

Effects of urbanization on plant flowering phenology: A review

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Abstract Studies of flowering and leafing phenology have dramatically increased during the last few decades because changes in plant phenology can be indicative of possible effects of climate change at multiple scales. This article reviews the available literature focusing on the effects of urbanization on flowering phenology. The literature of flowering phenology in urban environments suggests that spring-blooming plants in a variety of ecosystems in North America, Europe, and China tend to bloom earlier in the city than in the surrounding un-urbanized habitat. Moreover, ephemerals, early spring bloomers, and insect-pollinated plants in these environments tend to be more sensitive than perennials, mid- or late-spring bloomers, and wind-pollinated plants. Researchers attribute advanced flowering in urban environments to the Heat Island Effect. The potential ecological consequences of changes in flowering phenology in urbanized areas are not well understood or explicitly studied. However, studies in global biology have suggested that climate change may result in a series of important ecological consequences as well as human-related problems such as earlier and extended allergy seasons. More field-based studies are needed to elucidate this issue.

Keywords Urban ecology · Flowering phenology · Urban heat island · Ecosystem structure

Introduction

Urban climate conditions are considered similar to the changing global climate conditions; therefore, many researchers study urbanized areas as small-scale experiments, or models, of global climate change (Ziska et al., 2003). Studies of plant phenology, the seasonal timing of environment-mediated growth and reproduction events in plants and animals, and changes in phenology caused by urbanization will improve our understanding of intra- and inter-specific plant interactions and potential changes in their interactions in novel environments

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(Rathcke and Lacey, 1985; Mussey and Potter, 1997; Bishop and Schemske, 1998; Penuelas and Filella, 2001; Petit, 2001). Through studying these interactions in urban ecosystems, an opportunity is presented to test ecological theories (Pickett et al., 2001; Wu and David, 2002) related to coevolution, selective forces, community dynamics, population dynamics, and phenotypic plasticity. Indeed, the recent surge in phenological studies has occurred because phenology is a highly sensitive indicator that can be used to study the possible effects of climate change at multiple scales (Chuine et al., 2000; Schwartz and Reiter, 2000; Sparks and Menzel, 2002; Zhao and Schwartz, 2003; Penuelas et al., 2004; Williams and Abberton, 2004). Following phenological events also allows researchers to analyze net primary productivity (Schwartz et al., 2002; Badeck et al., 2004), energy and mass balance in the lower atmosphere (Schwartz and Chen, 2002; Kang et al., 2003), and multiscale plant dynamics (Schwartz and Chen, 2002).

Direct observations, remote sensing (via satellite), and modeling tools and techniques have been used to study plant phenology at regional scales. For example, onset of spring in Wisconsin (Zhao and Schwartz, 2003), China (Schwartz and Chen, 2002), the mid-latitudes of North America (Schwartz and Reiter, 2000), and Korea (Kang et al., 2003) have been studied using a combination of observation records, remote sensing, and modeling. However, Badeck et al. (2004) warns that direct ground observations and remote sensing data do not measure the same variables and researchers should consider this when they are using both data collection methods. These long-term studies indicate earlier green-up (start of seasonal photosynthesis) in high and mid latitude areas across the globe, although this is not a homogenous response (Penuelas and Filella, 2001; Sparks and Menzel, 2002; Walther et al., 2002; Schwartz, 2003; Badeck et al., 2004).

Selective forces acting on the timing of plant phenological events include abiotic and biotic elements, alone or in combination. Availability of light, nutrients, temperature, and moisture are key abiotic factors that may directly or indirectly limit the reproductive season of plants (Rathcke and Lacey, 1985). Biotic factors such as pollinators, pathogens, and herbivores are also recognized as potential selective forces on timing of flowering (Rathcke and Lacey, 1985; Brody, 1997).

Flowering phenology is often quantified by determining the time of onset and end of flowering, duration of flowering, skewness, and number of flowers produced (Augsburger, 1983; Rathcke and Lacey, 1985). Gene-environment interactions determine the timing of phenological events (e.g., new leaves of deciduous plants, flowers, and fruit). Events that break dormancy and initiate growth and reproductive development are called phenological triggers (Bowers and Dimmitt, 1994). Photoperiod, temperature, and soil moisture have been recognized as the main environmental triggers for leafing and flowering (Rathcke and Lacey, 1985); although many plants rely on multiple cues that may occur months apart or respond to different cues depending on the season (Yang and Abe, 1974; Rathcke and Lacey, 1985; Friedel et al., 1993; Bowers and Dimmitt, 1994). For example, some temperate forest plants require a chilling cue to begin biochemical reactions that will allow them to flower in response to the photoperiod cue several months later (Rathcke and Lacey, 1985). Bowers and Dimmitt (1994) found that several Sonora Desert perennials need both moisture and temperature cues to flower.

Photoperiod and temperature are regarded as the primary triggers of phenological events in many temperate forest, boreal, and Mediterranean plants. Unfortunately, temperature is often stated as the flowering trigger even though it is the interaction between temperature and photoperiod that is responsible for initiating flowering (Zhang et al., 2004). Moisture is thought to be the primary trigger for arid and semi-arid plants, but empirical studies have

shown that temperature and photoperiod also are important (Friedel et al., 1993; Bowers and Dimmitt, 1994; Abd El-Ghani, 1997).

The purpose of this paper is to synthesize the known spatiotemporal patterns of flowering in cities, the effects of urbanization on flowering phenology and potential consequences, and address unanswered questions and areas of research requiring further study, such as the mutual affects of landcover patterns of cities, spatiotemporal pattern of flowering within cities, ecological community structure and function within cities, and spatiotemporal pattern of flowering affect on human health and agriculture.

Patterns of flowering phenology in response to triggers

While there have been a number of recent studies of flowering and leafing phenology, the majority have focused on areas outside of urban ecosystems (Penuelas and Filella, 2001; Sparks and Menzel, 2002; Walther et al., 2002; Badeck et al., 2004). Nevertheless, field observations and remote sensing studies conducted across a range of habitats and in geographically widespread areas show an advancement of flowering phenology and greening (remote sensing used for the latter case only) anywhere from a few days to a couple of weeks in urban areas compared to the surrounding rural environment (Roetzer et al., 2000; Fitter and Fitter, 2002; White et al., 2002; Ziska et al., 2003; Zhang et al., 2004). These results are seen for both ephemerals and perennials; however, not all plants respond the same way. Early spring bloomers show more advancement than mid- or late-spring bloomers (Fitter and Fitter, 2002). In addition, animal-pollinated plants show more advancement than wind-pollinated plants (Fitter and Fitter, 2002). It is not clear from the current literature whether the same pattern exists in urban areas located in different biomes or ecosystem regions. There is also a paucity of information regarding the spatiotemporal pattern within cities. Existing studies only differentiate between urban and rural areas without looking at finer spatial or temporal (intra-annual) scales.

Historical temporal patterns

Phenological studies in urban areas of England, several central European countries, and Boston, Massachusetts, USA, demonstrate a historical trend of advanced timing of flowering over the last 50–100 years (Roetzer et al., 2000; Fitter and Fitter, 2002; Hepper, 2003; Primack et al., 2004). However, Hepper (2003) also reported that many garden plants at the Royal Botanical Gardens, England, demonstrated a delay or no change in flowering. The Royal Botanical Gardens is located within a large metropolitan area, about 10 km outside of London, near Richmond. Fitter and Fitter (2002) noted high variability in plant flowering time changes. For instance, many of their 385 plants did not show a significant change while only 3% of the 24% of the plants that flowered later were significant.

Both Fitter and Fitter (2002) and Roetzer et al. (2000) observed greater advances in the flowering time of some plants post 1980s and 1990s compared to earlier in the century. Roetzer et al. (2000) also observed a lack of difference in responses between urban and rural areas over time. Roetzer et al. (2000) stated the high variability may be a result of higher temperature trends in early spring and lower temperature trends in late spring as well as great spatial variability in flowering responses. A key issue is how much of the historical changes are attributable to global warming versus temperature changes associated with urbanization.

Spatial patterns

A clear difference in timing of flowering between urban and rural areas has been observed in the United States, Europe, and Asia (Roetzer et al., 2000; White et al., 2002; Ziska et al., 2003; Zhang et al., 2004). Zhang et al. (2004) used the moderate-resolution imaging spectroradiometer (MODIS) to study the timing of green-up and dormancy in the northern hemisphere (between 35°N and 70°N) in 2001. Their data show vegetation in large urban areas greening about 4–9 days earlier and going dormant about 2–16 days later than in the surrounding rural environment. This could imply a similar large-grain response in flowering. Using Advanced Very High Resolution Radiometer (AVHRR) data from 1990s, White et al. (2002) studied phenological differences in plant green-up between urban and rural areas in eastern United States broadleaf forests. They observed an expansion of the growing season of about 7.6 days in urban areas. Most of the expansion was due to an earlier start of the growing season and the rest was due to delayed dormancy. Not all areas showed the same trends; for instance, some areas showed a delay in green-up.

Ziska et al. (2003) studied ragweed (*Ambrosia artemisiifolia*) in Baltimore, Maryland, USA along an urban-rural gradient. Ragweed grew faster, flowered earlier, senesced earlier, and had greater above-ground biomass at the urban sites than at the rural sites, although the pollen allergenicity was greater at the rural sites. Flowering time of ragweed occurred earlier in the season the closer the plants were to the urban center. Roetzer et al. (2000) analyzed data for four spring blooming plants from 10 central European observation stations between 1951 and 1995. At almost all stations (except Zurich), the plants tended to bloom earlier in urban areas than in surrounding rural areas by about 2–4 days. However, not all differences were significant and there was great variability, part of which might be a result of observation stations not being in completely urbanized or completely rural areas.

Even though most of the above-mentioned studies demonstrate a difference between rural and urban areas, finer-scale spatial resolution patterns within cities are not completely clear. Will the same patterns be observed among cities? Also, the phenological studies indicate variability in flowering responses. Do different land cover/land use types affect flowering phenology differentially? Will this result in a multiscale pattern from local (neighborhood) to regional (whole cities or groups of cities) scales? For example, will there be differences between urban commercial, residential, xeriscaping, and mesicaping? This is particularly interesting when one considers cities not built in a concentric pattern. Will the urban-rural gradient pattern observed by Ziska et al. (2003) be observed in multi-nuclei, or polycentric and patchy, cities like Phoenix in which agriculture, residential, and commercial land cover are interspersed (Luck and Wu, 2002)?

Patterns by plant functional type

Several of the studies reviewed reported differences in plant responses based on plant functional type. Insect-pollinated plants tended to have greater advancement of flowering than wind-pollinated plants (Fitter and Fitter, 2002), annuals demonstrated greater advancement than perennials (Fitter and Fitter, 2002), and early spring bloomers showed greater advancement than mid- and late-spring bloomers (Fitter and Fitter, 2002; Hepper, 2003; Traidl-Hoffmann et al., 2003). Moreover, Zhang et al. (2004) observed that forest land cover is more sensitive (showed more advancement of green-up) than savanna land cover, which showed more advancement than grass land cover. United States urban areas tend to show more advancement than European or Asian urban areas. Thus, most studies suggest that

short-lived plants (with life history strategies that avoid environmental stresses) and plants reliant upon animals for reproductive success may be affected the most by urbanization-caused environmental change. This makes sense because these types of plants are known to be highly responsive to environmental variables. However, questions remain: Do self-fertile plants differ in response from obligate out-crossing plants? Do generalist pollinator plants differ in response from specialist pollinator plants? Are there general characteristics that define the types of plants blooming later vs. earlier? How are plants that flower in the summer, fall, or winter affected by urban climate conditions?

Causes of flowering phenological changes in urban environments

A mechanistic understanding of the causes and processes of changing flowering phenology in urban environments is severely lacking (Battey, 2000) although there have been an increasing number of studies on flowering phenology in cities (Table 1). In the following section, we summarize the major factors believed to cause changes in plant flowering phenology.

Temperature

All the studies of flowering phenology in cities attributed the advancement in flowering to the urban heat island effect. Zhang et al. (2004) stated different land cover types in their study demonstrated differential responses to temperature as a phenological trigger: forest land cover type being the most sensitive and grassland cover type the least sensitive. Zhang et al. (2004) also attributed the difference in advancement between United States urban areas and European and Asian urban areas to higher urban temperatures: 1–3°C warmer in US cities compared to surrounding rural environments and about 0.8°C warmer in European and Asian cities compared to surrounding rural environments (Zhang et al., 2004). White et al. (2002) also hypothesized the delay in green-up in some regions was a result of higher winter temperatures, which might have delayed the fulfillment of chilling requirements.

Fitter and Fitter (2002) suggested that insect-pollinated plants and annuals are more sensitive to temperature than wind-pollinated plants or perennials as a result of life history strategies that depend heavily on temperature as a cue for phenological events. Ziska et al. (2003) reported a high correlation between temperature/CO₂ concentration and earlier flowering time, but did not separate temperature effects from CO₂ effects. Hepper (2003) attributed observed advancement in flowering to global warming, but urbanization is more likely to have played a role at the local scale since local landscape characteristics (e.g., pattern of built features, vegetation amount, etc.) strongly affect microclimatic conditions. Primack et al. (2004) reported a correlation between winter and spring temperatures and flowering phenology at the Arnold Arboretum of Boston, MA, USA. However, when they statistically controlled for temperature in multiple regression analysis, they still found earlier flowering suggesting an additional cause. Other variables Primack et al. (2004) hypothesized as causes for earlier flowering included changes in rainfall, humidity, land cover change at the arboretum affecting temperature (temperature was obtained from a weather station), and age and size of the plants. Because they followed specific plants over the years, it was possible that increases in size and aging could have affected flowering time. This would need to be addressed on a species by species basis.

It appears that increase in temperature is considered the primary cause of flowering advancement as global climate change studies and numerous laboratory experiments

Table 1 Cited literature explicitly addressing flowering phenology and green-up (leafing) in urban ecosystems

Reference	Studied	Location	Period	Findings
Blankenship et al., 1993	Easter lilies and the effects of long-term exposure to ethylene.	Greenhouse in North Carolina	1990–1991	Total bud initiation decreased, bud abortion increased, many flowers did not open completely, buds abnormally curved, flowered earlier, and senesced earlier.
Roetzer et al., 2000	Flowering time of four perennials	Europe	1951–1995	Advanced flowering in spring in urban areas compared to the surrounding rural areas by 2–4 days. Early spring bloomers were more variable but tended to be more sensitive to the heat island effect than mid- to late-spring bloomers.
Fitter and Fitter 2002	First flowering date of a set of 557 plant species	A single location in South-central England	1954–2000	385 species show an advancement of flowering (increasing more in the 1990s) and 10 species flowered later. High variability.
White et al., 2002	Green-up of urban deciduous broadleaf forests using AVHRR.	Eastern United States	1990–1999	Expansion of the growing season by ~7.8 days—most of it from an earlier start.
Ziska et al., 2003	The effects of urbanization on <i>Ambrosia artemisiifolia</i> along an urban-rural gradient	Baltimore, Maryland, USA	2000–2001	Higher CO ₂ concentrations/temperatures along an urban-rural gradient appear to significantly affect phenology (advancement), allergenicity (decrease), and pollen production (increase).
Traidl-Hoffman et al., 2003	Reviewed health literature on pollenosis.	Europe, North America	–	High spatial variability in responses of plants to climate change such as: premature start of the pollen season, earlier peaks, decrease in number of days with pollen count, and increased strength of the pollen season.
Cape 2003	Reviewed studies addressing the effects of VOCs on plants.	–	–	More long term, low dose studies (field and lab) need to be done since current research is incomplete.
Hepper 2003	First flowering dates of common perennial garden plants	Leeds and Richmond, Britain	1946–2002	Spring plants tend to bloom earlier and summer plants tend to bloom later.
Zhang et al., 2004	Leafing phenology (i.e., green-up and dormancy) using MODIS	Mid to high latitudes in the United States, Europe, Asia	2001	Green-up occurred 4–9 days earlier and dormancy 2–16 days later in urban areas than in adjacent natural areas. Suggested UHI correlation.
Primack et al., 2004	Peak flowering dates of indigenous and non-indigenous woody plants	Arnold Arboretum, Boston, Massachusetts	1885–2003	Plants showed advancement in flowering (peak) of about 8 days; flowering in 2003 (with winter temperature well below recent normal temps.) showed similar timing as seen in early 1900s.

demonstrate earlier flowering at higher temperatures. For example, Peñuelas and Filella (2001) showed that the advancements of phenological events were significantly correlated with temperature increase over the last 30 years. However, correlation cannot be equated to cause-effect relationship. Moisture, CO₂, volatile organic compounds (VOCs), photoperiod, humidity, and ultra-violet radiation may also cause changes in flowering phenology, although their importance is still controversial. Nevertheless, with accelerating urbanization expected in the future, it is likely that increasing temperature due to urban heat islands will continue to be an important cause for phenological changes. How much will urban temperatures change in the future? Will global warming magnify urban climate changes or mask them? Another interesting question yet to be explored is: Will plants continue to advance flowering time? Or will a threshold temperature be reached?

Moisture and humidity

Peñuelas et al. (2004) pointed out that many studies have ignored the potential role of soil moisture on flowering phenology even though rainfall is known to affect phenology in seasonal tropical forests, in dry regions, and even in some places with “good water supply” like Norway. While not conducted specifically in an urban area, the experimental field studies on plants in the Mediterranean conducted by Peñuelas et al. (2004) demonstrated a correlation between decreased moisture availability and delayed flowering. Spatial variation in precipitation across the landscape also can produce patchy flowering phenology in tropical areas (Rathcke and Lacey, 1985).

Humidity may affect flowering phenology of some plants, particularly as a secondary trigger (Pavon and Briones, 2001), although the mechanism is unclear. Primack et al. (2004) pointed out that soil moisture or humidity could have contributed to earlier flowering in their study. Urbanization can change humidity in an area either by increasing or decreasing surface water and/or number of plants (Adebayo, 1991; Lipfert et al., 1991; Chow, 1992; Unger, 1999; Jonsson, 2004). How strong is the effect of humidity on flowering phenology in urban areas as compared to temperature? Which plants are most sensitive to humidity changes? These are questions to be addressed in future studies.

Photoperiod

While photoperiod and photoperiod-temperature interactions are known to affect flowering phenology (Deen et al., 1998; Yan and Wallace, 1998; Borchert and Rivera, 2001; Rivera and Borchert, 2001; Franklin and Whitelam, 2004), no studies have been found that have examined how urbanization might modify day length (night length) perception by plants. Light pollution (from buildings and outdoor lighting) has been studied, but only in relation to impacts on animal life (e.g., Longcore and Rich, 2004), human health (e.g., Pauley, 2004), energy conservation (e.g., Osman et al., 2001), and stargazing (e.g., Crawford, 2001). Changes in the far red/red light ratio would be most likely to cause problems since those are the wavelengths plants use for photoperiod perception. Moreover, experimental studies demonstrate that circadian clocks and light perception interact to trigger flowering. If the circadian clock-light perception synchrony is disrupted by light (including artificial) at the wrong time, day/night perception may be disrupted (Yanovsky and Kay, 2003), which can retard growth and reproduction. Experimental (*in situ* and *ex situ*) studies are necessary to determine if and how ecological light pollution affects flowering phenology and plant life in general.

Other factors

Rusterholz and Erhardt (1998) studied the effects of increased CO₂ concentration on two legumes and two non-legumes in the context of predictions from global climate change models rather than changes caused by urbanization. The authors observed varied responses: no effect, advanced flowering, delayed flowering, and an increase in flower number. However, there is controversy over how higher CO₂ concentrations influence flowering phenology and if it is species-specific (Badeck et al., 2004): directly via affecting internal mechanisms or indirectly via increased vegetation mass, which produces more flowers. Higher CO₂ concentrations are also found in urban areas relative to non-urbanized areas (Idso et al., 2001; Day et al., 2002; Nasrallah et al., 2003) and may affect the flowering phenology of some plants.

Cape (2003) hypothesized that volatile organic compounds (VOCs) also affect flowering phenology. VOCs do not appear to affect flowering phenology; however, Cape (2003) counters that the studies usually only tested VOCs at high concentrations for less than two weeks. One of the exceptions was a study conducted with ethylene for a longer time period and with lower concentrations in which floret reduction was observed. Another experiment conducted for more than 100 days with Easter lilies demonstrated decreased total bud initiation, increased bud abortion, incomplete flower opening, abnormally curved buds, earlier flower, and earlier senescence at ethylene concentrations (≥ 0.5 microliters per liter of air) similar to those found in urban areas (Blankenship et al., 1993). Since exposure to long periods (relative to plant life) of low amounts of VOCs is more realistic than short durations of high concentrations for plants near roadsides, further experimental study is important. Chauhan et al. (2004) reported delayed flowering of *Cassia siamea* near heavily used roadsides compared to plants in a botanical garden. They attributed the difference to pollution given off by vehicles.

Another controversial potential influence on flower phenology is ultraviolet-B (UV-B) radiation. Concerns over ozone depletion and the resulting increase in UV radiation have spurred studies of the effects of UV radiation on plants. Studies on the effects of increased UV-B show increased flowering duration (Conner and Neumeier, 2002), delayed flowering time (Sampson and Cane, 1999), and delayed or no change in flowering phenology of crop plants (Kakani et al., 2003). In contrast to these studies is the effect of decreased UV-B exposure in urban areas due to pollution (e.g., Papayannis et al., 1998; Repapis et al., 1998). If UV-B radiation affects flowering phenology, how does decreased UV-B exposure affect flowering? Which kinds of plants have flowering phenologies affected by UV-B? Is reduction in UV-B exposure caused by pollution strong enough to affect flowering phenology? Do other urban environmental factors counteract any effects of UV-B? These questions still await answers.

Consequences of changes in flowering phenology

Most, if not all, existing studies of urbanization effects on flowering phenology are descriptive, and associated hypotheses have largely not been directly tested. Many of the potential consequences of phenological changes discussed below are based on studies of global climate changes. Their relevance here rests on the assumption that urbanization and global climate change are similar in ways of affecting plant phenology through increasing temperature accompanied by elevated CO₂. In the following, we discuss the consequences of phenological changes in terms of ecological patterns and processes, human health, and economic ramifications.

Ecological consequences

Changes in flowering phenology across an urban landscape have the potential to affect plant population dynamics. Early and late flowering have been correlated with decreased seed set (Rathcke and Lacey, 1985; Santandreu and Lloret, 1999). In addition, spatial isolation due to habitat fragmentation has been addressed by many researchers (e.g., Fischer et al., 2000; Aizen et al., 2002; Murren, 2002); however, temporal isolation has not. Even if plants were not isolated spatially, if plants across an urban landscape flower at times that do not overlap or have only a small amount of overlap then they can become reproductively isolated (Fitter and Fitter, 2002; Hendry and Day, 2005). Genetic variability may then be positively (e.g., keeping landscape and indigenous plants from interbreeding and local adaptation) or negatively (e.g., inbreeding depression) affected. This may not be a problem with non-indigenous plants that human entities do not want proliferating, but can be one for other non-indigenous plants or indigenous plants in which successful reproduction is desirable. On the other hand, since changes in flowering phenology are not the same for every plant, increased overlap in flowering time is also possible (Fitter and Fitter, 2002). Increased synchrony of flowering between different cultivars, subspecies, and species of the same genus may result in increased hybridization and, therefore, genetic variability. Again, this may be desirable or not because it may lead to out-breeding depression or prevent in-breeding depression.

The effects of urbanization on flowering phenology may become important at the community level. Affects on other plant species, pollinators, herbivores, secondary consumers, and pathogens due to changes in flowering phenology must be considered. Depending on the species involved, a change in flowering time and/or duration may create an asynchronous mismatch between pollinators and their flowers. This is more likely for plants and animals that have different environmental cues for development. For example, Kudo et al. (2004) observed that some ephemerals had a smaller seed set than others during a couple of unseasonably warm years. They hypothesized that the differences were caused by the type of pollinator. The ephemerals with lower seed sets tended to be bee pollinated whereas the ephemerals with relatively steady seed set tended to be pollinated by flies. Although all the ephemerals tended to flower earlier, bees may not have come out of hibernation earlier and the flies did not hibernate at all.

On the other hand, there is no guarantee that specialization will make a plant or its dependent pollinators more vulnerable. Wcislo and Cane (1996) found that even specialized bees will switch plants when their “normal” pollen source is unavailable—this benefits the bees and may have varied consequences for the plants they “normally” pollinate. Moreover, although pollinators and plants are considered important mutualists, the importance of specific species interactions on long-term survival is still controversial (e.g., Rathcke and Lacey, 1985). Are mutualistic relationships the result of opportunistic exploitation or strong co-evolutionary interactions? How we answer this question will influence how we interpret any potential changes in indigenous and non-indigenous animal-plant interactions.

Another example of community dynamics impacts is the European winter moth (*Operophtera brumata*), great tit nestlings (*Parus major*), and oak trees. *O. brumata* is not negatively affected by the earlier bud burst of the oak they feed on because they keep synchronous by hatching earlier. However, *P. major*, which eat *O. brumata*, do not hatch earlier (Walther et al., 2002). This results in the peak in food availability for the birds occurring too soon for the nestlings. As a further consequence, traditional population controls of *O. brumata* by *P. major* may become decoupled and result in unpredictable consequences for this community (Penuelas and Filella, 2001). Complex changes in herbivore and pathogen interactions with plants, and their management, may also occur (Hepper, 2003; Badeck et al., 2004).

Walther et al. (2002) also discussed consequences for long distance migratory birds relying on plants for food during and after migration. If birds obtain nectar and pollen from plants which flower earlier, then there may be less food available and increased interspecific and intraspecific competition.

Community changes may cause further changes in ecosystem functioning. Resource use and cycling by plants may change due to changes in plant resource needs for reproduction. Moreover, urbanization may modify community structure and the timing of pollen and nectar availability which may in turn cause further modification due to new interspecific interactions such as competition for resources like water, nutrients, and pollinators.

Generally, changes in interspecific plant interactions will be complex and somewhat unpredictable. For instance, competition for resources (biotic and abiotic) could increase if more plants are flowering earlier (Fitter and Fitter, 2002) because reproduction requires a lot of resources. Urbanization effects on flowering phenology may also result in unpredictable changes in ecosystem structure because species previously able to coexist due to niche differentiation may interact differently (Fitter and Fitter, 2002). Another potential community affect involves pollination facilitation. This controversial theory states that flower display of one plant may help attract pollinators to neighboring plants, facilitating greater pollination than would occur if the plant were alone—even at high densities. The pollination facilitation theory was introduced since plants are known to facilitate the growth of other plant species via microclimate amelioration (Rathcke and Lacey, 1985; Feldman et al., 2004). Only a few examples of this phenomenon are known, contributing to the controversy (Feldman et al., 2004). If pollination facilitation does occur and is important for some species, then changes in flowering phenology may be beneficial or detrimental depending on the specific species involved. Non-indigenous flora and fauna in urban centers add another level of complexity whose effects are not fully understood at this time. This area is ripe for further investigation—particularly with the abundance of non-indigenous plants prevalent in urban ecosystems.

Human health

The impact of changes in flowering phenology on human health has focused on pollen allergies, or pollinosis. Advancement in allergy seasons and their peaks (by 3–22 days), lengthening of allergy seasons, and increase in the severity of allergies have been reported world-wide (Van Vliet et al., 2002; Traidl-Hoffmann et al., 2003), and correlated with higher temperatures and possibly higher CO₂ concentrations. Van Vliet et al. (2002) also found that grasses have advanced flowering by fewer days than many trees and shrubs. This observation fits with other studies that report less of an effect on wind-pollinated plants. On the other hand, this seems contradictory to reports of earlier allergy seasons since the most widespread known offenders are wind-pollinated grass, ragweed, tree, and shrub species. The work by Ziska et al. (2003) is apparently one of the few *in situ* experiments to study allergenicity and phenology of an allergenic plant along an urban-rural gradient. More studies are needed to better understand how changes in flowering phenology are related to the different aspects of human allergies.

Economic ramifications

Economic impacts of changes in flowering phenology within urban centers have not been studied although those of general phenological changes have to some extent. A few studies examining global climate change and urban heat island effects on agriculture and other plant-based food production suggest important implications for agriculture and plant-based food

production within and/or close to urban centers. For instance, Baker et al. (2002) reported that in the Phoenix metropolitan area from 1997–2000 cotton was planted about 14 days earlier in agriculture fields within the city and city fringe areas than in agriculture fields outside the reach of the urban heat island footprint. This implies that plants close to the city flowered earlier than those outside of the city. Moreover, even though cotton can self-pollinate, more cotton is obtained when pollinators are present (Rhodes, 2002). The advancement in cotton planting may have implications for pollination by insects—especially bees—if the pollinating insects are not (as) available when the plants are blooming. If pollinators are not available, then there may be less yield. On the other hand, if the pollinating insects are developing quicker due to increased heat exposure, then there may not be significant differences. In addition, changes in flowering phenology may impact the quality and quantity of chemical substance extracted from plants (Badeck et al., 2004).

Liu et al. (2004) hypothesized that a reduction in honey production in China in the 1990s may have resulted from warmer temperatures during that decade. Cape (2003) also discusses the potential impacts of VOCs on agriculture—specifically on plants grown for their flowers. The economic costs of increased allergy problems should also be considered. Finally, changing flowering phenology could also have implications for gardeners and landscapers. Hepper (2003) reported earlier flowering of common garden perennials in Britain. Successful plantings from seeds or from started stock from stores and planned landscaping effects (from flower displays) may change due to urbanization effects on microclimate.

Discussion and conclusions

Several important patterns have emerged from this review of urbanization and flowering phenology (Table 1 and Fig. 1). First, there is a general trend towards earlier spring-time flowering in urbanized areas compared to surrounding rural areas; although, many plants also show delayed flowering or no significant change in flowering. Second, some types of plants appear to be affected more strongly by urbanization than others; specifically, insect-pollinated plants, early-spring bloomers, annuals, and non-woody plants. Third, temperature appears to be the most frequently cited cause for changes in flowering phenology.

From this review, we can identify several knowledge gaps that need to be addressed by the following research questions. First, will we see earlier flowering in urbanized areas in tropical, arid, or semi-arid ecosystems? The existing studies have focused only on temperate forest, Mediterranean, and boreal ecosystems which all have a single distinct growing season. Will plants in urban areas in aseasonal tropical forest ecosystems, desert ecosystems, or seasons delineated by moisture (e.g., wet/dry) show similar phenological affects?

Second, which kind of plants do not show changes phenological changes related to urbanization and why? Is it because of photoperiod or interactions between phenological triggers that “cancel” changes in each other? How will plants dominated by moisture or moisture-temperature phenological triggers be affected by urbanization? Does ecological light pollution affect plants dominated by photoperiod triggers?

Third, what is the fine-scale spatial pattern of flowering phenology in cities? Does the spatiotemporal pattern of flowering change within a city? Are changes in the timing of plant flowering consistent along an urban-rural gradient? Or, will plants show spatial or temporal patchiness in flowering across the urban landscape within a city? Researchers have studied flowering patterns in rural ecosystems to decipher resource use by plants, resource use by animals, ecosystem structure, niche differentiation, and evolution (e.g., Gentry, 1974; Pávon and Briones, 2001; Lobo et al., 2003). This work should also be done for different urban

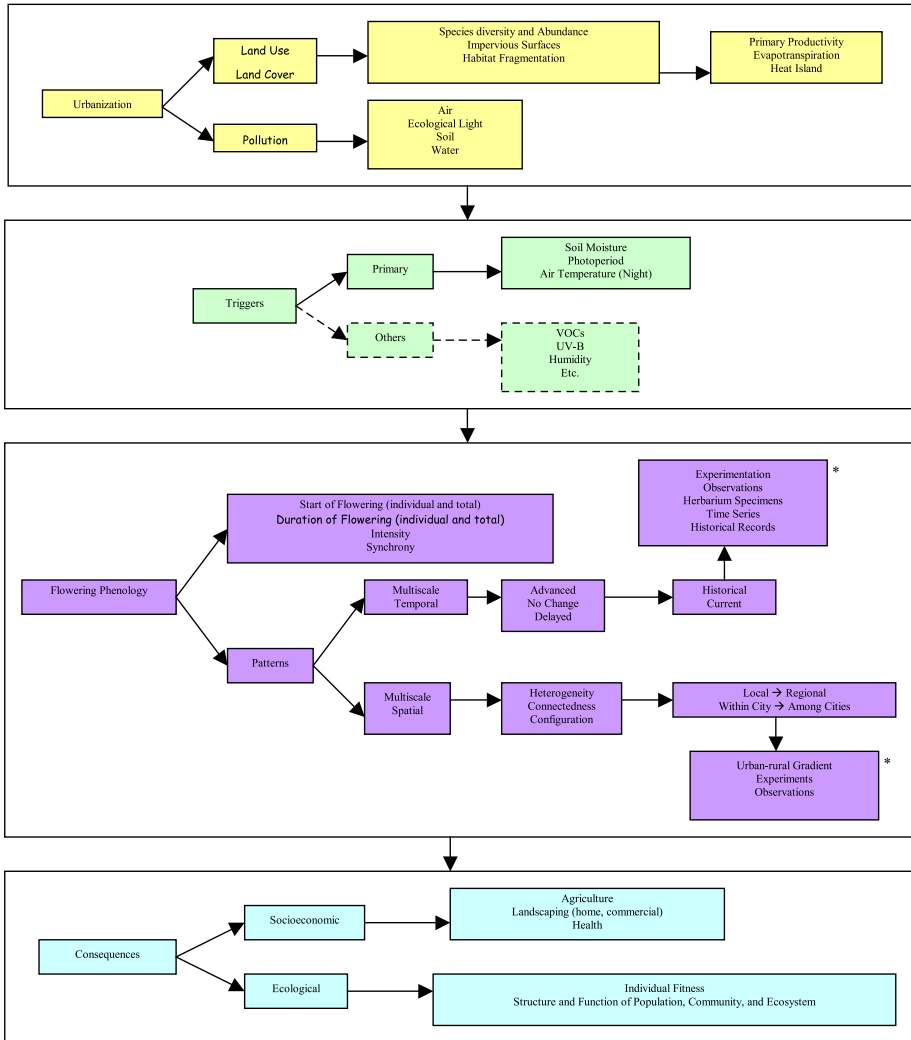


Fig. 1 Diagram summarizing urbanization factor that can affect phenological triggers and the resulting potential effect. Dashed lines indicate weak or controversial triggers of flowering. * Method of study

ecosystems. Moreover, these kinds of studies will reveal more about how socioeconomic factors, such as land cover type and land use affect flowering phenology and, therefore, interspecific and intraspecific interactions. For instance, are plants of the same species becoming more or less reproductively isolated? Is there more or less competition for resources for reproduction? Is there higher phenotypic plasticity in flowering phenology in urban ecosystems?

Lastly, how do non-indigenous species affect urban ecosystem structure and function? Non-indigenous species (flora and fauna) are a fact for urban ecosystems. Are non-indigenous plants flowering at the same times as the indigenous plants? Do they provide pollen and nectar for indigenous animals, non-indigenous animals, or both? Do they out-compete indigenous plants by taking pollinators away? Are non-indigenous plants, or cultivars, hybridizing with indigenous plants?

Understanding the causes, mechanisms, and consequences of changes in flowering phenology in urban environment has a number of important ecological and economic implications. It is time that we move beyond descriptive studies that show differences in phenology between urban areas and surrounding rural environments. We now need to focus more on mechanistic studies that address what, how, and why plants are affected and what are the ecological and environmental consequences of these effects. To achieve this goal, a spatially explicit framework based on landscape ecology (Turner et al., 2001; Wu and Hobbs, 2002) should be used that integrates spatial patterns of flowering phenology and environmental factors with various causes and consequences of phenological changes on multiple scales. While the potential is yet to be explored for studying flowering phenology, such a landscape ecological approach has been quite successful in a variety of ecological studies, including a number of urban ecological examples (e.g., Pickett et al., 2001; Luck and Wu, 2002; Wu and David, 2002). While remote sensing is helpful in many ways, most of these questions have to be addressed by direct observation or experimentation in the field.

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