Urban plant physiology: adaptation-mitigation strategies under permanent stress

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Urban environments that are stressful for plant function and growth will become increasingly widespread in future. In this opinion article, we define the concept of 'urban plant physiology', which focuses on plant responses and long term adaptations to urban conditions and on the capacity of urban vegetation to mitigate environmental hazards in urbanized settings such as air and soil pollution. Use of appropriate control treatments would allow for studies in urban environments to be comparable to expensive manipulative experiments. In this opinion article, we propose to couple two approaches, based either on environmental gradients or manipulated gradients, to develop the concept of urban plant physiology for assessing how single or multiple environmental factors affect the key environmental services provided by urban forests.

Urban environments as test beds for plant physiological studies

From hundreds to thousands of plant species grow in urban environments, providing rich species pools to study the diversity of responses to stressful conditions. Analyzing plant responses to urban conditions, defined here as 'urban plant physiology', represents an important opportunity to gain an insight into immediate physiological responses, tolerance of plants, and the extent and mechanisms of short and long term plant adaptations. Woody species are particularly important in this context, because of their longevity and the possibility of studying the mechanisms of long term adaptation. Moreover, dendrochronology based on tree ring analysis offers an unique opportunity to retrospectively investigate how tree growth has changed with past urban conditions, including water availability and temperature [1,2].

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Provided that plants cope with altered conditions similarly in urban environments and in laboratory experiments simulating climate change, urban microenvironmental conditions can represent a unique 'open lab' where environmental manipulations occur at no cost and without the restrictions of the laboratory. Therefore, plants growing in urban environments are a resource that could be exploited much more by researchers studying how future environmental changes affect plants. This opportunity applies mainly, but not exclusively, to conditions such as high temperatures (the 'urban heat island effect', [3]) or high concentrations of pollutants in air, water, or soil. It is important to highlight that the heat island effect is highly stressful for plants in hot climates, but can be beneficial in cold environments by prolonging the growing season of some species as well as bringing the rate of plant physiological processes closer to their thermal optimum [4].

In the urban plant physiology approach, scientists should consider particularly the transition zones between urban centers and rural and natural areas, including the urban–rural interface. This interface represents a gradient of stress conditions and thus provides a scene for unique case studies along stress gradients. Ideally the collection of data in selected experimental plots along this gradient should allow for the study of the impact of a single specific factor or multiple factors on target plant physiological processes. Unfortunately, despite the research possibilities offered by the urban environment, urban vegetation remains an underused resource for predicting the performance of plants under future conditions.

The studies on the effects of the components of global change, such as carbon dioxide (CO_2) and ozone (O_3) concentrations, temperature (T), and the availabilities of nitrogen (N) and water (W) have used large scale and very expensive facilities to manipulate one or more factors at a time. Examples of such experiments include free air CO_2 enrichment (FACE) [5,6], free air O_3 enrichment [7,8], and free air humidity enrichment (FAHM) [9] experiments. Many of these large experimental facilities, however, have recently been closed due to high costs, reinforcing the need to develop more cost-efficient approaches to focus on multifactorial treatments [10]. We argue that insufficient attention has been paid to using the urban–rural gradient as an open lab with 'experimental' treatments already in place for physiological studies, despite the availability of some promising case studies that have already been conducted, mainly in the USA [11–13].

Clearly, the extreme species richness of urban areas presents challenges, because the physiological potentials of only a few species are known [14,15]. Furthermore, there is often an important intraspecific variability among populations of given species [16]. Although urban forestry often uses clones or cultivars of given species with reduced genetic variability among individuals, there is a large variability among cultivars and clones of widely planted urban species in their responses to global change drivers [17]. Despite these difficulties, we argue that the extrapolation of vegetation carbon balance from native ecosystems to urban habitats is not justified. Increasing urbanization calls for more studies of urban environments for also gaining insight into the roles of urban habitats on other components of global change, such as plant invasion, biodiversity, and global carbon balance [15]. We also stress the point that, in the context of global change, few studies have focused on the growth of urban trees, including allometry, which is crucial to estimate leaf area development and carbon sequestration capacity. Studies demonstrate that allometric relationships can differ considerably between isolated urban trees and trees in forests [18].

Studying vegetation along the urban–rural gradient

The possibility of studying vegetation, particularly forests, along urban–rural gradients was first suggested approximately a decade ago [19].

A small number of available urban studies, one recently carried out with oak species in New York (USA), suggest that O_3 can have a larger influence on urban plants than changes in T or [CO_2] [11]. This intriguing aspect, however, might vary with species and climate, because the environmental variations along natural–urban gradients can differ considerably from town to town. Because of the soil compaction, water shortage, especially in interaction with other environmental drivers, can be also an important factor in urban environments. A number of studies have recently focused on plant water use and thresholds of water stress [20,21]. It has been further demonstrated that higher temperature and increased drought in urban environments significantly affected the growth of urban trees [2,22]. Usually T, [CO_2] and [N] increase from the suburbs to the city center, but [O_3] can increase or decrease because it depends on several factors such as the positioning of wind corridors, positioning of major roads, traffic intensity, and the typology of urban vegetation [14,15,23,24]. The physical–chemical conditions of the troposphere, which determine the reactivity of the O_3 precursors, are also particularly important, as well as the turbulence which determines the mix of the air masses in the different layers of the troposphere [23]. Moreover, the emission of biogenic volatile organic compounds (BVOCs) by urban vegetation can exacerbate photochemical reactivity, and thus O_3 formation, especially when VOC/NO_x ratios are relatively low [15,24].

In addition to widespread pollutants, we should also consider specific air, water, and soil pollutants, especially from specialized industrial activities, that could be typical only in some urban areas. The ability to identify gradients and determine their magnitude would represent a great opportunity to monitor pollutant dispersion, concentration, and accumulation and to study the responses of plants, and in the worst cases, even the thresholds for survival.

In this opinion article, we suggest the integration of two levels of investigation (Figure 1). The first level uses an urban–rural environmental gradient where multiple factors can change simultaneously in a multifactorial treatment. The lack of homogeneity in the levels of a target factor in each study area over time, and the concurrent heterogeneity in a number of secondary factors can complicate the evaluation of the dose–response relationship when focusing on the effects of a specific factor in any physiological process. Several of the inherent limitations of the urban–rural gradients can be accounted for by replicating the gradients within the same urban area and by including different urban–rural gradients. These limitations may restrict the interpretation of the data but may also represent an added value, because they can provide opportunities for performing long term multifactorial experiments under real conditions. These types of experiments are important for understanding the responses of plants to urban conditions, but can also represent a perfect simulation of the predicted conditions in some scenarios of climate change. This level of investigation employing the available long term environmental gradients generated by urban environments can be achieved by using the existing urban vegetation and/or potted seedlings placed in specific locations along the gradient.

Studying urban vegetation would allow for the evaluation of long term adaptations of the plants, especially when the same species are available along an urban–rural transect. The key challenge, however, is the choice of an appropriate 'control treatment' for studies of urban gradients, which include similar soil conditions. Urban plants grow under a variety of conditions, for example, in competitive conditions in dense forests along urban margins, or in noncompetitive conditions in linear alleys along streets and managed parklands. In addition, urban tree plantations are often monocultures of given species, but urban parks and gardens support highly diverse combinations of species. Such limitations could be overcome by growing conspecific seedlings along a transect in pots containing the same soil. In addition, gradient studies are convenient because physiological trends can be extrapolated to zero or to a particular level of pollutant concentration, thereby allowing us to gain an insight into the potential effect of the given pollutant [25].

In addition to the traditional eco-physiological, molecular, and biochemical techniques, reflectance indices such as the Normalized Difference Vegetation Index (NDVI) and the Photochemical Reflectance Index (PRI) [26] obtained from remote sensors or from the ground could be used as nondestructive indicators of the plant physiological status along the urban–rural gradient. Reflectance has, for example, been used to monitor the N content of leaves along an

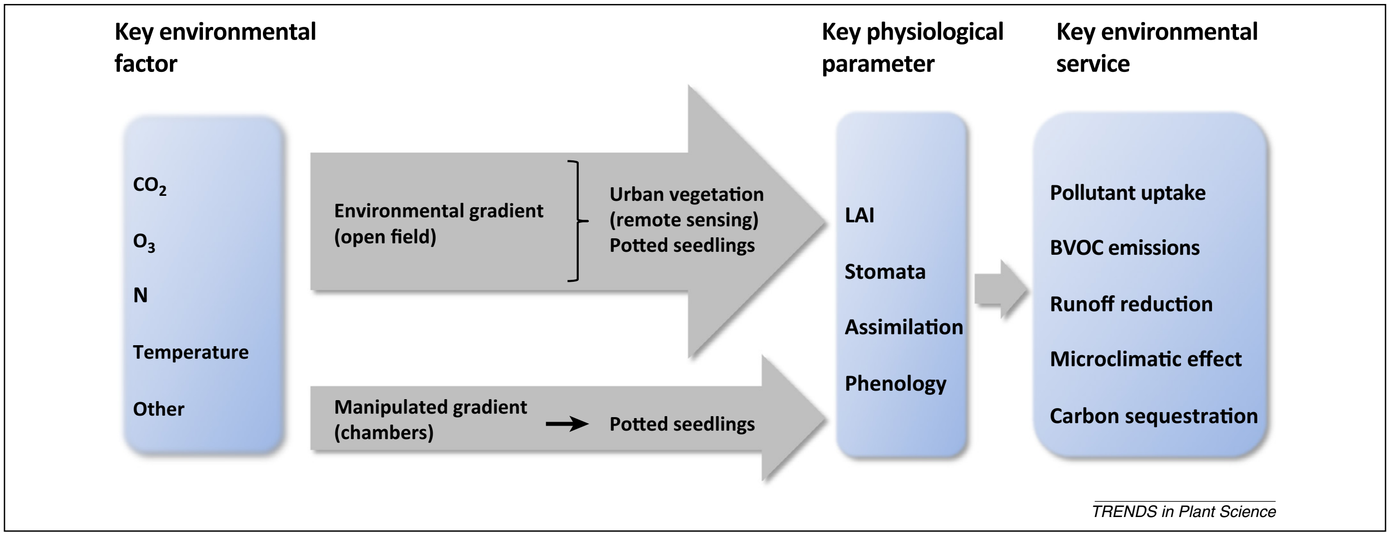

Figure 1. Two approaches are proposed to develop the concept of urban plant physiology for assessing the effect of single or multiple factors on key physiological parameters that drive key environmental services in urban areas. The field 'open lab' approach is based on the multifactorial variability along the urban–rural gradient and on the ability to use either urban vegetation (the implementation of remote sensing techniques is recommended) or potted seedlings along the gradient. The second approach is to simulate the changing conditions along the urban–rural gradient in growth chambers or in open top chambers (OTCs) installed in the urban area for disentangling the effects of multiple factors on potted seedlings. Abbreviations: Assim., assimilation; BVOC, biogenic volatile organic compound; LAI, Leaf Area Index.

urban–rural N-deposition gradient in Boston, USA [27], but could possibly be expanded to other physiological factors and to other urban areas. Changes in the physiological status of plants, for example, those induced by sudden industrial emissions along a transect, could therefore be quickly detected from satellite images, and thus reflectance represents a powerful biomonitoring tool.

Gradient studies can be supplemented by a second level of investigation: manipulated gradients in growth chambers using potted seedlings. This level of investigation, coupled with the observations from the environmental gradient studies, would allow disentangling the combined effects of multiple factors, in particular, by individually testing the same factor levels as observed in the field along the urban–rural transect. In the laboratory, replicated growth chambers can be used to manipulate microclimatic and growth conditions testing one factor at a time, as well as the various combinations of the different factors. The focus here should be the evaluation of the short term effects of a single factor or the effects of combinations of factors, as well as trying to establish a causal relationship between the level(s) of the factor(s) and the response of the plant.

Clearly, growth chamber experiments are ideal to understand the mechanisms of the response, especially when one wants to identify whether the response occurs at molecular, biochemical, or eco-physiological levels. However, in the case of trees, studies in growth chambers do not allow for carrying out experiments with relatively mature trees.

Another approach for 'manipulated gradient' would be the use of open top chambers (OTCs) in the urban environment. OTCs can be constructed to a sufficient size to accommodate even large saplings or entire trees, and thus, such an experimental setup is particularly important for tree species which usually require bigger space than herbaceous species, and also allow for studying the response for longer periods than with the growth chambers. OTCs in urban environments are mainly relevant when one wants to focus on air pollutants effects on plants [28,29]. When studying the air pollution effects in the control treatment OTCs, pollutants should be filtered out, particularly O_3, from the ambient air.

Another advantage of OTCs, compared with growth chambers in the lab, is that OTCs only partially modify the surrounding environment (chamber effect [30]), and plants are subjected to fluctuating ecological factors. OTCs can be installed either in private or in public areas depending on the availability of the owners, soil homogeneity, and power availability. OTCs can be constructed directly around the larger plants, or plants can be planted inside OTCs. When the homogeneity of soil is not guaranteed among different areas representing different levels of pollutants, plants can be grown in large pots with the same soil to avoid soil effects interfering with the air pollution treatment effects. Using plants in pots either in growth chambers or in OTCs, however, can be a major weakness in longer term experiments because of the restriction of the below-ground growth, which can confound the plant response to the target stress factor(s).

Urban plant physiology and environmental services

The concept of urban plant physiology also includes the implications for the capacity of the plants to mitigate environmental changes (Figure 1), particularly for trees under urban conditions, where uptake of air pollutants and carbon, cooling, or runoff reduction are crucial environmental services at risk of being compromised because of stressful urban conditions. In particular, most of these beneficial effects occur through the development of extensive plant canopies, which are able to capture air pollutants, radiation, CO_2, and water. Therefore, the leaf area index (LAI), which is normally directly related to the health status of the plant, becomes a crucial parameter to estimate. The stomatal conductance and the assimilation rate are other important parameters to explain several environmental services connected with the physiological status of the plant. Clearly, any effect of the urban environment on these parameters can deeply influence the capacity of the plants to mitigate environmental changes.

In this article, we highlight the link between urban plant physiology and the previously adopted concept of urban ecology, where urban ecosystems and anthropogenic factors interact on a larger scale [31]. In this view, the effect of urban conditions on the mitigative capacity of plants will influence the dynamic interactions where plants not only passively endure stressful urban conditions, but also influence them [15,32]. For example, among the biogeochemical effects, urban plants may increase their emission of BVOCs, and thus the formation of photochemical smog, but may also enhance the uptake of pollutants and CO_2 and the use of water (consuming more water, but also reducing water runoff, thereby reducing erosion and risk of dangerous floods). Among the biophysical effects, urban plants influence the convection of heat, changing aerodynamic resistance to heat diffusion. In vegetated areas, the coupling between the land and the atmosphere becomes more efficient because an increase in surface roughness lowers aerodynamic resistance, generates more turbulence and higher sensible and latent heat fluxes, and leads to a wetter, cooler atmospheric boundary layer through higher evapotranspiration. Understanding the interactions between urban conditions and urban vegetation would benefit from knowledge of the physiological responses of plants, for example, transpiration or BVOC emissions, to the urban conditions. The key physiological parameters that drive the main environmental services of urban plants (Figure 1) are potential foci of future studies of urban plant physiology. An important topic related to the physiology of urban plants is the need to develop a strategic selection and/or breeding program to select specific genotypes able to tolerate the often harsh conditions of urban environments, but also able to maximize ecosystem services and thus improve the quality of plant life.

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