ECOSYSTEMS

Sensitivity of Canopy Phenology to Local Urban Environmental Characteristics in a Tropical City

Peter Kabano,[1,2]* Angela Harris,[1] and Sarah Lindley[1]

[1]Department of Geography, School of Environment, Education and Development, The University of Manchester, Manchester, UK; [2]Department of Urban and Regional Planning and Geo-Information Management, Faculty of Geo-Information Science and Earth Observation (ITC), University of Twente, Enschede, The Netherlands

ABSTRACT

Canopy phenology is sensitive to variability in local environmental settings. In temperate climates, urban phenological processes and their determinants are relatively well understood. Equivalent understanding of processes in tropical urban settings is, however, less resolved. In this paper, we explore the influence of local urban environmental characteristics (that is, degree of urbanization, land cover and urban climate) on canopy phenology of two deciduous tree species (*Jacaranda mimosifolia*, $n = 48$, and *Tabebuia rosea*, $n = 24$) in a tropical city (Kampala, Uganda). Our study design involved ground monitoring and field sampling in 2017, with a focus on the dry season. We found that both species experienced significantly higher rates of canopy cover decline in heavily built-up neighborhoods ($p < 0.05$ for both species). Moreover, *Jacaranda* was more sensitive to differences in the degree of urbanization than *Tabebuia*, both in terms of total percentage tree canopy cover ($p < 0.01$) and net leaf loss ($p < 0.05$). Total percentage tree canopy cover for *Jacaranda* declined with increasing proportion of impervious cover (that is, roads and paved cover) and was positively related to relative humidity ($p < 0.01$), a variable correlated with soil moisture. Net leaf loss in *Jacaranda* increased with the decreasing proportion of pervious land cover and as nighttime air temperature increased ($p < 0.01$). In contrast, land cover and urban climate had no significant influence on either measure of phenological traits for *Tabebuia*. These results provide new evidence of the effect of urbanization on canopy phenology of different tree species in the tropics. Such knowledge offers new insights into the spatial and temporal differences in the physiological functional traits of trees and also serves as a proxy for possible species responses under future climate change.

Key words: Tropics; Dry season; land cover; Urban climate; UHI effect; Relative humidity; Soil moisture; Vegetation; Tree canopy phenology.

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*Corresponding author; e-mail: ptkabano@gmail.com

HIGHLIGHTS

- Rate of decline in canopy cover is greatest in heavily built-up locations.
- Tree species vary in their sensitivity to the effects of urbanization.
- High temperature and a high proportion of impervious land cover suppress canopy cover.

INTRODUCTION

Urbanization is a major driver of environmental change through the intensive modification of the landscape, increased human habitation and energy consumption (Wu 2014). The increase in area covered by artificial surfaces in cities enhances thermal admittance and heat storage resulting in the urban heat island (UHI) effect (Roth 2007; Giridharan and Emmanuel 2018). Moreover, increased potential evapotranspiration due to the UHI effect, coupled with restricted water uptake, accounts for lower levels of surface moisture and atmospheric humidity in cities, commonly referred to as the Urban Dryness Island (UDI) effect (Adebayo 1991; Hao and others 2018). As much as 90% of urban growth predicted to occur over the next 30 years is expected to be concentrated in tropical Africa and Asia (United Nations 2019) where high levels of vulnerability to climate change are already being observed (du Toit and others 2018; Lindley and others 2018). Consequently, it is imperative to improve our understanding of the potential consequences of degraded urban environments on the quality of life and public health.

The UHI effect has been observed in many cities in the tropics and poses a public health concern due to the potential for population exposure to high temperature events (Roth 2007; Scott and others 2017; Giridharan and Emmanuel 2018; Kotharkar and others 2018; Simwanda and others 2019). This is particularly important in the context of climate change and associated trends toward higher temperatures and more extreme events (du Toit and others 2018; Lindley and others 2018). Vegetation is important in tropical cities for mitigating against the effects of urbanization through the provision of ecosystem benefits, including thermal regulation (Cavan and others 2014; Feyisa and others 2014), provision of shade (de Abreu-Harbicha and others 2015) and flood control (du Toit and others 2018; Lindley and others 2018). However, urban vegetation is being lost at unprecedented rates in much of the tropics (Yao and others 2019), which poses a public health concern for the urban populace.

Other than the spatial extent of vegetation cover in tropical cities, vegetation seasonal growth patterns [commonly referred to as vegetation phenology (Lieth 1974)] are equally crucial for understanding vegetation ecosystem processes, yet phenological processes in tropical cities often remain overlooked. Evidence suggests that vegetation in temperate cities experiences longer growing seasons with earlier starts than in rural areas due to the UHI effect (for example, Neil and Wu 2006;

Jochner and Menzel 2015). Far fewer phenological studies have been carried out in tropical urban settings. Those that exist have focussed on understanding how the UHI effect influences the timing of the start of the vegetation growing season in both temperate and tropical cities (for example, Gazal and others 2008; Jochner and others 2013a). Findings suggest that the UHI effect generally plays a more limited role in controlling the timing of the start of the growing season in the tropics (Gazal and others 2008; Jochner and others 2013a), possibly as a consequence of milder seasonal temperature changes as compared to temperate regions. However, relative humidity has been shown to correlate strongly with season onset dates of some tropical tree species (Jochner and others 2013a), highlighting a potential effect of surface moisture as the two variables often show a positive association (for example, Huxley and Vaneck 1974; Borchert 1983; Williams and others 1997; Zhang and others 2005; Archibald and Scholes 2007; Clinton and others 2014; de Camargo and others 2018; Cai and others 2019). Therefore, other than the UHI effect, soil moisture is an essential variable driving phenology in temperate cities (Jochner and others 2011; Buyantuyev and Wu 2012; Walker and others 2015) necessitating the inclusion of a wide range of spatially varying abiotic factors in the analysis of drivers of phenology in tropical cities.

Existing vegetation phenological knowledge in tropical urban settings emanates exclusively from studies that have focused upon the timing of the start of the growing season alone (for example, Gazal and others 2008; Jochner and others 2013a). Knowledge about the seasonal growth of vegetation over an extended period is scarce despite being widely studied in natural tropical habitats (for example, Williams and others 1997; Condit and others 2000; Valdez-Hernandez and others 2010; Dalmolin and others 2015; de Camargo and others 2018). These studies have shown that soil moisture depletion with the advancement of the dry season drives leaf loss and that the extent of leaf loss is dependent upon species type and local environmental conditions. Whether changes in canopy cover follow similar patterns in tropical cities due to variation in local environmental settings, is currently unknown. Unusually, high levels of leaf loss may impact upon the fitness of trees in successive growing seasons (Singh and Kushwaha 2016) and affect the extent of shading offered from tree stands and their thermal regulation benefits.

Here, we study tree canopy cover change of two deciduous tree species (*Jacaranda mimosifolia* and *Tabebuia rosea*) in response to differences in the

degree of urbanization, land cover and intra-urban climate in Kampala, Uganda in 2017, with a particular focus on the dry season. We test three key hypotheses: (1) The degree of urbanization of a given location influences the rate of change of canopy cover. We expect that heavily built-up neighborhoods would experience higher rates of decline in tree canopy cover in comparison with less built-up neighborhoods. (2) We anticipate that tree canopy cover change represented by total percentage tree canopy cover and net leaf loss, between heavily and lightly or moderately built-up neighborhoods will differ between the species. (3) Variations in total percentage tree canopy cover and net leaf loss for each species are accounted for by differences in land cover and urban climate.

METHODS

Study Area

The study was undertaken in Kampala, East Africa (located at 00°18′49″ N 32°34′52″ E) between March and September 2017. Kampala covers an approximate area of 181 km^2 and has a population of over 1.6 million inhabitants (that is, a population density of approximately 9300 inhabitants/km^2; https://www.citypopulation.de/). Kampala has a tropical rainforest (equatorial) climate (Af) according to the Köppen climate classification. Climate records over 30 years show that Kampala has two wet seasons annually (March–May and September–November) and annual precipitation of about 1200 mm (data source: WMO, World Meteorological Organization). The heaviest monthly rains are in the shorter rain season (generally March to May) with April typically recording the heaviest rains (approximately 169 mm), whereas July is the driest month (about 63 mm). In 2017, the dry season started in May and continued through September (Figure 1A), and nighttime temperature and relative humidity varied across the city (Figure 1B).

Selected Tree Species

Two deciduous tree species (*Jacaranda mimosifolia* and *Tabebuia rosea*) that are commonly found throughout Kampala were selected for the analysis of canopy cover change (Figure 2). *Jacaranda mimosifolia* (D. Don) and *Tabebuia rosea* (Bertol.) DC both belong to the family *Bignoniaceae*. They are native to the neo-tropics (for example, Argentina, Brazil, Mexico, Venezuela and Ecuador) but are grown in other tropical countries (for example, Uganda, Sri Lanka, South Africa and Australia).

Jacaranda trees grow up to 20 m in height with spreading branches to make a light crown (data source: World Agroforestry). *Jacaranda* trees undergo leaf flush with the onset of the rain season, while leaf fall starts early in the rain season and extends into the dry season (Huxley and Vaneck 1974). *Tabebuia* trees grow up to 25 m high and exhibit considerable shoot growth and leaf flushing during the rainy season (data source: World Agroforestry), while leaf fall is pronounced during the dry season in response to increasing air temperature (Figueroa and Fournier 1996).

Individual Tree and Phenology Site Selection

Traditionally, an urban–rural dichotomy has been the basis for examining the effects of urbanization on phenology (for example, Roetzer and others 2000; White and others 2002; Zhang and others 2004; Gazal and others 2008). However, the local scale effects associated with differences in land cover within cities are known to influence phenology (Jochner and others 2012, 2013a; Zhang and others 2014; Melaas and others 2016; Zipper and others 2016) and ought to be considered when undertaking phenological observations in tropical cities. Therefore, nine phenology sites were selected within the city to represent the wide range in land cover, structure and land use types (that is, commercial, residential and park) that can be observed across the city (Figure 3; Table 1). Each phenology site contained between 3 and 8 individual trees of one of the candidate species ($n_{Jacaranda}$ = 48; $n_{Tabebuia}$ = 24). To minimize the potential phenological influence of elevation, each phenology site was located within an 80 m altitudinal range of one another (Jochner and others 2012). Differences in tree size and age were minimized by selecting trees with a similar height and trunk size (that is, diameter at breast height).

A cloud-free WorldView-3 (WV3) satellite image acquired on 25/10/2016 was selected for the characterization of pervious land covers (grass and bare soil), trees, impervious land covers (road and paved ground) and buildings as the land cover types and structural features that influence local climate and phenology (Stewart and Oke 2012; Jochner and Menzel 2015). Despite being taken from the wet season, the image was ideal for characterization of the land cover types of interest whose spatial extent is expected to remain the same regardless of season. The creation of regions of interest (radius = 200 m) at each phenology site for attribution of phenology to land cover and structure was done according to
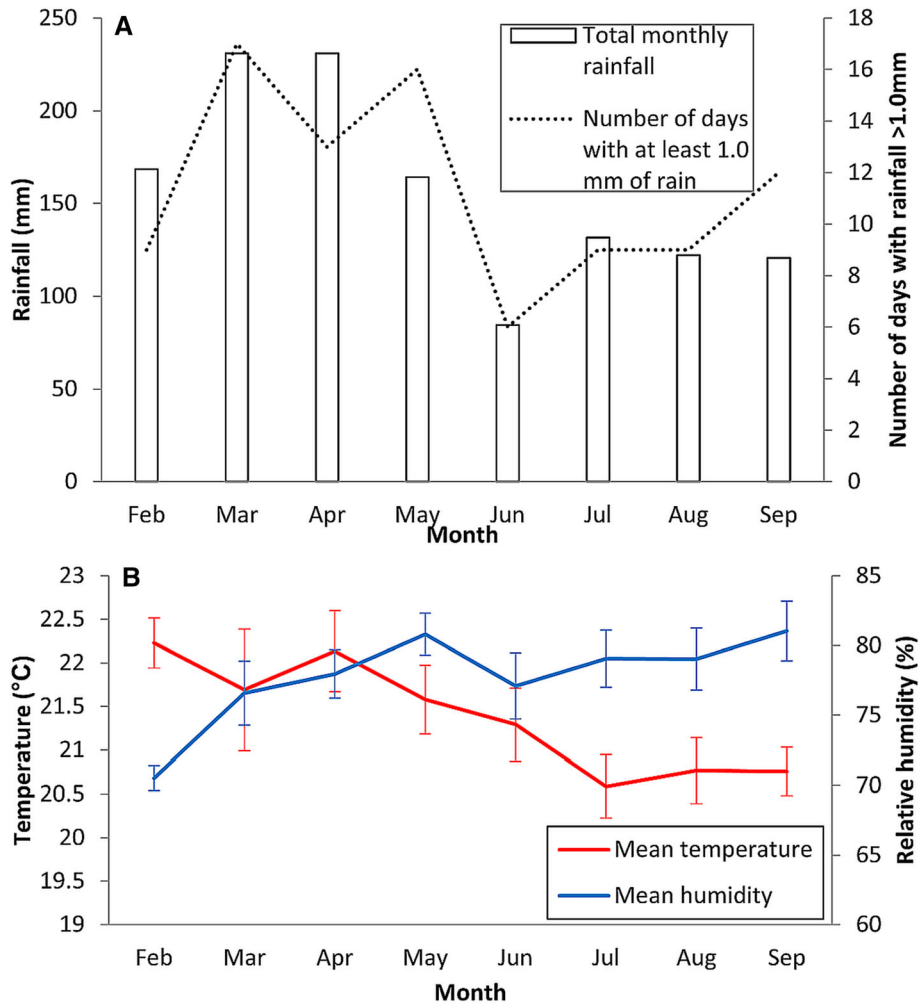
Figure 1. Kampala's climate between February and September 2017, (**A**) monthly rainfall and number of days with more than 1 mm of rain and (**B**) monthly nighttime air temperature and relative humidity. Errors bars represent the standard deviation and show the monthly variation of nighttime temperature and relative humidity across the phenology sites.

Figure 2. (**A**) *Jacaranda* and (**B**) *Tabebuia* are ornamental trees commonly found throughout Kampala.

Figure 3. Land cover and structure at each individual phenology site (site number is shown in the top left corner). A summary of each phenology site's characteristics is presented in Table 1.

Stewart and Oke (2012), where an area with a minimum radius of 200 m is recommended for attribution of urban climate to land cover and structure. All trees selected for phenological observations were centrally located in relation to the positioning of the region of interest such that any given tree was at a distance of less than 100 m from the center of the region of interest (Figure 3).

The WV3 image consisted of 8 multispectral bands: coastal blue, blue, green, yellow, red, 2 NIR (near-infrared) bands (NIR1 & NIR2) and a panchromatic band. The image was geometrically

corrected and projected to the WGS-84 UTM Zone 36 N coordinate system. Pansharpening was applied to increase the spatial resolution of the image from 1.24 to 0.5 m using the panchromatic band. The spectral band set was supplemented with a NIR/Red ratio and Normalized Difference Vegetation Index bands (using the NIR and Red band) to increase classification accuracy.

The image was classified using eCognition Developer (version 9) using an Object-Based Image Analysis (OBIA). OBIA exploits spectral, spatial, textural and topological characteristics of the image

Table 1. Characteristics of the Nine Phenology Sites, Their Associated Urban Form (Proportion of Pervious Cover, Trees, Impervious Cover and Buildings) and Number of Individual Trees (per Species) Sampled at Each Phenology Site

Phenology sites	One	Two	Three	Four	Five	Six	Seven	Eight	Nine
Pervious land cover (bare soil and grass) (%)	12	13	38	69	42	41	46	50	42
Tree cover (%)	24	18	8	16	30	32	23	48	52
Impervious land cover (road and paved ground) (%)	37	44	31	08	13	09	16	01	02
Buildings (%)	27	25	22	7	15	19	14	00	04
Jacaranda	5	2	6	5	6	5	5	8	6
Tabebuia	4	5	0	5	0	3	0	0	7
Degree of urbanization category	Heavily built-up			Moderately built-up				Lightly built-up	

The last row indicates the degree of urbanization category assigned to each phenology site.

and is often used to classify very high-resolution imagery. OBIA is performed in a two-step process involving segmentation (creation of objects) and classification of objects, as opposed to individual pixels. Consequently, OBIA overcomes the within feature variation, salt-and-pepper effect and mis-classifications associated with the pixel-based classification (Blaschke 2010; Blaschke and others 2014; Momeni and others 2016). Segmentation creates objects whereby grouped pixels in a given object share similar characteristics such as spectral value. Experimentation was conducted to determine the selected OBIA approach, and a multi-stage object-based classification undertaken using a multiresolution segmentation algorithm. Multi-stage OBIA is a widely used approach in heterogeneous urban environments (Momeni and others 2016). Land cover was sequentially classified via rule-based classification to discriminate objects on the basis of spectral information, object size and shapes (for example, rectangular fit for buildings). Unclassified objects in the classification output were manually assigned to the correct class. The final classified image was exported as a shapefile into ArcGIS (version 10.0) to derive the proportion (percentage) of land cover and structural features at each phenology site (Table 1).

Hierarchical cluster analysis was used to generate a generic qualifier of the degree of urbanization for each phenology site using R (version 3.5.0). Clustering was based on the proportion of land cover and structural features at the phenology sites, resulting in three categories of degree of urbanization: lightly built-up, moderately built-up and heavily built-up (Table 1). This way, trees under the same category of degree of urbanization could be treated as a single population.

Phenology Data

Phenological observations were undertaken between March and September 2017 and each tree observed twice a week to increase the accuracy of characterizing tree canopy change. A single observer visually estimated the canopy cover of the entire tree crown on north–south and east–west orientations. Leaf abundance was assigned in a two-step process. In step 1, the canopy cover was assigned a cover score relating to the relative level of leaf presence (0 = absence of leaves, 1 = 1–25%, 2 = 26–50%, 3 = 51–75% and 4 = 76–100%). In step 2, each canopy score was refined by assigning a sub-score of 1, 2 or 3. A 1 or 3 was appended if the percentage estimates in the first score were distinguishable as being within the upper half or lower half of the associated range, otherwise, a 2 (median) was appended. For example, a tree with a 3 in the first step would be assigned either 3.1 or 3.3 to distinguish between 51 and 75%, or a 3.2 would be assigned if the estimate was indistinct. The final categorical scores were subsequently converted to their indicative percentage values for use in further analysis (for example, Williams and others 1997; Morellato and others 2010; Valdez-Hernandez and others 2010). To ensure that the data recorded by the main observer was robust throughout the study, quality assurance was done by comparing the observations to those taken by a second observer on a biweekly basis. We also ensured that the selected trees and phenology sites were not actively managed during the period of field data collection.

Phenology Data Processing

Time-series profiles of percentage canopy cover were generated for each individual tree sampled
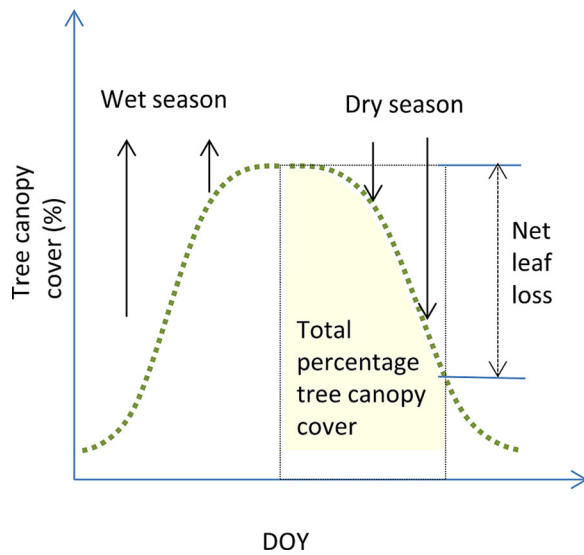
Figure 4. Conceptual diagram showing tree canopy change across time and traits of canopy cover change (total percentage canopy cover and net leaf loss) that were extracted from the time series as indicators of leaf production and leaf loss.

($n_{Jacaranda}$ = 48; $n_{Tabebuia}$ = 24) using R (version 3.5.0). A LOESS smoothing algorithm was applied to each time series to minimize the noise in the temporal profile (Figure 4). To quantify canopy cover changes across the entire dry season (that is, DOY 150 to 250), two measures of leaf phenological traits were derived for each individual tree time series. Firstly, total percentage tree canopy cover was calculated as the area under the curve between the first and last phenological observation as a proxy for leaf production. Secondly, net leaf loss was calculated as the difference between the maximum and minimum percentage tree canopy cover over the observation period (Figure 4). This way variability in total percentage tree canopy cover and net leaf loss could be attributed to intra-urban differences in local urban environmental characteristics of land cover and structure and urban climate.

Urban Climate

To relate differences in tree canopy cover change to urban-induced climatic differences, we collected information on soil volumetric moisture content, relative humidity and air temperature at each phenology site. Soil volumetric water content (expressed as a percentage) was measured using a ThetaProbe (model ML3 ThetaProbe, Delta-T Devices), at a fixed point 3 m from each tree trunk, twice a week simultaneous with the phenological

data collection. Air temperature and relative humidity data were acquired from HOBO sensors (model HOBO U23-001 Pro v2, Onset Corporation) housed in a radiation shield at the height of 3 m, which was centrally located at each phenology site. Each sensor collected data at 30-min intervals and was calibrated every three months against a factory-calibrated sensor. We calculated the dry season average of each urban climate variable (that is, nighttime temperature (sunset 18:00 to sunrise 06:00), volumetric soil moisture content and relative humidity) for comparison with differences in total percentage tree canopy cover and net leaf loss.

Data Analysis

For each tree species, a linear mixed model was used to determine whether the degree of urbanization influenced rates of decline in tree canopy cover over the duration of the observation period. Each data point represented observed canopy cover for an individual tree on a given day ($n_{Jacaranda\ model}$ = 672; $n_{Tabebuia\ model}$ = 336) and was used as the response variable. The fixed effects were Julian day (DOY) and the degree of urbanization (categorical with three levels: high, moderate or low) and their interaction. The individual tree was included as a random effect to allow for correlated error terms caused by repeated observations on the same tree. The significance of the full models was compared to a corresponding null model (a model that did not account for temporal autocorrelation) using a likelihood ratio test. Visual inspection of Q–Q plots and plots of residuals plotted against fitted values for the significant models revealed normally distributed and homogeneous residuals. DOY was centered around zero for interpretation of model coefficients. The modeling was implemented using the ''lme'' function of the ''nlme'' package in R (Pinheiro and others 2018; R Core Team 2018).

General linear models were used to determine whether the effect of urbanization on total percentage tree canopy cover and net leaf loss varied between species. We used only locations where both species occurred, and each data point represented an individual tree ($n_{Jacaranda}$ = 23; $n_{Tabebuia}$ = 24). Total percentage tree canopy cover and net leaf loss were modeled separately. Species, the degree of urbanization and their interaction, were explanatory variables in both models. The significance of the full models was tested against a reduced model with a single explanatory variable of degree of urbanization, using a likelihood ratio test to assess the effect of species. Prior to modeling, total percentage tree canopy cover and net leaf loss

were log-transformed. An exact Mann–Whitney U test was used to determine whether total percentage tree canopy cover and net leaf loss differed between the species. Again, a visual inspection of Q-Q plots and plots of residuals plotted against fitted values for the significant models revealed normally distributed and homogeneous residuals.

We used an information-theoretic approach (Burnham and others 2011) to explore the relative influence of different urban climate variables and land cover composition on each of the measured phenological traits. This was undertaken to identify the explanatory effect of individual elements of urban climate and land cover. We derived linear models for each response variable (total percentage tree canopy cover and net leaf loss) into which land cover (proportion of buildings, trees, impervious and pervious cover) or urban climate (nighttime temperature, relative humidity and volumetric soil moisture) were included as explanatory variables. This resulted in two sets of models; one for land cover and the other for urban climate, with each model-set comprising all combinations of their input variables. Variance inflation factors (VIFs) were calculated (''vif'' function of the R package car) for each model to assess collinearity between continuous explanatory variables, resulting in the sequential exclusion of models in which explanatory variables had a VIF greater than 3. We also formulated a null model with the intercept only to represent the explanatory nature of other variables not covered in this study. Model selection approaches were used to determine the structure of the simplest model explaining the phenology–land cover–urban climate relationships using the MuMIn package in R [R version 3.5.0 (Barton 2018; R Core Team 2018)]. The Akaike information criterion corrected for small sample size (AICc) was used to rank and assess individual model performance. The correlative relationship between land cover, urban climate and phenology were considered to be weak if the null model (intercept only) had a ΔAICc = 0. Models with ΔAICc less than 2 when comparing models with the top-ranked model were considered as potentially suitable models. For all remaining models, the relative influence of land cover and urban climate (separately) on total percentage tree canopy cover and net leaf loss was assessed. The sum of Akaike weights for each model was used to obtain the relative importance value (RIV) for a given explanatory variable (Burnham and Anderson 2003), in order to identify variables that were most closely associated with total canopy cover and net leaf loss.

RESULTS

Rate of Change of Tree Canopy Cover in Relation to the Degree of Urbanization

Both species showed a general pattern of increasing canopy cover with increasing soil moisture during the wet season, followed by canopy cover decline as soil moisture declined during the dry season (Figure 5).

The combined effect of time (DOY) and the degree of urbanization significantly influenced canopy cover for both tree species (likelihood ratio test: $p < 0.0001$). Both species experienced significantly higher rates of tree canopy cover decline in heavily built-up neighborhoods in comparison with less built-up neighborhoods ($p < 0.05$ in both models). The change in slope (that is, rate of change in canopy cover) from lightly built-up to heavily built-up neighborhoods was significant for both *Jacaranda* (estimate = 0.16, standard error = 0.02, $p < 0.01$; Table 2) and *Tabebuia* (estimate = 0.03, standard error = 0.01, $p < 0.01$; Table 2). Similarly, the change in slope from moderately built-up to heavily built-up neighborhoods was highly significant for *Jacaranda* (estimate = 0.11, standard error = 0.01, $p < 0.01$; Table 2) and *Tabebuia* (estimate = 0.02, standard error = 0.01, $p < 0.05$; Table 2).

Species Influence on Total Percentage Tree Canopy Cover

Species had an effect on the relationship between degree of urbanization and total percentage tree canopy cover (comparison of full with reduced
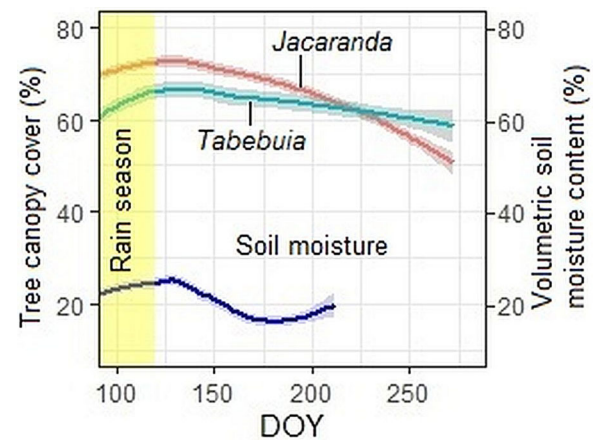

Figure 5. Temporal changes in canopy cover for all trees of each species compared to changes in volumetric soil moisture content across the entire city. Soil moisture data after DOY = 212 were removed prior to analysis due to equipment malfunction.

Table 2. Estimated Regression Parameters, Standard Errors (in Brackets) and Significance Levels for the Relationship Between Degree of Urbanization and Canopy Cover Decline

	Dependent variable	
	Leaves (%)	
	Tabebuia	*Jacaranda*
	(1)	(2)
DOY	− 0.216***	− 0.047***
	(0.011)	(0.006)
Lightly built-up	11.539***	0.648
	(3.537)	(3.474)
Moderately built-up	9.963***	− 0.250
	(3.241)	(3.349)
DOY:Lightly built-up	0.160***	0.027***
	(0.015)	(0.009)
DOY:Moderately built-up	0.105***	0.022**
	(0.014)	(0.009)
Intercept	57.966***	64.224***
	(2.547)	(2.298)
Observations	672	336

*$p < 0.1$; **$p < 0.05$; ***$p < 0.01$.

model: $\chi^2 = -0.18$, $df = 3$, $p < 0.01$). A Mann–Whitney U test ($U = 394$, $p = 0.028$) confirmed differences in total percentage tree canopy cover between the two species across all neighborhood categories. In comparison with *Jacaranda*, *Tabebuia* showed negligible differences in total percentage tree canopy cover between lightly and heavily built-up neighborhoods (estimate = − 0.257, standard error = 0.087, $p < 0.01$) and between moderately built-up and heavily built-up neighborhoods (estimate = − 0.22, standard error = 0.08, $p < 0.01$) as shown in Table 3.

Species Influence on Net Leaf Loss

The relationship between the degree of urbanization and net leaf loss was influenced by species (likelihood ratio test: $\chi^2 = 13.583$, $df = 3$, $p = 0.0000$). Overall, mean net leaf loss across all neighborhood categories differed between *Jacaranda* and *Tabebuia* (Mann–Whitney U test: $U = 430$, $p = 0.002805$). *Tabebuia* showed negligible differences in mean net leaf loss between lightly and heavily built-up neighborhoods in comparison with *Jacaranda* (estimate = 1.266, standard error = 0.591, $p < 0.05$; Table 3). However, differences in net leaf loss between moderately built-up and heavily built-up neighborhoods were similar for *Tabebuia* and *Jacaranda* (estimate = 0.420, standard error = 0.545, $p > 0.05$; Table 3).

Table 3. Estimated Regression Parameters, Standard Errors (in Brackets) and Significance Levels for the Effects of Species on the Relationship Between Degree of Urbanization and (1) Net Leaf Loss (2) Total Percentage Canopy Cover

	Dependent variable	
	log(Net leaf loss)	log(Total percentage canopy cover
	(1)	(2)
Tabebuia	− 1.472***	0.103*
	(0.397)	(0.058)
Lightly built-up	− 1.265***	0.242***
	(0.438)	(0.064)
Moderately built-up	− 0.767*	0.197***
	(0.388)	(0.057)
Tabebuia:Lightly built-up	1.266**	− 0.257***
	(0.591)	(0.087)
Tabebuia:Moderately built-up	0.420	− 0.217***
	(0.545)	(0.080)
Intercept	2.723***	8.575***
	(0.297)	(0.044)
Observations	47	47

*$p < 0.1$; **$p < 0.05$; ***$p < 0.01$.

Table 4. Results for Regression Models for Determinants of Phenological Traits

Metric	Species	Model class	Model variables	AICc	logLik	df	Adjusted R^2	p	delta
Total percentage canopy cover	Jacaranda	Land cover	Impervious	− 56	31.4	3	0.24	0.0002	0
			Pervious	− 55	30.9	3	0.23	0.0003	0.8
		Urban climate	Relative humidity	− 55	− 30.8	3	0.22	0.0004	0
			Night temp	− 53.7	30.14	3	0.20	0.0007	1.25
	Tabebuia	Land cover	Intercept only	− 32.8	18.7	2			0
		Urban climate	Intercept only	− 32.8	18.7	2			0
			Night temp	− 31.1	19.2	3	− 0.01	0.356	1.68
Net leaf loss	Jacaranda	Land cover	Buildings	128.1	− 60.8	3	0.21	0.0006	0
		Urban climate	Pervious	128.8	− 61.1	3	0.2	0.0008	0.74
			Night temp	126.05	− 59.8	3	0.24	0.0002	0
			Night temp, soil moisture	127.5	− 59.3	4	0.24	0.0007	1.44
	Tabebuia	Land cover	Intercept only	53.79	− 24.6	2			0
		Urban climate	Intercept only	53.79	− 24.6	2			0

Influence of Land Cover

The total percentage tree canopy cover for *Jacaranda* trees was significantly influenced by the proportion of pervious land cover ($F_{1,46}$ = 14.9, $p < 0.01$) and impervious land cover ($F_{1,46}$ = 16.0, $p < 0.01$). The significance of the influence of the proportion of impervious (that is, roads and paved cover) and pervious land cover is supported by high RIV scores in comparison with other predictor variables (Table 5). Total percentage tree canopy cover increased with an increase in the proportion of pervious cover (R^2 = 0.23, estimate ± SE: 0.003 ± 0.001, t_{46} = 4.0; Table 4; Figure 6), and increased as the proportion of impervious cover declined (R^2 = 0.24, estimate ± SE: − 0.005 ± 0.001, t_{46} = − 4.0; Table 4).

Net leaf loss showed a strong relationship with the proportion of pervious cover ($F_{1,46}$ = 12.8, $p < 0.01$) and the proportion of buildings ($F_{1,46}$ = 13.7, $p < 0.01$), with high RIV recorded by both predictor variables (Table 5). Locations with high proportions of pervious cover were associated with low net leaf loss (R^2 = 0.2, estimate ± SE: − 0.021 ± 0.006, t_{46} = − 3.6; Table 4; Figure 6), whereas areas with a high proportion of buildings resulted in a high net leaf loss (R^2 = 0.21, estimate ± SE: 0.05 ± 0.014, t_{46} = 3.7; Table 4).

Influence of Urban Climate

Total percentage tree canopy cover and net leaf loss for *Jacaranda* were significantly influenced by differences in relative humidity ($F_{1,46}$ = 14.47, $p = 0.0004$; Table 4) and nighttime temperature ($F_{1,46}$ = 16.24, $p = 0.0002$; Table 4), respectively. Total percentage tree canopy cover increased with increase in relative humidity (R^2 = 0.22, estimate ± SE: 0.04 ± 0.01, t_{46} = 3.804; Table 4; Figure 6) while increased nighttime temperatures resulted in higher net leaf loss (R^2 = 0.24, estimate ± SE: 1.425 ± 0.354, t_{46} = 4.03; Table 4; Figure 6). However, models explaining the relationship between urban climate and phenological traits in *Tabebuia* were not statistically significant (Tables 4, 5).

DISCUSSION

Our results suggest that the degree of urbanization surrounding tree locations is a key factor determining the rate of canopy cover decline of two deciduous species (that is, *Jacaranda mimosifolia* and *Tabebuia rosea*) during the dry season in the tropical city of Kampala. Specifically, heavily built-up neighborhoods experienced the highest rates of tree canopy cover decline across both species. Moreover, *Jacaranda* was more sensitive than *Tabebuia* to the degree of urbanization, evidenced by greater differences in total percentage tree canopy cover and net leaf loss between heavily built-up and less built-up neighborhoods. *Jacaranda* trees exhibited high total percentage canopy cover in locations with low proportions of impervious land cover types (that is, roads and paved cover) and high relative humidity (high soil moisture content). High net leaf loss was attributed to low proportions of pervious land cover and high nighttime temperature. However, there was no evidence to sug-
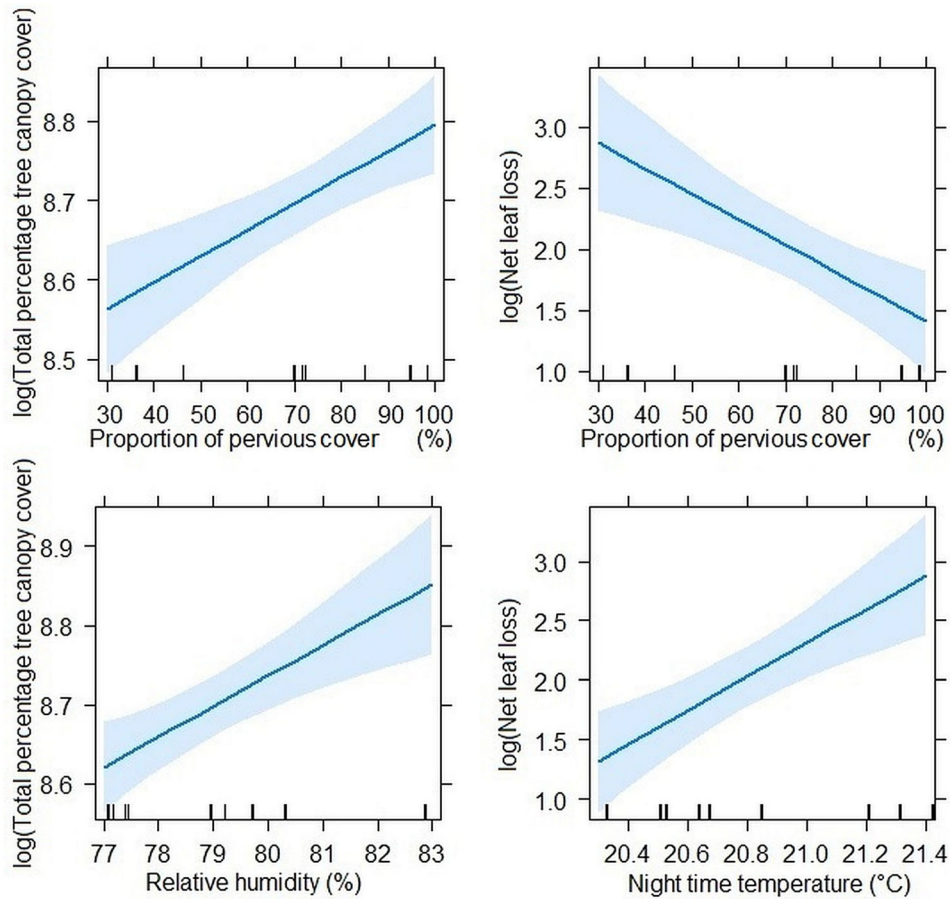
Figure 6. Effect plots showing the influence of proportion of pervious land cover and urban climate on total percentage tree canopy cover and net leaf loss.

Table 5. Relative Importance Values (RIV) of Determinants of Phenological Traits

Metric	Species	Model category						
		Land cover				Urban climate		
		Impervious	Trees	Pervious	Buildings	Night temp	Soil moisture	Relative humidity
Total percentage	*Jacaranda*	0.48	0.12	0.43	0.08	0.36	0.26	0.63
canopy cover	*Tabebuia*	0.13	0.16	0.18	0.14	0.29	0.26	0.15
Net leaf loss	*Jacaranda*	0.15	0.11	0.39	0.44	0.83	0.33	0.16
	Tabebuia	0.13	0.17	0.16	0.12	0.21	0.22	0.168

gest that land cover composition or the measured urban climate variables influenced the phenology of *Tabebuia*. Our observation of low relative humidity and high temperature in heavily built-up locations is consistent with the observed urban–rural patterns in Ibadan, Nigeria during the dry season (Adebayo 1991). This alludes to an UDI effect in Kampala, which is caused by a high pro-

portion of impervious land covers that restrict water uptake and retention, and a low proportion of vegetation cover which leads to low rates of evapotranspiration and an intensification of the UHI effect (Hao and others 2018). However, like UHI, urban–rural humidity differences vary diurnally despite tending toward UDI effect on a seasonal scale (Adebayo 1991; Hao and others 2018).

Similar patterns of canopy cover decline with decreasing soil moisture content during the dry season, and species differences have been observed in natural habitats (for example, Williams and others 1997; Condit and others 2000; de Camargo and others 2018). This study, however, provides substantial new evidence of these processes in tropical urban environments. Differences between tree species have been linked with species-specific endogenous mechanisms (for example, Borchert 1983; Williams and others 1997). *Jacaranda* and *Tabebuia* have been observed to show different mechanisms for the timing of leaf loss in relation to leaf production. For example, Huxley and Vaneck (1974) observed that *Jacaranda* exhibited extended periods of leaf production that coincided with the rainy season and that leaf loss occurred simultaneously with leaf production. Start of leaf loss in *Tabebuia*, however, has been observed to occur much later after leaf production and to coincide with the dry season (Borchert 1983). Moreover, *Tabebuia* has been observed to exhibit weak tree canopy cover change under moderate seasonal climatic conditions (Reich 1995) and to show slight leaf loss in some dry seasons (Condit and others 2000).

The intra-urban differences in canopy cover change (total percentage tree canopy cover and net leaf loss) between the two species showed *Jacaranda* to be more sensitive than *Tabebuia* to the combined effect of urbanization and the dry season. Species differences in the sensitivity of phenology to urbanization have been observed in the tropics with respect to the timing of start of the season (for example, Gazal and others 2008; Jochner and others 2013a). However, this study improves our understanding of the impacts of urbanization on seasonal tree canopy cover change, justifying the need for extended observational periods for future phenological studies in tropical cities.

Our analysis showed that *Jacaranda* trees in sites that had low proportions of impervious land cover (that is, roads and paved cover), high relative humidity and high soil moisture (positively correlated with relative humidity; Pearson's $r = 0.63$) exhibited high total percentage tree canopy cover. In turn, *Jacaranda* trees in sites with a low proportion of pervious land cover and high nighttime air temperature (low volumetric soil moisture) experienced high net leaf loss. Total percentage tree canopy cover and net leaf loss have been observed to have a strong relationship with relative humidity and air temperature, respectively (Do and others 2005). Although we were not able to identify a strong statistical relationship between soil moisture and total percentage tree canopy cover as expected (Huxley and Vaneck 1974; Borchert 1983), the positive correlation between soil moisture and humidity observed in this study might be indicative of the effect of soil moisture at deeper soil layers, as some studies have shown (for example, Archibald and Scholes 2007; Cai and others 2019). Trees in tropical environments have complex water use mechanisms that rely on underground water (Do and others 2005; Guan and others 2014), and the relative differences in underground soil moisture content in this study were not adequately depicted by our measures of volumetric soil moisture within the topmost soil layer (within ~ 8 cm).

The observed pattern of high leaf loss in locations with high proportions of impervious land cover might also allude to levels of exposure to traffic-related air pollutants due to a high proportion of roads. Jochner and Menzel (2015) observed that ozone, NO_2, NOx and PM levels were significantly associated with delays in phenology in a temperate city. Future research is needed to compare the mechanisms by which pollution affects phenology in the tropics by taking into account the effect of different types of pollutants and their concentrations, along with the proportion of area covered by roads in the phenology sites.

Although the rate of decline of canopy cover for *Tabebuia* was sensitive to the degree of urbanization, there was little to no evidence to show that land cover and urban climate influenced total percentage tree canopy cover and net leaf loss. Jochner and others (2013a) observed that some species were less sensitive to intra-urban variation in urban climate, which is the case with *Tabebuia* in our study. Moreover, *Tabebuia* is known to be relatively insensitive to intra-seasonal changes in meteorological conditions (Reich 1995; Condit and others 2000). Consequently, the differences in the rate of change in canopy cover decline for *Tabebuia* observed in the present study, may be linked to environmental conditions not included within the scope of this study, such as nutrient availability (Jochner and others 2013b).

CONCLUSION

We provide new evidence that shows that urbanization affects the rate of change of deciduous tree canopy cover in tropical urban environments during the dry season, and that the dynamics of these processes vary among species. Moreover, the differences in sensitivity of species to the degree of urbanization, land cover and urban climate imply that some species may be better adapted than

others to urban environments. Therefore, the direction for future research that assesses the regulatory services of trees ought to account for locational differences in degree of urbanization, land cover and temporal changes in canopy cover of trees. Equally, future studies on vegetation phenology in tropical urban environments should explore the effect of wider range of environmental factors (for example, nutrients and pollution) in addition to the degree of urbanization, land cover and urban climate.

Our findings have direct implications for understanding the provision of vital regulatory functions of vegetation in tropical urban environments. Suppressed tree canopy cover in heavily built-up neighborhoods may limit mitigation of the UHI through shading and evaporative cooling. Furthermore, the amplified effect of the dry season as a result of intensified urbanization is indicative of potential impacts of climate change, which is expected to result in extreme dry seasons. The observations made on both *Jacaranda mimosifolia* and *Tabebuia rosea* in the heavily built-up neighborhoods in comparison with the less built-up neighborhoods of Kampala offer insights as to how these species, and other taxonomically related species may respond to extreme events, like drought, that are linked to climate change in natural habitats. Our findings form the baseline for further studies to be undertaken which relate the degree of urbanization, land cover and urban climate to tree canopy cover change in tropical environments. Although this study focussed on the effect of spatial differences in urban climate, averaged across the entire dry season, on canopy cover change, more research is needed examining the effect of atmospheric processes occurring at finer temporal resolutions (for example, diurnally) as sudden extreme events are expected to occur more frequently under climate change and in disturbed environments. Such studies are required to improve our understanding of temporal changes in primary production and their effects on nutrient cycling, water and energy fluxes and resource availability at the ecosystem level.

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