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Climate and Lawn Management Interact to Control C4 Plant Distribution in Residential Lawns Across Seven U.S. Cities

Tara Trammell
University of Delaware

Diane E. Pataki
University of Utah

Christopher Still
Oregon State University

James Ehleringer
Oregon State University

Meghan Avolio
University of Utah

See next page for additional authors

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Authors
Tara Trammell, Diane E. Pataki, Christopher Still, James Ehleringer, Meghan Avolio, Jennifer L. Morse, and multiple additional authors

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Climate and lawn management interact to control C_4 plant distribution in residential lawns across seven U.S. cities

Tara L. E. Trammell,[1,20] Diane E. Pataki,[2] Christopher J. Still,[3] James R. Ehleringer,[2] Meghan L. Avolio,[4] Neil Bettez,[5] Jeannine Cavender-Bares,[6] Peter M. Groffman,[7] Morgan Grove,[8] Sharon J. Hall,[9] James Heffernan,[10] Sarah E. Hobbie,[6] Kelli L. Larson,[11] Jennifer L. Morse,[12] Christopher Neill,[13,19] Kristen C. Nelson,[14] Jarlath O'Neil-Dunne,[15] William D. Pearse,[6,16] Rinku Roy Chowdhury,[17] Meredith Steele,[18] and Megan M. Wheeler[9]

[1]*Department of Plant and Soil Sciences, University of Delaware, 531 S. College Ave, 152 Townsend Hall, Newark, Delaware 19716 USA*
[2]*Department of Biology, University of Utah, Salt Lake City, Utah 84112 USA*
[3]*Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331 USA*
[4]*Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, Maryland 21218 USA*
[5]*Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA*
[6]*Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108 USA*
[7]*City University of New York, Advanced Science Research Center at the Graduate Center, New York, New York 10031 USA*
[8]*USDA Forest Service, Baltimore Ecosystem Study, University of Maryland, Baltimore County, Baltimore, Maryland 21227 USA*
[9]*School of Life Sciences, Arizona State University, Tempe, Arizona 85287 USA*
[10]*Nicholas School of the Environment, Duke University, Durham, North Carolina 27708 USA*
[11]*School of Geographic Science and Urban Planning, School of Sustainability, Arizona State University, Tempe, Arizona 85287 USA*
[12]*Department of Environmental Science and Management, School of Environment, Portland State University, Portland, Oregon 97207 USA*
[13]*Marine Biological Laboratory, Ecosystems Center, Woods Hole, Massachusetts 02543 USA*
[14]*Department of Forest Resources and Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108 USA*
[15]*Spatial Analysis Laboratory, Rubenstein School of Environment & Natural Resources, University of Vermont, Burlington, Vermont 05405 USA*
[16]*Department of Biology & Ecology Center, Utah State University, Logan, Utah 84322 USA*
[17]*Department of Geography, Indiana University, Bloomington, Indiana 47405 USA*
[18]*Department of Crop and Soil Environmental Science, Virginia Tech, Blacksburg, Virginia 24061 USA*

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Abstract. In natural grasslands, C_4 plant dominance increases with growing season temperatures and reflects distinct differences in plant growth rates and water use efficiencies of C_3 vs. C_4 photosynthetic pathways. However, in lawns, management decisions influence interactions between planted turfgrass and weed species, leading to some uncertainty about the degree of human vs. climatic controls on lawn species distributions. We measured herbaceous plant carbon isotope ratios ($\delta^{13}C$, index of C_3/C_4 relative abundance) and C_4 cover in residential lawns across seven U.S. cities to determine how climate, lawn plant management, or interactions between climate and plant management influenced C_4 lawn cover. We also calculated theoretical C_4 carbon gain predicted by a plant physiological model as an index of expected C_4 cover due to growing season climatic conditions in each city. Contrary to theoretical predictions, plant $\delta^{13}C$ and C_4 cover in urban lawns were more strongly related to mean annual temperature than to growing season temperature. Wintertime temperatures influenced the distribution of C_4 lawn turf plants, contrary to natural ecosystems where growing season temperatures primarily drive C_4 distributions. C_4 cover in lawns was greatest in the three warmest cities, due to an interaction between climate and homeowner plant management (e.g., planting C_4 turf species) in these cities. The proportion of C_4 lawn species was similar to the proportion of C_4 species in the regional grass flora. However, the majority of C_4 species were nonnative turf grasses, and not of regional origin. While temperature was a strong control on lawn species composition across the United States, cities differed as to whether these patterns were driven by cultivated lawn grasses vs. weedy species. In some cities, biotic interactions with weedy

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[19] Present address: Woods Hole Research Center, 149 Woods Hole Road, Falmouth, Massachusetts 02540 USA
[20] E-mail: ttram@udel.edu

plants appeared to dominate, while in other cities, C_4 plants were predominantly imported and cultivated. Elevated CO_2 and temperature in cities can influence C_3/C_4 competitive outcomes; however, this study provides evidence that climate and plant management dynamics influence biogeography and ecology of C_3/C_4 plants in lawns. Their differing water and nutrient use efficiency may have substantial impacts on carbon, water, energy, and nutrient budgets across cities.

Key words: C_4 plant distribution; lawns; macroecology; plant $\delta^{13}C$; residential; urban; yard management.

Introduction

Turf grasses across the continental United States occupy over 160,000 km^2 with important consequences for air and water quality as well as human health and well-being (Milesi et al. 2005). Residential land covers the majority of urban greenspace (62%), and lawns account for most of this greenspace (52–80%; Richards et al. 1984). While lawns are a significant component of residential landscapes, we still know very little about the ecological structure and function of this widespread American Residential Macrosystem (Groffman et al. 2009, 2014). In intensively managed lawns, the distribution of plant functional types is likely to reflect interactions between human decisions (e.g., planting and maintenance), biophysical factors (e.g., climate), and biological interactions (e.g., plant dispersal and competition). However, at present there are insufficient data on the distribution of urban plant species to understand the roles of biophysical and human factors in structuring plant communities in cities.

Throughout the United States, nurseries and sod companies offer different lawn species and cultivars, and lawn grasses that form an even turf are typically preferred (Christians and Engelke 1994). Weedy species and forbs (non-turf species) are also common in lawns and can vary by region and lawn management practices, such as fertilizer or herbicide application (Stewart et al. 2009, Bertoncini et al. 2012). Turf scientists have long investigated turf performance and made recommendations for which turf grasses to plant based on climate (e.g., Christians and Engelke 1994, Dionne et al. 2010, Bertrand et al. 2013). Historically, recommendations were based on growing season temperatures and wintertime freeze tolerance (Madison 1971, Beard and Beard 2005). However, empirical evidence for the prevalence of warm-season vs. cool-season grass and forb species (i.e., C_4 vs. C_3 photosynthesis) in in situ residential lawns is lacking at continental scales. Following planting, turf grasses and weedy species undergo ecological dynamics due to abiotic and biotic interactions that are not well studied in situ (Bell 2011). At regional scales, previous research demonstrated the importance of elevated urban temperature and atmospheric CO_2 on the competitive dynamics of C_3 and C_4 plants in lawns (Bijoor et al. 2008, Duffy and Chown 2016, Hobbie et al. 2017). However, understanding the controls on C_3/C_4 plant distribution in cities across continental scales is necessary to contribute to the growing understanding of how human-dominated and natural ecosystems differ (or do not differ) in ecological dynamics (Pickett and Cadenasso 2017).

Grass species that utilize the C_4 photosynthetic pathway account for only 3% of land plant species, yet they have a wide global distribution and contribute about 25% of global terrestrial primary production (Sage 2004). Various metrics of local air temperature are significantly correlated with continental and global distributions of C_4 grass abundance and dominance (e.g., growing-season minimum temperature; Terri and Stowe 1976, Ehleringer et al. 1997). The theoretical basis for these patterns in grasslands is the difference between photosynthetic light-use efficiencies in C_3 vs. C_4 plants, or the ratio of photosynthetic carbon (C) gain to photons absorbed (Ehleringer and Björkman 1977). At high temperatures, photosynthetic light-use efficiencies of C_3 plants are low because of increased photorespiration (Ehleringer et al. 1997, Collatz et al. 1998), favoring C_4 plants. However, C_4 photosynthesis has energetic costs (Ehleringer 1978, Ehleringer et al. 1991). As a result, C_4 plants are expected to outcompete C_3 species only in regions with warmer growing-season conditions and adequate rainfall to support grass growth (Ehleringer 1978, Ehleringer et al. 1997).

While temperature is a dominant control on the distribution of C_4 plants globally, human-mediated changes in land cover and use, such as agricultural crop production and altered fire regimes, also influence natural C_4 grassland and pasture distributions (Still et al. 2003). Furthermore, in cities across the United States, residential landowners may plant turf-forming grass species irrespective of local climatic conditions since local resource limitations can be overcome by water and fertilizer subsidies and competitive outcomes can be influenced by use of selective herbicides (Ward 1969). While planting recommendations for warm season vs. cool season grasses tend to be based on climate (Christians and Engelke 1994, Bertrand et al. 2013), we do not know the impacts of planting choices on the continental distribution of turf grasses when multiple species and cultivars are available from local commercial sources. In addition, the ecological dynamics that subsequently take place, such as the invasion of lawns by weed species, are not well documented. As a result, the extent to which the distribution of C_3 vs. C_4 species in lawns follows similar biogeographical patterns as natural ecosystems is still a significant gap in our basic understanding of the biogeography and ecology of major plant functional types.

The carbon stable isotope ratio ($\delta^{13}C$) of plant tissues can be a valuable tool to measure the relative abundance of C_3 and C_4 grasses (O'Leary 1981). For all plants, the natural abundance $\delta^{13}C$ in plants is depleted in ^{13}C relative to atmospheric CO_2 because of discrimination against ^{13}C during photosynthesis (Farquhar et al. 1989). The greater discrimination against ^{13}C by Rubisco compared with PEP (phosphoenolpyruvate) carboxylase during photosynthesis causes isotopically distinct plant $\delta^{13}C$ values in C_3 (average $\delta^{13}C = -27‰$) and C_4 (average $\delta^{13}C = -13‰$) plants (O'Leary 1988, Boutton 1996). Biogenic and anthropogenic factors control plant $\delta^{13}C$ values in urban lawns through the relative proportion of C_3 vs. C_4 plant composition.

We sought to understand how C_4 plants are distributed in lawns throughout the United States by (1) sampling the composition of lawns in seven cities of varying climate (BOS, Boston, Massachusetts; BAL, Baltimore, Maryland; LA, Los Angeles, California; MIA, Miami, Florida; MSP, Minneapolis-St. Paul, Minnesota; PHX, Phoenix, Arizona; SLC, Salt Lake City, Utah), and (2) comparing observed C_4 lawn distribution with theoretical carbon gain for C_4 plants (i.e., simulated C_4 carbon assimilation as a function of temperature for each city; Ehleringer 1978, Sage et al. 1999, Still et al. 2003). We evaluated how direct climate and an interaction between climate and lawn management controls the distribution of C_4 plants in lawns. Climatic constraints on large-scale C_3 and C_4 plant distributions have been commonly evaluated using a mean monthly temperature threshold of 22°C and a minimum precipitation constraint for C_4 competitive advantage (Collatz et al. 1998, Sage and Kubien 2003, Still et al. 2003). Based solely on this temperature threshold, we predicted that BAL, BOS, LA, MSP, and SLC residential lawns would be C_3 dominated, whereas MIA and PHX would be C_4 dominated (Table 1). If there is a direct influence of climate on C_3 vs. C_4 plant growth, then we expected C_4 lawn cover to be quantitatively related to growing-season temperature (GST) and to the theoretical carbon gain that C_4 plants would have in each city. Alternatively, if lawn management practices (e.g., planting, weeding, irrigation, and fertilization) override climatic constraints on grass performance and interspecific competition, then C_4 lawn cover will be unrelated to climate parameters (such as MAT) and to the theoretical C_4 carbon gain in lawns.

The distribution of spontaneous (i.e., weedy non-turf) vs. cultivated (i.e., turf) plant species in urban lawns across these cities should provide insight as to which species are most successful under varying climatic conditions. If human management of residential lawns interacts with climate to determine the availability and/or selection of seed or sod, then we expected to see a relationship between temperature (MAT) and turf C_4 lawn cover, whereas non-turf (weed species) C_4 lawn cover will be related to precipitation (mean annual precipitation, MAP), suggesting homeowners can select C_4 lawn turf for optimal year-round temperatures and override any soil moisture constraints (i.e., irrigation). Furthermore, a relationship between winter minimum temperatures and C_3/C_4 turf lawn cover, and no relationship with C_3 and C_4 non-turf species supports an interaction between climate and human management influence on C_3/C_4 turf distribution since spontaneous and cultivated plants are not similarly controlled by low temperatures. Finally, a high proportion of nonnative C_4 turf species would support the idea that homeowner planting of C_4 turf species is a dominant control in these residential lawns. This analysis adds a new dimension to our understanding of the processes governing biodiversity, composition, and ecological dynamics of urban plant communities.

Methods

Study area

Plant samples were collected in residential lawns in seven major metropolitan areas across the United States: Baltimore, Maryland; Boston, Massachusetts; Los Angeles, California; Miami, Florida; Minneapolis-

Table 1. The expected dominance of C_3 or C_4 plants based on each city's climate.

City	Temperature (°C)	Precipitation (cm)	Climate prediction	Turfgrass climate zone	Dominant lawn community
BAL	12.8	106.4	C_3	humid transitional	warm/cool grass mix
BOS	10.8	111.2	C_3	semi-cool humid	cool season grasses
LA	17.0	32.6	C_3	cool semiarid Pacific	warm/cool grass mix
MIA	25.1	157.2	C_4	warm tropical	warm season grasses
MSP	7.9	77.7	C_3	semi-cool humid	cool season grasses
PHX	23.9	20.4	C_4	warm arid	warm season grasses
SLC	11.6	40.9	C_3	cool semiarid	cool season grasses

Notes: Cities are Baltimore, Maryland (BAL); Boston, Massachusetts (BOS); Los Angeles, California (LA); Miami, Florida (MIA); Minneapolis-St. Paul, Minnesota (MSP); Phoenix, Arizona (PHX); and Salt Lake City, Utah (SLC). Temperature and precipitation data are shown for mean annual 30-yr norms (National Climatic Data Center 2016), and the climate prediction is based on whether temperatures are > 22°C. Turfgrass climate zones and potential lawn management practices are incorporated into recommendations for dominant lawn communities across the United States (Cook and Ervin 2010).

St. Paul, Minnesota; Phoenix, Arizona; and Salt Lake City, Utah. These cities represented multiple ecological biomes and climatic regions across the United States. In all cities, the experimental design included residential parcels (n = 17–30 per city) stratified by urban density classes (i.e., urban, suburban, and exurban [settlements outside the city, usually a prosperous area beyond the suburbs]) and socioeconomic status (i.e., high, medium, or low), which were identified using the PRIZM (Potential Rating Index for Zipcode Markets) market classification system (Claritas 2008). The PRIZM classification utilizes demographics (based on census data) and consumer behavior to define social groups and life stage groups. Social groups are defined by urban density (i.e., population and housing density) and socioeconomic status (i.e., income, education, occupation, and home value), whereas life stage groups are defined by resident age, socioeconomic rank, and presence of children at home. The experimental design varied slightly in each city to account for local variation in factors controlling yard structure and function in different regions across the United States, (i.e., previous land use in BAL, BOS, and PHX; soil conditions in MIA and MSP; temperature in LA; and yard landscaping in PHX [i.e., xeriscaping]). For further details about experimental designs, see Trammell et al. (2016). All yards were randomly selected from a list of willing participants originally identified from a telephone survey (9,480 respondents across the cities). For the purposes of this study, we analyzed data from yards with lawns, thus only excluding yards with xeriscaping in PHX.

Plant $\delta^{13}C$

In each residential yard, bulk plant leaf samples were collected in two random locations in the lawn during peak growing season for each city (i.e., summer 2012 for BAL, BOS, MSP, and MIA, spring 2013 for LA and PHX, summer 2013 for SLC). In LA and SLC, replicate bulk plant samples were collected within 30 cm of each other at each sampling location. Replicate samples were not collected in BAL, BOS, MIA, and PHX, so each bulk plant sample was divided prior to sample processing to create within-sample replicates. In MSP, species-specific plant leaf samples were collected instead of bulk plant samples. Thus, the weighted average for each species was calculated from lawn quadrat abundance data (see *C_4 proportion of lawn cover*) and applied to $\delta^{13}C$ data. Thus, MSP data are not included in the analysis of relationships between plant $\delta^{13}C$ and C_4 lawn cover across the seven cities (i.e., Appendix S1: Fig. S1). After collection, plant leaves were dried at 60°C for at least 48 hours.

All leaves were selected from the bulk plant samples in order to exclude other plant material (i.e., flowers, roots) prior to C analysis. Plant leaf samples were ground to a fine powder using a Retsch Ball Mixer Mill (MM200, Haan, Germany). Natural abundance isotopic C composition, $\delta^{13}C$, was measured with a DELTA Plus Isotope Ratio Mass Spectrometer (Finnigan-MAT, Bremen, Germany) interfaced with an elemental analyzer (Model 1110, Carlo Erba, Milan, Italy) at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah, Salt Lake City. Two primary (PLRM) reference materials, calibrated against National Institute of Standards and Technology and International Atomic Energy Agency certified reference materials, and one secondary (SLRM, spinach leaf) reference material were used as internal standards with $\delta^{13}C$ precision of $\pm$ 0.1‰. The plant $\delta^{13}C$ values were expressed relative to the international standard (Vienna-PeeDee Belemnite) in the conventional δ notation:

$$\delta^{13}C = [(^{13}C_{sample}/^{12}C_{sample})/(^{13}C_{standard}/^{12}C_{standard}) - 1] \times 1000‰.$$

C_4 proportion of lawn cover

The plant species cover in each lawn was assessed using three randomly placed 1-m^2 quadrats in the front and back lawns of each residential yard (6-m^2 total). For each species identified in the quadrats, percent cover was estimated and species were assigned a cover category (<1%, 1–2%, 3–5%, 6–15%, 16–25%, 26–50%, 51–75%, 76–100%). The median of each cover category was used in data analysis (e.g., <1%, median = 0.5%; 76–100%, median = 88%). Plant species were identified as having the C_3 or C_4 photosynthetic pathway according to Waller and Lewis (1979), Sage and Monson (1999), Smith and Knapp (1999), Sage (2001), Bruhl and Wilson (2007), and Sage et al. (2011). The proportion of total plant cover contributed by plants with C_4 photosynthesis was calculated for each quadrat (C_4 proportion of total plant cover). We separated the cultivated lawn grass ("turf") species (Table 2) from all other species such as weeds ("non-turf") according to Wheeler et al. (2017; Appendix S1: Table S1).

Modeling theoretical C_4 carbon gain

Modeling photosynthesis and photosynthetic carbon isotope fractionation.—Net photosynthetic and transpiration rates for grasses in each pathway (C_3 and C_4) were calculated at hourly intervals for a representative day in each month of the growing season. The growing season for each city was defined as the warm months with ample precipitation for grass growth (>25 mm/yr; Collatz et al. 1998), which may not coincide with irrigation inputs alleviating this moisture constraint (e.g., LA growing season November–April, whereas irrigation increases growing season through September). This approach simplifies the calculation of fluxes at subhourly intervals for each day of the month, which requires comprehensive and gap-free data not easily

Table 2. Residential lawn turf species found in the seven cities.

Latin name	Common name	Photosynthetic pathway	Cities present
Agrostis capillaris L.	colonial bentgrass	C_3	BAL, BOS, MSP
Agrostis stolonifera L.	creeping bentgrass	C_3	BAL, BOS, MSP
Cynodon dactylon (L.) Pers.	Bermuda grass	C_4	BAL, BOS, LA, MIA, PHX, SLC
Festuca filiformis Pourr.	fineleaf sheep fescue	C_3	BAL, BOS
Festuca ovina L.	sheep fescue	C_3	BOS
Festuca rubra L.	red fescue	C_3	BOS, LA, MSP, SLC
Lolium perenne ssp. *multiflorum* Lam.	Italian ryegrass	C_3	PHX
Lolium perenne L.	perennial ryegrass	C_3	BAL, BOS, LA, MSP, PHX, SLC
Paspalum notatum Fluegge	Bahia grass	C_4	MIA
Pennisetum clandestinum Hochst. ex Chlov.	Kikuyu grass	C_4	LA
Poa pratensis L.	Kentucky bluegrass	C_3	BAL, BOS, LA, MSP, SLC
Poa trivialis L.	rough bluegrass	C_3	MSP
Schedonorus arundinaceus (Schreb.) Dumort.	tall fescue	C_3	BAL, LA, MSP, SLC
Stenotaphrum secundatum (Walter) Kuntze	St. Augustine grass	C_4	LA, MIA, PHX
Zoysia tenuifolia Willd. ex Thiele	Mascarene grass	C_4	MIA

Notes: City codes are identified in Table 1. Cities present represents the cities where turf species were identified in the lawn.

attainable across all sites. Simulating sub-hourly fluxes using real weather and radiation data would also require a comprehensive biosphere model with soil moisture calculations, canopy leaf area and radiation attenuation, and a host of other processes. Rather, our simplified approach was meant to capture the dominant photosynthetic physiology differences between C_3 and C_4 grasses, and compare the modeled predictions against site data on C_3 and C_4 distributions.

Representative fluxes were predicted using the coupled C_3 and C_4 leaf photosynthesis and stomatal conductance models of Collatz et al. (1991, 1992). Parameter values, such as maximum carboxylation rates (V_{max}) and temperature response functions, were taken from Sellers et al. (1996). V_{max} for C_3 grasses was assumed to be 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 298 K, and 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for C_4 grasses at 298 K. These models, described in Collatz et al. (1991, 1992) in detail, estimate net leaf photosynthetic rates as a function of temperature, relative humidity, insolation, and the partial pressure of atmospheric carbon dioxide and dioxygen. The latter quantities were calculated from fixed concentrations (400 and 20,900 ppm, respectively) and elevation-dependent atmospheric pressures. The other (diurnally varying) driving radiation and weather variables were calculated as described in *Diurnal variations in air temperature, relative humidity, and surface insolation*.

Diurnal variations in air temperature, relative humidity, and surface insolation.—Representative hourly air temperature values (T_{air}) were calculated from mean monthly minimum (T_{min}) and maximum (T_{max}) air temperatures (Campbell and Norman 2012), and monthly T_{min} and T_{max} data for each city's airport were obtained from NOAA (2015). Mean daily time courses of air temperature and relative humidity (%) were calculated based on the following empirical functions (Campbell and Norman 2012):

$$T_{air} = T_{max} \times \gamma + T_{min} \times (1 - \gamma)$$

$$\gamma = 0.44 - 0.46 \times \sin\left(\left(\frac{\pi}{12}\right) \times \text{time} + 0.9\right) + 0.11 \times \sin\left(\left(\frac{\pi}{12}\right) \times \text{time} + 0.9\right)$$

where T_{max} and T_{min} represent the mean daily maximum and minimum temperatures for a given month, and time represents hourly values from 1 to 24. T_{min} was used as a proxy for dew point temperature (T_{dew}). Daily mean ambient vapor pressure (e_a, in mbar; 1 bar = 1 × 10^5 Pa) and hourly saturation vapor pressure (e_{sat}, in mbar) were estimated using T_{dew} and hourly modeled T_{air}, respectively, using the following formula (Campbell and Norman 2012):

$$e_{sat} = 6.112 \times \exp\left(\frac{17.67 \times \text{temp}}{(\text{temp} + 243.5)}\right)$$

where e_{sat} is the saturation vapor pressure (mbar) and temp is air temperature (°C).

Downwelling solar irradiance or shortwave insolation at hourly time steps was modeled using the method described in Bonan (2008). In short, surface solar irradiance at a given location depends on latitude, altitude, and time of year. For each month, the mid-month day of year (DOY) was used (i.e., 15 May is DOY 135 in a non-leap year), and the latitude and altitude of each city's airport were used. These calculations require an estimate of cloud-free atmospheric transmittance, and for these simulations, a value of 0.7 was used in all locations. Total shortwave insolation (direct and diffuse in W/m^2) was converted to the flux of photosynthetically active radiation (PAR, in $\mu mol \cdot m^{-1} \cdot s^{-1}$) by assuming that one-half of shortwave insolation was in the PAR wavelengths

(Campbell and Norman 2012). All process model calculations were performed in R version 3.2.0 (R Core Team 2013).

Data and statistical analyses

Regression analysis was used to determine if there was a relationship between (1) mean plant $\delta^{13}C$ and C_4 proportion of lawn cover at the national scale (i.e., across cities), (2) C_4 proportion of lawn cover or the theoretical C_4 carbon gain and mean growing season temperature (GST, °C), (3) C_4 proportion of lawn cover and mean annual temperature (MAT, °C) or the theoretical C_4 carbon gain, (4) turf or non-turf C_4 proportion of lawn cover and MAT or MAP, and (5) proportion of C_3/C_4 or turf/non-turf and mean annual winter minimum temperature (°C). Pearson correlation analysis was used to assess whether the C_4 proportion of regional grass flora (Sage et al. 1999) was correlated with C_4 proportion of lawn species in residential yards across these seven cities. The GST was calculated for months with average temperature above 18.3°C. All statistical analyses were performed in R version 3.2.1 (R Core Team 2013). All tests for significance are reported at the $\alpha = 0.05$ critical value.

Results

Mean plant $\delta^{13}C$ in residential lawns across the cities was positively related to the C_4 proportion of lawn cover ($r^2 = 0.82$, $P < 0.01$; Appendix S1: Fig. S1). The theoretical C_4 carbon gain was related to mean growing season temperature (GST; $r^2 = 0.89$, $P < 0.001$), but the relationship between C_4 proportion of lawn cover and mean GST was weak ($r^2 = 0.55$, $P > 0.05$; Fig. 1). In fact, the C_4 proportion of lawn cover was more strongly related to MAT ($r^2 = 0.95$, $P < 0.001$), and C_4 proportion was not related to the theoretical C_4 carbon gain in lawns ($r^2 = 0.39$, $P > 0.05$; Fig. 2). Turf C_4 proportion of lawn cover was positively related to MAT ($r^2 = 0.94$, $P < 0.001$), whereas the non-turf C_4 proportion of lawn cover was related to MAP ($r^2 = 0.85$, $P < 0.05$); however, the degree of change (slope) in C_4 lawn cover with MAT is much greater than for non-turf C_4 lawn cover with MAP (Fig. 3). Furthermore, turf C_3 and C_4 proportion of lawn cover was related to mean annual winter minimum temperatures ($r^2 = 0.71$, $P = 0.02$ and $r^2 = 0.78$, $P = 0.01$, respectively), whereas the non-turf C_3 and C_4 proportion of lawn cover were not related to winter temperatures (Fig. 4).

The contributions of C_3 vs. C_4 and turf vs. non-turf species to the total lawn cover broadly reflected differences in climate among the seven cities. In BAL, BOS, LA, MSP, and SLC, the majority of lawn cover consisted of C_3 species (66–97% of total plant cover), whereas in MIA and PHX, the majority of lawn cover was composed of C_4 species (77% and 70%, respectively; Fig. 5). The proportion of C_3 and C_4 turf (Table 2) and non-turf (Appendix S1: Table S1) species differed among the seven cities. MIA and PHX had the greatest C_4 turf cover, whereas C_3 turf was at least one-half of the total lawn cover in the other five cities (Fig. 5). The C_3 non-turf cover comprised 17–37% of the lawn cover in all cities except in SLC, which had 6% C_3 non-turf cover. Alternatively, the C_4 non-turf cover was below 14% across all the cities, and was especially low in the arid cities (<1.0%; Fig. 5). While the C_4 proportion of lawn species was significantly correlated with the C_4 proportion of regional grass flora ($R = 0.90$, $P < 0.01$; Fig. 6), the majority (73%) of all C_4 turf species present in the lawns were nonnative in origin.

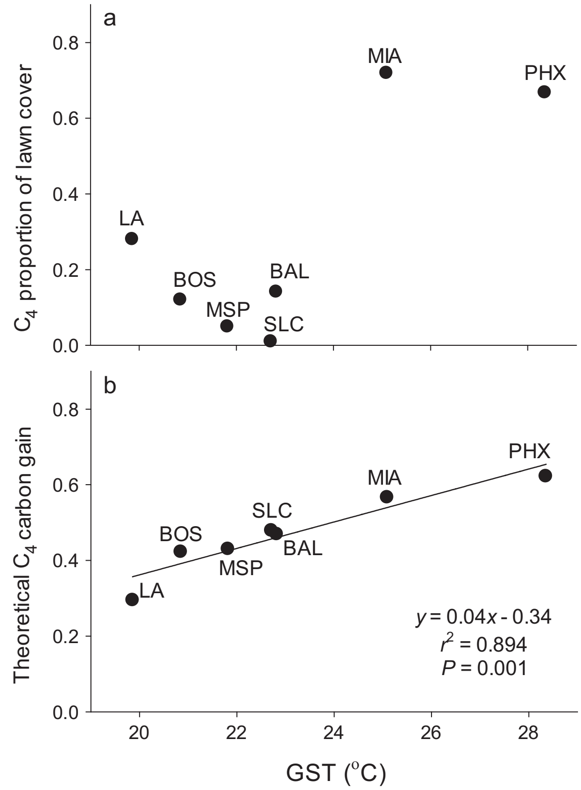

Fig. 1. Observed C_4 proportion of lawn cover (a) and theoretical C_4 carbon gain (b) vs. mean growing season temperature (GST) across seven U.S. cities; Baltimore, Maryland (BAL); Boston, Massachusetts (BOS); Los Angeles, California (LA); Miami, Florida (MIA); Minneapolis-St. Paul, Minnesota (MSP); Phoenix, Arizona (PHX); and Salt Lake City, Utah (SLC).

Discussion

Complex relationships between climate and homeowner plant management drive the distribution of C_4 plants in residential lawns. Across seven U.S. cities, plant $\delta^{13}C$ and C_4 proportion of lawn cover were lower in the cities with lower MAT, whereas C_4 proportion and plant $\delta^{13}C$ increased in the warmer cities (Appendix S1: Fig. S1). This temperature control was driven more strongly by MAT than GST across these cities (Figs. 1,

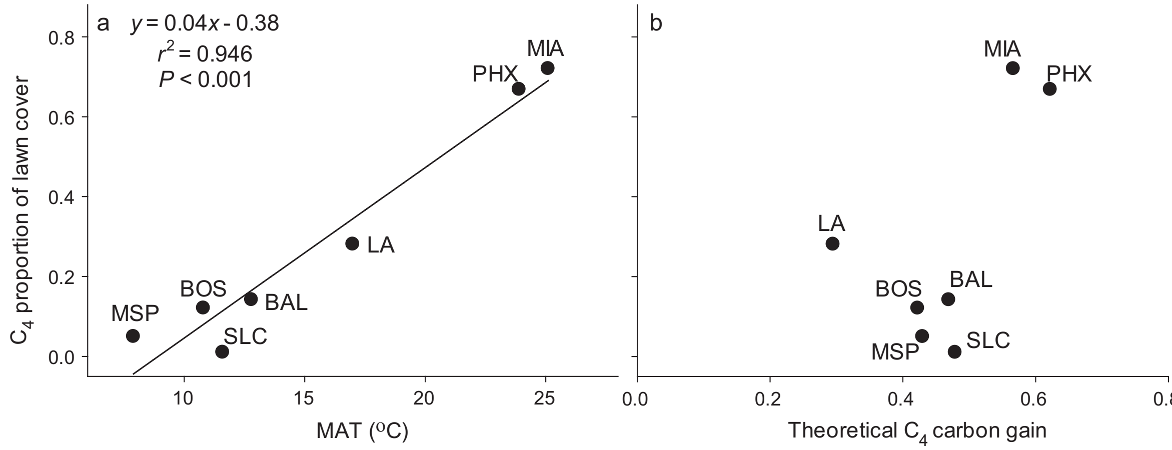

FIG. 2. C_4 proportion of lawn cover in residential lawns vs. mean annual temperature (a) (MAT; °C) and the theoretical C_4 carbon gain in lawns (b). For city abbreviations, see Fig. 1.

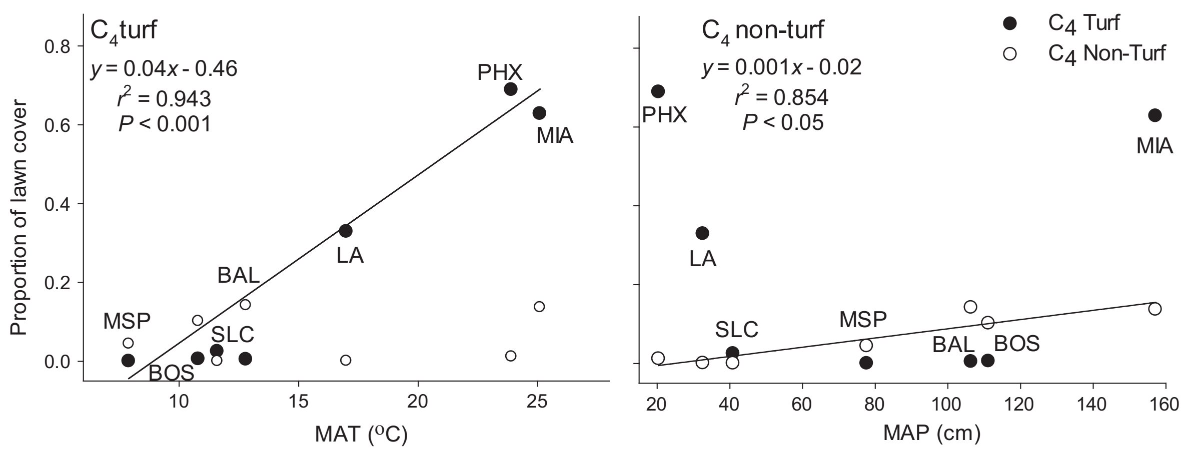

FIG. 3. C_4 proportion of turf (black circles) and non-turf (white circles) lawn cover vs. mean annual temperature (MAT, °C) and mean annual precipitation (MAP, cm) across seven cities. Regression line shown for turf C_4 proportion of lawn cover and MAT, and for non-turf C_4 proportion of lawn cover and MAP. For city abbreviations, see Fig. 1.

2), and wintertime temperatures influenced the distribution of C_4 lawn turf plants (Fig. 4). This pattern differs from the relationship between C_4 distributions and temperature in natural ecosystems (Terri and Stowe 1976) and therefore suggests a human-mediated mechanism for selection of wintertime temperature tolerance in C_4 species. Our results suggest that persistence of turf performance (i.e., green) beyond the growing season is an important attribute for homeowners since persistent warm temperatures (i.e., MAT) are a stronger predictor than the growing season temperatures in determining C_4 lawn cover. In fact, MAT and winter minimum temperature were more significant predictors of the distribution of C_4 turf species than non-turf species (Figs. 3, 4), indicating that C_4 turf species in warmer climates are (1) sold by nurseries, seed suppliers, sod companies, and other turf suppliers, (2) preferentially selected and planted by homeowners, and/or (3) more successful after establishment. Alternatively, C_4 weed species, whose dynamics are the result of natural plant community assembly processes (e.g., dispersal, biotic interactions) and homeowner management (e.g., weeding), are not successful or are removed from lawns by homeowners in these warm cities and are more successful in mesic cities (Fig. 3).

The majority of C_4 turf species were of nonnative origin and imported from warmer climates, compared to the dominant C_4 non-turf species, which originate from cooler climates and demonstrated a positive relationship with MAP. While previous research provided evidence for direct temperature control of C_4 productivity and abundance in lawns (Duffy and Chown 2016, Hobbie et al. 2017) and for direct homeowner management control of lawn composition (Stewart et al. 2009, Bertoncini et al. 2012), our study documents how climate and homeowner plant management interact to control C_4

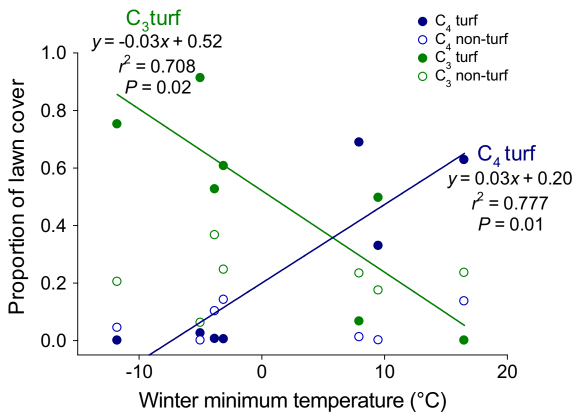

Fig. 4. Proportion of C_3 turf (dark green), C_3 non-turf (light green), C_4 turf (dark blue), and C_4 non-turf (light blue) lawn cover vs. mean annual winter minimum temperature (°C). Regression line shown for turf C_3 (dark green) and turf C_4 proportion of lawn cover and winter minimum temperature.

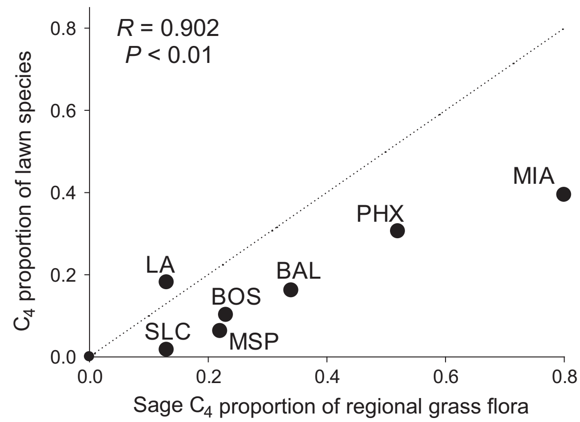

Fig. 6. C_4 proportion of lawn species (i.e., number of lawn species that are C_4) vs. Sage et al. (1999) C_4 proportion of regional grass flora (i.e., number of grass species that are C_4). The dotted line represents a 1:1 line. For city abbreviations, see Fig. 1.

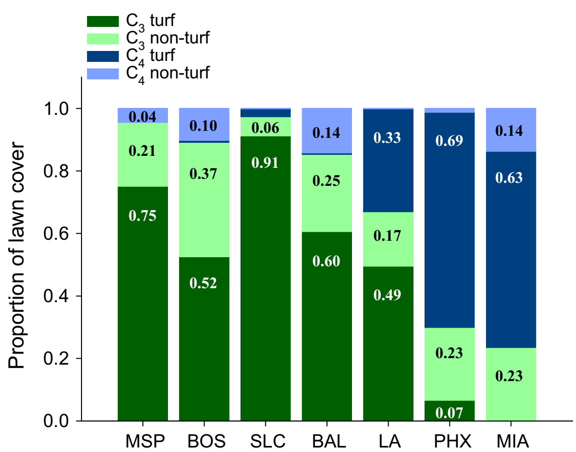

Fig. 5. The C_3 turf (dark green), C_3 non-turf (light green), C_4 turf (dark blue), and C_4 non-turf (light blue) proportion of lawn cover across the seven cities. Proportion for the C_3 and C_4 turf (white) and non-turf (black) components of the lawn are shown, except when the proportion is below 0.03. Cities are shown in order of increasing mean annual temperature, from coolest (MSP) to warmest (MIA) city. For city abbreviations, see Fig. 1.

lawn cover at continental scales. C_4 turf lawn cover is positively related to MAT, and most turf species are nonnative species (i.e., not of regional origin).

The relationship between C_4 distributions and climatic variables provides a means of evaluating the role of horticultural and management practices vs. biotic factors in structuring these plant communities in differing climates. In MSP and SLC, which have a continental climate, both turf and non-turf (i.e., weedy species) were predominately C_3 (Fig. 5). This suggests that C_4 species are not competitive irrespective of homeowner lawn management, and/or the regional C_4 grass flora species pool for these cities is low, most likely due to land use change and fewer native prairie grasses (Fig. 6). The two East Coast cities, BOS and BAL, had larger proportions of C_4 weedy species, suggesting that during the hot, mesic summers in these regions, C_4 species were somewhat competitive, which is expected when cool season grasses weaken and C_4 species are seldom planted (Cook and Ervin 2010). In contrast, the arid cities (LA and PHX) had minimal C_4 non-turf cover (0.4–5% of non-turf cover), and C_4 plants in these cities were predominantly planted turf grasses. This suggests that competitive dynamics among C_3 and C_4 grasses played less of a role in the C_4 dominance compared to planting choices, or that C_4 species were more competitive once planted with ample irrigation in these arid cities (Bijoor et al. 2008). In MIA, the majority of turf grasses were C_4 species, whereas both C_3 and C_4 non-turf species were present. Many C_4 weedy sedges (e.g., *Cyperus croceus*, *Kyllinga brevifolia*) and grasses (e.g., *Digitaria ciliaris*, *Eleusine indica*) can thrive in this warm, moist climate. The strong climatic influence on plant composition appears to be driven by a combination of both direct effects of temperature on plant performance, and more indirect effects that influence the homeowner management of turf grass species in a given region.

While MAT was a strong predictor of C_4 lawn cover across these cities (Fig. 2), C_4 lawn cover was not related to mean annual precipitation across these cities ($P > 0.10$) indicating that irrigation inputs in the warm arid cities provide ample water for plant growth (Collatz et al. 1998, Romero and Dukes 2013, Wang et al. 2014, Volo et al. 2015). Turf scientists' recommendations were developed for the best-predicted establishment and performance of turf based on climate, as well as other factors (e.g., light). However, cultivation of turfgrass species not adapted to local conditions is feasible since management of other factors (e.g., precipitation alleviation via irrigation, mowing height) can offset environmental limitations (Ward 1969). More recent turf adaptation zones include potential competitive dynamics and lawn management practices to predict C_3/C_4 lawn plant communities (Cook and Ervin 2010). Our empirical findings demonstrate the importance of lawn management on the distribution of warm and cool-season grasses in residential lawns. In LA, local climatic conditions predict dominance of C_3 grasses (ample precipitation for grass productivity occurs during the cool months; Sage and Monson 1999; Table 1). Yet the substantial C_4 lawn cover observed in LA lawns suggests irrigation practices alleviate precipitation constraints on the distribution of C_4 plant species (precipitation < 25 mm/yr constrains grass growth; Collatz et al. 1998). Similarly, climate conditions in SLC predict dominance by C_3 species (Table 1). However, in contrast to LA, SLC homeowners appear to be primarily cultivating C_3 turf species, suggesting that year-round climatic conditions exert some influence on homeowner lawn planting choices or competitive dynamics between lawn species in SLC residential lawns (Fig. 5). It is possible that, in addition to summer months, SLC residents desire green lawns during cold spring and fall months when C_3 species are more competitive than C_4 species (Cook and Ervin 2010).

As expected, the proportion of C_4 species in residential lawns was correlated with the proportion of C_4 species in the regional grass flora (Fig. 6). For six cities, C_4 species were under-represented in the lawns compared to the regional flora. The exception is LA, where the number of C_4 species found in residential lawns is slightly greater than the number of C_4 species in the regional grass flora (Fig. 6). This supports the idea that homeowners plant C_4 species in this city in greater numbers than represented in the regional flora. Furthermore, the majority of C_4 turf species present in these residential lawns (73%) are not native to the United States, suggesting nonnative C_4 turf species are competitive and persistent in LA lawns with dynamics that differ from the regional native ecosystem.

The plant composition in residential lawns is a result of dynamics between homeowner plant management and competition between cultivated (turf) and spontaneous (non-turf) plants. Across the United States, urban residents have created a new biome, i.e., the American Residential Macrosystem (Groffman et al. 2017), which reflects land management, planting choices, and irrigation practices that increase lawn cover. This has implications for water use, especially in arid climates, and energy balance in urban landscapes. For example, greater water-efficient C_4 turf species planted in LA lawns may decrease landscape water requirements in the warm, arid summer months. Furthermore, using regionally adapted native species for turf is a more sustainable approach for lawn management as these species allow for reduced resource inputs and increased performance compared with nonnative turf monocultures (Simmons et al. 2011). Future work will focus on how alterations to current lawn management practices modify energy and water cycles within this American Residential Macrosystem.

Conclusion

The species composition of residential lawns is a result of complex relationships between climate controls on the competitive dynamics between C_3 and C_4 plants and resident lawn management and horticultural practices, such as cultivating desirable turf species and weeding undesirable plants. We showed that $\delta^{13}C$ of lawns across seven cities was strongly correlated with the proportion of observed C_4 plant cover, providing a simple means of assessing the distribution of C_3 vs. C_4 species in lawns. MAT was a strong control on lawn species composition across the United States, but cities differed as to whether these patterns were driven by cultivated lawn grasses vs. weedy species. In some cities, biotic interactions with weedy plants appeared to dominate, while in other cities, C_4 plants were predominantly imported and cultivated. C_4 lawn cover exhibited no relationship with MAP, demonstrating the importance of irrigation in overriding climate constraints in arid cities (e.g., PHX). In cities with hot, mesic summers (BAL, BOS), substantial cover by C_4 non-turf species suggests that weedy species may be responding to warm summer temperatures in these cities even though homeowners select C_3 turf species. Furthermore, minimal C_4 non-turf cover in LA, PHX, and SLC suggests weed species are not thriving in these arid cities, and either are not competitive or are not present in the local seed pool. These results provide the first comprehensive assessment of lawn biogeography in the United States, and advance our understanding of the complex interactions between social and biophysical drivers of plant species composition in urban residential lawns.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1884/full

Data Availability

The data that support the findings of this study are openly available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/ae6a8154bf0df6492a7358e19ee08fc6