural light via photosynthetic pigments [130]. Thus, the photosynthetic capacity of trees can be indirectly assumed to be related to the foliar Chl contents [130,132], and Chl content was investigated in combination with measurements such as leaf area index (LAI) for plant productivity [133]. This parameter can be a marker of abiotic stress effect on trees in a forest ecosystem [134]. Car consists of carotenes and xanthophylls and this group of photo-pigments is regarded as another stress indicator besides the ratio of chlorophyll a and chlorophyll b (Chl*a*/Chl*b*) [9]. Car is an essential structural component of the photosynthetic antenna with Chl and participates in harvesting light energy for carbon assimilation [135]. Lee et al. [72] reported the Chl*a*/Chl*b* and the ratio of total chlorophyll and total carotenoids content (Chl_T/Car_T)

in poplar seedlings under severe drought conditions decreased compared with control treatment. Car can also be utilized in the defence mechanism against abiotic extremes such as the imbalance of reactive oxygen species and the manifestation of oxidative stress [136]. Moreover, Car plays a central role in the dissipation of excess light energy and provides protection to photosynthetic reaction centres (PSRC) [137].

3.4. Changes in Biochemical Parameters in Response to Drought

In plant stress physiology, Farquhar et al. [91] and Farquhar et al. [138] have described a quantitative biochemical model on photosynthesis, and it is utilized in many experimental botany and forestry studies. More studies have been focused on the relationship between physiological and biochemical characteristics of a leaf such as photosynthetic rate (P_n), maximum carboxylation rate (V_{cmax}), and maximum electron transport rate (J_{max}) in relation to tree growth rate and to specific leaf area (SLA) [76,139]. A quantitative plant biochemical analysis through V_{cmax} and J_{max} is a key factor in biochemical reactions with foliar gas exchange models under different experimental conditions [140,141]. Lee et al. [72] reported that trees grown in extremely dry conditions such as arid areas had physiological adaptation strategies through stomatal aperture limitation to minimize leaf gas exchange under drought conditions. The photosynthetic efficiency of trees might be restricted by photoinhibition, but generally trees could reduce their Chl antennae to reduce carbon uptake under drought [72,128]. The changes in the biochemical parameters of *Quercus* and *Populus* spp., two common exotic species, under abiotic extremes such as different water deficit levels can be the first important step in a study to gain a better understanding of the decline phenomenon associated with water deficit in trees [72,142].

To maintain cell turgor pressure, high cellular concentrations of osmolytes including proline and betaine are accumulated [103,104]. These ‘compatible solutes’ are considered not only to protect enzymes and membrane structures but also to scavenge reactive oxygen species (ROS) in addition to ‘osmotic adjustment’ [79]. As a result of excess energy, ROS are produced and the lipid peroxidation (malondialdehyde; MDA) level is increased under drought [72,105,106]. To remove these ROS, plants develop their antioxidant mechanisms through enhancing the activities of superoxide dismutase (SOD) and catalase (CAT) [79,86,111,127,128]. Weber and Gates [88] reported that the rate of photosynthesis of *Quercus* spp. rapidly decreased when drought was prolonged and dropped to zero under severe drought. It has been reported that *Quercus* spp. has two types of drought resistance mechanisms, such as avoidance mechanisms (e.g., deep root system, leaf curling, and smaller leaf area) and tolerance mechanisms (osmotic adjustment and stomatal control to maintain a moderate photosynthetic rate) during a severe drought event [143]. Quero et al. [144] also reported that a study of the effect of abiotic stresses, such as drought on leaf morphological and physiological responses, should be conducted in relation to the changes at the leaf level and whole plant growth and development. Niinemets et al. [70] reported that a lower photosynthetic capacity of *Quercus* seedlings was closely related to foliar biochemical changes (i.e., Rubisco, electron transport, maximum carboxylation rate (V_{cmax}), and maximum electron transport rate (J_{max}) of leaves). Generally, trees can acclimate in response to different environmental stress conditions. For instance, trees can control biomass and nutrient allocation from roots at the cellular level. Trees can also reallocate nitrogen budget through photosynthesis at the leaf level [107].

Hare and Cress [105] reported that proline content in plants increased under severe drought (i.e., severe water stress) to protect antioxidant enzymes and plasma membranes. It is also accumulated in response to other environmental stresses, including high temperature, nutrient deficiency, and atmospheric pollution. The accumulation of proline in response to water deficit is the result of enhanced synthesis from glutamate [105,145]. Besides, Miller et al. [146] revealed that proline might be able to stabilize plasma membranes and antioxidant enzyme, such as superoxide dismutase. Based on previous studies, the key mechanisms and tolerance strategies of urban trees to drought stress are summarized in this paper (Figure 3). Few studies, however, have been conducted on the relationship among morphological, phenological, biochemical and physiological characteristics of many indigenous trees or regionally important tree species in cities. For instance, pruning is one of the most common ecosystem services by urban dwellers. However, pruning could be a benefit and drawback to urban trees. This is because few studies suggested that crown thinning improves either urban tree health or structural stability [147]. However, Suchocka et al. [147] reported that pruned trees still had fully green foliage while unpruned tree leaves exhibited leaf discolourations or leaf fall in roadside affected by soil salinity, osmotic stress and heavy traffic in cities. Swoczyna and Borowski [148] also reported the delay in leaf phenology stages of roadside trees (*Platanus* × *hispanica* 'Acerifolia') in London with heavy traffic conditions and vehicle speed in the city. Therefore, it is necessary that biochemical traits and relationships with phenological/physiological responses of trees are investigated, and then to conduct a comparative study among different species to find the superior species under urban stress conditions.

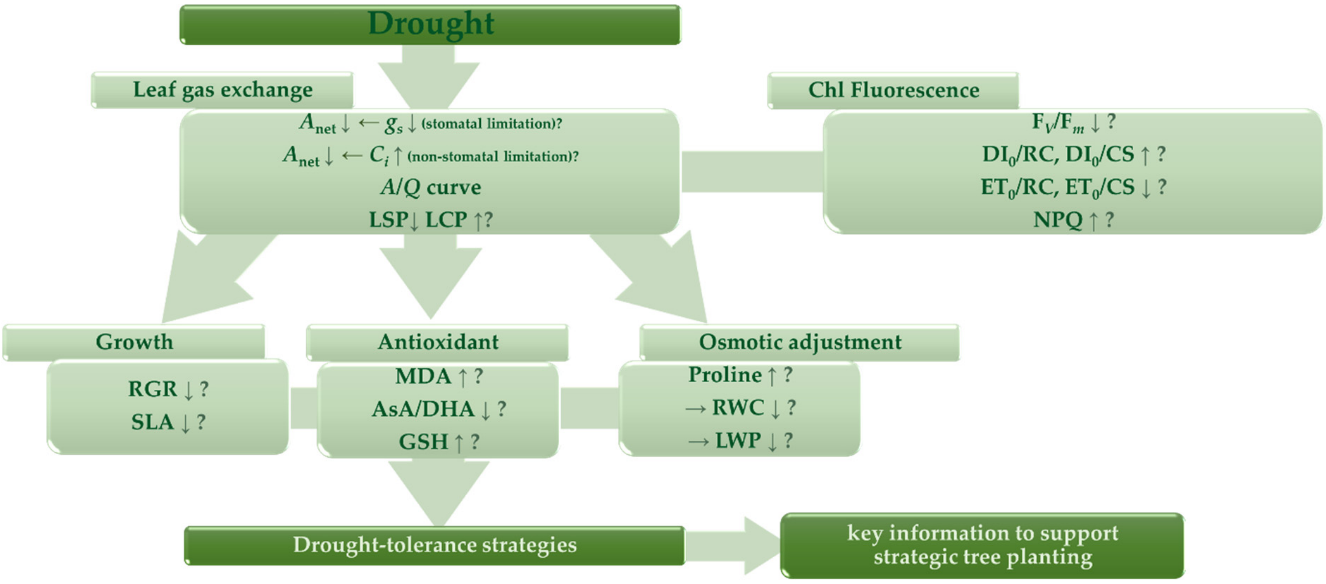

Figure 3. Key mechanisms and tolerance strategies to drought stresses in a tree. ↑ refers to the increase, ↓ refers to the decrease and a question mark means a scientific inference. ← or → means the deduction of a physiological or biochemical reaction in a tree response.

4. Responses of Trees to High Temperature and Elevated CO_2: Synthesis and Discussion

4.1. Changes of Leaf Gas Exchange in Response to Atmospheric Temperature

Higher temperatures can foster tree growth, but if higher than a tree's ideal range of growth temperature, tree growth can be adversely affected. High temperature and/or heat stress can cause a myriad of morphological and physiological adaptations in the trees. The anticipated GCC projections are that atmospheric temperature in cities is likely to increase in both day- and nighttime [39]. The transpiration rate (Tr) of trees is significantly affected by the vapour pressure differences between the humidity of the inside of leaves and that surrounding trees [3]. Kirschbaum [149] reported that tree transpiration and the associated cooling effects will increase if daytime and nighttime temperatures increase because vapour pressure deficits (VPD) increase with increasing temperature. However, effects of increased atmospheric CO_2 concentrations on trees include reductions in stomatal conductance (Gs). Hence, a decrease in the transpiration rate might also be triggered, which could affect plant growth and aboveground biomass production [149–151]. Allen [152] and Bert et al. [153] reported that if CO_2 concentration was doubled, Gs would be reduced by 20–40%. Therefore, stomatal closure by CO_2 might have invalidated any increase in transpiration with increased air temperature [154].

4.2. Effects of Elevated CO_2 Levels on Abiotic Stress Mitigation

Elevated CO_2 concentrations generally foster tree growth because a higher photosynthetic rate and water-use efficiency could be induced through a rise in internal CO_2 concentrations in leaves due to a change in the ratio between water loss and carbon gain [155]. On the contrary, elevated CO_2 concentrations mitigate adverse effects of abiotic stress through increment in or maintaining photosynthetic rates in response to high external CO_2 concentrations even if Gs is declined [156,157]. These results suggest that it is possible to buffer abiotic stress and trees' damages from abiotic stress such as heat. However, it has been reported that the mitigation of adverse effects does not include protection of chlorophyll content and maximal photochemical efficiency (F_v/F_m), and there are no previous reports on the 'CO_2 ameliorating effect' on light utilization [102]. Moreover, Kitao et al. [158] reported a reduction in photochemical quenching and increased susceptibility to photoinhibition in *Betula platyphylla*. However, the threat of photoinhibition was mitigated by the long-term soil drought condition. Poorter et al. [97] reported that the leaf mass per area (LMA) increased under elevated CO_2 conditions, and was inversely related to the specific leaf area (SLA). Yin [159] also reported that SLA increased under elevated CO_2 concentrations because leaf size increased whereas leaf mass was decreased and thinned. However, high temperature and dry conditions might change SLA and leaf traits. Lin et al. [160] reported that elevated CO_2 concentrations under dry conditions affected the thickness of the needles of *Pinus sylvestris* and that of mesophyll tissue increased. These results imply that an increase in CO_2 concentration might lead to an increase in leaf thickness or dense tissues. Thus, supplementation of carbon by elevated CO_2 concentration is expected to alter leaf morphological traits under dry conditions. Finally, understanding urban trees' conceptual model of key mechanisms and reaction scenarios to climate change is likely to provide new information on species tolerance to climate change in cities (Figure 4).

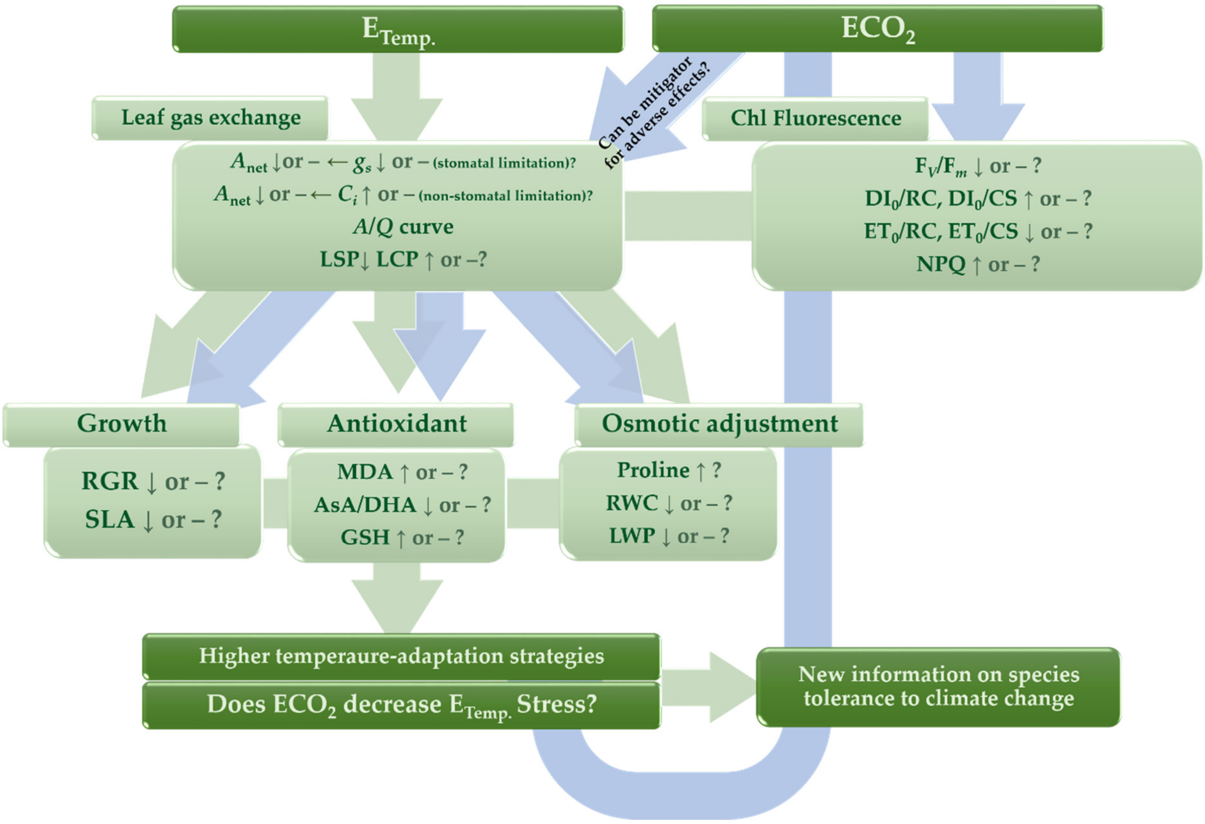

Figure 4. Key mechanisms and adaptation strategies to urban climate changes in a tree. ↑ refers to the increase, ↓ refers to the decrease, – means no change and a question mark means a scientific inference. ← or → means the deduction of a physiological or biochemical reaction in a tree response.

5. Conclusions and Future Perspectives

Growing conditions of trees largely differ between urban areas and non-urban land areas (i.e., forest sites, silvopasture areas and riparian forest buffer) [3,10]. This is because urbanization means changes in trophic structure, biotic diversity, element cycles as well as microclimate [6,21]. The trees' morphological, physiological and biochemical traits under drought, high atmospheric temperature and elevated CO_2 concentration, which are common characteristics in cities under global climate change trends, have been the focus of this review. Here, a survey of the relevant literature, the current progress in urban tree diversity and morpho-physio-biochemical attributes for urban ecosystem resilience under climate change conditions has been presented. Many studies have shown physiological, biochemical, and morphological characteristics of small numbers of specific tree species (i.e., *Platanus* spp., *Quercus* spp., *Populus* spp., *Salix* spp., *Pinus* spp., *Picea* spp., *Betula* spp., and *Eucalyptus* spp.) in GCC projection scenarios and urban abiotic extreme settings [161]. To evaluate urban trees' health conditions and environmental acclimation of municipal trees, it was found that the fundamental and substantial criteria to consider are: (1) leaf gas exchange patterns by time and local climate, (2) chlorophyll fluorescence, (3) annual relative growth rate, (4) specific leaf area, (5) antioxidant capabilities, and (6) osmotic adjustment by tree species based on local climate and urban environment. However, in the urban science context, few studies have been conducted on the combined effects of elevated temperature and elevated CO_2 level on trees' physiological responses [162]. Specifically, those combined effects of elevated CO_2 concentration and/or drought on indigenous trees have not yet been clarified in the urban area settings at both the seedling and canopy levels. The phenological, morphological and physiological responses as well as the mechanism associated with the effects of elevated CO_2 level and high temperature and/or drought might be species-specific (i.e., overall tree vitality, premature leaf shedding, canopy dieback, reduced photosynthesis or damage of photosynthetic apparatus). Understanding the role of species diversity, including indigenous tree species, in the ecosystem resilience of cities is key to strategic ecosystem management for disturbances from anthropogenic impacts. Thus, to understand indigenous trees' role in GCC scenarios and urban environmental settings, it is likely important to investigate their physiological, morphological, and biochemical actions altogether.

In this review, it seems that the physiology-based model concept supports the future urban tree physiology research needs. In particular, it is necessary to develop integral methodologies and an urban tree research concept to assess how the main and combined effects of drought and/or climate changes affect indigenous and exotic trees that are commonly grown in cities. This concept can facilitate the provision of more ideas in urban tree selection for urban forest construction.

However, further discussion of the use of various species including indigenous trees for sustainable urban forest management and ecosystem services is required. In addition, it is necessary to quantify integrating morpho-physio-biochemical attributes regarding tree responses to other environmental factors in cities. Examples of the relevant morpho-physio-biochemical attributes in relation to urban ecosystem resilience against rapidly changing urban environments include ozone (O_3), air-borne pollutants of various sizes (PM_{10}, $PM_{2.5}$), disturbance to trees' circadian rhythm by nighttime light pollution from street lighting, soil compaction and pollution from pavement and microplastic particles, and osmotic stress from soil salinity change caused by canopy pruning and loss of microbial diversity in soils. Further studies will uncover the benefits and drawbacks of planting urban trees, and the current limitations and future management of urban trees. This will answer the question of whether the role of unexploited trees such as indigenous trees and new tree species in urban forests/streets would have more benefits or drawbacks for the urban forestry management at the canopy and seedling levels.

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