4 Urban Plant Ecophysiology

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Introduction

Plants have long been cultivated to improve quality of life in dense human settlements, mitigating the environmental stresses of urban living. Urban landscape elements include gardens, trees and lawns designed to provide aesthetic and functional benefits to local residents, as well as urban natural areas that reflect the native biome vegetation. Different types of informal green space are typically found in interstitial urban areas wherever plants find space, light, water and nutrients to grow (Rupprecht and Byrne, 2014). A growing body of literature evaluates the health and well-being benefits of these diverse types of intentional and unintentional urban nature, and advocates for their inclusion in sustainable urban design (Konijnendijk *et al.*, 2013; Kowarik, 2018; Threlfall and Kendal, 2018). But how does the urban environment impact plant physiological function, whether cultivated or not, native or introduced species, across the range of habitats found within a metropolitan area? And how might those impacts affect the ability of urban plants to perform the ecosystem services desired by urban residents?

Plant ecophysiology (or physiological plant ecology) is a field of study concerned with the function and performance of plants under constraints imposed by their growing environment. Ecophysiological research is integral to understanding and managing the fluxes of heat, water, gases and nutrients that underlie urban ecosystem science and that help make cities both liveable and sustainable (Alberti, 2005). The past few decades have seen a rise in research on plant community ecology, but ecophysiological studies have lagged behind, possibly due to methodological challenges, or due to the recent popularity of other topics in plant biology (Beyschlag and Ryel, 2007).

A systematic approach to urban plant ecophysiology that is tied to decision making can support efforts to improve both liveability and sustainability of cities via plant physiological function. Plants are the foundation of most nature-based solutions to environmental, social and economic challenges, and physiological function is the engine that drives the provision of associated ecosystem services. Knowledge about variation in plant physiological function across genotypes, species, urban site types or regions that accounts for differences in management intensity or land use history will help inform the continued (and equitable) provision of these services. This chapter presents a comprehensive approach to the study of urban plant ecophysiology and provides a framework for future study, examining existing research, methodological challenges and linkages to nature-based solutions in cities.

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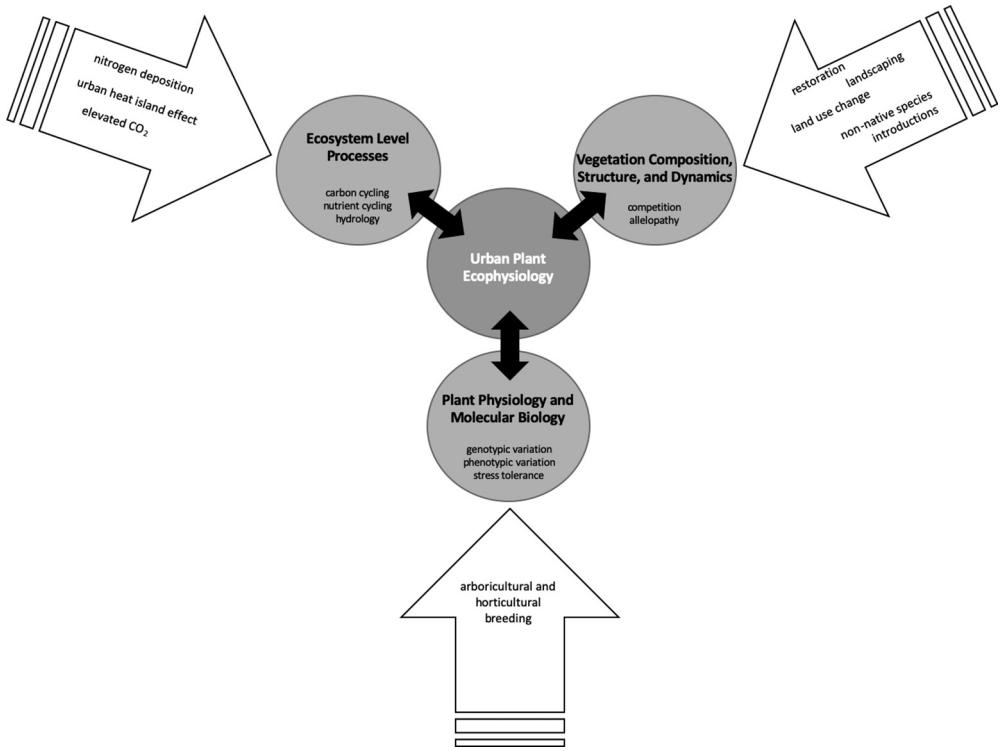

Fig. 4.1. A framework for understanding urban plant ecophysiology in relation to other fields of study and related social-ecological processes. Circles represent the major disciplines in plant biology and include examples of phenomena studied within each discipline. Black arrows represent the feedbacks between urban plant ecophysiology and these ecosystem, community or organismal processes. Clear arrows illustrate examples of social and biophysical processes that impact urban ecosystems at different scales of space and time through direct or indirect human activity. (Adapted from Beyschlag and Ryel, 2007 to include examples of phenomena within each discipline and of social and biophysical processes)

Approaches to the Study of Urban Plant Ecophysiology

The study of plant ecophysiology in any environmental context creates an important link between scales and disciplines in plant science (Beyschlag and Ryel, 2007; Fig. 4.1). Research in plant ecophysiology addresses spatial scales from organelles to ecosystems and corresponding timescales from seconds to millennia across biochemical, physiological, ecological, and evolutionary processes (Osmond *et al.*, 1980). In the urban context, plant ecophysiology provides a mechanistic understanding underlying current advances in the study of urban ecosystem fluxes (e.g. Reisinger *et al.*, 2016; Menzer and McFadden, 2017) and plant community ecology (e.g. Aronson *et al.*, 2016; Kowarik and von der Lippe, 2018).

Predictions of individual plant, community and ecosystem responses to social-ecological urban environmental factors are only possible with knowledge of the underlying physiological mechanisms. Figure 4.1 illustrates examples of social and biophysical processes that impact urban ecosystems at different scales of space and time through direct or indirect human activity. Some processes, such as the urban heat island effect or non-native species introductions have been well studied across many urban areas. In contrast, the processes of natural selection compared to domestic selection through

arboricultural and horticultural practices and resulting impacts on plant ecology are an emerging area of research that has received little attention.

Until now, the study of urban plant physiology has been dominated by the paradigm of urban environmental stress as well as dominated by the urban-to-rural gradient approach. The two concepts may be combined, such that an urban–rural gradient is described as a 'stress gradient' (Calfapietra *et al.*, 2015). Although these paradigms have provided an initial approach to urban plant ecophysiology and resulted in important research findings, they are incomplete and reveal the need for a more comprehensive framework.

It is commonly assumed that urban plants must acclimate or adapt to conditions of 'permanent stress' (Calfapietra *et al.*, 2015). Indeed, there are many scenarios in which plants experience stress in urban environments, resulting in less vegetative growth, reduced flowering and seed production, failure to germinate, or mortality. The harsh growing conditions of street trees in particular have been studied for several decades (Bassuk and Whitlow, 1987; Cregg and Dix, 2001; Meineke *et al.*, 2013), leading to a search for stress-tolerant tree species suitable for highly developed urban sites (Sjöman and Busse Nielsen, 2010). Street tree pits surrounded by pavement are known to provide particularly stressful environments due to soil compaction, high soil pH, soil solution chemistry affected by dog urine and de-icing salts, waterlogging, lack of water, air pollution, high summer temperatures, and mechanical damage from people and vehicles (Whitlow and Bassuk, 1988). However, there are many environmental constraints to plant growth that are reduced in urban environments, depending on the plant species and site type (Table 4.1). While highly visible, the street tree pit represents only a fraction of urban tree sites, let alone the habitats of all vegetation contained within a city. Trees planted in lawn strips, residential gardens, parks, institutional grounds, or naturally regenerating across a variety of public and private land uses may have access to more light, nutrients and water than trees in a rural forested condition, and the added heat or heavy metals may not be enough to negatively impact physiological function, depending on the species and site type (Iakovoglou *et al.*, 2001; Pretzsch *et al.*, 2017; Sonti, 2019). Even street trees are likely to experience less competition and reduced herbivory from deer and other mammals compared to forest-grown trees. The variety of plant species and site types found within cities means that various abiotic and biotic aspects of the urban environment may be stressful or beneficial to plant physiological function.

Urban influences on environmental constraints do not occur in isolation, but interact to determine plant growth, physiological function and reproductive success, which in turn influence community composition and ecosystem fluxes. For example, research from the eastern and midwestern USA shows that insect herbivore density increases with elevated urban temperatures (Youngsteadt *et al.*, 2015), and that drought stress can predispose urban trees to insect pest infestation (Cregg and Dix, 2001). Management practices, including irrigation and pruning, reduce water-use efficiency and lead to sunscald on urban trees in the arid south-west USA (Martin and Stabler, 2004; Martin and Stutz, 2013). However, interactions between urban environmental factors can also reduce constraints to plant growth and function. Nitrogen availability in urban conditions may interact with changes in temperature and water availability to either enhance or limit tree growth (Searle *et al.*, 2011; Osone *et al.*, 2014). A nuanced view of environmental constraints across plant species, cities and urban site types will allow for a more accurate picture that reflects the values of urban green spaces for ecosystem function.

A second common approach to urban plant physiology has been the use of urban-to-rural gradients to understand the influence of the urban environment on plant physiology. This approach can help gain insight into future global change conditions (Gregg *et al.*, 2003; Searle *et al.*, 2012; Calfapietra *et al.*, 2015). The gradient approach can be a useful construct for examining the impact of large-scale anthropogenic factors such as CO_2 emissions, nitrogen deposition, changes in ozone concentration and precipitation patterns (Lahr *et al.*, 2018a). Urban–rural gradient experiments conducted using uniform soil conditions (in pots or constructed plots) demonstrate that the elevated temperatures, increased levels of atmospheric

Table 4.1. Urban influences on abiotic and biotic environmental factors affecting plant growth, including direct and indirect human impacts.

Environmental factors	Urban influence
Abiotic	
Radiation	Shade from tall buildings or planted trees Reflected UV radiation from built surfaces Reduced UV radiation due to air pollution
Temperature	Urban heat island effect Soil freezing affected by soil compaction; snow/leaf litter removal
Water	
Humidity	Wind tunnels Urban heat island effect
Soil moisture	Changes in soil organic matter Soil compaction Flashy precipitation and stormwater run-off Engineered stormwater controls Stream channelization
Gas	
Oxygen deficiency	Modified flooding frequency Soil compaction
Ozone exposure Atmospheric CO_2 Particulate matter	Elevation or depletion Elevation from local point sources Modified seasonal dynamics Increased exposure and deposition
Chemicals/minerals	Nutrient excess, deficiency, or imbalance from pollution or fertilizer Altered pH from fertilizer or anthropogenic construction materials Changes in salinity from road salt or altered coastal flooding patterns Increased heavy metals Pesticide or herbicide application
Mechanical effects	
Wind	Wind tunnels or wind breaks from tall buildings
Burial	Construction activities Planting practices
Snow and ice cover	Urban heat island effect Snow clearing
Fire	Fire suppression Arson
Vegetation management	Pruning Weeding Lawn mowing
Biotic	
Plants	Reduced competition through vegetation control Increased competition from invasive species or planting Allelopathy from introduced species

Continued

Table 4.1. Continued

Environmental factors	Urban influence
Microorganisms	Introduced diseases (virus, bacteria, fungi) Loss of mycorrhizal fungi Changes in microorganism biodiversity Altered rates of nitrification
Animals	Herbivory from insect pests (native and introduced) Trampling and soil compaction from pets Herbivory and seed predation by urban mammals (e.g. deer, rodents) Increased faeces and urine from pets

CO_2 and/or reduced ozone found in urban areas can lead to greater plant productivity (Gregg *et al.*, 2003; George *et al.*, 2009; Searle *et al.*, 2012). Mature urban trees growing *in situ* are also more productive than their rural counterparts across both open-grown and forested settings (Pretzsch *et al.*, 2017; Sonti *et al.*, 2019), although tree longevity may be reduced in urban areas (Smith *et al.*, 2019). This increase in productivity has been observed using remote sensing as well (Zhao *et al.*, 2016). Urban conditions can also enhance growth of species that are problematic for human health, including ragweed and poison ivy (Ziska, 2003; Ziska *et al.*, 2007). Urbanization is also known to alter nutrient availability, with implications for foliar nitrogen content and physiological function (Vallano and Sparks, 2013; Falxa-Raymond *et al.*, 2014;; Trammell *et al.*, 2016). However, urbanization gradients are applied inconsistently across studies and can be an oversimplified and misleading concept in many situations (McDonnell and Hahs, 2008; Raciti *et al.*, 2012a; Short Gianotti *et al.*, 2016). Urban–rural gradients are inadequate to capture many of the environmental factors affecting plant physiology that vary on small spatial scales within cities and suburbs. These factors include impervious surfaces, fertilizer or pesticide application, soil disturbance history, and the influence of domestic versus natural selection.

By focusing on terrestrial and aquatic patches within cities and suburbs as analogues of non-urban habitats, the gradient approach tends to examine ecology *in* the city, rather than a more comprehensive ecology *of* the city that treats the entire urban mosaic as a social-ecological system (Pickett *et al.*, 2016). As illustrated in Fig. 4.2, differences in human-management intensity and land-use history both within a city and across urban–rural gradients will impact both plant community composition and physiological function across different site types. This approach provides a comprehensive framework in which to design specific studies of urban plant ecophysiology. For example, in Baltimore, Maryland, we find vacant lots with ruderal plant species and patches of closed canopy forest (Avins, 2013; Johnson *et al.*, 2018); both are examples of sites with little management or cultivation, but their species composition and ecophysiological function vary greatly due to the history of development or disturbance on that site. Even within a particular type of urban green space, there may be a great deal of variation in environmental conditions due to land-use history. For example, urban soils collected from several New York City forest restoration sites supported significantly different levels of tree seedling health and growth (Pregitzer *et al.*, 2016). In addition, we may find particular site types, such as a lawn or a patch of forest, that occur within urban, suburban and rural areas. Rather than frame research questions around an urbanization gradient, it may make more sense to conceptualize and compare sites within cities or metropolitan areas that vary according to specific combinations of environmental parameters (McDonnell and Hahs, 2008).

Within urban areas, there is a variety of formal and informal green spaces that provide habitat for plant life (Kowarik, 2011; Rupprecht and Byrne, 2014). Management practices vary across these sites, leading to differences in physiological function (Fig. 4.2). For example, water use (measured as sap flux) varies between native and non-native tree species, as well as between natural, irrigated, unirrigated and street tree

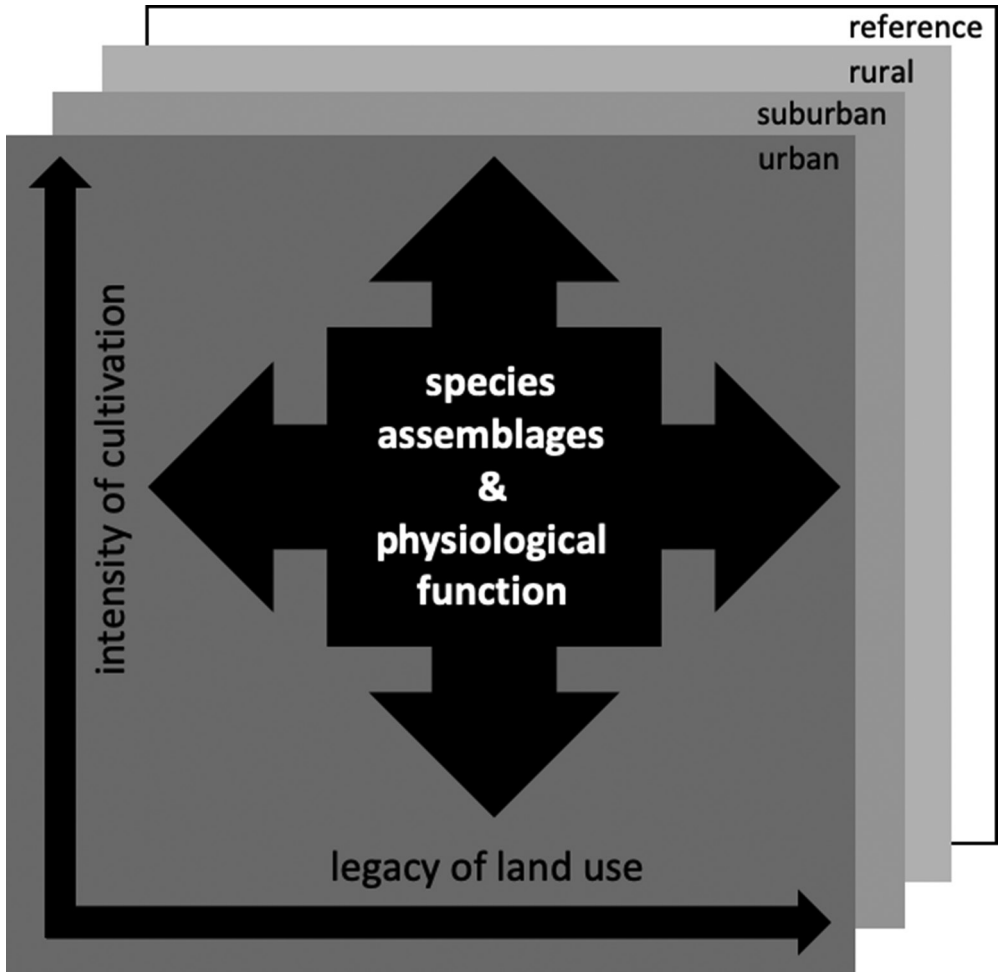

Fig. 4.2. Urban plants grow in a variety of site types that vary along axes of land-use history and intensity of cultivation or management, leading to differences in community composition and physiological function. These site types are found throughout the urban-to-rural gradient and can be utilized to construct or refine experimental studies of plant ecophysiological function.

sites in Los Angeles, California (McCarthy and Pataki, 2010; Pataki *et al.*, 2011). Research has also found that landscaping choices may have socio-economic drivers (Kinzig *et al.*, 2005) and result in different ecophysiological outcomes. Empirical models of turfgrass and tree evapotranspiration combined with remotely sensed estimates of Los Angeles vegetation cover reveal that coniferous and palm tree species contribute little transpiration compared to angiosperms, and that total modelled evapotranspiration is correlated with median household income (Litvak *et al.*, 2017).

Private residential lands are beginning to receive recognition from ecologists as one of the most prevalent land uses in cities, with important consequences for urban biodiversity and ecosystem function (Locke *et al.*, 2018; Pearse *et al.*, 2018). Lawns in particular dominate urban green space land cover across many cities (Ignatieva *et al.*, 2015), and much remains to be learned about their role in urban ecosystem

functioning. Microclimate factors such as shading may have a strong influence on turfgrass water use, which has implications for lawn irrigation practices (Litvak and Pataki, 2016). Analysis of residential lawns across the USA suggests that nitrogen additions interact with overall rates of nitrogen cycling and losses to drive foliar nitrogen concentration and isotopic composition (Trammell *et al.*, 2016). Carbon assimilation was found to be greater in arid residential landscapes than in the surrounding native desert across different plant life forms (Martin and Stabler, 2002).

In addition to gradients of urbanization, it is important to consider the impact of latitudinal gradients and range limits of both native and introduced species found in urban areas. For example, elevated urban temperatures may switch from beneficial to harmful in the lower latitudes of a species's range (Ghannoum and Way, 2011). Plant ecophysiology also underlies theory and practice related to the role of cities in plant migration related to climate change (Woodall *et al.*, 2010). The role of urban landscapes in plant migration and species range distributions deserves further study, particularly in light of projected changes in climatic conditions influencing ecophysiological function.

Across biomes and land uses, root function and other below-ground processes are notoriously difficult to measure, and this is even more true in urban systems where soil is often locked under impervious surfaces and destructive sampling is discouraged (Raciti *et al.*, 2012b). However, below-ground processes are a critical link in understanding urban plant productivity and ecosystem function (Högberg and Read, 2006). Research from several cities across the USA suggests that paved surfaces can reduce tree growth due to increased rhizosphere temperatures, among other factors (Martin *et al.*, 2002; McClung and Ibáñez, 2018). Soils beneath pavement may become compacted without the use of structural materials to maintain pore spaces (Grabosky *et al.*, 2009). Soil compaction is considered a major stress to urban plants, potentially restricting root access to oxygen and water (Mullaney *et al.*, 2015). Urban soils may also become waterlogged if drainage is inadequate, causing a lack of oxygen in the root zone. De-icing salts can cause 'chemical drought' to roots; chloride ions taken up by plant roots can accumulate to toxic levels in the leaves and result in leaf necrosis (Bassuk and Whitlow, 1987). Urban fill contains cement with limestone and is often alkaline, which limits availability of nutrients like iron and manganese in some urban sites. However, less heavily disturbed urban soils may provide greater nutrient availability than surrounding native ecosystems (Sonti *et al.*, 2019). Urban soils from a variety of land uses may support lower rates of tree root colonization by mycorrhizal fungi, which provide increased water and nutrient absorption to the host plant (Martin *et al.*, 2002; Karpati *et al.*, 2011; Tyburska *et al.*, 2013). The impacts of urbanization on root herbivory also remain largely unexplored (Rasmann and Agrawal, 2008).

Urban plant populations and communities are shaped by the forces of both natural selection and domestic selection (i.e. artificial selection, propagation and dissemination of plant genotypes with traits deemed advantageous or desirable for human use). Species or cultivars planted in gardens and other highly cultivated sites are selected for specific traits related to their physiological function (shade, water use), aesthetic appeal (flowers, fall foliage) and/or ease of maintenance (male dioecious trees that do not produce seeds or fruit) (Cariñanos and Casares-Porcel, 2011; Pataki *et al.*, 2013; Avolio *et al.*, 2018). In sites with less maintenance, conventional traits related to natural selection may be more relevant to reproductive success (Johnson *et al.*, 2018). The success of ubiquitous urban species such as *Ailanthus altissima* and *Ginkgo biloba* may be explained by ecophysiological traits allowing for high rates of photosynthesis and water-use efficiency in urban growing conditions (Hamerlynck, 2001; Osone *et al.*, 2014). There is little research comparing physiological function of ornamental species compared to the native wildtypes they replace across different plant functional groups (Lahr *et al.*, 2018b) compared to photosynthesis and stomatal conductance rates among red maple urban-planted cultivars and wildtype trees, finding that cultivars had higher maximum rates of photosynthesis but lower water-use efficiency than wildtype trees. Red maple is a common urban tree species that occurs naturally in urban-to-rural landscapes through the eastern USA and has also been used to develop dozens of cultivars available for purchase in nurseries. However,

cultivars and varieties of many other native species are available to urban residents and land managers, and it is not clear how these domestic selection processes and the resulting genotypic and phenotypic variation in urban plant populations impact physiological function across the urban landscape.

In addition to below-ground processes and horticultural practices, there are other urban environmental factors affecting plant growth (Table 4.1) that have received little attention in the literature. For example, although it has been suggested that wind tunnels caused by tall buildings may increase leaf desiccation (Bassuk and Whitlow, 1987), there is far more research about the role of trees as wind breaks in urban areas (Trowbridge and Bassuk, 2004). Presumably, if trees are strategically placed to block strong winds, there may be impacts to growth and physiological function. The ability of tall buildings to block and reflect light may also impact plant growth form or phenology.

Social-ecological factors may influence urban plant ecology in completely different ways across humid versus arid cities, necessitating different approaches to ecophysiological study. In temperate regions of North America and Europe, many cities have reduced tree canopy cover compared to the native forest biome they replaced, often leading to general changes such as more sunlight and less soil organic matter. However, arid cities generally have more tree cover than the surrounding native ecosystem, resulting in more shade and soil organic matter. In addition, regional differences in irrigation, fertilizer application and pesticide application practices affect plant physiological function differently across local land uses and site types. Comparative plant ecophysiology research across urban areas will be critical to determine whether these environmental impacts are similar across urban geographies (Sonti, 2019). Urban site conditions of different regions vary according to the unique sets of interacting human and biophysical variables at each location, including latitudinal gradient, physiography and land-use history, requiring careful consideration of each of these factors and their interactions. Traditionally, the study of ecophysiology tends to focus on either model plant systems (e.g. *Arabidopsis thaliana*), natural systems, or crops (Ainsworth *et al.*, 2016). In this context, urban systems may be viewed as natural systems, or may be akin to agricultural systems, depending on the level of cultivation, intensity of continued maintenance, and expected performance of the urban plants in question.

Methodological Considerations for Field Studies of Urban Plant Physiology

The focus of plant ecophysiology is often on the scale of a single leaf and extends up to a whole plant, although the discipline includes techniques for examining processes from molecular to global scales (Pearcy *et al.*, 1989). Field methods include assessments of all of the environmental factors listed in Table 4.1 and their resulting impacts on myriad physiological processes including gas exchange, nutrient uptake, water use, carbon allocation, growth and reproduction. Field methods in plant ecophysiology have been adapted to urban conditions with varying levels of success, and there may be opportunities to develop new directions and research techniques suited to urban ecology (Fig. 4.3).

As the study of urban ecology has advanced, field researchers are recognizing the need to include sites beyond formal protected areas such as parks or other institutional grounds. However, fieldwork on private urban land or informal green spaces requires careful precautions to ensure security of equipment, researchers and the local community. Studies of urban plant biodiversity and ecosystem fluxes have outpaced research on urban plant physiology, which may be partly due to the challenges associated with plant ecophysiology methods and their reliance on expensive instrumentation. A study of common problems experienced by urban ecology researchers includes several issues of particular relevance to plant physiological ecologists, who often need to destructively sample plants and/or leave expensive equipment on site that is not easy to hide (Dyson *et al.*, 2019). Though rare, property damage may occur during collection of tree cores or other plant tissues, as well as during soil sampling or root studies, making it particularly difficult to receive permission to conduct

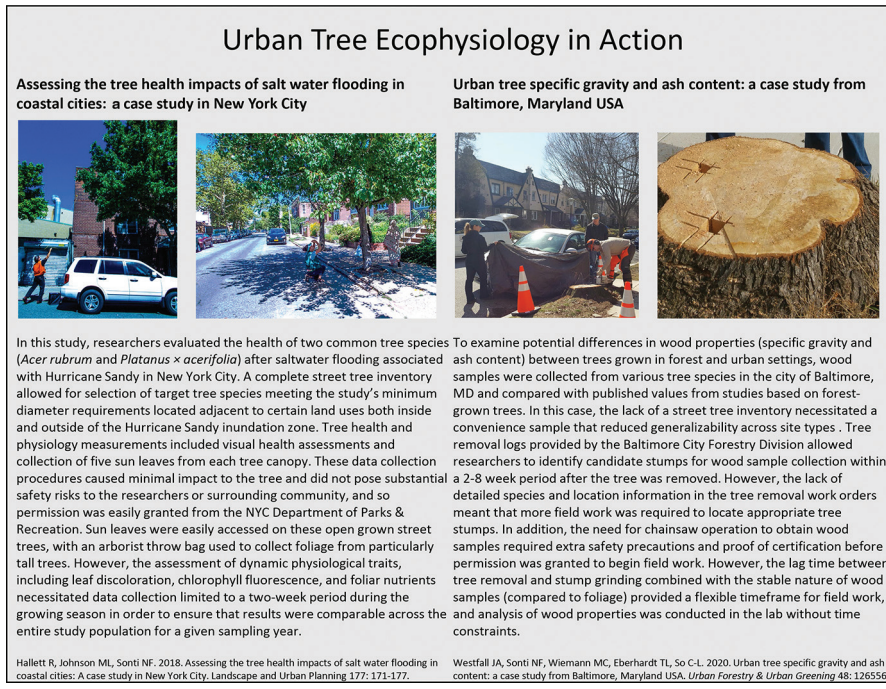

Fig. 4.3. Two street tree studies conducted by scientists from the USDA Forest Service Northern Research Station illustrate the challenges and feasibility associated with design and implementation of ecophysiological research methods in urban contexts (Hallett *et al*., 2018; Westfall *et al*., 2019)

these types of studies on some urban land uses or ownerships. Because small-scale management practices can impact individual plant function, there is also a need to control or document these types of activities during the course of a research project. For example, a study of residential tree water use or lawn nutrient dynamics will be impacted by irrigation or fertilizer application, so it is important to communicate with property owners about the frequency of these activities or request that they suspend management for the duration of the research. This is not a unique consideration for urban research, but the large number of property owners involved in a given urban ecology study makes these types of communications and management activities more complex.

Traditional ecophysiology methods include instrumentation of individual plants to measure physical and chemical parameters (Pearcy *et al*., 1989). For example, measurements of tree sap flux or leaf-level gas exchange require expensive equipment to be attached to plants *in situ* and left in place anywhere from hours to months at a time. As a result, many of these studies have been conducted in protected urban sites such as an arboretum or university campus (but see, for example, Osone *et al*., 2014; Lahr *et al*., 2018b). Access to tree canopies is a challenge in many ecophysiological studies, but the urban setting may preclude the use of techniques like scaffolding to reach the canopy or shotgun use to collect foliage. Pre-dawn measurements of chlorophyll fluorescence or leaf-water potential may be challenging if sites are not considered safe in the dark. At the same time, urban sites are generally more accessible and less remote than wilderness areas, making it easier to transport heavy equipment or find supplies to make repairs.

Methods that require collection of a minimal amount of foliage can be successfully employed in urban areas, including assessments of foliar nutrients, isotopic composition, chlorophyll fluorescence, or chlorophyll content.

For example, foliar nitrogen concentration and isotopic composition of residential lawns may be associated with fertilization practices and housing age and may differ from associated native ecosystems in many cities (Trammell *et al.*, 2016). Nitrogen and oxygen isotope ratios of winter annual plants in Los Angeles, CAalifornia, vary with the spatial distribution of atmospheric NO_2 and ozone, suggesting that these pollutants influence stomatal conductance (Wang and Pataki, 2010). Foliar nitrogen concentrations and isotope signatures may also reveal differences in species responses to altered nitrogen availability in urban green spaces, with implications for differential growth and survival (Falxa-Raymond *et al.*, 2014).

Growth rates of woody plants across urban site types and management regimes may be assessed easily using repeated measurements of stem diameter, or sometimes through increment cores when permission is granted (e.g. Pretzsch *et al.*, 2017; Bialecki *et al.*, 2018). Because of the difficulty in assessing tree root growth and function in urban sites, some researchers have made use of ground-penetrating radar to assess rooting depth in different site conditions (Bassuk *et al.*, 2011; Grabosky and Bassuk, 2016).

One approach to studying ecophysiology along an urbanization gradient is to use potted plants that may be grown and harvested without harming existing vegetation. These types of studies measure plant physiological responses to atmospheric factors such as ozone, carbon dioxide, temperature and nitrogen deposition, but do not account for below-ground influences of the urban environment (e.g. Gregg *et al.*, 2003; Searle *et al.*, 2012; Vallano and Sparks, 2013). Of course, greenhouses, growth chambers and experimental plots may also be used to simulate urban environmental conditions, avoiding many of the difficulties of urban ecophysiology field research (e.g. Mueller and Day, 2005; Bartens *et al.*, 2008; Searle *et al.*, 2011, 2012; Rahman *et al.*, 2014; Pregitzer *et al.*, 2016). These methods also have the advantage of direct experimental manipulation and subsequent determination of causal relationships between environment and plant physiological response, which is difficult to achieve in the urban setting. However, the applicability of these results to urban field conditions may be more limited.

Flux towers can be used to examine the influence of urban vegetation on atmospheric CO_2 fluxes (Briber *et al.*, 2013), particularly when combined with empirical data such as leaf-level gas exchange (Ng *et al.*, 2015) or tree-level carbon sequestration estimates (Velasco *et al.*, 2016). Flux tower data has also shown that tree canopy can augment atmospheric elemental inputs to urban ground surfaces (Decina *et al.*, 2018). Although flux towers are large installations that may be difficult to establish initially, they can be used to collect continuous long-term data unobtrusively once they are installed.

High spatial resolution remote sensing may also provide insight into urban plant ecophysiology. For example, evapotranspiration rates of different types of urban vegetation cover may be associated with Normalized Difference Vegetation Index (NDVI) values derived from high spatial resolution imagery (Nouri *et al.*, 2013); although, at a lower spatial resolution, Moderate Resolution Imaging Spectroradiometer (MODIS) data have been used to demonstrate the effect of the urban heat island on vegetation phenology (Zhang *et al.*, 2004) as well as to estimate net primary productivity in urban areas (Lu *et al.*, 2010; Yan *et al.*, 2018). High-resolution hyperspectral imagery and LiDAR data may be used to map tree species, health status, leaf area index (LAI) and carbon storage (Alonzo *et al.*, 2016; Pontius *et al.*, 2017). Ground-based LiDAR can also be used to model urban tree biomass in a non-destructive manner (McHale *et al.*, 2009). Unmanned aerial vehicle (UAV) remote sensing also has great potential for ultra-high-resolution (both spatial and temporal) mapping of vegetation structure and function in complex urban landscapes provided that safety and privacy concerns of this emerging technology are addressed (Feng *et al.*, 2015; Gallacher, 2016). The increased availability of high-resolution data about the structure and arrangement of urban vegetation in relation to the built environment also allows for improved design of plant ecophysiology studies. For example, mapping of woody and herbaceous vegetation in front versus backyards in Boston, Massachusetts, would allow for investigation of physiological function of these different vegetation types across

residential management contexts (Ossola *et al.*, 2019).

Urban Plant Ecophysiology as the Foundation of Nature-based Solutions

The field of plant ecophysiology has long been central to the mitigation of anthropogenic global change factors, as well as maintaining humankind's supply of goods and service in the face of increasing environmental stress (Ainsworth *et al.*, 2016). Thus, the discipline is a natural fit with urban ecology, which also seeks to address issues of sustainability, environmental quality and human well-being (McDonnell and MacGregor-Fors, 2016). Using an approach which has been termed ecology *for* the city, interdisciplinary scientists seek to inform the design, planning, construction and management of cities and towns through the study of the structure and function of urban ecosystems (Childers *et al.*, 2015). The provision of such evidence-based knowledge is essential for the success of 'nature-based solutions' that aim to promote public health and safety, enhance quality of life, and restore natural hydrologic and ecological processes in urban areas (Nesshöver *et al.*, 2017; Keeler *et al.*, 2019). Cost-effective, nature-based solutions are often presented as 'green infrastructure' that provide additional social-ecological co-benefits, unlike costly technological 'grey infrastructure'. Plants provide the foundation of most nature-based solutions, and a comprehensive understanding of their physiological functioning in relation to current and future urban environmental conditions will allow for more effective design, implementation and maintenance of these ecological features. Of course, it is important to consider the ways in which interactions among social, ecological and technological factors (including climate change) will impact the efficacy with which plants provide urban ecosystem services and disservices (Keeler *et al.*, 2019).

As the use of nature-based solutions becomes more widespread in urban areas, there is a need to evaluate the current physiological performance of plants within these installations as well as the suitability of species and cultivars or varieties of plants for future installations. To this end, Ordóñez *et al.* (2019) have developed a performance assessment framework, using street trees as a model nature-based solution. Unsurprisingly, tree ecophysiology is central to the conceptual and methodological framework, as the performance indicators centre around measures of tree physiological performance and the abiotic and biotic environmental conditions that influence it (Ordóñez *et al.*, 2019). Research by Ballinas and Barradas (2015,2016) illustrates the utility of this approach, showing that measurements of transpiration and stomatal conductance may be used to inform urban tree-planting arrangements that will dissipate the greatest possible amount of heat, mitigating the urban heat island. Similarly, water-use efficiency can be used as a metric of urban ecosystem service provision by different species in arid cities, given that it captures the trade-off between plant water use and growth (McCarthy *et al.*, 2011).

Ecophysiological function of certain nature-based solutions has been studied more thoroughly than others, including green roofs. In these highly designed settings, species selection and management practices are extremely important in order to achieve the desired physiological performance and environmental outcomes. For example, research shows that green roof substrate design, vegetation type and species have been found to affect plant performance (e.g. photosynthesis or water use) and/or green roof performance (water run-off) (VanWoert *et al.*, 2005; Nagase and Dunnett, 2012; Starry *et al.*, 2014). Green roof plant functional traits may also impact provision of ecosystem services such as canopy density, substrate organic matter, substrate temperature index, and substrate nutrient retention (Xie *et al.*, 2018). Selection of green roof plant species based on evapotranspiration rates provides a tangible example of the use of ecophysiological properties to inform design of nature-based solutions (Kemp *et al.*, 2019). Interactions between species are also important in these systems. For example, mycorrhizae may be introduced into green roofs or other nature-based solutions to enhance productivity and performance (John *et al.*, 2017). Sedum groundcover may be used strategically to enhance performance and phenolic concentrations in edible plants used as part of a

sustainable urban agriculture green roof programme (Ahmed *et al.*, 2017).

Phytoremediation systems are another example of nature-based solutions that use more advanced species and genotype selection processes in order to achieve specific ecosystem service outcomes. Dozens of plant species have been identified as hyperaccumulators of heavy metals and at least ten uptake mechanisms have been identified as part of a comprehensive model of phytoremediation technology (Mahar *et al.*, 2016). Salicaceae species are particularly well studied, with a combination of field and laboratory trials exploring the growth and physiology of *Populus* and *Salix* spp. genotypes used in phytoremediation of heavy metals and organics (Marmiroli *et al.*, 2011). Further research is needed on both intraspecific and interspecific variation in productivity across a range of urban conditions in order to maximize plant function and associated performance of nature-based solutions.

Conclusions: Future Directions for Urban Plant Ecophysiology Research

In 1988, Whitlow and Bassuk published 'An Agenda for Urban Ecophysiological Research', focused on street trees, which are highly visible and managed components of many cities, and which provide important benefits to urban residents (Whitlow and Bassuk, 1988). Many of the questions they identified remain to be answered, both for street trees and other types of urban vegetation. However, our increased recognition of the value of urban plants across a diverse range of habitats, and their central role in the function of nature-based solutions, requires an expansion of this research agenda. Over half of the world's population already lives in urban areas and it is projected that 60% will live in cities by 2030 (United Nations *et al.*, 2018). Ambitious urban greening agendas worldwide recognize the value of urban vegetation in sustaining and enhancing human and ecosystem health and well-being, particularly in the face of changing climate conditions (Tan *et al.*, 2013; Anguelovski *et al.*, 2018). Successful implementation of these greening initiatives will require a mechanistic understanding of plant productivity that is critical to the design and management of urban green spaces.

Several areas of urban ecophysiological research have received little attention but have particular potential to inform the practice of urban natural resource management. There is a need to elucidate the impacts of domestic selection on genotypic and species diversity of urban plants and on associated ecosystem function. Continued research on both inter- and intraspecific variation in physiological function of native and introduced urban plants can help inform planning and design of urban landscapes. The ability to match plant species and genotypes with specific urban site conditions can help reduce the resources needed to sustain urban landscapes that provide a high quality of life to residents. There is also a need to quantify plant performance and physiological function across a range of urban site types, from the most intensively managed to urban wilderness areas. When informed by an ecophysiological approach, patch analysis of the urban mosaic using remotely sensed data may be used to estimate the extent of urban vegetation site types, with implications for ecosystem function at a metropolitan or regional scale (e.g. Cadenasso *et al.*, 2007). In addition, plant growth in each of these social-ecological contexts will lead to different positive and negative outcomes for human health and well-being. Research from landscape architecture and social science perspectives can provide complementary information about human values and perceptions of urban vegetation form and function (e.g. Heynen *et al.*, 2006; Jansson *et al.*, 2013). Together, social and ecophysiological research can inform optimization of the trade-offs between resources (carbon emissions, water) and ecosystem services or disservices (biophysical and socio-cultural).

Cities are dynamic ecosystems made up of a mosaic of heterogeneous sites that may be heavily managed or not managed at all. Plants may be integrated into urban landscapes in highly intentional ways with expected or unanticipated functional outcomes (Pataki, 2015), or they may exist and function in ways that are not intentional at all. As large-scale urban greening initiatives become increasingly widespread and the impact of their changes to the urban landscape are borne out, a greater understanding of plant ecophysiology will provide insight into

carbon, water and nutrient dynamics essential to sustaining life in cities. Urban ecology and plant ecophysiology are both areas of study that cross scales and disciplines in order to describe mechanisms underlying observed ecological patterns, but also to inform desired ecosystem function and related impacts on human health and well-being. Advancing an urban plant ecophysiology research agenda can help support the design and implementation of more sustainable and resilient cities in the face of complex and uncertain future social-ecological conditions.

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