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Climate and lawn management interact to control C4 plant distribution in residential lawns across seven U.S. cities

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Abstract. In natural grasslands, C4 plant dominance increases with growing season temperatures and reflects distinct differences in plant growth rates and water use efficiencies of C3 vs. C4 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 C3/C4 relative abundance) and C4 cover in residential lawns across seven U.S. cities to determine how climate, lawn plant management, or interactions between climate and plant management influenced C4 lawn cover. We also calculated theoretical C4 carbon gain predicted by a plant physiological model as an index of expected C4 cover due to growing season climatic conditions in each city. Contrary to theoretical predictions, plant $\delta^{13}C$ and C4 cover in urban lawns were more strongly related to mean annual temperature than to growing season temperature. Wintertime temperatures influenced the distribution of C4 lawn turf plants, contrary to natural ecosystems where growing season temperatures primarily drive C4 distributions. C4 cover in lawns was greatest in the three warmest cities, due to an interaction between climate and homeowner plant management (e.g., planting C4 turf species) in these cities. The proportion of C4 lawn species was similar to the proportion of C4 species in the regional grass flora. However, the majority of C4 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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Turf grasses across the continental United States occupy over 160,000 km² with important consequences for air and water quality as well as human health and well-being (Milesi et al. 2005). Residential lawns cover 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., C₄ vs. C₃ photosynthesis) 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 CO₂ on the competitive dynamics of C₃ and C₄ plants in lawns (Bijoor et al. 2008, Duffy and Chown 2016, Hobbie et al. 2017). However, understanding the controls on C₃/C₄ 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 C₄ 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 C₄ 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 C₃ vs. C₄ plants, or the ratio of photosynthetic carbon (C) gain to photons absorbed (Ehleringer and Björkman 1977). At high temperatures, photosynthetic light-use efficiencies of C₃ plants are low because of increased photorespiration (Ehleringer et al. 1997, Collatz et al. 1998), favoring C₄ plants. However, C₄ photosynthesis has energetic costs (Ehleringer 1978, Ehleringer et al. 1991). As a result, C₄ plants are expected to outcompete C₃ 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 C₄ plants globally, human-mediated changes in land cover and use, such as agricultural crop production and altered fire regimes, also influence natural C₄ 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 C₃ vs. C₄ species in lawns follows similar biogeographical patterns as natural ecosystems is still a significant gap in our basic understanding of
The carbon stable isotope ratio (δ13C) of plant tissues can be a valuable tool to measure the relative abundance of C3 and C4 grasses (O’Leary 1981). For all plants, the natural abundance δ13C in plants is depleted in 13C relative to atmospheric CO2 because of discrimination against 13C during photosynthesis (Farquhar et al. 1989). The greater discrimination against 13C by Rubisco compared with PEP (phosphoenolpyruvate) carboxylase during photosynthesis causes isotopically distinct plant δ13C values in C3 (average δ13C = −27‰) and C4 (average δ13C = −13‰) plants (O’Leary 1988, Boutton 1996). Biogenic and anthropogenic factors control plant δ13C values in urban lawns through the relative proportion of C3 vs. C4 plant composition.

We sought to understand how C4 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 C4 lawn distribution with theoretical carbon gain for C4 plants (i.e., simulated C4 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 C4 plants in lawns. Climatic constraints on large-scale C3 and C4 plant distributions have been commonly evaluated using a mean monthly temperature threshold of 22°C and a minimum precipitation constraint for C4 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 C3 dominated, whereas MIA and PHX would be C4 dominated (Table 1). If there is a direct influence of climate on C3 vs. C4 plant growth, then we expected C4 lawn cover to be quantitatively related to growing-season temperature (GST) and to the theoretical carbon gain that C4 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 C4 lawn cover will be unrelated to climate parameters (such as MAT) and to the theoretical C4 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 C4 lawn cover, whereas non-turf (weed species) C4 lawn cover will be related to precipitation (mean annual precipitation, MAP), suggesting homeowners can select C4 lawn turf for optimal year-round temperatures and override any soil moisture constraints (i.e., irrigation). Furthermore, a relationship between winter minimum temperatures and C3/C4 turf lawn cover, and no relationship with C3 and C4 non-turf species supports an interaction between climate and human management influence on C3/C4 turf distribution since spontaneous and cultivated plants are not similarly controlled by low temperatures. Finally, a high proportion of nonnative C4 turf species would support the idea that homeowner planting of C4 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-

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**Table 1.** The expected dominance of C3 or C4 plants based on each city’s climate.

<table>
<thead>
<tr>
<th>City</th>
<th>Temperature (°C)</th>
<th>Precipitation (cm)</th>
<th>Climate prediction</th>
<th>Turfgrass climate zone</th>
<th>Dominant lawn community</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAL</td>
<td>12.8</td>
<td>106.4</td>
<td>C3</td>
<td>humid transitional</td>
<td>warm/cold grass mix</td>
</tr>
<tr>
<td>BOS</td>
<td>10.8</td>
<td>111.2</td>
<td>C3</td>
<td>semi-cool humid</td>
<td>cool season grasses</td>
</tr>
<tr>
<td>LA</td>
<td>17.0</td>
<td>32.6</td>
<td>C3</td>
<td>cool semiarid Pacific</td>
<td>warm/cold grass mix</td>
</tr>
<tr>
<td>MIA</td>
<td>25.1</td>
<td>157.2</td>
<td>C4</td>
<td>warm tropical</td>
<td>warm season grasses</td>
</tr>
<tr>
<td>MSP</td>
<td>7.9</td>
<td>77.7</td>
<td>C3</td>
<td>semi-cool humid</td>
<td>cool season grasses</td>
</tr>
<tr>
<td>PHX</td>
<td>23.9</td>
<td>20.4</td>
<td>C4</td>
<td>warm arid</td>
<td>warm season grasses</td>
</tr>
<tr>
<td>SLC</td>
<td>11.6</td>
<td>40.9</td>
<td>C3</td>
<td>cool semiarid</td>
<td>cool season grasses</td>
</tr>
</tbody>
</table>

**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 δ13C**

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 C₄ proportion of lawn cover) and applied to δ¹³C data. Thus, MSP data are not included in the analysis of relationships between plant δ¹³C and C₄ 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, δ¹³C, 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 δ¹³C precision of ±0.1‰. The plant δ¹³C values were expressed relative to the international standard (Vienna-PeeDee Belemnite) in the conventional δ notation:

$$\delta^{13}C = \left[ \frac{^{13}C_{sample}}{^{12}C_{standard}} \right] - 1 \times 1000$$

**C₄ proportion of lawn cover**

The plant species cover in each lawn was assessed using three randomly placed 1-m² quadrats in the front and back lawns of each residential yard (6-m² 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 C₃ or C₄ photosynthetic pathway according to Walker 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 C₄ photosynthesis was calculated for each quadrat (C₄ 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 C₄ carbon gain**

*Modeling photosynthesis and photosynthetic carbon isotope fractionation.*—Net photosynthetic and transpiration rates for grasses in each pathway (C₃ and C₄) 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; Collett 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 sub-hourly 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.

<table>
<thead>
<tr>
<th>Latin name</th>
<th>Common name</th>
<th>Photosynthetic pathway</th>
<th>Cities present</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agrostis capillaris</em> L.</td>
<td>colonial bentgrass</td>
<td><em>C</em>₃</td>
<td>BAL, BOS, MSP</td>
</tr>
<tr>
<td><em>Agrostis stolonifera</em> L.</td>
<td>creeping bentgrass</td>
<td><em>C</em>₃</td>
<td>BAL, BOS, MSP</td>
</tr>
<tr>
<td><em>Cynodon dactylon</em> (L.) Pers.</td>
<td>Bermuda grass</td>
<td><em>C</em>₄</td>
<td>BAL, BOS, LA, MIA, PHX, SLC</td>
</tr>
<tr>
<td><em>Festuca filiformis</em> Pourr.</td>
<td>fineleaf sheep fescue</td>
<td><em>C</em>₃</td>
<td>BAL, BOS</td>
</tr>
<tr>
<td><em>Festuca ovina</em> L.</td>
<td>sheep fescue</td>
<td><em>C</em>₃</td>
<td>BOS</td>
</tr>
<tr>
<td><em>Festuca rubra</em> L.</td>
<td>red fescue</td>
<td><em>C</em>₃</td>
<td>BOS, LA, MSP, SLC</td>
</tr>
<tr>
<td><em>Lolium perenne</em> ssp. <em>multiflorum</em> Lam.</td>
<td>Italian ryegrass</td>
<td><em>C</em>₃</td>
<td>PHX</td>
</tr>
<tr>
<td><em>Lolium perenne</em> L.</td>
<td>perennial ryegrass</td>
<td><em>C</em>₃</td>
<td>BAL, BOS, LA, MSP, PHX, SLC</td>
</tr>
<tr>
<td><em>Paspalum notatum</em> Fluege</td>
<td>Bahia grass</td>
<td><em>C</em>₄</td>
<td>MIA</td>
</tr>
<tr>
<td><em>Pennisetum clandestinum</em> Hochst. ex Chiov.</td>
<td>Kikuyu grass</td>
<td><em>C</em>₄</td>
<td>LA</td>
</tr>
<tr>
<td><em>Poa pratensis</em> L.</td>
<td>Kentucky bluegrass</td>
<td><em>C</em>₃</td>
<td>BAL, BOS, LA, MSP, SLC</td>
</tr>
<tr>
<td><em>Poa trivialis</em> L.</td>
<td>rough bluegrass</td>
<td><em>C</em>₄</td>
<td>MSP</td>
</tr>
<tr>
<td><em>Schedonorus arundinaceus</em> (Schreb.) Dumort.</td>
<td>tall fescue</td>
<td><em>C</em>₃</td>
<td>BAL, LA, MSP, SLC</td>
</tr>
<tr>
<td><em>Stenotaphrum secundatum</em> (Walter) Kuntze</td>
<td>St. Augustine grass</td>
<td><em>C</em>₄</td>
<td>LA, MIA, PHX</td>
</tr>
<tr>
<td><em>Zoysia tenuifolia</em> Willd. ex Thiele</td>
<td>Mascarene grass</td>
<td><em>C</em>₄</td>
<td>MIA</td>
</tr>
</tbody>
</table>

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 C₃ and C₄ grasses, and compare the modeled predictions against site data on C₃ and C₄ distributions.

Representative fluxes were predicted using the coupled C₃ and C₄ 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 C₃ grasses was assumed to be 90 $\mu$mol-m⁻²-s⁻¹ at 298 K, and 30 $\mu$mol-m⁻²-s⁻¹ for C₄ 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):

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

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

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 $\times$ 10⁵ 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/m²) was converted to the flux of photosynthetically active radiation (PAR, in $\mu$mol-m⁻¹-s⁻¹) by assuming that one-half of shortwave insolation was in the PAR wavelengths.
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.

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,
2), and wintertime temperatures influenced the distribution of C₄ lawn turf plants (Fig. 4). This pattern differs from the relationship between C₄ distributions and temperature in natural ecosystems (Terri and Stowe 1976) and therefore suggests a human-mediated mechanism for selection of wintertime temperature tolerance in C₄ 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 C₄ lawn cover. In fact, MAT and winter minimum temperature were more significant predictors of the distribution of C₄ turf species than non-turf species (Figs. 3, 4), indicating that C₄ 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, C₄ 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 C₄ turf species were of nonnative origin and imported from warmer climates, compared to the dominant C₄ 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 C₄ 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 C₄
lawn cover at continental scales. C4 turf lawn cover is positively related to MAT, and most turf species are nonnative species (i.e., not of regional origin). The relationship between C4 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 C3 (Fig. 5). This suggests that C4 species are not competitive irrespective of homeowner lawn management, and/or the regional C4 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 C4 weedy species, suggesting that during the hot, mesic summers in these regions, C4 species were somewhat competitive, which is expected when cool season grasses weaken and C4 species are seldom planted (Cook and Ervin 2010). In contrast, the arid cities (LA and PHX) had minimal C4 non-turf cover (0.4–5% of non-turf cover), and C4 plants in these cities were predominantly planted turf grasses. This suggests that competitive dynamics among C3 and C4 grasses played less of a role in the C4 dominance compared to planting choices, or that C4 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 C4 species, whereas both C3 and C4 non-turf species were present. Many C4 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 C4 lawn cover across these cities (Fig. 2), C4 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 C3/C4 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 C3 grasses (ample precipitation for grass productivity occurs during the cool months; Sage and Monson 1999; Table 1). Yet the substantial C4 lawn cover observed in LA lawns suggests irrigation practices alleviate precipitation constraints on the distribution of C4 plant species (precipitation < 25 mm/yr constrains grass growth; Collatz et al. 1998). Similarly, climate conditions in SLC predict dominance by C3 species (Table 1). However, in contrast to LA, SLC homeowners appear to be primarily cultivating C4 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 C3 species are more competitive than C4 species (Cook and Ervin 2010).

As expected, the proportion of C4 species in residential lawns was correlated with the proportion of C4 species in the regional grass flora (Fig. 6). For six cities, C4 species were under-represented in the lawns compared to the regional flora. The exception is LA, where the number of C4 species found in residential lawns is slightly greater than the number of C4 species in the regional grass flora (Fig. 6). This supports the idea that homeowners plant C4 species in this city in greater numbers than represented in the regional flora. Furthermore, the majority of C4 turf species present in these residential lawns (73%) are not native to the United States, suggesting nonnative C4 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 C4 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 C3 and C4 plants and resident lawn management and horticultural practices, such as cultivating desirable turf species and weeding undesirable plants. We showed that δ13C of lawns across seven cities was strongly correlated with the proportion of observed C4 plant cover, providing a simple means of assessing the distribution of C3 vs. C4 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, C4 plants were predominantly imported and cultivated. C4 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 C4 non-turf species suggests that weedy species may be responding to warm summer temperatures in these cities even though homeowners select C3 turf species. Furthermore, minimal C4 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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**LITERATURE CITED**


**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/ae6a8154bf0df6492a7358e19e088fc6