

Effects of urbanization on flowering phenology in the metropolitan phoenix region of USA: Findings from herbarium records

Kaesha L. Neil^{a,*}, Leslie Landrum^a, Jianguo Wu^{a,b}

^aSchool of Life Sciences, Arizona State University, P.O. Box 874601, Tempe AZ 85287-4601, USA

^bGlobal Institute of Sustainability, Arizona State University, Tempe AZ 85287, USA

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ABSTRACT

Phenological studies have become more prominent recently because of rising interests in understanding how plants, communities, and ecosystems respond to global climate change and urban climate modifications. Herbarium records of plants can be a particularly useful source of information for studying historical trends in phenology in areas where long-term phenological records do not exist. In this study, we used herbarium records to examine the historical patterns of flowering phenology of 87 shrubs and ephemerals in the Phoenix metropolitan region in the southwestern United States from 1902 through 2006. We found that 19% of plant species examined either advanced or delayed their flowering. Also, the flowering responses of 28% of the species examined showed significant differences between urban and non-urban areas: 24% advanced in urban areas and 5% delayed. Our study indicates that urbanization may have a significant effect on the flowering phenology of a small but substantial proportion of plants, which will likely affect native biological diversity and ecosystem services due to potential changes in population and community dynamics.

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1. Introduction

Phenology is the seasonal timing of environment-mediated events such as growth and reproduction (Augspurger, 1983; Rathcke and Lacey, 1985). Photoperiod, temperature, and soil moisture have been recognized as the main environmental triggers for leafing and flowering (Rathcke and Lacey, 1985), and many plants rely on multiple cues that may occur months apart (Bowers and Dimmitt, 1994; Friedel et al., 1993; Rathcke and Lacey, 1985). Phenological studies have become increasingly prominent in the last decade because they are directly and indirectly connected to urban and global climate change (Neil and Wu, 2006).

One of the several methods of studying how climate change affects plant phenology (and therefore population and community dynamics) is the use of herbarium records (e.g., Lavoie and Lachance, 2006; Miller-Rushing et al., 2006). European countries have a long tradition of keeping plant phenological records which have enabled researchers to study long-term climate change (Menzel et al., 2006). Such phenological records also have been used to detect flowering phenological changes in response to climatic modifications by urbanization in temperate, boreal, and

Mediterranean ecosystems (see Neil and Wu, 2006 for a recent review). These studies indicated that some species flower earlier, some later, others had no change in flower timing.

Herbarium records can also be a valuable resource in studying plant phenological changes in places like the United States that do not have a tradition of keeping such records. Whereas programs for keeping phenological records are becoming more popular in the United States, the herbarium records kept in botanical gardens and universities across the country are an excellent resource for studying historical trends (Bowers, 2007; Primack et al., 2004). However, this potentially important resource has yet to be fully used.

The purpose of this study was to explore if urbanization-induced climatic changes have resulted in any shifts in plant flowering phenology detectable using the herbarium records at Arizona State University (ASU), which is located in the Phoenix metropolitan region, Arizona, USA. The Phoenix metropolitan area provides a unique opportunity for studying urbanization because it is relatively young (less than 100 years old) and also one of the fastest growing metropolitan regions in the USA during the last 50 years.

Our main hypothesis was that urbanization-induced climatic changes may have resulted in detectable plant phenological changes in the Phoenix metropolitan area; specifically some plants would flower earlier than before during the past several decades as a consequence of warmer temperature. This hypothesis was based on previous findings that temperature is a main flowering trigger in

* Corresponding author. Tel.: +1 602 538 8098.

E-mail address: kaesha.neil@scmail.maricopa.edu (K.L. Neil).

many plants (Rathcke and Lacey, 1985)—including desert plants (Bowers and Dimmitt, 1994) and that temperature in cities increase due to the urban heat island effect (Grimm et al., 2008; Buyantuyev and Wu, 2009). So far, plant phenological studies have been conducted in temperate and Mediterranean ecosystems, and none is found in semi-arid or arid ecosystems (Neil and Wu, 2006). Thus, our study not only sheds new light on the effects of urbanization on the flowering phenology of native plants in the Phoenix region, but also provides an early example of phenological studies of urbanization in arid environments, particularly using herbarium records.

2. Materials and methods

2.1. Study area

The Phoenix metropolitan area is located mostly within Maricopa County of the State of Arizona in southwestern USA, and is home to the Central Arizona-Phoenix Long-Term Ecological Research project (Grimm and Redman, 2004). This region is the northern portion of the Sonoran Desert which has a warm (mean summer high temperature of 40 °C) and dry (mean annual precipitation of 193 mm) climate with two distinct wet seasons—one in winter and the other in summer (Bowers and Dimmitt, 1994). Urban development has been concentrated in the flat and broad Salt River Valley (Luck and Wu, 2002). The Phoenix metropolitan area consists of urban and residential developments, agricultural fields, desert remnants, and undeveloped desert land. Morphologically, while the Phoenix metropolitan area has a distinct densely developed urban core with decreasing urban and residential density further away from the core, development does not reflect a concentric zone or multi-nucleus pattern. Instead, agriculture and desert land is interspersed with urban and residential development (Luck and Wu, 2002). Most of the area's exponential growth has occurred since the 1950s (Berling-Wolff and Wu, 2004; Jenerette and Wu, 2001). Moreover, while there has not been an increase in the average annual maximum temperature in the Phoenix metropolitan area, there has been a steady and significant increase in the average annual minimum temperature by about 3 °C (Brazel et al., 2000).

2.2. Methods

The Arizona State University herbarium contains plant specimens collected from all over the State of Arizona for more than a century, some of which do not have complete herbarium records. While there is no indication that the time of year for specimen collection has significantly changed over the past century (Bowers, 2007), collection peaked in the 1960s and 1970s and has fallen steadily since then. We analyzed the ASU herbarium records of 87 species of native Sonoran desert plants that were collected from 1902 through 2006. Specimens were collected from areas not surrounded by urban structures, but some were near roadsides. Records were analyzed by species and functional groups: spring ephemerals, spring shrubs, fall ephemerals, winter-spring ephemerals, and winter-spring shrubs (Appendix 1). Functional groups were identified using criteria based on growth form and flowering season (Daniel and Butterwick, 1992).

Data were analyzed with functional groups in addition to individual species to determine if patterns could be discerned using larger data sets because fewer individual species had enough herbarium records to allow for a statistically robust species-level analysis. The ASU Herbarium has digitized its herbarium records, including whether or not the plants were flowering. The date of collection (month and day) for each specimen was converted to Julian Day to standardize years. Because winter and spring together spans the end and start of the year, the dates for winter-spring flowering plants were adjusted to begin on the 200th day of the

year (about 19 July), well before winter begins. Around that date is also where there appeared a break in the data. Records missing the collection or flowering date or containing no information on flowering were removed from the dataset. The data set was further divided into two groups: inside Maricopa County (where most of the urban growth has occurred) and outside Maricopa County. The data for each functional group were analyzed in raw form that used all individual records and averaged by decade (i.e., 1910s, 1920s, etc.); in which all records for each functional group in a decade were averaged together to smooth out data trends. The data were averaged to determine if a pattern could be discerned after smoothing out the “noise” of using raw data.

The exact number of days that flowering date changed was not assessed because the data set only had information on whether the individual plants were flowering at the time of collection, but not on the first day of flowering. The data were not standardized to a significant climatic event, such as snowmelt, because Arizona does not have such wide spread significant events that spread slowly over the region. Moreover, it is a relatively small area compared to other regions, such as Canada, studied in a similar manner (Lavoie and Lachance, 2006). SPSS was used for linear regression analysis to test significance of trends over time and for Student's t-test to compare plants inside and outside Maricopa County.

3. Results

3.1. Trends over time

When the plants were analyzed by functional group for historical trends in flowering time, most groups did not show a significant change ($p < 0.05$). We did, however, find that winter-spring ephemerals inside Maricopa County advanced in flowering based on our analysis using both the raw and averaged data ($p < 0.001$, $p = 0.01$; respectively; Table 1). Also, our analysis using only the raw data suggested that spring ephemerals significantly delayed ($p = 0.001$) flowering time over the last century outside of Maricopa County. The analysis using the averaged data, however, showed no significant change ($p = 0.96$).

None of the fall ephemerals changed significantly in flowering date over the last century (data not shown). Only three of the 14 spring ephemerals showed a significant change over time:

Table 1

Linear regression analysis of historical flowering times by group and species and inside and outside Maricopa County. Most show no significant change; however, several spring and winter-spring ephemerals show significant advancement or delay.

Functional Group	Plant	p-value	r ²	Slope
<i>Inside</i>				
Grouped-Averaged	Winter-Spring Ephemeral	0.011	0.631	-0.795
Grouped-Raw	Winter-Spring Ephemeral	0.000	0.013	-0.113
Spring Ephemerals	<i>Antirrhinum filipes</i>	0.030	0.998	0.999
Spring Ephemerals	<i>Mimulus guttatus</i>	0.002	0.278	-0.527
Spring Ephemerals	<i>Oligomeris linifolia</i>	0.018	0.240	-0.490
Winter-Spring Ephem.	<i>Mentzelia affinis</i>	0.018	0.261	-0.511
Winter-Spring Ephem.	<i>Perityle emoryi</i>	0.016	0.097	-0.311
Winter-Spring Ephem.	<i>Sisymbrium irio</i>	0.043	0.104	-0.322
Winter-Spring Ephem.	<i>Stylocline micropoides</i>	0.030	0.144	-0.379
Spring Shrubs	<i>Olneya tesota</i>	0.049	0.199	-0.446
Summer-Fall Ephem.	<i>Trianthema portulacastrum</i>	0.050	0.333	-0.577
<i>Outside</i>				
Grouped-Raw	Spring Ephemeral	0.001	0.016	0.128
Winter-Spring Ephem.	<i>Eriastrum deflexum</i>	0.001	0.111	-0.334
Winter-Spring Ephem.	<i>Eschscholzia californica</i>	0.004	0.127	0.357
Winter-Spring Ephem.	<i>Lepidium lasiocarpum</i>	0.045	0.044	-0.210
Winter-Spring Ephem.	<i>Lupinus arizonicus</i>	0.043	0.103	-0.321
Winter-Spring Ephem.	<i>Silene antirrhina</i>	0.006	0.161	0.401
Spring Shrubs	<i>Larrea tridentata</i>	0.015	0.160	-0.325

Oligomeris linifolia (advanced), *Antirrhinum filipes* (delayed), and *Mimulus guttatus* (advanced) inside Maricopa county (Table 1). One (*Olneya tesota*) of the 11 spring flowering shrubs advanced flowering time inside Maricopa County while another (*Larrea tridentata*) delayed flowering time outside of Maricopa county (Table 1). Four (*Perityle emoryi*, *Stylocline micropoides*, *Sisymbrium irio*, and *Mentzelia affinis*) of the 38 winter-spring ephemerals demonstrated significant advancement in flowering time inside Maricopa County while five other winter-spring ephemerals (*Silene antirrhina* (delayed); *Lepidium lasiocarpum* (advancement); *Lupinus arizonicus* (advancement); *Eschscholzia californica* (delayed); and *Eriogonum deflexum* (advancement)) demonstrated significant change outside of Maricopa County (Table 1). No winter-spring flowering shrubs demonstrated a significant change over time. One of the two summer-fall ephemerals (*Trianthema portulacastrum*) advanced flowering time within Maricopa County over time.

3.2. Inside vs. outside Maricopa County

Only spring ephemerals as a group showed a significant difference in flowering time (inside Maricopa County earlier than outside) when averaged by decade and when using raw data (data not shown). Half of the spring ephemerals (seven out of 14), three of the eleven spring shrubs, nine of the 38 winter-spring ephemerals, one of the two summer-fall ephemerals, and three of the 12 winter-spring shrubs had a significant difference between outside and inside Maricopa County (Fig. 1). All but the winter-spring shrubs and the fall ephemeral bloomed earlier within Maricopa County than without.

4. Discussion and conclusions

Functional groups demonstrated no significant trends except for winter-spring ephemerals which have advanced in flowering date inside of Maricopa County over time, but not outside of Maricopa County. We suggest the limited response by functional groups may be attributable, at least in part, to the following reasons: (1) the responses of individual plant species to changing environmental conditions varied greatly even within the same functional group, (2) there were not sufficient data for each year for the beginning of flowering time, or (3) a combination of the two. However, when plants were analyzed by species, eight showed a historical trend towards advancing flowering inside Maricopa County while seven appear to be delayed. Similar results were found in urban areas by Hepper (2003) in England and Fitter and Fitter (2002) for plants across Britain. Only two of the thirteen plants that showed a significant historical trend in our dataset were shrubs, which is consistent with past findings that ephemerals respond more than shrubs (Fitter and Fitter, 2002; Hepper, 2003).

Spring ephemerals as a group and many as individual species, some spring shrubs, several winter-spring ephemerals, and one of the two summer-fall ephemerals demonstrated a significant earlier flowering time within Maricopa County than outside. The most likely explanation for the earlier flowering times inside versus outside Maricopa County is higher nighttime temperatures. Nighttime, but not daytime, temperatures have been increasing in the Phoenix metropolitan region for the last fifty years by about 3 °C (Brazel et al., 2000). The urban heat island effect has been hypothesized to cause differences in flowering time between urban and rural areas across the globe (Lu et al., 2006; Luo et al., 2007), and is empirically supported by at least one study (Ziska et al., 2003).

Very little research has been conducted on the flowering phenology cues for Sonoran desert plants, especially ephemerals; but what has been conducted suggests temperature, moisture, or both may be responsible (photoperiod has not been studied;

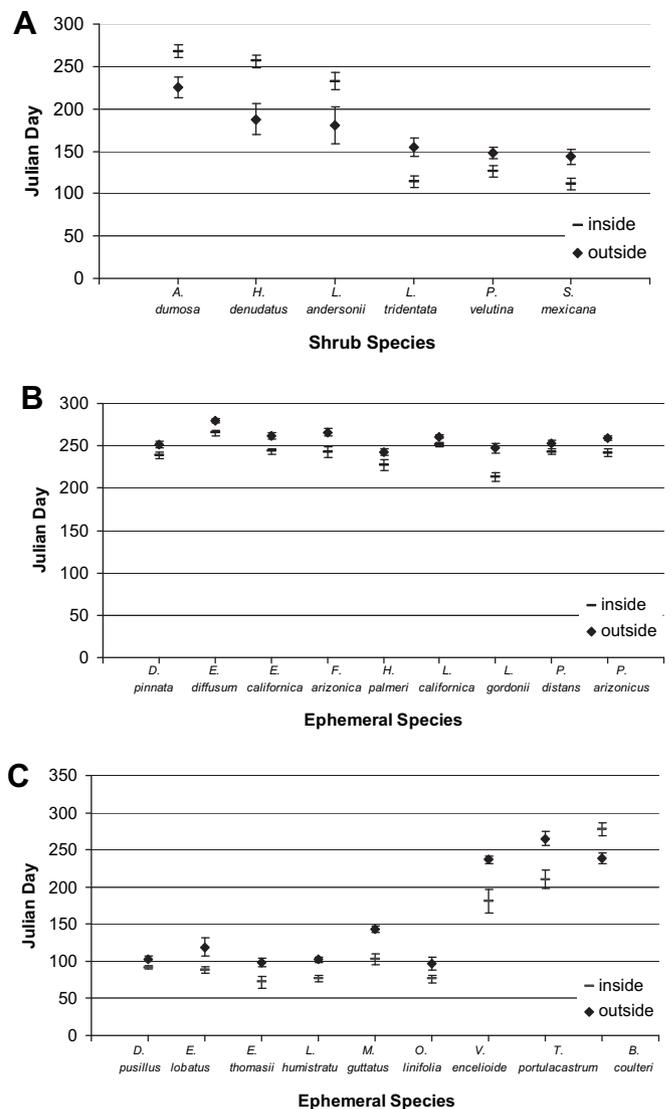


Fig. 1. Species with different ($p < 0.05$) flowering times inside and outside Maricopa County were: (a) shrub species: the winter-spring shrubs exhibit later flowering inside Maricopa County, while the spring shrubs show advanced flowering; (b) winter-spring ephemerals: All exhibit earlier flowering inside Maricopa County; (c) ephemeral species: All but the fall ephemeral (*B. coulteri*) exhibit earlier flowering inside Maricopa County.

Bowers and Dimmitt, 1994). Our results suggest that if urbanization causes modified flowering phenology, temperature is probably a strong trigger for spring and winter-spring desert ephemerals. The fall ephemeral and three winter-spring shrubs that showed a significant difference between inside and outside Maricopa County bloomed later within Maricopa County than outside of Maricopa County. This corresponds to findings by others that fall plants tend to bloom later and spring plants earlier (Fitter and Fitter, 2002; Hepper, 2003; Luo et al., 2007). The disparity most likely results from fall plants not responding to temperature triggers for flowering. Because the Sonoran desert has two growing seasons (winter/spring and summer), this study had the additional group of winter-spring plants. These plants were similar in response to fall/summer-fall plants. Perhaps they require a chilling time that takes longer to reach within Maricopa County due to the higher nighttime temperatures.

Southern Arizona is generally flat and subtropical, and the plants chosen for this study are lowland desert plants. Nevertheless, we were concerned that possible elevation-caused temperature effects

might affect our results. To examine this potential problem, we grouped the data by functional groups in counties of higher mean elevation than Maricopa County (Mohave, Yavapi, Coconino, Navajo, Apache, Santa Cruz, Cochise, Gila, Graham, and Greenlee; 1000–21,000 m), the same mean elevation as Maricopa County (Pima and Pinal; 300–1000 m), and mean elevation lower than Maricopa County (Yuma and La Paz; <300 m). If elevation is the cause for the differences in flowering phenology, then we predicted counties of lower elevation than Maricopa would have spring plants bloom earlier and fall plants bloom later, flowers in counties at the same elevation as Maricopa would bloom at the same time, and flowers in counties of higher elevation would have spring plants bloom later and fall plants bloom earlier. We found that Maricopa County plants flowered significantly earlier than those in counties at the same elevation for summer-fall ephemerals ($p = 0.016$), winter-spring ephemerals ($p < 0.001$), and winter-spring shrubs ($p = 0.019$). Moreover, the fall ephemerals bloomed later ($p < 0.001$) in Maricopa than in counties at lower elevations. These results lend support to our hypothesis that urbanization contributed significantly to the differences in flowering phenology observed for most of the plants although elevation does affect air temperatures.

Temperature changes are not the only potential cause for the changes in flowering phenology in our study. Along with wind, VOCs, photoperiod, UV radiation, and possibly arthropod community on plants (Faeth et al., 2005; Neil and Wu, 2006), changes in precipitation patterns may also play a role in changing phenological patterns (Penuelas et al., 2004). Research indicates relative humidity and precipitation patterns can be changed by urbanization (Diem and Brown, 2003; Dixon and Mote, 2003; Jonsson, 2004; Lipfert et al., 1991; Shepherd, 2006; Unger, 1999). To analyze precipitation influences, however, fine scale precipitation data are necessary because precipitation patterns are highly spatially and temporally variable in arid systems. As such data were not available, we did not address this potential problem in our study. Nevertheless, we believe that the general pattern of shifting flowering phenology observed in our study, not the exact time of flowering advanced by urbanization, remains robust.

In conclusion, 19% of the 81 Sonoran desert species examined in this study demonstrated a change in flowering phenology over time. Moreover, 28% of them demonstrated a difference in flowering time between urban and non-urban areas. While this data does not demonstrate cause and effect between urbanization and flowering phenology pattern observed, it does suggest a correlation between urbanization and phenology patterns. Because all the plants were collected as part of different research projects of numerous different researchers, this project is limited by when and where the researchers chose their research areas. The data will be strengthened by combining flowering data from multiple institutions (i.e., other universities and botanical gardens). Despite these limitations, our study using data from the herbarium collection has provided valuable insights into flowering phenology trends concurrent with urbanization in the southwestern USA. Our study indicates that urbanization may significantly affect the phenology of a small but substantial proportion of plants, and consequently native biodiversity and ecosystem services through potential alterations of the structure and function of populations and communities. Furthermore, because of the rapid urbanization worldwide and certain similar environmental effects between urbanization and climate change, our findings may be relevant to other regions of the world or at the global level.

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Appendix 1. Native Sonoran desert plants used in this study.

Winter–Spring Ephemerals (WSE)			
<i>Amsinckia intermedia</i>	<i>Descurainia pinnata</i>	<i>Lesquerella gordonii</i>	<i>Phacelia distans</i>
<i>Astragalus nuttallianus</i>	<i>Draba cuneifolia</i>	<i>Linanthus bigelovii</i>	<i>Pholistoma auritum</i>
<i>Bowlesia incana</i>	<i>Eriastrum diffusum</i>	<i>Lupinus arizonicus</i>	<i>Plagiobothrys arizonicus</i>
<i>Baileya multiradiata</i> ^a	<i>Eriogonum deflexum</i>	<i>Machaeranthera arida</i>	<i>Silene antirrhina</i>
<i>Calycosotis wrightii</i>	<i>Eschscholzia californica</i>	<i>Mentzelia affinis</i>	<i>Sisymbrium irio</i>
<i>Camissonia californica</i>	<i>Eucrypta chrysanthemifolia</i>	<i>Monoptilon bellioides</i>	<i>Sphaeralcea coulteri</i>
<i>Caulanthus lasiophyllus</i>	<i>Filago arizonica</i>	<i>Parietaria hespera</i>	<i>Stylocline micropoides</i>
<i>Chaenactis carphoclinia</i>	<i>Harpagonella palmeri</i>	<i>Pectocarya heterocarpa</i>	<i>Thysanocarpus curvipes</i>
<i>Chorizanthe brevicornu</i>	<i>Lasthenia californica</i>	<i>Pectocarya setosa</i>	<i>Trichoptilium incisum</i>
<i>Cryptantha angustifolia</i>	<i>Lepidium lasiocarpum</i>	<i>Perityle emoryi</i>	
Spring Ephemerals (SE)			
<i>Antirrhinum filipes</i>	<i>Eriogonum thomasi</i>	<i>Nama demissum</i>	<i>Salvia columbariae</i>
<i>Centaureium calycosum</i>	<i>Juncus bufonius</i>	<i>Oligomeris linifolia</i>	<i>Spermelepis echinata</i>
<i>Daucus pusillus</i>	<i>Lotus humistratus</i>	<i>Pterostegia drymarioides</i>	<i>Verbesina encelioides</i>
<i>Erigeron lobatus</i>	<i>Mimulus guttatus</i>		
Summer–Fall Ephemerals ^b (SFE)			
<i>Trianthema portulacastrum</i>	<i>Tidestromia lanuginosa</i>		
Fall Ephemerals (FE)			
<i>Boerhavia coulteri</i>	<i>Conyza canadensis</i>	<i>Cuscuta tuberculata</i>	<i>Pectis papposa</i>
Winter–Spring Shrubs (WSS)			
<i>Ambrosia deltoidea</i>	<i>Crossosoma bigelovii</i>	<i>Galium stellatum</i> ^a	<i>Lycium exsertum</i>
<i>Ambrosia dumosa</i>	<i>Encelia farinosa</i>	<i>Gymnosperma glutinosum</i>	<i>Nicotiana glauca</i>
<i>Atriplex canescens</i>	<i>Forestiera shrevei</i> ^a	<i>Hibiscus denudatus</i>	<i>Viguiera deltoidea</i>
<i>Atriplex polycarpa</i> ^a	<i>Fouquieria splendens</i>	<i>Lycium andersonii</i>	<i>Ziziphus obtusifolia</i> ^a
<i>Brickellia coulteri</i>			
Spring Shrubs (SS)			
<i>Acacia greggii</i>	<i>Hymenoclea salsola</i>	<i>Lycium fremontii</i>	<i>Prosopis velutina</i>
<i>Celtis pallida</i>	<i>Krameria grayi</i>	<i>Olneya tesota</i>	<i>Salazaria mexicana</i>
<i>Horsfordia newberryi</i>	<i>Larrea tridentata</i>	<i>Parkinsonia florida</i>	

^a Used in functional group analysis but not sufficient data to analyze individually.

^b Analyzed individually but not as a group.

References

- Augspurger, C.K., 1983. Phenology, flowering synchrony, and fruit-set of 6 neotropical shrubs. *Biotropica* 15, 257–267.
- Berling-Wolff, S., Wu, J., 2004. Modeling urban landscape dynamics: a case study in Phoenix, USA. *Urban-Ecosystems* 7, 215–240.
- Bowers, J.E., 2007. Has climatic warming altered spring flowering date of sonoran desert shrubs? *Southwestern Naturalist* 52, 347–355.
- Bowers, J.E., Dimmitt, M.A., 1994. Flowering phenology of 6 woody-plants in the Northern Sonoran Desert. *Bulletin of the Torrey Botanical Club* 121, 215–229.
- Brazel, A., Selover, N., Vose, R., Heisler, G., 2000. The tale of two climates – Baltimore and Phoenix urban LTER sites. *Climate Research* 15, 123–135.

- Buyantuyev, A., Wu, J., 2009. Urbanization alters spatiotemporal patterns of ecosystem primary production: A case study of the Phoenix Metropolitan region, USA. *Journal of Arid Environments* 73, 512–520.
- Daniel, T.F., Butterwick, M.L., 1992. Flora of the South Mountains of South-Central Arizona. *Desert Plants* 10, 99–119.
- Diem, J.E., Brown, D.P., 2003. Anthropogenic impacts on summer precipitation in central Arizona, USA. *Professional Geographer* 55, 343–355.
- Dixon, P.G., Mote, T.L., 2003. Patterns and causes of Atlanta's urban heat island-initiated precipitation. *Journal of Applied Meteorology* 42, 1273–1284.
- Faeth, S.H., Warren, P.S., Shochat, E., Marussich, W.A., 2005. Trophic dynamics in urban communities. *Bioscience* 55, 399–407.
- Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. *Science* 296, 1689–1691.
- Friedel, M.H., Nelson, D.J., Sparrow, A.D., Kinloch, J.E., Maconochie, J.R., 1993. What induces Central Australian Arid Zone trees and shrubs to flower and fruit. *Australian Journal of Botany* 41, 307–319.
- Grimm, N.B., Redman, C.L., 2004. Approaches to the study of urban ecosystems: The case of Central Arizona-Phoenix. *Urban-Ecosystems* 7, 199–213.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J.G., Bai, X.M., Briggs, J.M., 2008. Global change and the ecology of cities. *Science* 319, 756–760.
- Hepper, F.N., 2003. Phenological records of English garden plants in Leeds (Yorkshire) and Richmond (Surrey) from 1946 to 2002. An analysis relating to global warming. *Biodiversity and Conservation* 12, 2503–2520.
- Jenerette, G.D., Wu, J.G., 2001. Analysis and simulation of land-use change in the central Arizona-Phoenix region, USA. *Landscape Ecology* 16, 611–626.
- Jonsson, P., 2004. Vegetation as an urban climate control in the subtropical city of Gaborone, Botswana. *International Journal of Climatology* 24, 1307–1322.
- Lavoie, C., Lachance, D., 2006. A new herbarium-based method for reconstructing the phenology of plant species across large areas. *American Journal of Botany* 93, 512–516.
- Lipfert, F.W., Cohen, S., Dupuis, L.R., Peters, J., 1991. Relative-humidity predictor equations based on environmental-factors. *Atmospheric Environment Part B-Urban Atmosphere* 25, 435–441.
- Lu, P.L., Yu, Q., Liu, J.D., Lee, X.H., 2006. Advance of tree-flowering dates in response to urban climate change. *Agricultural and Forest Meteorology* 138, 120–131.
- Luck, M., Wu, J.G., 2002. A gradient analysis of urban landscape pattern: a case study from the Phoenix metropolitan region, Arizona, USA. *Landscape Ecology* 17, 327–339.
- Luo, Z.K., Sun, O.J., Ge, Q.S., Xu, W.T., Zheng, J.Y., 2007. Phenological responses of plants to climate change in an urban environment. *Ecological Research* 22, 507–514.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczka, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Pirinen, P., Remisova, V., Scheffinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Züst, A., 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12, 1969–1976.
- Miller-Rushing, A.J., Primack, R.B., Primack, D., Mukunda, S., 2006. Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany* 93, 1667–1674.
- Neil, K., Wu, J., 2006. Effects of urbanization on plant flowering phenology: A review. *Urban Ecosystems* 9, 243–257.
- Penuelas, J., Filella, I., Zhang, X.Y., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradas, J., 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist* 161, 837–846.
- Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J., Del Tredici, P., 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* 91, 1260–1264.
- Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16, 179–214.
- Shepherd, J.M., 2006. Evidence of urban-induced precipitation variability in arid climate regimes. *Journal of Arid Environments* 67, 607–628.
- Unger, J., 1999. Urban-rural air humidity differences in Szeged, Hungary. *International Journal of Climatology* 19, 1509–1515.
- Ziska, L.H., Gebhard, D.E., Frenz, D.A., Faulkner, S., Singer, B.D., Straka, J.G., 2003. Cities as harbingers of climate change: common ragweed, urbanization, and public health. *Journal of Allergy and Clinical Immunology* 111, 290–295.