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ARTICLE

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Urban net primary production: Concepts, field methods, and Baltimore, Maryland, USA case study

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Abstract

Given the large and increasing amount of urban, suburban, and exurban land use on Earth, there is a need to accurately assess net primary productivity (NPP) of urban ecosystems. However, the heterogeneous and dynamic urban mosaic presents challenges to the measurement of NPP, creating landscapes that may appear more similar to a savanna than to the native landscape replaced. Studies of urban biomass have tended to focus on one type of vegetation (e.g., lawns or trees). Yet a focus on the ecology of the city should include the entire urban ecosystem rather than the separate investigation of its parts. Furthermore, few studies have attempted to measure urban aboveground NPP (ANPP) using field-based methods. Most studies project growth rates from measurements of tree diameter to estimate annual ANPP or use remote sensing approaches. In addition, field-based methods for measuring NPP do not address any special considerations for adapting such field methods to urban landscapes. Frequent planting and partial or complete removal of herbaceous and woody plants can make it difficult to accurately quantify increments and losses of plant biomass throughout an urban landscape. In this study, we review how ANPP of urban landscapes can be estimated based on field measurements, highlighting the challenges specific to urban areas. We then estimated ANPP of woody and herbaceous vegetation over a 15-year period for Baltimore, MD, USA using a combination of plot-based field data and published values from the literature. Baltimore's citywide ANPP was estimated to be 355.8 g m^{-2}, a result that we then put into context through comparison with other North American Long-Term Ecological Research (LTER) sites and mean annual precipitation. We found our estimate of Baltimore citywide ANPP to be only approximately half as much (or less) than ANPP at forested LTER sites of the eastern United States, and more comparable to grassland, oldfield, desert, or boreal forest ANPP. We also found that Baltimore had low productivity for its level of precipitation. We conclude with a discussion of the significance of accurate assessment of primary productivity of urban ecosystems and critical future research needs.

KEYWORDS
biomass increment, carbon cycling, LTER, net primary production, urban ecology field methods, urban ecosystem, urban trees, shrubs, herbaceous vegetation, vegetation management

INTRODUCTION

Anthropogenic biomes, and urban areas in particular, are best characterized as landscape mosaics where social and ecological heterogeneities interact, combining a variety of different land uses and land covers where managed vegetation is mixed with seminatural vegetation (Ellis & Ramankutty, 2008; Pickett et al., 2017). Urban land area is expanding globally, with a projected increase of 38.6 million hectares in the United States alone between 2010 and 2060 (Nowak & Greenfield, 2018). This varied and growing urban mosaic presents challenges to the measurement of basic ecosystem processes, including net primary productivity (NPP), creating landscapes that may appear more similar to a savanna than to the native landscape replaced (Dorney et al., 1984). For example, in the United States, studies of urban vegetation biomass have tended to focus on either lawns or trees. However, a focus on the ecology of the city should include the entire urban ecosystem rather than the separate investigation of its parts (Grimm et al., 2000; Pickett et al., 1997). Here, we are referring to "urban ecosystems" as densely settled human dominated landscapes typically characterized by a mix of vegetation types, as well as the frequent planting and removal of plant material. Therefore, some of the considerations presented here may be analogous to mixed vegetation systems (e.g., savanna) or to agricultural and commercial forestry settings with regular harvests.

Although we can estimate NPP at global and regional scales across many anthropogenic biomes using remotely sensed data, it remains challenging to assess NPP accurately within heterogeneous urban landscapes (McHale et al., 2017). Few studies have attempted to measure urban aboveground net primary production (ANPP) using field-based methods (e.g., Jo & McPherson, 1995; Shen et al., 2005). Gross primary production (GPP) of entire urban ecosystems may be estimated from eddy covariance data (Briber et al., 2013), but comprehensive field measurements integrating all urban vegetation types are rare. Most studies project growth rates from measurements of tree diameter to estimate annual ANPP (McHale et al., 2017; Nowak & Crane, 2002) or use remote sensing approaches (Imhoff et al., 2004; Lu et al., 2010). Furthermore, field-based methods for measuring NPP do not include special considerations for urban landscapes (Clark et al., 2001; Fahey & Knapp, 2007). These challenges have led to a dearth of detailed estimates of ANPP in urban areas, leading to the exclusion of urban ecosystems from comparisons of field-based ANPP across biomes (Knapp & Smith, 2001). As cities and regions continue to develop and implement sustainability agendas and climate action plans, there is a need to improve our ability to characterize carbon dynamics within urban areas, and to understand how these fluxes compare with those of other ecosystems impacted by continued urban development (Briber et al., 2013).

In this paper, we examine how ANPP of urban landscapes can be estimated based on field measurements, highlighting the challenges specific to urban areas. We then estimate ANPP over a 15-year period for Baltimore, MD using a combination of plot-based field data and published values from the literature. This estimate of urban ANPP is put into context through comparison with other North American Long-Term Ecological Research (LTER) sites and mean annual precipitation. We conclude with a discussion of the significance of accurate assessment of primary productivity of urban ecosystems and considerations for future research.

DEFINING AND CONCEPTUALIZING URBAN ANPP

Net primary production is net carbon gain by plants per unit area of the Earth's surface, which is equal to the difference between the amount of energy fixed by plants in photosynthesis (GPP) and carbon released via leaf dark respiration plus the construction and maintenance respiration of non-photosynthetic plant tissue (Barnes et al., 1998). Aboveground and belowground components of NPP are measured separately, although belowground NPP is rarely measured and is often ignored or estimated as a proportion of aboveground NPP (ANPP) (Clark et al., 2001; Tierney & Fahey, 2007). Belowground NPP is particularly challenging to measure in urban areas, where tree roots located under impervious surfaces may be inaccessible to researchers, landowners may not tolerate major disruptions to their properties (such as soil displacement), and underground utilities further limit excavation activities (Day et al., 2010). Here, we limit our discussion to urban ANPP but suggest that a study of belowground NPP in urban areas would need to consider the same challenges described by other comprehensive discussions of NPP measurement (Clark et al., 2001; Fahey & Knapp, 2007).

Urban ANPP is the total new aboveground biomass produced by all plants in an urban landscape per unit area during an interval of time. This biomass production may include growth of woody and herbaceous plants that are newly planted, naturally regenerated, existing, or removed during the measurement interval. Many components of this organic matter production are difficult or impossible to measure directly, leading to the necessity of ANPP estimates based on a variety of measurements and associated underlying assumptions (Clark et al., 2001). Following Clark et al. (2001), we define the quantity urban ANPP* as the field-measurement-based operational estimate of actual urban ANPP. For purposes of measurement, ANPP* can be separated into growth increments and losses (Figure 1). Increments include aboveground biomass production of new, existing, or removed woody and herbaceous plants during the measurement interval. Losses include fine litterfall from aboveground woody vegetation, losses of woody or herbaceous biomass to consumers or human management activities, and volatile or leached organic compounds from aboveground woody and herbaceous vegetation.

A comprehensive assessment of urban ANPP should consider all woody and herbaceous vegetation, as urban landscapes are not always dominated by trees, even when cities replace a native forested landscape. Studies of aboveground carbon storage in cities have focused on trees, with the assumption that biomass of shrubs and herbaceous plants is negligible in comparison (Lagrosa IV et al., 2020; Nowak, 1994). Nowak (1994) found that carbon storage by shrubs in Chicago, IL, USA was ~4% of the amount stored by trees, and Davies et al. (2011) found that shrubs and herbaceous plants made up 2.7% of aboveground carbon stored in vegetation of Leicester, England. However, Jo and McPherson (1995) found that grass and other herbaceous plants made up ~5% and 8% of carbon uptake on two residential blocks of Chicago. Combining shrub, tree, and herbaceous measurement methods should allow for ANPP to be estimated in proportion to the plant growth forms present in the urban ecosystem (Young, 2007). We will review measurement considerations for each component of ANPP* in an urban context, as well as sampling design considerations and sources of error and uncertainty.

FIELD METHODS FOR ESTIMATING ANPP IN URBAN SETTINGS

Depending on the climate and land use, aboveground biomass in urban areas may be dominated by trees,

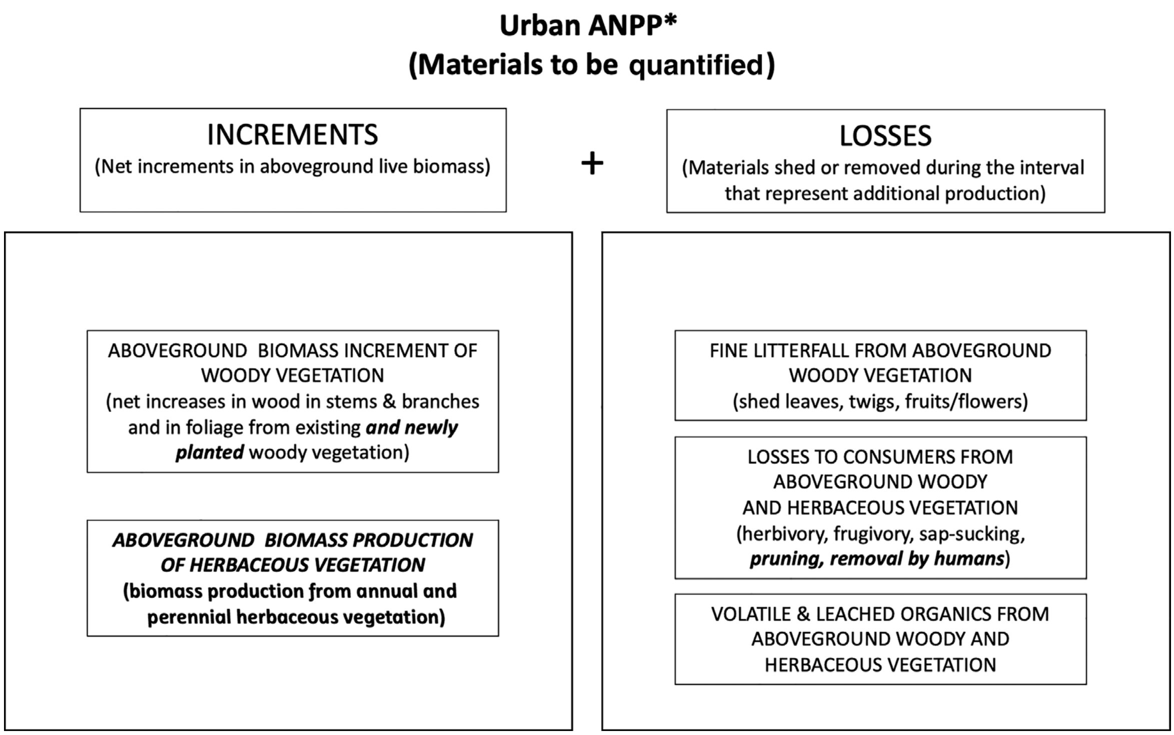

FIGURE 1 The components of urban ANPP*, including new organic matter retained by live plants at the end of the measurement interval (i.e., increments) and organic matter produced and lost by plants during the same interval (i.e., losses). Adapted from Clark et al. (2001)

shrubs, or herbaceous plants, and is often a mix of all three functional types. Many urban site types such as residential yards or institutional grounds resemble open woodlands where a dense shrub or herbaceous layer can make a significant contribution to biomass production. In addition, natural areas found within cities often reflect the surrounding native biome (e.g., desert, scrub/shrub, prairie, or forest) and may be dominated by non-woody vegetation in some ecoregions. Trees, shrubs, and herbaceous plants require different types of field measurements, and thorough descriptions of these methods may be found in resources designed for the native ecosystem from which these plants originate (e.g., Battles et al., 2008; Clark et al., 2001; Fahey & Knapp, 2007). However, there are special circumstances that arise in urban ecosystems that may require modifications to these established methods.

Woody vegetation

Aboveground biomass increments

The production of woody plant tissues with a short life span (deciduous leaves, flowers, and seeds) is often best estimated with fine litterfall collections, whereas long lifespan tissues are best estimated with allometric relationships developed from careful harvest of trees and shrubs (Kloeppel et al., 2007). Allometric equations are species-specific (or species group-specific) relationships that can be used to estimate volume or weight of trees based on their dimensions. Biomass increment is then calculated by making measurements of tree or shrub heights and diameters in successive years, computing the biomass for each year using allometric equations, and subtracting the biomass estimate in year 1 from that estimated in year 2. Diameter growth increment may also be measured from tree ring data. Few studies have developed allometric equations for tree volume or biomass specifically for urban sites, and there is not yet agreement in the literature about whether urban trees require modification to existing allometric equations developed for the same species in rural forests (Aguaron & McPherson, 2012; Hasenauer, 1997; McHale et al., 2009; Nowak, 2020; Yoon et al., 2013; Zhou et al., 2015). The widely used i-Tree Eco models use existing allometric equations developed in rural forest sites, but then reduce biomass estimates for trees with higher crown light exposure by 20% based on measurements of open-grown trees in urban areas found to have significantly less biomass than predicted using forest-derived equations (Nowak, 1994). McHale et al. (2009) tested this model assumption and found that many tree species in open-grown conditions exhibited similar or greater biomass than expected when compared with allometric equations developed in forested settings. Therefore, it is not clear whether or how allometric equations should be altered for trees growing across different urban site types (e.g., tree pits, lawns, maintained or unmaintained residential yards, forest patches). In general, more research is needed to determine under which conditions urban tree properties differ from published values developed from forest trees.

Differences in tree allometric relationships between urban and forest settings would be influenced by canopy architecture and wood density, which might vary between urban and rural sites and within urban areas. The canopy architecture and overall biomass of open-grown trees may reflect light availability, but may also be impacted by pruning or belowground growing conditions such as rooting space availability (Day et al., 2010; MacFarlane & Kane, 2017). Depending on the site type, surrounding land use, and management activities, urban tree biomass and growth rates may also be positively or negatively affected by pollution, nutrients, and water availability, and urban heat island effects (Calfapietra et al., 2015; Lahr et al., 2018; Reinmann et al., 2020; Sonti, 2020) with potential impacts on allometric relationships. Little information is known about how the wood density (specific gravity) of urban trees might vary across urban site types (Francis, 2000; MacFarlane, 2009), but research suggests that the use of existing forest-based wood density data may produce estimates of urban woody biomass that are 5%–10% too low (Westfall et al., 2020). Because it is not possible to track detailed site conditions or management actions for every urban tree in a study of ANPP, a more effective approach to urban tree biomass estimation will be to further refine urban tree wood densities and allometric equations to account for varied urban growth forms. In general, it is important to match the allometric equations as closely as possible to the site under study, and researchers in urban areas must be aware of the assumptions made when using allometric equations developed in rural forests.

Accurate measurement and careful remeasurement of tree diameter are critical to determining biomass increment given the slow growth rates of trees (Kloeppel et al., 2007). Dendrometer bands can provide greater measurement precision than diameter tapes (McMahon & Parker, 2015) but may be difficult to implement in urban settings where they may be subject to vandalism. Similarly, annual growth rings may be measured from extracted wood cores, but it can be difficult to gain permission to core trees from urban property owners (Dyson et al., 2019). Newly planted woody or herbaceous vegetation should be incorporated into estimates of urban ANPP as well, although without knowing when and at what size the woody vegetation was planted it may not be possible to estimate ANPP until after remeasurement has occurred. In mature forest stands, a minimum size cutoff is often used for tree measurements, with the justification that small trees (<10 cm diameter) account for less than 10% of vegetation biomass (Clark et al., 2001). However, ornamental small trees and shrubs are prominent features in many urban landscapes (Avolio et al., 2018; Nowak, Bodine, et al., 2016, Nowak et al., 2017). Previous research has found that trees and shrubs 2.54–15.3 cm in diameter account for ~60% of the number of trees in a city (Nowak & Aevermann, 2019), and trees 2.54–12.7 cm in diameter make up 2%–16% of urban tree biomass (Burrill et al., 2021).

Shrub biomass increment may be calculated from two successive biomass estimates, or one measure of ring width increment. However, allometric regression equations or other methods of estimating shrub biomass are poorly documented compared with common tree species (Battles et al., 2008; Conti et al., 2019; McHale et al., 2017). Furthermore, many shrub species planted in urban landscapes are exotic ornamental species or cultivars and have not been well studied in the ecological literature. These species may be heavily pruned or left to grow in their natural form depending on the urban site type and level of management activity. Allometric regression equations may be developed to relate shrub biomass to volume or crown dimensions rather than basal area or stem diameter (Conti et al., 2019; McHale et al., 2017; Young, 2007). Shrub volume may be relatively easy to measure in managed landscapes where shrubs are pruned into compact shapes. Shrub dimensions can be measured by hand, or volumes may be captured using lidar or structure-from-motion photogrammetry (Alonzo et al., 2020).

Shrub layer ANPP may also be estimated using light interception methods, given access to an LAI-2000 Plant Canopy Analyzer, or similar instrument (Battles et al., 2008). When measuring shrub volume or light interception over successive years, it is important to always measure during the same season (e.g., full leaf-out). However, it is still necessary to destructively sample shrubs to develop equations relating biomass to volume or leaf area index (LAI). Because it is difficult to gain permission to remove shrubs from urban plots, it may not be feasible to establish allometric relationships for every species in an urban ecosystem, given the large number of ornamental species that may be found in such landscapes (Avolio et al., 2020). In this case, regression equations may be established for shrub functional groups or growth forms, or even one general equation for all shrubs present (Conti et al., 2019, McHale et al., 2017).

In general, development of allometric equations that incorporate common pruning practices of common ornamental shrub species may be more effective than trying to quantify the amount of biomass removed from trees and shrubs on a plot each year. To capture a variety of urban management approaches, allometric equations should be built from a data set capturing as many management contexts as possible. However, it is possible that some shrubs are pruned to the same dimensions year after year, resulting in ANPP and stem diameter increment with no change in shrub volume. In these situations, coordination with urban land managers to quantify the amount of plant material removed may be necessary for accurate ANPP estimation.

Aboveground biomass losses

In addition to the accumulation of new biomass by woody plants, some of the organic matter produced is shed naturally or lost to herbivores or human management activities during the measurement interval. Fine litterfall includes leaf production as well as other short-lived woody plant material such as flowers, fruit, and twigs, and is relatively straightforward to measure in a closed-canopy forest using litterfall traps (Martínez-Yrízar et al., 1999; but please refer to Clark et al., 2001 for considerations of leaf longevity and size of woody material included). Foliage biomass of deciduous trees and shrubs can be estimated using allometric equations, or may be estimated from litterfall, but it is important to use only one method or the other to avoid accounting for the same foliage twice in ANPP estimates. Foliage biomass of evergreen trees and shrubs is generally included in allometric equations for total plant biomass.

Trees and shrubs in urban landscapes may be found in closed-canopy conditions, in which case the established methods for fine litterfall collection will be appropriate. However, in many residential and institutional landscapes, the spacing of trees and shrubs is much more irregular, making it difficult to calculate litterfall per unit area using traps on the ground. In these cases, it may be more effective to calculate fine litterfall per tree or shrub and scale up to the area of the plot depending on how many woody plants are present. However, it is not easy to collect fine litterfall from an entire tree, and so the use of allometric equations to estimate foliage production may be more appropriate in the urban environment. Furthermore, if a significant portion of organic matter is lost before twigs and/or leaves fall from the tree, then litterfall will underestimate foliage biomass production compared with allometric equations (Edwards, 1977; Frangi & Lugo, 1985; Kloeppel et al., 2007). However, open-grown trees may produce a different amount of foliage compared with forest trees of the same diameter, which is another reason that urban-specific allometric equations may be more reliable for estimates of urban ANPP.

Aboveground woody and herbaceous biomass production may be subject to losses to animal consumers through herbivory and seed and fruit predation, as well as to sap-sucking insects and nectarivores (Clark et al., 2001). In the urban landscape, pruning of trees and shrubs may also affect the amount of fine litterfall that is captured in litterfall traps. Jo and McPherson (1995) estimated that trees and shrubs on two residential blocks of Chicago lost 15% of annual carbon sequestered through pruning activities. Furthermore, litterfall traps should be installed in locations where leaves, fruit, or seeds are not raked or removed from a property. However, to produce accurate estimates of aboveground biomass production, it will be important to quantify fine litterfall production from ornamental species that are commonly found in heavily managed sites. Failure to account for any of these losses will lead to underestimation of urban ANPP.

Compared with vegetation in native biomes, plants of all functional types are frequently planted and removed in urban areas. An urban tree or shrub may be found standing dead or may have been removed during the measurement interval, making it difficult to track mortality. Careful documentation of woody vegetation locations within a plot is critical to determining whether plants have been removed. If a woody plant dies or is removed during a short measurement interval (<3 year), the plant can be assumed to have no growth increment contributing to ANPP* (Clark et al., 2001). If the measurement interval is longer, the growth increment of a woody plant that has died or has been removed can be estimated as half of the measurement interval using estimated growth rates (Bechtold & Patterson, 2005; Kohyama et al., 2018).

Other aboveground biomass losses include volatile organic compounds (VOCs) lost from foliage and organic compounds leached from aboveground plant parts. These components of ANPP* remain poorly quantified in natural biomes and have been considered minor components (<1%) of ANPP* in forests (Fahey et al., 2005; Guenther et al., 1995). It is unknown whether these losses make a more significant contribution to urban ANPP, although many aspects of the urban ecosystem are thought to influence VOC emission rates from trees (Fitzky et al., 2019; Owen et al., 2003). Sensitivity analysis of urban forest ecosystem service modeling has found that genus has the strongest impact on estimated VOC emissions from urban trees, followed by leaf biomass and temperature (Lin et al., 2020).

Biomass turnover in mature forests can be just 1%–2% per year (Fahey & Knapp, 2007), but this figure is likely to be much higher in the woody plant biomass of actively managed urban landscapes where entire live or dead trees and shrubs may be removed or planted on an urban site during a measurement interval (Nowak, Hoehn, et al., 2016). This higher rate of turnover makes it even more critical to record the locations of woody plants during plot surveys, as it will be impossible to determine which vegetation has been added or removed without this detailed information.

Herbaceous vegetation

Aboveground biomass increments

Aboveground biomass production of planted or naturally occurring herbaceous vegetation may be estimated by harvesting and weighing all herbaceous material from fixed area plots. When perennial plants are present, the current year's growth must be separated from dead and previous years' vegetation. When destructive harvesting is difficult, allometric techniques may be used to estimate herbaceous biomass from volume measurements, with regular harvests used as validation (Daoust & Childers, 1998).

Lawns, or urban grasslands, present some unique challenges to consider in ANPP assessments. It may be appropriate to make one measurement of peak standing biomass in an urban grassland where: (1) there is a significant dormant season leading to a clear distinction between the current and previous years' growth; (2) the growing season is short enough to prevent significant decomposition of biomass produced during the current season; and (3) there is no grazing or lawn mowing occurring (Knapp et al., 2007). When these conditions are met, green and current year's standing dead biomass may be summed to estimate urban grassland ANPP. However, when lawn mowing occurs, separate measurements of grass clippings, thatch, and stubble biomass must be combined (please refer to Falk, 1976, 1980; Qian et al., 2003). In tropical ecosystems where there is no dormant season, or significant decomposition occurs during one season, other techniques may be necessary (Knapp et al., 2007). In addition, herbaceous ANPP (including lawns) may vary strongly between shaded and sunny sites, fertilizer regimes, or across different soil conditions, such as time since development. Therefore, it is important to capture varied urban conditions when biomass harvests are used to estimate herbaceous productivity. Once local ANPP estimates are established for herbaceous cover types, such as mown and unmown urban grasslands, percent cover of these vegetation types may be recorded in field plots.

Aboveground biomass losses

In addition to losses to animal consumers described above, foraging, weeding, or other human activities may also account for significant losses of aboveground herbaceous biomass production. Although it may be relatively easy to determine whether an area is frequently mown, infrequent mowing (such as on some public or vacant properties) may be more difficult to detect. In addition, more targeted herbaceous plant removal (weeding) may be nearly impossible to account for. In addition to landscaping activities, large-scale plant removal may also occur when invasive species are targeted as part of restoration activities in urban natural areas and may be difficult to account for in urban ANPP estimates. Although time-consuming, urban biomass removal may be accounted for if researchers collaborate with land managers to quantify the amount and frequency of plant material removed (Jo & McPherson, 1995).

CHALLENGES: SOURCES OF ERROR AND UNCERTAINTY

Some of the challenges encountered in accurate estimation of ANPP are not unique to urban areas, whereas others may be exacerbated due to the lack of urban-specific literature. For example, establishing accurate allometric equations for palm trees (Brown, 1997) or exceptionally large trees (Brown & Lugo, 1992) remains challenging in urban environments, where they may account for high proportion of urban forest biomass. As previously mentioned, the lack of allometric equations for predicting aboveground biomass of urban trees and shrubs may lead to biased or less accurate estimates of ANPP in urban areas. In addition to pruning, urban trees may be more likely to experience branchfall or heart rot, which are not accounted for in allometric equations that estimate biomass of forest trees (Clark et al., 2001; Fahey et al., 2005). The contribution of shrubs to urban ANPP is likely to vary across urban regions, land uses, and with time since development. Given the smaller contribution of shrubs to urban NPP compared with trees, even in desert ecosystems where shrubs dominate NPP of the native landscape (McHale et al., 2017), accurate characterization of urban tree allometry is likely to be more important than similar efforts aimed at improving urban shrub NPP estimation. However, given that shrubs accounted for 5%–10% of urban NPP in Phoenix, AZ, USA (McHale et al., 2017) and 21%–25% of carbon uptake in residential Chicago, IL, USA (Jo & McPherson, 1995), the inclusion of shrubs in the study of urban ANPP remains important.

As in natural biomes, there may also be uncertainty associated with the separation of live and dead plant tissues, or difficulties in separating current-year senescent material from the previous year's senescent material. The biomass of lianas and hemiepiphytes are difficult to estimate in studies of forest ANPP (Clark et al., 2001), and urban forests are prone to heavy vine invasions in tree canopies (Simmons et al., 2016; Trammell et al., 2020; Ward et al., 2020). Finally, many components of ANPP* may be even more difficult to measure directly in urban settings, given the myriad property ownerships and permissions required for destructive sampling (Dyson et al., 2019; Nowak et al., 2008). Many of these challenges exist in forest productivity research settings but can be exacerbated in urban landscapes.

We did not include a discussion of belowground NPP here, but belowground measurements in urban areas would entail some of the same challenges present in non-urban systems (Tierney & Fahey, 2007) as well as the additional complications associated with destruction of urban property involved in digging up roots or potential disturbance to underground utilities (e.g., gas lines). However, belowground NPP is likely to contribute substantially to total urban NPP. Approximately half of grassland and turfgrass lawn NPP is allocated belowground (Lilly et al., 2015; Tierney & Fahey, 2007) and, although the fraction of forest NPP allocated belowground varies widely by forest type, fine root production in temperate forest ecosystems may account for up to 76% of total NPP (Vogt, 1991). It is not known how urban conditions such as soil compaction or limited soil volume might affect the accuracy of allometric equations developed to estimate woody root biomass in native ecosystems (e.g., Li et al., 2003). In addition to root biomass losses to herbivores, human landscaping or construction activities might lead to further losses of root biomass or impact root exudates (Day et al., 2010).

A lack of replication in space and time can decrease the reliability of ANPP estimates in any ecosystem, but the urban landscape is likely to be even more heterogeneous across space and time than natural biomes at the scale at which ANPP* is measured in the field, necessitating higher replication for reliable estimates. As found for natural biomes, urban ecosystems have irregularly distributed large trees, and irregularly distributed disturbance events, such as pest outbreaks, drought, or destructive storms. As a result, plot measurements should be well replicated over space and time, and plots may be arranged in a stratified random design with respect to the major gradients of variation (Clark et al., 2001). However, unlike many natural gradients such as soil type or slope, urban land uses and associated management regimes change frequently (in space and time) throughout the landscape, with significant impacts to standing biomass (Sonti, Henning, et al., 2021). Therefore, randomly placed plots may be the most appropriate strategy in a long-term study of urban ANPP (Edgar et al., 2021). Larger plots are more desirable for ANPP assessments in lower-density forests where individual large trees comprise a high proportion of total biomass (Kloeppel et al., 2007). However, establishing and accessing large plots in urban areas is challenging due to the number of built structures, roads, and property owners in proximity. A rule of thumb for forest plot measurements states that plot size should be chosen to encompass at least 75–100 trees larger than the minimum diameter included in the study (Kloeppel et al., 2007), but this is difficult to achieve in urban areas where many plots are not in a forested condition (Sonti, Henning, et al., 2021). Therefore, even in forested regions, a comprehensive estimate of urban ANPP cannot be solely modeled on forest measurement methods and must account for other vegetation types.

Because ANPP is estimated from a combination of measured variables, errors (both random and systematic) propagate as the variables are mathematically scaled and combined (Harmon et al., 2007). Estimates of uncertainty, such as confidence intervals, give important context for changes over time or comparisons to other ecosystems.

CASE STUDY: BALTIMORE ANPP* 1999–2014

Site description and methods

We calculated woody and herbaceous plant ANPP* components of the urban ecosystem in the City of Baltimore, MD, USA. Baltimore is located in the Chesapeake Bay watershed and is part of the deciduous forest ecoregion. The region has a long history of land clearing for agricultural activity followed by industrialization and urban development. More recently, Baltimore has experienced decades of depopulation and economic disinvestment (Grove et al., 2015).

Repeated measurements of tree size and condition were taken on permanent i-Tree Eco plots (formerly UFORE plots) established as part of the Baltimore Ecosystem Study LTER project (Appendix S1: Figure S1; Nowak, 2018). In total, 200 circular 0.04-ha plots were established with a stratified random sampling approach using land use categories obtained from a 1996 municipal land use map: high-density residential, medium-/low-density residential, forest, commercial/industrial, institutional, transportation, open urban land, and barren.

Full descriptions of all i-Tree Eco field data variables are available in the field manual (i-Tree Eco Field Guide v6.0, 2019). For each plot in this study, all woody vegetation with a minimum stem diameter at 1.37 m (diameter at breast height [dbh])) of 2.54 cm was measured and recorded as a tree. For each tree, species, dbh, total height, crown width, height to base of crown, percent crown missing, crown dieback, and crown light exposure (number of sides of the tree receiving sunlight from above) were recorded. For multistemmed trees, a tree dbh was calculated based on the combined basal area (cross-sectional area of stem at dbh) of all measured stems.

Plot centers were permanently referenced based on triangulation from fixed objects and individual tree locations were recorded (distance and azimuth from plot center) to facilitate remeasurement. Permanent tagging was not conducted due to the prevalence of plots on private land or in highly trafficked areas subject to potential vandalism. The plots were assessed by field crews in the summers of 1999, 2004, 2009, and 2014. Plots that were not assessed at all time periods were excluded from the analysis, which led to a total of 193 plots used in estimating ANPP for each measurement interval: high-density residential (50 plots), medium/low-density residential (42 plots), forest (39 plots), commercial/industrial (25 plots), institutional (10 plots), transportation (10 plots), open urban land (9 plots), and barren (8 plots).

Models contained within the i-Tree Eco software (version 6.0.19) were used to calculate biomass for individual trees at each time period. i-Tree Eco estimates total dry-weight woody biomass for each measured tree from tree height and diameter using species-specific forest-derived allometric equations from the literature (Nowak, 2020). In the i-Tree Eco software, if no biomass equation is found for an individual species, the average of results from equations of the same genus is used. If no genus coefficients exist, then the next phylogenetic level average is used as available. Whole tree biomass was then converted to aboveground biomass using a root-to-shoot ratio of 0.26 (Cairns et al., 1997). Equations that compute fresh-weight biomass were multiplied by species-specific or genus-specific conversion factors to yield dry-weight biomass (Nowak et al., 2002). Biomass results for open-grown trees were multiplied by a factor of 0.8 to account for the fact that open-grown, maintained trees tend to have less aboveground biomass than predicted by forest-derived biomass equations (Nowak, 1994). Open-grown trees were defined as having a crown light exposure of four or five sides, and accounted for 12%–24% of the

Baltimore tree population in a given sampling year. Deciduous tree leaf biomass (weight of dry leaves) was calculated by converting leaf area estimates (generated within i-Tree Eco from species crown density coefficients and crown volumes related to field-collected crown size variables) using species-specific conversion factors of grams of leaf dry weight per square meter of leaf area (Nowak, 2020). i-Tree Eco carbon sequestration models were used to estimate growth of trees that died or were removed between measurement intervals (growth from the initial measurement to the midpoint between measurement intervals; Bechtold & Patterson, 2005). These species-specific models of annual growth incorporate tree diameter, height, competition (crown light exposure), tree health (canopy dieback), and length of growing season (Nowak, 2020). Ingrowth of new trees was calculated as the difference between the biomass of the tree when it was measured at the end of the interval and the estimated biomass of the tree at 2.54 cm diameter when it would have entered the inventory. Citywide estimates were generated by summing biomass at the plot level and then extrapolating to population totals using stratified random sampling statistics with the land use stratification from the original 1999 study design described above (Cochran, 1977).

Assessments of ground cover on the permanent plots were used to estimate citywide percentage cover of maintained grass, unmaintained grass, and other herbaceous vegetation at each measurement interval. As with tree measurements, ground cover plot data were scaled to citywide estimates using stratified random sampling statistics and the land use stratification from the original study design. Ground cover was not assessed in 1999, and so the 1999–2004 herbaceous ANPP estimates were generated using only 2004 ground cover data. Maintained grass (i.e., lawn) covered from 24% to 27% of the city, whereas unmaintained grass cover was ~3% across all time periods, and other herbaceous vegetation cover ranged from 6% to 7% during the study period.

These citywide ground cover estimates were combined with published values of aboveground biomass (or local unpublished ANPP data for maintained grass) for each vegetation cover type to calculate citywide changes in ANPP* components over time. Maintained grass productivity was estimated using data collected from repeated measurements of Baltimore residential lawns (Jenkins et al., 2021; Raciti et al., 2011a, 2011b). Sites were selected across a gradient of housing age classes, prior land uses, and landscape configurations and were clipped once or twice weekly throughout the 2006 and 2007 growing seasons (1 April to 15 November) to simulate mowing regimes. In addition to clippings, stubble, thatch, and moss production were quantified to calculate total ANPP*. Unmaintained grass productivity was estimated using Hoeppner and Dukes' (2012) oldfield biomass measurements from Waltham, MA, USA. Other herbaceous vegetation productivity was estimated using a published equation for forest understory forb biomass (Thrippleton et al., 2016), given that most other herbaceous vegetation cover in the Baltimore data set occurred on forested plots.

Variance among plots for ground cover estimates and individual tree measurements was used to calculate the standard error of the mean, an estimate of sampling error, for each vegetation component and for total ANPP* during each time interval. Other sources of error were not considered in this study, including modeling errors associated with the ANPP rates of each vegetation type. Seedlings and shrubs less than 2.54 cm diameter at 1.37 m height were not assessed as part of the Baltimore i-Tree Eco protocol, so the contributions of those vegetation types to ANPP* are missing from these calculations.

Baltimore ANPP* across the three measurement intervals, and average ANPP* over 1999–2014 was compared with published values from other North American LTER sites (Knapp & Smith, 2001; Monk & Day Jr., 1988). ANPP* was also plotted against mean annual precipitation (MAP) for each site. Baltimore MAP was calculated using daily total precipitation data covering the years 1999–2014 from the NOAA weather station at Baltimore Washington International Airport (NOAA GHCN, 2020), Coweeta MAP data were previously published by Swift Jr. et al. (1988), and all other LTER precipitation data were previously published by Knapp and Smith (2001).

Results and discussion

Total citywide ANPP* for Baltimore across all time periods was 355.8 g m^{-2}. Baltimore's ANPP* is dominated by trees and maintained grass (i.e., lawn), with much smaller contributions from unmaintained grass and other herbaceous vegetation (Figure 2; Appendix S1: Table S1). Unmaintained grass is likely to be found in vacant lots or other unmanaged open sites, whereas other herbaceous vegetation cover is primarily found in the understory of forested sites as well as within residential, commercial, or institutional garden landscapes. Although the average annual rate of maintained grass productivity used in our case study is higher than unmaintained grass or herbaceous vegetation (558 g m^{-2} compared with 416 and 215 g m^{-2}, respectively), it is the higher proportion of maintained grass cover in Baltimore compared with the other herbaceous vegetation types that drive its large contribution to overall citywide ANPP*. These results

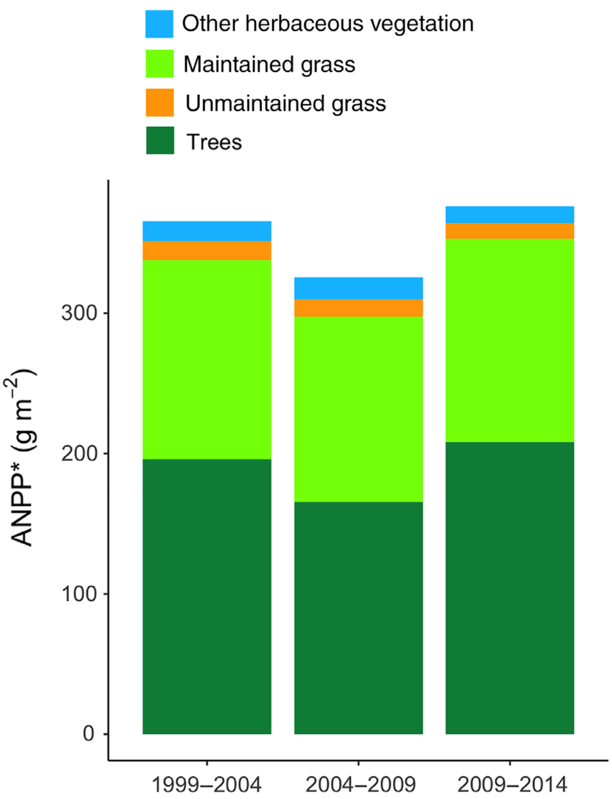

FIGURE 2 ANPP* of woody and herbaceous vegetation types assessed in Baltimore, MD during three time periods from 1999 to 2014

confirm that, even in a naturally forested ecosystem context such as Baltimore, lawn primary productivity should not be ignored in characterizations of urban biomass and carbon flux. In other urban settings with equally extensive lawn cover and less tree canopy cover, lawns would contribute even more to citywide urban ANPP*.

In our 15-year estimate of Baltimore's ANPP, woody (tree) ANPP* fluctuated over time, decreasing by 22% from the first to the second measurement interval and then increasing by 20% from the second to the third measurement interval. The number of trees in Baltimore's urban forest decreased during all three intervals, but the decrease was largest during 2004–2009 (Sonti, Henning, et al., 2021). Throughout the study time period, there was a consistent decrease in the proportion of trees in the smallest diameter class (2.54–15.24 cm) and a concurrent increase in the proportion of trees in larger diameter classes (Sonti, Henning, et al., 2021). This decrease in small diameter trees suggests that there is not enough planting or natural regeneration to sustain the city's urban forest, which may cause a long-term decrease in citywide ANPP over time. Net change in standing live tree biomass was positive during 1999–2004 but was negative during 2004–2009 and 2009–2014, driven by increasing removal of large diameter trees and lower total growth in the remaining population of large trees (Sonti, Henning, et al., 2021). Several large storms during these intervals may have contributed to the removal of mature trees, including Hurricane Irene in 2011, Hurricane Sandy in 2012, and a derecho in 2013. However, if larger declining trees with low growth rates were removed, this may explain why ANPP* increased from the second to third measurement intervals, as the remaining population of healthier trees contributed more to ANPP* as they grew larger over time.

The magnitude of tree ANPP* fluctuation in our study is similar to the ~20% decrease in northern hardwood forest ANPP* observed between successive 5-year intervals at the Hubbard Brook LTER in New Hampshire, USA during the 1950s to 1960s (Whittaker et al., 1974) and during the 2000s to 2010s (Battles et al., 2014). Hubbard Brook ANPP* also declined by 31% from 1956 to 1965 to the 1990s, a long-term trend explained by species-specific decreases in the growth rates of living trees, the causes of which may be complex and difficult to identify (Siccama et al., 2007). Continued monitoring of ANPP* of Baltimore's trees may reveal similar long-term trends or continued short-term fluctuations.

ANPP* of the other vegetation types did not fluctuate as strongly between measurement intervals, but this difference is likely to be due to our calculations only including changes in percent cover, and not in actual rates of herbaceous ANPP. Percentage cover of herbaceous plants may change over time due to environmental factors but is more likely to be tied to changes in human management activities, whereas interannual climate variability is more likely to result in changes in productivity within the existing amounts of herbaceous (and woody) vegetation cover. In particular, interannual variability in grassland ANPP is known to be high, and estimated errors associated with maintained and unmaintained grass ANPP* in this study are lower than that of grassland LTER sites (Knapp & Smith, 2001). This difference may be due in part to human inputs of water or fertilizer in urban systems, but more frequent measurements of urban herbaceous productivity would probably yield stronger fluctuations over time. For example, the maintained grass ANPP plot data used in our calculations ranged from a mean value (±SE) of 575 g m^{-2} (±70) in 2006 to 541 g m^{-2} (±40) in 2007. In contrast, estimated error associated with trees in this study is higher than that of forested LTER sites, which is unsurprising given the high variability among urban plots ranging from closed-canopy forest conditions to plots without any trees (Knapp & Smith, 2001).

When compared with other LTER ecosystems, Baltimore citywide ANPP* is only about half as much (or less) than ANPP* at forested sites of the eastern United States

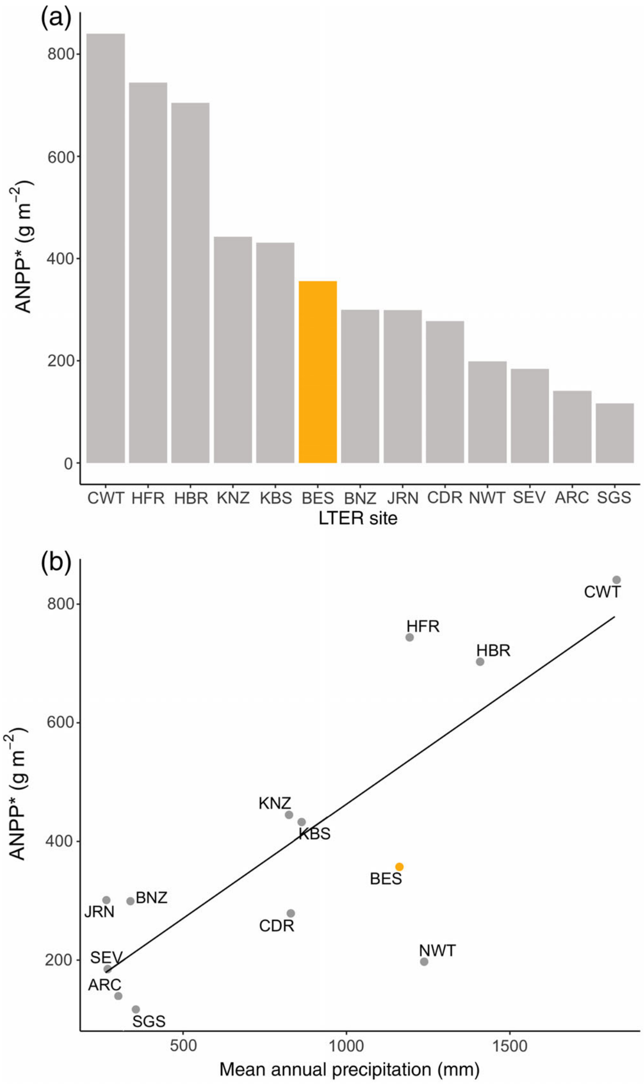

FIGURE 3 (a) Long-term average ANPP* for 13 sites in the LTER network: CWT (Coweeta), HFR (Harvard Forest), HBR (Hubbard Brook), KNZ (Konza Prairie), KBS (Kellogg Biological Station), BES (Baltimore Ecosystem Study), BNZ (Bonanza Creek), JRN (Jornada), CDR (Cedar Creek), NWT (Niwot Ridge), SEV (Sevilleta), ARC (Arctic Tundra), and SGS (Shortgrass Steppe). (b) Relationship between mean annual precipitation and long-term average annual ANPP* for 13 LTER sites. Data from all sites except CWT and BES are from Knapp and Smith (2001)

(CWT, HFR, and HBR), and is more comparable with grassland (KNZ and CDR), oldfield (KBS), desert (JRN), or boreal forest (BNZ) sites (Figure 3a). Although Baltimore is located in a temperate deciduous forested region, tree canopy only covers 28% of the city's area (O'Neil-Dunne, 2017), and impervious surfaces that contribute little to ANPP cover almost half (45%) of the city's area (City of Baltimore, 2009). Similarly, Briber et al. (2013) found that the GPP of Boston, MA, USA was ~75% lower than that of nearby Harvard Forest (HFR). However, there is evidence that tree and herbaceous plant growth rates are enhanced in urban areas worldwide, due to a combination of factors including elevated air temperature, atmospheric CO_2, light availability, and nutrient availability (Briber et al., 2015; George et al., 2009; Pretzsch et al., 2017; Reinmann et al., 2020; Ruan et al., 2019; Searle et al., 2012; Sonti et al., 2019, Sonti, Griffin, et al., 2021; Zhao et al., 2016; Ziska et al., 2004). Despite enhanced growth rates, urban trees in some settings may not live as long as trees in rural forests (Smith et al., 2019), and fragmentation associated with urbanization may lead to increased climate stress (Reinmann & Hutyra, 2017). These varied environmental impacts on urban plant physiology will probably have interacting effects on productivity and carbon cycling in urban systems.

When compared with MAP, we found that Baltimore (BES) ANPP* lies below the trend line, indicating it has low productivity for its level of precipitation, similar to the temperature- and nutrient-limited alpine (NWT) and grassland (CDR) sites (Figure 3b). Because urban ecosystems contain a mix of woody and herbaceous vegetation (particularly grass), they may exhibit ANPP characteristics of grassland, forest, and other ecosystem types. For example, Knapp and Smith (2001) found that maximum interannual variability in ANPP* occurred in grassland and oldfield biomes where high potential growth rates of herbaceous vegetation were combined with moderate variability in precipitation. Low variability in ANPP* occurred in forested biomes, which had consistently high ANPP* and less variation in precipitation. The continental homogenization of urban residential landscapes has led to a similar mix of trees and lawn throughout urban ecosystems in varying climates (Locke et al., 2019; Pearse et al., 2018). An arid or semiarid city might be expected to have greater ANPP* than predicted for its MAP given the prevalence of human irrigation inputs and intensive landscaping efforts in these urban ecosystems (Imhoff et al., 2004), although McHale et al. (2017) found the opposite to be true in their estimate of Phoenix, AZ NPP. Comparison of native biomes, Baltimore, and additional urban areas will help elucidate the extent to which ANPP is converging across the urban macrosystem, similar to other ecological patterns and processes (Groffman et al., 2014).

Our case study calculation of urban ANPP* does have some limitations that should be improved upon in further research. In general, we may be underestimating ANPP in our Baltimore case study due to the lack of data on small shrubs, the 20% reduction in open-grown urban tree biomass used in the i-Tree Eco model (Nowak, 2020), which affected 12%–24% of trees in our analyses depending on the year, and the probable underestimate of urban tree wood density in our case study (Westfall et al., 2020). Although not likely to be a large component of urban ANPP, seedlings and shrubs less than 2.54 cm diameter at 1.37 m height are missing from our data set and should be included in woody biomass production. As mentioned previously, the further development and use of urban-specific allometric equations to calculate tree biomass from diameter and height measurements would also reduce the error associated with the differences between urban and rural tree growth forms. Finally, our estimates of herbaceous biomass production would also be improved with additional data collection from the study system over time. In general, our error calculation should be considered an estimate of minimum error, as there is modeling error associated with productivity rates of all vegetation types that was not incorporated into this analysis. The differences discussed here between Baltimore's ANPP* and other biomes, as well the relationship with MAP, may be influenced by these limitations, and further data collection and analysis will improve our understanding of these relationships across urban areas.

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Knowledge about urban ecosystem productivity and carbon fluxes is still relatively undeveloped compared with the body of research on native ecosystems. We do not know how biomass accumulation curves of urban ecosystems compare with other ecosystem types or how urban plant biodiversity and demography impact biomass production rates across urban site types and ecoregions. In addition, many of the research questions posed by House et al. (2003) in relation to the "NPP conundrum" in mixed woody-herbaceous plant systems are also compelling in urban landscapes given their savanna-like structure. For example, how do spatial patterns of urban vegetation distribution affect NPP (i.e., does NPP for a given woody plant basal area vary if trees or shrubs are clumped or dispersed)?

Future research should pursue field-based calculation of ANPP* in urban areas throughout different geographic regions, reflecting differences in climate and patterns of urban development. Establishment of the USDA Forest Service's Urban Forest Inventory and Analysis (FIA) program (Edgar et al., 2021) may help to enable future calculations of urban tree ANPP* nationwide, as FIA data from rural lands have been used to estimate forest NPP across the United States for decades (Gray et al., 2016; Hudiburg et al., 2009; Jenkins et al., 2001; Raymond & McKenzie, 2013). In the absence of nationwide urban vegetation sampling programs, coordinated long-term research networks such as the International Long-Term Research (ILTER) Network may promote the collection of urban ANPP data using standardized protocols. The i-Tree Eco protocol used in our Baltimore case study has also been used in dozens of countries worldwide (Nowak et al., 2018) and can be used to generate urban tree ANPP estimates if repeated at regular intervals.

Sampling designs other than randomly located fixed area plots may be established to target measurement of different urban vegetation types across a gradient of environmental conditions (e.g., time since urban development). Remotely sensed data may also be used in conjunction with field-collected data to estimate contributions of different vegetation types across an urban region. In our case study, we found that field-collected plot data provided more useful herbaceous vegetation cover categories, given that remotely sensed vegetation cover classes are generally not as specific (e.g., maintained grass vs. unmaintained grass vs. other herbaceous vegetation) and may be obscured by overhanging tree canopy.

Here we present a conceptual framework and detailed methodological considerations for field-based measurements of urban ANPP*, as well as the first effort to estimate citywide urban ANPP from a combination of repeated field measurements and other data sources. As cities around the world invest millions of dollars into tree-planting initiatives (Campbell, 2017; Oldfield et al., 2013; Pincetl et al., 2013) and prioritize conservation of urban natural areas (Forgione et al., 2016; Salbitano et al., 2016), it will be important to understand the contribution of these different green spaces and their component vegetation types to overall urban plant biomass production and associated ecosystem services. In addition, the prevalence of residential and other privately owned lands throughout urban areas has led to their inclusion in urban sustainability initiatives aimed at increasing vegetation cover (Aronson et al., 2017; Lerman & Warren, 2011). Individual decisions made by urban land managers about the type of vegetation present on their property and the intensity of management practices used can scale up to shape landscape-scale trends in ecosystem productivity and carbon and nutrient fluxes (Briber et al., 2013; Polsky et al., 2014).

A more accurate assessment of urban primary production within cities, between cities, and over time can help to inform effective urban sustainability and climate policy.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Environmental Data Initiative: Nowak, 2018 (https://doi.org/10.6073/pasta/f499b08931ce01b01280f1f89e5c1ee9) and Jenkins et al., 2021 (https://doi.org/10.6073/pasta/07bf9a491ea7d08459b5849ba703634f).

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