THE FLOWERING RESPONSE OF GREATER PHILADELPHIA NATIVE PIEDMONT PLANTS TO LONG TERM CLIMATE CHANGE

by

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ABSTRACT

There is growing evidence that many plant species are flowering earlier in recent years and that climate change is a contributing factor. These studies have predominantly used field observations as their data source while an increasing number of reports are utilising herbarium specimens. The current research uniquely combined different data sources in the form of herbarium specimens, field observations and dated photographic images to study plant species response to rising temperatures. An analysis of 28 Greater Philadelphia species, native to Pennsylvania and Delaware Piedmont, and 2539 flowering records from 1840 to 2010 indicated that plants are responding to rising minimum monthly temperatures. On average, these species are flowering 16 days earlier over this 170 year period and 2.7 days earlier per °C rise in monthly minimum temperature. Monthly minimum temperatures one or two months prior to flowering correlate with flowering time most significantly. Short flowering plants and woody plants are better indicators of climate change. Phenological studies across areas of at least 80 km in radius produce significant results. Individuals, public gardens and institutions holding historic botanical data can play an important role in topical research such as climate change.

Chapter 1

INTRODUCTION

Globally, the average surface temperature of the world has risen by 0.74˚C in the last 100 years, with the rate of increase doubling in the last 50 years to 0.13˚C per decade (Trenberth et al., 2007). Climate change is believed to have altered the timing of such phenological events as flowering time in plants (Fitter et al., 1995; Bradley et al., 1999; Ledneva et al., 2004; Hawkins et al., 2008). Plant species may respond to this changing climate by adapting, migrating or becoming extinct (Hawkins et al., 2008). Predictive models indicate that temperatures will rise by as much as 2.4 to 6.4˚C in the next 100 years (Trenberth et al., 2007) thus, with the rate of climate change increasing, the risk of extinction increases because species may not be able to adapt rapidly enough (Hawkins et al., 2008).

The interdependent relationships amongst plants, insects, birds and animals is being altered by an uneven response to climate change (Fitter et al., 1995; Bradley et al., 1999; Hawkins et al., 2008; Kudo et al., 2008). The change in these interdependent relationships may potentially alter the ecological community structure (Fitter et al., 1995; Bradley et al., 1999; Chapin et al., 2002; Hawkins et al., 2008;

MacGillivray et al., 2010). Unique ecological communities on mountain tops or islands are particularly at risk as they could ultimately be eliminated as the environment necessary for these communities to exist disappears (Hawkins et al., 2008; Inouye, 2008; Gallagher et al., 2009). The warming trend is likely to favour non-native species (Abu-Asab et al., 2001; Willis et al., 2010), further precipitating ecological imbalance. The impacts of such ecological relational changes could be far reaching, affecting both agriculture and the environment (Hawkins et al., 2008).

Phenology is defined as the study of the timing of an organism's periodic events or phenophases and is invariably stimulated by the yearly periodicity of the climate (Chapin et al., 2002; Hudson and Keatley, 2010). Flowering time of plants can be a good indicator of climate variations, as many plants have a sudden, mostly temperature-dependent start and finish to flowering (Primack, 2003; Hawkins et al., 2008; Hudson and Keatley, 2010). For successful cross-pollination, flowering time for a species' population must be synchronised (Aniśko, 2008; Hawkins et al., 2008; Kudo et al., 2008). This, together with short flowering duration for many species, aids in the assessment of climate induced changes in the timing of flowering (Primack, 2003; Primack et al., 2004; Miller-Rushing et al., 2006; Primack et al., 2007; Hudson and Keatley, 2010).

Historical records of phenological events, such as botanists' field observations, dated photographs and herbarium specimens, have emerging value in

climate change research. Herbarium specimens and dated photographs are most frequently taken when species are in full flower, providing a good historical record of the assumed peak flowering time (Primack, 2003; Primack et al., 2004; MacGillivray et al., 2010). Amateur naturalists' and botanists field observations often include first flowering, providing invaluable historical records of phenological events that can be used in the analysis of climate change and related ecological impacts (Miller-Rushing and Primack, 2008; MacGillivray et al., 2010). Miller-Rushing et al. (2008) reported peak flowering is less variable than first flowering date and hence provides a more accurate assessments of the impact of climate change.

Winter and early season temperatures are rising more rapidly than summer and late season temperatures while night time temperatures are increasing faster than day time temperatures (Hawkins et al., 2008; Knight, 2010; Leathers, 2010; Neil et al., 2010). Hence, studying spring flowering plants response to minimum temperatures will likely result in a more detectable and significant response than summer flowering plants response (Fitter et al., 1995; Abu-Asab et al., 2001).

The vast majority of phenology studies related to climate change use data from post Second World War (Fitter et al., 1995; Abu-Asab et al., 2001; Cayan et al., 2001; Chmielewski and Rötzer, 2001; Menzel et al., 2001; Wolfe et al., 2005; Menzel et al., 2006). While scant, some studies use data back to the early 1900s and even into the depths of the 1800s (Sparks et al., 2000; Primack et al., 2004; Miller-Rushing and

Primack, 2008; Robbirt et al., 2010). Short term phenological studies may obscure long term trends (Hudson and Keatley, 2010; Robbirt et al., 2010), hence the ability to analyse phenological data over a long period may realise more substantial results. From the 1850s onwards, there is suitable temperature data for climate change studies (Pethica, 2010), facilitating phenological research back to this era. Furthermore many North American studies that relate phenology to climate change have focused on non-native species (Schwartz, 1994; Cayan et al., 2001; Primack et al., 2004; Wolfe et al., 2005; Lavoie and Lachance, 2006; Miller-Rushing et al., 2006). Studying the phenological response of native species may add a different perspective and more insight into the impact of climate change in North America.

The Philadelphia region has a long and rich history of botanical study and documentation, with herbarium specimen and field observation records dating back to the 1680s. The depth and breadth of these records, combined with a focus on native plants, may provide new insight into the impact of climate change on plant phenology. In addition, Philadelphia has not been treated before in climate change research and, with the substantial amount of data available in the region, provides an opportunity to determine if the methods employed by other research are applicable to Philadelphia.

The objectives of this thesis are to assess the impact of climate change on flowering time of spring flowering plants native to the Piedmont region surrounding Philadelphia. The research goal is to compare, substantiate and expand on the

evidence and methodologies of comparable phenological studies. Other factors that may affect the responsiveness of plant species to climate change are also assessed. The research employs the novel approach of combining field observations, herbarium specimens and photograph data dating back to the 1840s and from a wide geographical area to study the phenological response to climate change.

Chapter 2

LITERATURE SURVEY

Plant Phenological Response to Climate Change

Worldwide, there is growing evidence that some plant species are flowering earlier in more recent years and that rising temperatures are a contributing factor. Plant species in Eastern North America are flowering from 0.5 to 2.8 days per decade earlier (Bradley et al., 1999; Abu-Asab et al., 2001; Ledneva et al., 2004; Primack et al., 2004; Wolfe et al., 2005; Lavoie and Lachance, 2006; Miller-Rushing et al., 2006; Miller-Rushing and Primack, 2008) and 0.5 to 4.2 days per °C earlier (Abu-Asab et al., 2001; Ledneva et al., 2004; Primack et al., 2004; Miller-Rushing et al., 2006; Miller-Rushing and Primack, 2008) while those in Western United States are experiencing greater advances of two to eight days per decade earlier (Cayan et al., 2001; Neil et al., 2010). There are similar findings in Europe, where plants are flowering from 1.0 to 2.5 days per decade earlier (Menzel, 2000; Chmielewski and Rötzer, 2001; Menzel et al., 2001; Menzel et al., 2006) and two to ten days per °C earlier (Fitter et al., 1995; Sparks et al., 2000; Chmielewski and Rötzer, 2001; Menzel

et al., 2006; Robbirt et al., 2010). Australian plants are showing the greatest change, flowering from 3.1 to 8.1 days per decade earlier and four to twelve days per °C earlier (Gallagher et al., 2009; Rumpff et al., 2010).

Prevailing temperatures one or two months prior to flowering have the most influence on flowering time (Fitter et al., 1995; Cayan et al., 2001; Chmielewski and Rötzer, 2001; Primack et al., 2004; Menzel et al., 2006; Miller-Rushing and Primack, 2008; Robbirt et al., 2010). In England, February temperatures were important in determining flowering time (Fitter et al., 1995) while January, but not February, had significance in north-eastern United States (Miller-Rushing and Primack, 2008). Plants showed a stronger response to temperature in warmer European countries (Menzel et al., 2006). Urban heat islands are also having a greater impact on flowering times (Primack et al., 2004; Lavoie and Lachance, 2006; Neil et al., 2010).

The growing season, from leafing out to leaf fall, has lengthened by 3.5 days per decade (Menzel and Fabian, 1999; Chmielewski and Rötzer, 2001), 60% of this increase is due to advances in spring phenophases (Menzel, 2000). In addition, the spring phenological event changes were more significant and distinctive than the autumn phenological event changes (Menzel, 2000). Spring phenological events appear to be more affected by climate change (Bradley et al., 1999), with earlier flowering species showing greater responses (Fitter et al., 1995; Menzel et al., 2006;

Miller-Rushing and Primack, 2008; Neil et al., 2010). However, some phenophases are reported to be shorter with higher temperatures (Post et al., 2008) even though the overall growing season has lengthened.

Woody plants are more responsive to temperature than herbaceous species (Fitter et al., 1995; Miller-Rushing and Primack, 2008). Within defined areas, non-native species respond more to temperature change than native species (Abu-Asab et al., 2001; Miller-Rushing and Primack, 2008; Willis et al., 2010). Closely related species respond quite differently to temperature (Fitter et al., 1995; Miller-Rushing and Primack, 2008), however there is evidence of a phylogenetic pattern to climate change response (Willis et al., 2008) and phenological response linked to reproductive traits (Bolmgren and Lonnberg, 2005; Kudo et al., 2008).

Latitude, longitude and altitude all have a small, but significant, influence on phenophase timing (Menzel, 2000; Menzel et al., 2001; Robbirt et al., 2010). In Europe, the green wave (the progression of leafing out from south to north) advances 44 km per day south to north, 200 km per day west to east and 32 m per day with increased altitude (Chmielewski and Rötzer, 2001).

Sources of Phenological Data

The three principle sources for phenological research are field observations, herbarium specimens and photographs. The overwhelming majority of

research uses field observations from phenology networks or botanists' or amateur naturalists' field notes and diaries (Fitter et al., 1995; Bradley et al., 1999; Abu-Asab et al., 2001; Cayan et al., 2001; Chmielewski and Rötzer, 2001; Menzel et al., 2001; Ledneva et al., 2004; Wolfe et al., 2005; Menzel et al., 2006; Inouye, 2008; Miller-Rushing and Primack, 2008; Rumpff et al., 2010). However, an increasing number of studies use herbarium specimens (Primack et al., 2004; Bolmgren and Lonnberg, 2005; Lavoie and Lachance, 2006; Miller-Rushing et al., 2006; Gallagher et al., 2009; Neil et al., 2010; Robbirt et al., 2010; Rumpff et al., 2010). A few studies have used dated photographs (Miller-Rushing et al., 2006; MacGillivray et al., 2010) and only a small number have combined two data sources (Primack et al., 2004; Miller-Rushing et al., 2006; Robbirt et al., 2010; Rumpff et al., 2010).

Many museums and botanical gardens are now digitizing their herbarium collection records and making them available online. Lead players in the digitization of herbarium records in North America include New York Botanic Garden (NYBG, 2007) and Missouri Botanic Garden (Tropicos.org, 2010). Organisations are being established from the regional level (e.g. Consortium of North-eastern Herbaria (CNH, 2010)) to the global level (e.g. Global Biodiversity Information Facility (GBIF, 2010) to share the herbaria data online. These technological advancements enhance the accessibility and speed with which such data can be analysed for phenological studies (Gallagher et al., 2009).

Since the Second World War, phenological networks have been set up in many parts of the world and their data is now being used as a source for researching phenology and the impact of climate change (Koch, 2010). Those in the United States often focus on non-native species (Schwartz, 1994; Cayan et al., 2001; Wolfe et al., 2005), while European botanical gardens formed the International Phenology Network ((Institute of Crop Sciennce, Humboldt University of Berlin, 2010) to monitor both vegetative and flowering stages of cloned woody plants (Menzel, 2000; Chmielewski and Rötzer, 2001; van Vliet et al., 2003; Menzel et al., 2006). Meteorological organizations and societies have also set up phenological networks (Sparks et al., 2000; Menzel et al., 2001; Koch, 2010). With the recent revival of interest in phenology, the current interest in climate change and improved accessibility to electronic data gathering, a number of citizen science projects have been set up to monitor flowering times in the United States (Cornell University, 2009; Budburst, 2010) and Europe (Natuurkalender, 2010; WoodlandTrust, 2010). In South Africa, citizen science phenological projects have provided valuable data for conservation efforts (Donaldson, 2009). Communication and collaboration across phenological networks could lead to a unified global view of the phenological impact of climate change and hence drive related policy decisions (van Vliet et al., 2003).

Many institutions, such as botanical gardens, museums of natural history or universities, have herbarium collections that support research and other scholarly

activities. They collectively possess more than 140 million herbarium specimens that could be used for analysis of contemporary issues including climate change (Donaldson, 2009). Therefore, these institutions can contribute to the important study of climate change and its impact on the environment (Hawkins et al., 2008; BGCI, 2009; Donaldson, 2009; Primack and Miller-Rushing, 2009).

Phenological Data Analytical Approaches

Studies of phenological trends in relation to climate change are in their infancy, with a few studies undertaken in the 1990s (Beaubien and Johnson, 1994; Fitter et al., 1995; Bradley et al., 1999) and the majority documented from the 2000s onwards. Hence, methods of analysis are still being established and trialled (Hudson, 2010). Most studies have used linear regression techniques, however, use of a linear approach for non-linear climate phenomena is affected by start and duration of the data set; therefore non-linear approaches that identify change points are being researched (Hudson and Keatley, 2010; Hudson, 2010; MacGillivray et al., 2010). Use of non-linear Bayesian and Generalised Additive Model for Location, Scale and Shape (GAMLSS) models indicate there are change points to earlier phenological timing in the latter half of the twentieth century (MacGillivray et al., 2010). GAMLSS models have also indicated that some change points align with cyclic climatic events such as El Niño (MacGillivray et al., 2010).

The use of herbarium specimens to reconstruct flowering time has proven to be as statistically reliable as using field data (Primack et al., 2004; Bolmgren and Lonnberg, 2005; Miller-Rushing et al., 2006; Robbirt et al., 2010). Reliable results have also been obtained from the analysis of combined data sources, either herbarium and field observation data (Primack et al., 2004; Bolmgren and Lonnberg, 2005; Robbirt et al., 2010; Rumpff et al., 2010) or herbarium and photographic data (Miller-Rushing et al., 2006; MacGillivray et al., 2010). Studies that combine field observation, herbarium specimen and photographic or field observation and photographic data sources are either scarce or non-existant.

The original intent of herbarium specimens was not to aid in phenological studies. Thus, in order to obtain reliable data, stringent criteria are required for selecting specimens to include in a phenological study (Gallagher et al., 2009). Variations in phenological data can occur if the herbarium specimens are not collected at true peak flowering time (Primack et al., 2004), are collected by different people (Lavoie and Lachance, 2006; Miller-Rushing and Primack, 2008) or collected from different locations (Bolmgren and Lonnberg, 2005; Lavoie and Lachance, 2006). To minimize variations in the date of peak flowering, the use of plants with short flowering durations would therefore seem advisable; however the use of herbarium specimens of plants with either short or long flowering duration can provide reliable data on the phenological response to climate change (Primack et al., 2004).

Plant phenology is not truly a series of discrete events, rather a progression of developmental stages. This poses a challenge in defining a phenological event such as flowering and leafing out. Hence, guidelines need to be established to standardise phenological data and enable studies to be compared. (van Vliet et al., 2003; Hudson, 2010)

Phenology data is most often collected from a small area where the climatic conditions are similar, thus enabling easy comparison of phenological data and climate (Bolmgren and Lonnberg, 2005). Analysing phenology data collected from a variety of sites, however, is problematic (Bolmgren and Lonnberg, 2005). In Quebec, Canada, the use of the spacial distribution of snow cover disappearance has been used to normalise temperatures across a wide area in order to analyse the effect of climate change on the flowering time of plants collected from a wide area (Lavoie and Lachance, 2006). In Australia, where snow disappearance data was not available, gridded temperature data was used to normalise the temperature across a wide area (Gallagher et al., 2009).

An issue with nineteenth century herbarium specimens, particularly those prior to the 1880s, is that they often lack an exact collection date, resulting in their exclusion from the analyses (Gallagher et al., 2009; Robbirt et al., 2010). However, one unusual approach was to assume the collection date was the mid-point of the collection month given on the herbarium specimen (Rumpff et al., 2010).

When there have been insufficient data points to provide meaningful phenological time series data for a single species, several species' phenological data have been adjusted to form a normalised data set (Menzel et al., 2001; Miller-Rushing et al., 2006).

Field observations, herbarium specimens or photographs have been used in a number of different types of phenological studies: analysis of plant responses to climate change (Sparks et al., 2000; Abu-Asab et al., 2001; Chmielewski and Rötzer, 2001; Primack et al., 2004; Lavoie and Lachance, 2006; Miller-Rushing et al., 2006; Miller-Rushing and Primack, 2008; Robbirt et al., 2010), identification of climate change indicator species (Cayan et al., 2001; Gallagher et al., 2009; Rumpff et al., 2010), assessment of heat island effects (Neil et al., 2010), determination of which species show flowering time responses to temperature versus photoperiod (Fitter et al., 1995) and the study of the ecological effects of climate change (Bradley et al., 1999; Ledneva et al., 2004; Hawkins et al., 2008; Kudo et al., 2008).

Chapter 3

MATERIALS AND METHODS

Overall Research Approach

The research fell into four phases. The first phase identified the plant species to be studied. The second phase was a field study of the 2010 flowering time and duration of the selected species. The third phase determined the plant species' historical flowering times from field notes, herbarium specimens and dated images. The fourth phase was a quantitative statistical analysis of the data.

The study area was limited to the Greater Philadelphia Piedmont areas of Pennsylvania and Delaware counties within an approximately 80 km radius of the city Philadelphia, namely: Bucks, Chester, Delaware, Lancaster, Montgomery and Philadelphia, Pennsylvania and New Castle, Delaware. For New Castle County, Delaware only data from areas above or on the fall line (US Geological Survey, 2000) and considered Piedmont was included.

Terms and Definitions

Throughout this thesis the term "flowering day" defines the day on which a species was observed in flower and is expressed as the number of days from 1st January of the year in which the species was observed in flower. Where there was a range of dates on which the species was observed to be in flower at a particular location in a particular year, a calculated midpoint of the range was taken as the flowering day. If there was clear evidence of peak flowering, the peak flower date was recorded as the flowering day. The observation of a species in flower could coincide with the peak flower day or extremely close to that day, particularly for short-flowering species. However, since there was no way to conclusively prove this, the more general term flowering day was used instead.

Obvious peak flowering was defined as when there was significantly more flowers in one week than in any other week. Obvious start and finish to flowering was defined as when the population went from no flowers one week to a significant number of flowers the next week or vice versa.

The term "monthly minimum temperature" is the monthly average of the daily minimum temperature similarly the "monthly average temperature" is the monthly average of the daily average temperature.

Plant Species Selection

Twenty-eight species, native to the Greater Philadelphia Piedmont area were selected for the field study and the historic data collection phases (Table 3.1). *The Plants of Pennsylvania* (Rhoads and Block, 2007) was used as the reference for nomenclature and nativity of the selected species.

The first species selection criterion was herbarium specimen availability, as indicated by The Pennsylvania Flora Project's database (The Pennsylvania Flora Project, 2010) and *The Vascular Flora of Pennsylvania: Annotated Checklist and Atlas* (Rhoads and Klein, 1993). The second criterion was that the species selected have a short flowering time in order to minimise the variance in the flowering day. Where persistent petals or unclear differences between flower and fruit development make flowering day estimation difficult, a third criterion mandated that the selected species have an obvious, visible flower with a clearly observable start and finish to flowering. Since early season flowering species respond more to temperature rises, March to June flowering season species were selected. To investigate the evidence of a phylogenetic pattern to climate change response (Willis et al., 2008), species from a phylogenetically diverse range of families were selected. The remaining selection criteria were: including both woody and herbaceous species; only one species per genus and species observable at the primary field study site of Mt. Cuba Center.

The Plants of Pennsylvania (Rhoads and Block, 2007); Tim Block, Director of Botany, Morris Arboretum of the University of Pennsylvania; Rick Lewandowski, Director, Mt. Cuba Center and Richard Primack, Professor of Biology, Boston University were consulted regarding information relevant to the criteria.

Table 3.1. Native plant species selected for study within the Greater Philadelphia Piedmont area, representing an phylogenetically diverse range of families and a representative proportion of woody (13) and herbaceous (15) species.

Species	Common Name	Family	Habit
Amelanchier canadensis	Serviceberry	Rosaceae	woody
Asimina triloba	Pawpaw	Annonaceae	woody
Caltha palustris	Marsh Marigold	Ranunculaceae	herbaceous
Caulophyllum thalictroides	Blue Cohosh	Berberidaceae	herbaceous
Cercis canadensis	Redbud	Fabaceae	woody
Claytonia virginica	Spring-beauty	Portulacaceae	herbaceous
Cornus alternifolia	Pagoda Dogwood	Cornaceae	woody
Cypripedium acaule	Pink Lady's-slipper	Orchidaceae	herbaceous
Dicentra cucullaria	Dutchman's-breeches	Papaveraceae	herbaceous
Erythronium americanum	Yellow Trout-lily	Liliaceae	herbaceous
Kalmia latifolia	Mountain Laurel	Ericaceae	woody
Lindera benzoin	Spice Bush	Lauraceae	woody
Liriodendron tulipifera	Tuliptree	Magnoliaceae	woody
Magnolia virginiana	Sweetbay Magnolia	Magnoliaceae	woody
Maianthemum racemosum	False Solomon's-seal	Ruscaceae	herbaceous
Mertensia virginica	Virginia Bluebell	Boraginaceae	herbaceous
Panax trifolius	Dwarf Ginseng	Araliaceae	herbaceous
Podophyllum peltatum	Mayapple	Berberidaceae	herbaceous
Prunus serotina	Wild Black Cherry	Rosaceae	woody
Rhododendron periclymenoides	Pinxter-flower	Ericaceae	woody
Sanguinaria canadensis	Bloodroot	Papaveraceae	herbaceous
Saxifraga virginiensis	Early Saxifrage	Saxifragaceae	herbaceous
Staphylea trifolia	Bladdernut	Staphyleaceae	woody
Trillium cernuum	Nodding Trillium	Melanthiaceae	herbaceous
Triosteum aurantiacum	Wild-coffee	Caprifoliaceae	herbaceous
Uvularia sessilifolia	Bellwort	Colchicaceae	herbaceous
Vaccinium corymbosum	Highbush Blueberry	Ericaceae	woody
Viburnum acerifolium	Maple-leaved Viburnum	Adoxaceae	woody

Field Study

Two field study sites were used to record the 2010 flowering time and duration of the selected species. The primary field study site was the Mt. Cuba Center, New Castle County, Delaware (Mt. Cuba Center, 2011). The secondary field study site was the Natural Lands Trust's Crow's Nest Preserve, Chester County, Pennsylvania (Natural Lands Trust, 2011). Mt. Cuba Center is a public garden focusing on Piedmont native plant species and is located at the southernmost point of the study area. Crow's Nest Preserve is a managed natural area located towards the northern end of the study area. All 28 species were present at the Mt. Cuba Center, while 22 were present at Crow's Nest Preserve (Table 3.2).

The field study sites were visited weekly from 19th March 2010 to 24th June 2010 to record species flowering data. Observations at the sites included start, peak and finish date of flowering; obviousness of the start and end of flowering; the obviousness of peak flowering and whether it was sunny or cloudy. Each species was photographed weekly to record the developmental progress of the flowers. A herbarium voucher was taken for each species, except for *Cornus alternifolia*, *Cypripedium acaule*, *Magnolia virginiana*, *Trillium cernuum*, *Triosteum aurantiacum* and *Viburnum acerifolium* due to too small populations. The herbarium vouchers are held at the Longwood Gardens Herbarium (KEN) with duplicates held at the Claude E. Phillips Herbarium at Delaware State University (DOV).

Table 3.2. Mt. Cuba Center and Crow's Nest Preserve species population types.

Species	Mt. Cuba Population Type	Crow's Nest Population Type
Amelanchier canadensis	Planted (two specimens)	Planted (single specimen)
Asimina triloba	Planted (two specimens)	Planted (single specimen)
Caltha palustris	Planted	Wild
Caulophyllum thalictroides	Planted & wild	Not present
Cercis canadensis	Planted	Planted (two specimens)
Claytonia virginica	Planted	Wild
Cornus alternifolia	Planted (two specimens)	Planted (single specimen)
Cypripedium acaule	Planted (single specimen)	Wild
Dicentra cucullaria	Planted	Wild
Erythronium americanum	Planted	Wild
Kalmia latifolia	Planted & wild	Wild
Lindera benzoin	Planted & wild	Wild
Liriodendron tulipifera	Planted & wild	Wild
Magnolia virginiana	Planted (three specimens)	Not present
Maianthemum racemosum	Planted	Wild
Mertensia virginica	Planted & wild	Planted
Panax trifolius	Planted	Wild
Podophyllum peltatum	Planted & wild	Wild
Prunus serotina	Planted & wild	Wild
Rhododendron periclymenoides	Planted	Wild
Sanguinaria canadensis	Planted	Wild
Saxifraga virginiensis	Planted (two specimens)	Not present
Staphylea trifolia	Planted & wild	Not present
Trillium cernuum	Planted	Wild
Triosteum aurantiacum	Planted (two specimens)	Not present
Uvularia sessilifolia	Planted	Not present
Vaccinium corymbosum	Planted (two specimens)	Wild
Viburnum acerifolium	Planted & wild	Wild

Historic Data Collection

The principle source of historic flowering time data for each species was herbarium specimens. However, fewer herbarium specimens existed from the 1960s onwards so the herbarium data was supplemented with data from dated images and field notes. A total of 2581 data points were obtained for the 28 species, up to and including 2010 data. Of these, 63% were from herbarium specimens, 26% from field notes (including the field study observations) and 11% from dated images.

The distribution of data points across the counties included in the study was uneven (Figure 3.1). New Castle County, Delaware had the fewest data points but that was to be expected as only the very northernmost part of the county was included in the study. Bucks and Chester Counties, Pennsylvania had the most data points because the field study sites and some of the main data sources were from these counties (Bowman's Hill Wild Flower Preserve and Morris Arboretum from Bucks County and Crow's Nest Preserve, Longwood Gardens and West Chester University Herbarium from Chester County).

The distribution of data points over the years followed somewhat of a bi-modal distribution (Figure 3.2).

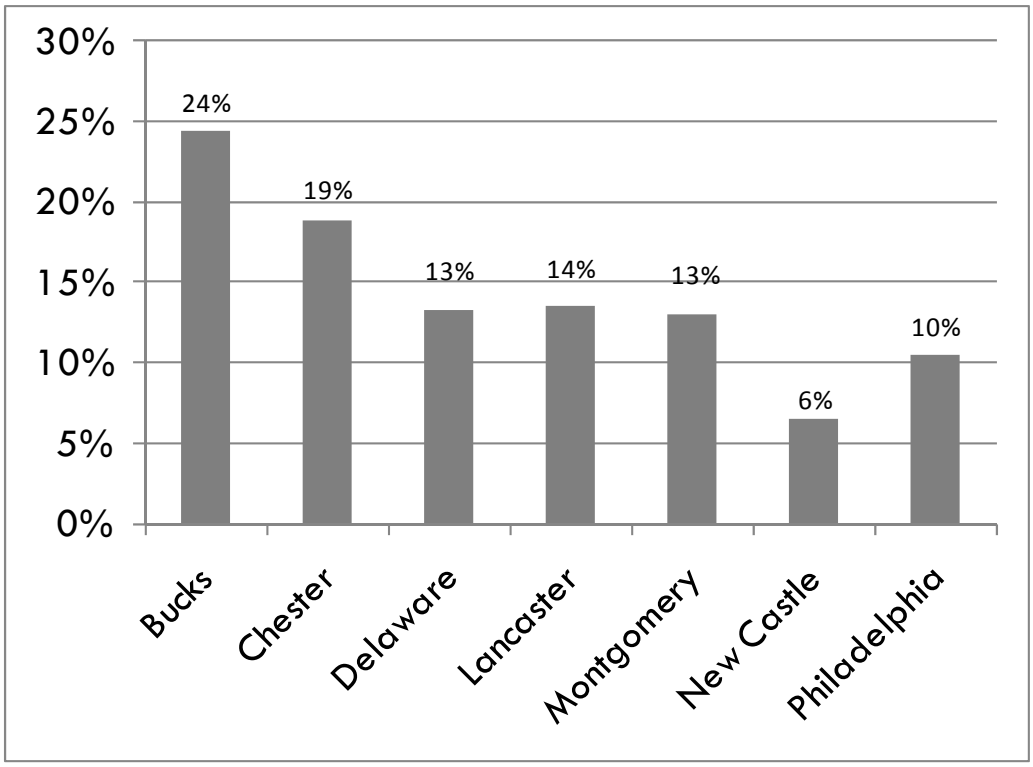

Figure 3.1. Distribution of field notes, herbarium specimen and image data points across counties included in the research.

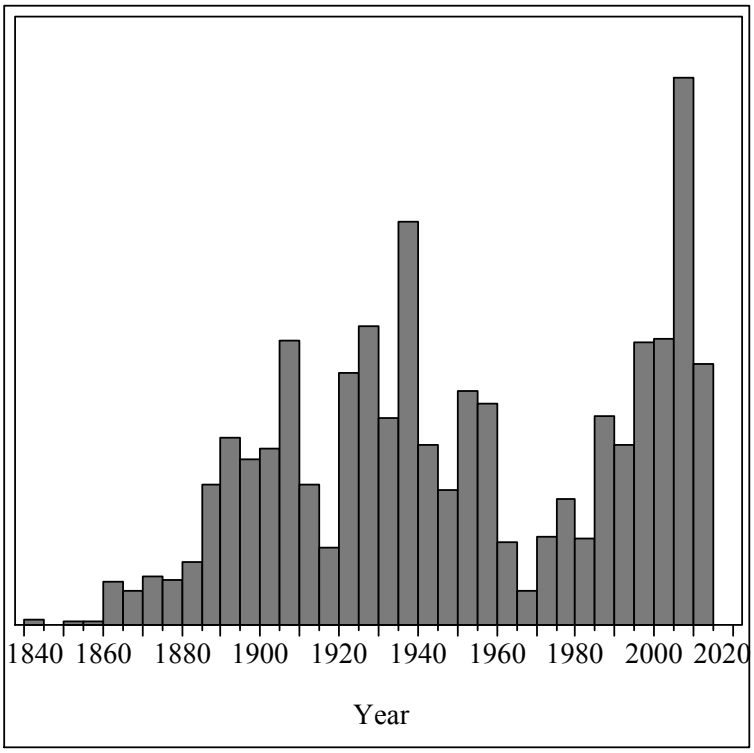

Figure 3.2. Distribution of field notes herbarium specimen and image data points over the years 1840-2010.

Herbarium Specimen Data Collection

The principle source of herbarium specimens was The Academy of Natural Sciences' Vascular Herbarium (PH) (The Academy of Natural Sciences, 2010) with other sources being the West Chester University's William Darlington Herbarium

(DWC) (West Chester University, 2010), Swarthmore College Herbarium (SWC) (Swarthmore College, 2010), Morris Arboretum Herbarium (MOAR) and Harvard University Herbaria (GH) (Harvard University Herbaria, 2011) (Appendix A).

For herbarium specimens in flower, the year, date, county, location, collector, collector number and accession number were recorded. Herbarium specimens not in flower or lacking the exact collection date or county information were excluded from the study. The majority of the herbarium specimens prior to the 1880s did not include the exact date and could therefore not be included in the study. Duplicate herbarium specimens were also excluded.

Image and Field Notes Data Collection

Herbarium specimens from The Academy of Natural Sciences' Vascular Herbarium were primarily from the 1880s to 1960s, hence dated images and field notes were sought from clubs, societies, list-servs, public garden organisations and natural area organisations (Appendix A).

For each image or field note indicating a species was in flower, the year, date of photo or field note, county, location and who provided the image or field note was recorded. When there was a series of photos from a single site over a series of weeks, the flowering day was considered the midpoint between the first and last date of the photo series. For data from Longwood Gardens (Longwood Gardens, 2010) and

Bowman's Hill Wild Flower Preserve (BHWP, 2011), the flowering day was calculated from the Longwood Garden's Plant Explorer and BG-Base phenology records and Bowman's Hill Wild Flower Preserve "What's in Bloom this Week" records by taking the midpoint between first recorded flowering date and last recorded flowering date.

Temperature Data

The 1895-2010 West Chester monthly minimum temperature was obtained from the National Oceanic and Atmospheric Administration's (NOAA) US Historical Climatology Network (HCN) website (Menne et al., 2010). West Chester was the only HCN site within the study area but is located approximately centrally in the study area. For the period from 1839-1894, the monthly minimum temperatures for West Chester were reconstructed using a methodology described by Leathers et al. (2008). A correlation equation for each month was determined by taking the 1895-1930 Philadelphia monthly minimum temperatures (Martin, 1933) and correlating it against the 1895-1930 West Chester monthly minimum temperatures. The resulting correlation equations (Table 3.3) were then applied to the 1839-1894 Philadelphia monthly minimum temperatures to calculate the estimated 1839-1894 West Chester monthly minimum temperatures.

Table 3.3. Correlation equation and R^2 ($P < 0.0001$*) for the regression of 1895-1930 West Chester monthly minimum temperature (y) with 1895-1930 Philadelphia monthly minimum temperature (x). All temperatures in °C.

Month	Correlation Equation	R^2
January	y = 1.0220x - 4.9886	0.88*
February	y = 0.9307x - 5.3891	0.90*
March	y = 1.0624x - 4.7354	0.88*
April	y = 1.0534x - 5.0004	0.72*
May	y = 1.0823x - 5.5405	0.64*
June	y = 0.8236x - 1.3594	0.74*

The West Chester monthly minimum temperature showed a significant trend towards warming temperatures from 1839-2010 (Table 3.4, Figure 3.3).

Table 3.4. Linear regression results showing change in West Chester monthly minimum temperature over the years 1840-2010.

Month	Regression Coefficient (°C/Year)	R^2	*P*
January	0.0109	0.04	0.0067*
February	0.0158	0.11	<0.0001*
March	0.0144	0.11	<0.0001*
April	0.0098	0.10	<0.0001*
May	0.0043	0.02	0.0668
June	0.0047	0.04	0.0081*

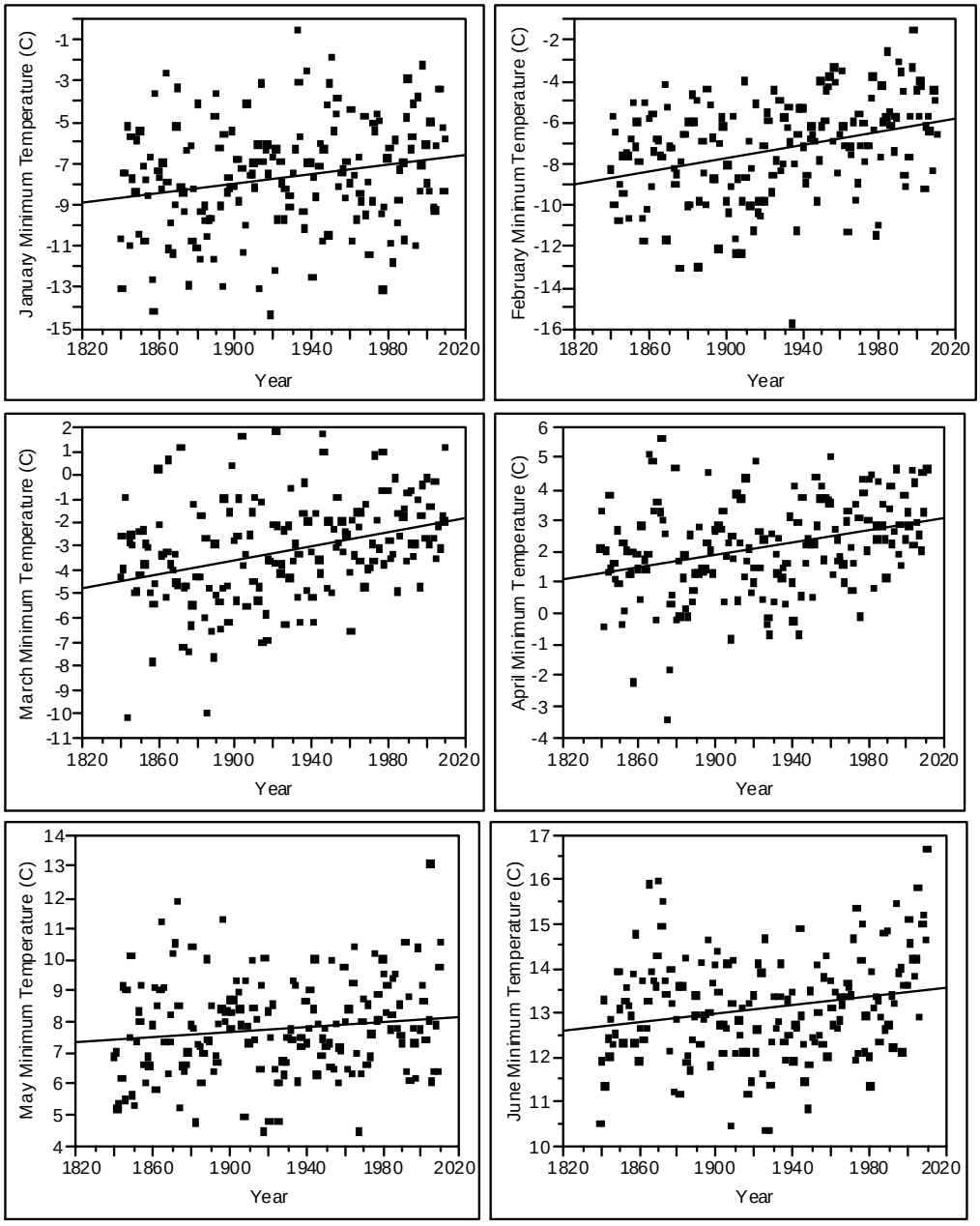

Figure 3.3. West Chester monthly minimum temperatures showing a significant trend towards higher temperatures over the years 1839-2010. The solid line represents the best fit linear regression. The correlation statistics are in Table 3.4.

Statistical Analysis

All statistical analysis was performed using Microsoft Excel and SAS Institute Inc. JMP, Cary, North Carolina software programs. Seventeen data points for years prior to 1839 were excluded as there were no monthly minimum temperature records available prior to 1839. Twenty-five data points were identified as outliers due to record-capturing errors and excluded from the statistical analysis. Hence a total of 2539 data points were used in the statistical analysis.

Individual Species Analysis

Based on the findings of the field study and the number of historic data points obtained for each species, a subset of the initial list of 28 species was selected for the individual species statistical analysis. The criteria used to select the species were:

- The length of flowering time of the species population (as observed at Mt. Cuba Center in 2010).
- The number of data points for the species.
- The obviousness of start, peak and finish of flowering of the species population (as observed at Mt. Cuba Center and Crow's Nest Preserve in 2010).

For ease of determining which species to include in the statistical analysis phase, the species were grouped into four categories:

1. Species with short flowering duration (three weeks or less), many data points (>110) and obvious start, peak and finish to flowering.

2. Species with very short flowering duration (two weeks or less), few data points (50-74) and obvious start, peak and finish to flowering.

3. Species with long flowering duration (>18 days) but many data points (75-200).

4. Species with long flowering duration (>18 days), few data points (<76) and/or indistinct start, peak and finish to flowering.

Twenty species, corresponding to categories 1, 2 and 3 were selected for individual species statistical analysis (Table 3.5). Species in category 4 were excluded from the individual species statistical analysis, as there was insufficient data and/or too much variance in the data due to indistinct start, peak and finish to flowering.

Table 3.5. Species Flowering Duration and number of Data Points. Category 1: ≤ three weeks flowering duration, ≥ 110 data points and obvious start, peak and finish to flowering. Category 2: ≤ two weeks flowering duration, 50-74 data points and obvious start, peak and finish to flowering. Category 3: ≥18 days flowering duration and 75 - 200 data points. Category 4: >18 days flowering duration, <76 data points and/or indistinct start, peak and finish to flowering.

Species	2010 Mt. Cuba Flowering Duration	Data Points	Category
Erythronium americanum	6	136	1
Sanguinaria canadensis	7	142	1
Dicentra cucullaria	12	146	1
Lindera benzoin	13	109	1
Podophyllum peltatum	21	135	1
Prunus serotina	6	64	2
Uvularia sessilifolia	6	56	2
Cornus alternifolia	6	53	2
Amelanchier canadensis	6	54	2
Liriodendron tulipifera	12	63	2
Vaccinium corymbosum	14	60	2
Viburnum acerifolium	19	79	3
Cercis canadensis	19	79	3
Panax trifolius	20	95	3
Staphylea trifolia	20	85	3
Rhododendron periclymenoides	27	144	3
Mertensia virginica	27	135	3
Trillium cernuum	33	103	3
Saxifraga virginiensis	34	180	3
Claytonia virginica	42	198	3
Maianthemum racemosum	19	72	4
Cypripedium acaule	19	68	4
Caltha palustris	19	55	4
Asimina triloba	20	52	4
Triosteum aurantiacum	23	28	4
Caulophyllum thalictroides	27	54	4
Magnolia virginiana	28	39	4
Kalmia latifolia	40	55	4

The following linear regression analysis was performed to analyse the statistical significance of trends towards earlier flowering of the 20 species.

- Bi-variant linear regression of the flowering day with year.
- Bi-variant linear regression of the flowering day with monthly minimum temperature for the months of January to June.
- Multi-linear regression of the flowering day with year and January to June monthly minimum temperatures.

Analysis of 28 Species Combined into a Single, Adjusted Dataset

To confirm the findings of the individual species analysis and to analyse the species for which there was insufficient data, a combined data set of all 28 species was analysed using an adjusted flowering day. The adjusted flowering day for each data point for all 28 species was calculated by adding the species adjustment factor (Table 3.6) to the flowering day of the data point. The species adjustment factor was calculated by subtracting the mean flowering days for the species from the mean flowering days for all 28 species (flowering day 129) (Table 3.6).

Table 3.6. Species Mean Flowering Day and the flowering day Adjustment Factor. The Adjustment Factor was added to the flowering day to obtain the adjusted flowering day used in the combined adjusted data set for the 28 species.

Species	Mean Flowering Day	Adjustment Factor
Amelanchier canadensis	112	17
Asimina triloba	130	-1
Caltha palustris	112	17
Caulophyllum thalictroides	122	7
Cercis canadensis	121	8
Claytonia virginica	115	14
Cornus alternifolia	144	-15
Cypripedium acaule	137	-8
Dicentra cucullaria	111	18
Erythronium americanum	112	17
Kalmia latifolia	157	-28
Lindera benzoin	103	26
Liriodendron tulipifera	149	-20
Magnolia virginiana	172	-43
Maianthemum racemosum	146	-17
Mertensia virginica	117	12
Panax trifolius	122	7
Podophyllum peltatum	131	-2
Prunus serotina	142	-13
Rhododendron periclymenoides	133	-4
Sanguinaria canadensis	106	23
Saxifraga virginiensis	116	13
Staphylea trifolia	130	-1
Trillium cernuum	131	-2
Triosteum aurantiacum	143	-14
Uvularia sessilifolia	124	5
Vaccinium corymbosum	128	1
Viburnum acerifolium	151	-22

The following linear regression analysis was performed on the combined dataset to analyse the statistical significance of trends towards earlier flowering.

- Bi-variant linear regression of adjusted flowering day with year.
- Bi-variant linear regression of the adjusted flowering day with monthly minimum temperature for January to June.
- Multi-linear regression of the adjusted flowering day with year and January to June monthly minimum temperatures.

Chapter 4

RESULTS

Field Study Observations

The 28 species were observed in flower at Mt. Cuba Center and Crow's Nest Preserve over the period of 26th March to 7th June 2010 (Table 4.1 and Table 4.2 respectively). The flowering day ranged from day 88 (29th March 2010) to day 161 (10th June 2010) and the days in flower ranged from six to 54 days (Table 4.1 and Table 4.2). There was significant correlation between the two sites for flowering day ($R^2 = 0.92$, $P < 0.001$) and the days in flower ($R^2 = 0.40$, $P = 0.0017$). The weekly photos provided excellent flower development documentation from flower bud to fruit, examples of which are given in the Appendix B.

Table 4.1. Dates when species were observed in flower at Mt. Cuba Center in 2010. The Days in Flower is the number of days from the first to last date the species was seen in flower. The Flowering Date is the peak flowering date, if apparent, or the midpoint between the first and last date the species was seen in flower. The Flowering Day is the flowering date in number of days from 1st January 2010.

Species	March 26th	April 1st	April 9th	April 16th	April 22nd	April 29th	May 7th	May 14th	May 20th	May 27th	June 7th	Days in Flower	Flowering Date	Flowering Day
Amelanchier canadensis												6	5-Apr	95
Asimina triloba												20	22-Apr	112
Caltha palustris												19	13-Apr	103
Caulophyllum thalictroides												27	19-Apr	109
Cercis canadensis												19	13-Apr	103
Claytonia virginica												42	22-Apr	112
Cornus alternifolia												6	3-May	123
Cypripedium acaule												19	7-May	127
Dicentra cucullaria												12	9-Apr	99
Erythronium americanum												6	9-Apr	99
Kalmia latifolia												40	27-May	147
Lindera benzoin												13	29-Mar	88
Liriodendron tulipifera												12	20-May	140
Magnolia virginiana												28	10-Jun	161
Maianthemum racemosum												19	14-May	134
Mertensia virginica												27	9-Apr	99
Panax trifolius												20	22-Apr	112
Podophyllum peltatum												21	29-Apr	119
Prunus serotina												6	7-May	127
Rhododendron periclymenoides												27	29-Apr	119
Sanguinaria canadensis												7	1-Apr	91
Saxifraga virginiensis												34	22-Apr	112
Staphylea trifolia												20	22-Apr	112
Trillium cernuum												33	22-Apr	112
Triosteum aurantiacum												23	20-May	140
Uvularia sessilifolia												6	9-Apr	99
Vaccinium corymbosum												14	25-Apr	115
Viburnum acerifolium												19	14-May	134

Table 4.2. Dates when species were observed in flower at Crow's Nest Preserve in 2010. The Days in Flower is the number of days from the first to last date the species was seen in flower. The Flowering Date is the peak flowering date, if apparent, or the midpoint between the first and last date the species was seen in flower. The Flowering Day is the flowering date in number of days from 1st January 2010.

Species	March 26th	April 1st	April 10th	April 16th	April 23rd	May 1st	May 7th	May 14th	May 20th	May 27th	June 7th	Days in Flower	Flowering Date	Flowering Day
Amelanchier canadensis			■									5	7-Apr	97
Asimina triloba				■	■	■	■	■	■			40	4-May	124
Caltha palustris			■	■	■							20	13-Apr	103
Cercis canadensis			■	■	■							23	13-Apr	103
Claytonia virginica	■	■	■	■	■	■	■	■				54	19-Apr	109
Cornus alternifolia							■	■	■			19	9-May	129
Cypripedium acaule					■	■	■	■				26	4-May	124
Dicentra cucullaria			■	■								12	10-Apr	100
Erythronium americanum			■									5	10-Apr	100
Kalmia latifolia									■	■	■	18	27-May	147
Lindera benzoin	■	■										14	29-Mar	88
Liriodendron tulipifera								■	■	■		23	20-May	140
Maianthemum racemosum							■	■	■			19	14-May	134
Mertensia virginica			■	■	■	■						26	16-Apr	106
Panax trifolius				■	■	■						19	23-Apr	113
Podophyllum peltatum						■	■					12	4-May	124
Prunus serotina						■						5	4-May	124
Rhododendron periclymenoides					■	■	■					20	1-May	121
Sanguinaria canadensis			■									20	1-Apr	91
Trillium cernuum					■	■	■	■				26	1-May	121
Vaccinium corymbosum			■	■	■	■						26	16-Apr	106
Viburnum acerifolium								■	■	■		23	20-May	140

There was variability in the flowering day or days in flower for some species at the two different field study sites but for the majority, the timing and/or duration were only a week different. There was no obvious pattern of one site always flowering earlier or longer. *Asimina triloba* started flowering at the same time at both sites but was in flower for six weeks at Crow's Nest yet for only three weeks at Mt. Cuba. *Claytonia virginica* started flowering one week earlier and finished one week later at Crow's Nest than at Mt. Cuba. *Cornus alternifolia* started flowering at the same time at both sites but finished flowering within a week at Mt. Cuba and continued flowering for two more weeks at Crow's Nest. The population of seven *Cyprepedium acaule* started flowering two weeks earlier at Crow's Nest and was in flower for four weeks while the two plants at Mt. Cuba were in flower for three weeks. *Kalmia latifolia* started flowering one week earlier at Mt. Cuba than at Crow's Nest yet finished flowering at the same time at both sites. *Liriodendron tulipifera* started flowering at the same time at both sites but stayed in flower for one week longer at Crow's Nest. *Podophyllum peltatum* started flowering one week earlier and flowered for three weeks at Mt. Cuba, while at Crow's Nest it flowered for two weeks. *Prunus serotina* flowered for less than a week at both sites but one week earlier at Crow's Nest than at Mt. Cuba. *Rhododendron periclymenoides* started flowering one week earlier at Mt. Cuba and flowered for four weeks, compared to three weeks at Crow's Nest. *Sanguinaria canadensis* started flowering one week earlier at Crow's Nest and

flowered for three weeks but flowered for just one week at Mt. Cuba. *Trillium cernuum* started flowering one week earlier at Mt. Cuba but finished flowering at the same time at both sites. *Vaccinium corymbosum* started flowering two weeks earlier and for four weeks at Crow's Nest while it flowered for just two weeks at Mt. Cuba. *Viburnum acerifolium* flowered for three weeks at both sites but started a week earlier at Mt. Cuba than at Crow's Nest. The remaining species, *Amelanchier canadensis*, *Caltha palustris*, *Cercis canadensis*, *Dicentra cucullaria*, *Erythronium americanum*, *Lindera benzoin*, *Maianthemum racemosum*, *Mertensia virginica* and *Panax trifolius*, flowered for the same length of time and in the same weeks at both sites.

Of the species studied at Mt. Cuba Center, the flowering time of the wild populations was approximately the same as for the planted populations. The start, peak and finish of the flowering time for both wild and planted populations were within the one week window of observation.

Many of the species had an obvious start, peak and finish to their flowering. *Amelanchier canadensis* had a very obvious flowering period. *Asimina triloba* did not have an obvious peak flowering or finish to flowering. *Caltha palustris* had an obvious start and finish to flowering and the peak flowering time was obvious. It was difficult to observe an obvious start, peak and finish to flowering for *Caulophyllum thalictroides*. *Cercis canadensis* had an obvious start and finish to flowering but peak flowering was less discernable. *Claytonia virginica* was in flower

for a long time and the peak and finish were not obvious. *Cornus alternifolia* had a sudden bloom with an obvious peak flowering. *Cypripedium acaule* did not have an obvious peak flowering. *Dicentra cucullaria* and *Erythronium americanum* both had an obvious flowering period. *Kalmia latifolia* buds were present and slowly enlarging for many weeks before flowering, however the peak flowering was obvious. *Lindera benzoin* had a very sudden start and finish to flowering; there was a yellow haze for two weeks, and then it was gone. It was difficult to observe when *Liriodendron tulipifera* was in bloom as the flowers were often high up in the canopy. Fallen or low branches were used for observations and was likely the approach taken for taking herbarium specimens, field notes or images. The flowering of *Magnolia virginiana* was sporadic with no obvious start, peak or finish to flowering. The start, peak and finish to flowering of *Maianthemum racemosum* was not very obvious. *Mertensia virginica* had a steady progression of flowers to seed pods along an individual raceme clearly indicating flowering progression. The *Panax trifolius* petals are very small and fragile, especially on the female flower, making it difficult to really know when it had finished flowering. *Podophyllum peltatum* had an obvious start and finish to flowering but no obvious peak flowering. *Prunus serotina* had a very obvious flowering period. *Rhododendron periclymenoides* had an obvious start, peak and finish to flowering. *Sanguinaria canadensis* had a very obvious peak flowering with just a few flowers flowering earlier or later than the one-week peak flowering period. *Saxifraga*

virginiensis had no obvious start, finish or peak flowering. The finish of flowering of *Trillium cernuum* was indistinct, as the flowers slowly faded and the petals turned brown. Flowering start, peak and finish of *Triosteum aurantiacum* was indistinct as flowering progressed up the stem from one leaf axle to the next. *Vaccinium corymbosum* did not have a particularly obvious start, peak or finish to flowering. *Viburnum acerifolium* had an obvious start, peak and finish to flowering.

Individual Species Analysis

Response of Species' Flowering Day to Year

Of the 20 species analysed, 19 showed a significant trend towards earlier flowering over the past 170 years (1840-2010) (Appendix C). These species are flowering from 0.43 to 1.69 days per decade earlier or 7.31 to 28.73 days earlier over the 170 year period studied (Table 3.4), with an average of 0.94 days per decade or 15.98 days earlier over the 170 year period. Nine of the 20 species are flowering more than one day per decade earlier ($R^2 = 0.12$ to 0.38, $P < 0.001$). *Claytonia virginica* and *Amelanchier canadensis* showed the greatest trend, with more than 1.5 days per decade earlier flowering ($R^2 = 0.13$, 0.32 respectively, $P < 0.0001$). The flowering day for *Liriodendron tulipifera*, *Amelanchier canadensis*, *Cercis canadensis* and *Mertensia virginica* had the strongest correlation with year ($R^2 = 0.26$ to 0.38,

P<0.0001). The correlation of flowering day with year was very low ($R^2 < 0.1$) for *Viburnum acerifolium*, *Staphylea trifolia, Rhododendron periclymenoides, Lindera benzoin* and *Trillium cernuum*. In addition, each of these five species is flowering fewer than 0.6 days per decade earlier and showed the least significant trends ($P < 0.05$). *Prunus serotina* was the only species that showed no significant trend towards earlier flowering.

Although *Amelanchier canadensis* was a very short flowering species and had a strong correlation of flowering day with year, this was not, however, the general trend as there was no significant correlation between days in flower (as observed at Mt. Cuba in 2010) (Table 4.1) and strength of correlation of flowering day with year (Table 4.3) for the 19 species.

Table 4.3. Linear regression results showing species' change in flowering day over the years 1840-2010.

Species	Regression Coefficient Days/Year	R^2	N	*P*
Claytonia virginica	-0.169	0.13	198	<0.0001
Amelanchier canadensis	-0.158	0.32	54	<0.0001
Liriodendron tulipifera	-0.137	0.38	63	<0.0001
Vaccinium corymbosum	-0.121	0.17	60	0.0010
Mertensia virginica	-0.116	0.26	135	<0.0001
Cercis canadensis	-0.115	0.26	79	<0.0001
Saxifraga virginiensis	-0.115	0.12	180	<0.0001
Dicentra cucullaria	-0.102	0.20	146	<0.0001
Uvularia sessilifolia	-0.101	0.18	56	0.0010
Sanguinaria canadensis	-0.093	0.14	142	<0.0001
Cornus alternifolia	-0.091	0.20	53	0.0008
Podophyllum peltatum	-0.084	0.21	135	<0.0001
Panax trifolius	-0.080	0.13	95	0.0002
Erythronium americanum	-0.064	0.11	136	<0.0001
Rhododendron periclymenoides	-0.059	0.05	144	0.0053
Staphylea trifolia	-0.052	0.07	85	0.0137
Lindera benzoin	-0.050	0.04	109	0.0292
Trillium cernuum	-0.044	0.04	103	0.0342
Viburnum acerifolium	-0.043	0.08	79	0.0141
Prunus serotina	Not significant		64	

Response of Species' Flowering Day to Monthly Minimum Temperature

All 20 species showed a significant trend towards earlier flowering with increased monthly minimum temperature (Table 4.4 -Table 4.8). The month or two months prior to flowering showed the highest correlation of flowering day to monthly minimum temperature and the greatest change in flowering day per °C rise in monthly minimum temperature. These 20 species are flowering from 0.67 to 4.49 days earlier per °C rise in monthly minimum temperature and an average of 2.7 days earlier per °C rise in monthly minimum temperature (for the month with highest correlation). The greatest correlation of flowering day with monthly minimum temperature (R^2 = 0.3 to 0.46, P<0.0001) was seen for *Amelanchier canadensis*, *Prunus serotina*, *Lindera benzoin*, *Vaccinium corymbosum* and *Cornus alternifolia*. The species that showed the largest rate of change (>3.5 days/°C, P < 0.0001) were *Vaccinium corymbosum*, *Claytonia virginica*, *Amelanchier canadensis*, *Cornus alternifolia* and *Liriodendron tulipifera*.

There was a significant inverse relationship between days in flower (as observed at Mt. Cuba in 2010) (Table 4.1) and correlation of flowering day with monthly minimum temperature (for the month with highest correlation) (Table 4.4 - Table 4.8) (R^2 = 0.375, P = 0.0041).

A student's t difference of means test showed that the correlation of flowering day with monthly minimum temperature (for the month with highest correlation) (Table 4.4 - Table 4.8) was significantly higher for woody plants than for herbaceous plants ($t = 2.1$, $P = 0.006$).

Table 4.4. Linear regression results showing species' significant change in flowering day with monthly minimum temperatures. The months for which the species was observed in flower from 1840 to 2010 is shown in parentheses.

Month	Regression Coefficient Days/°C	R^2	*P*
Amelanchier canadensis **(April, May)**			
January	-1.46	0.11	0.0165
February	-1.39	0.14	0.0046
March	-3.34	0.46	<0.0001
April	-3.84	0.28	<0.0001
May	-2.11	0.12	0.0104
Cercis canadensis **(April, May)**			
January	-0.89	0.06	0.0257
February	-1.34	0.13	0.0013
March	-2.59	0.27	<0.0001
April	-3.38	0.25	<0.0001
May	-1.61	0.08	0.0108
Claytonia virginica **(March, April, May)**			
January	-1.96	0.07	0.0003
February	-2.19	0.11	<0.0001
March	-2.28	0.07	0.0001
April	-4.37	0.14	<0.0001
May	-3.24	0.09	<0.0001
Cornus alternifolia **(May, June)**			
January	-1.19	0.09	0.0263
February	-1.08	0.08	0.0393
March	-1.92	0.22	0.0005
April	-3.36	0.30	<0.0001
May	-2.52	0.18	0.0017
June	-3.73	0.27	<0.0001

Table 4.5. Linear regression results showing species' significant change in flowering day with monthly minimum temperatures. The months for which the species was observed in flower from 1840 to 2010 is shown in parentheses.

Month	Regression Coefficient Days/°C	R^2	*P*
Dicentra cucullaria **(March, April, May)**			
January	-1.23	0.11	<0.0001
February	-1.26	0.10	<0.0001
March	-2.28	0.21	<0.0001
April	-3.21	0.22	<0.0001
May	-1.43	0.05	0.008
Erythronium americanum **(April, May)**			
January	Not significant		
February	Not significant		
March	-1.27	0.11	0.0001
April	-1.87	0.13	<0.0001
May	-0.97	0.04	0.0235
Lindera benzoin **(March, April)**			
January	Not significant		
February	-0.67	0.04	0.032
March	-2.77	0.36	<0.0001
April	-2.44	0.12	0.0002
May	Not significant		
Liriodendron tulipifera **(May, June)**			
January	Not significant		
February	Not significant		
March	-2.42	0.23	<0.0001
April	-3.61	0.22	<0.0001
May	Not significant		
June	-2.11	0.08	0.0234

Table 4.6. Linear regression results showing species' significant change in flowering day with monthly minimum temperatures. The months for which the species was observed in flower from 1840 to 2010 is shown in parentheses.

Month	Regression Coefficient Days/°C	R^2	*P*
***Mertensia virginica* (April, May)**			
January	-1.24	0.10	0.0002
February	-1.53	0.15	<0.0001
March	-2.56	0.24	<0.0001
April	-3.39	0.21	<0.0001
May	Not significant		
***Panax trifolius* (April, May)**			
January	Not significant		
February	-1.2	0.12	0.0006
March	-1.71	0.16	<0.0001
April	-2.4	0.15	<0.0001
May	Not significant		
***Podophyllum peltatum* (April, May)**			
January	Not significant		
February	-0.87	0.07	0.016
March	-1.77	0.21	<0.0001
April	-2.48	0.22	<0.0001
May	-1.3	0.08	0.001
***Prunus serotina* (May)**			
January	Not significant		
February	Not significant		
March	-1.79	0.27	<0.0001
April	-3	0.36	<0.0001
May	-2.27	0.20	0.0002

Table 4.7. Linear regression results showing species' significant change in flowering day with monthly minimum temperatures. The months for which the species was observed in flower from 1840 to 2010 is shown in parentheses.

Month	Regression Coefficient Days/°C	R^2	*P*
Rhododendron periclymenoides **(April, May)**			
January	Not significant		
February	Not significant		
March	-1.6	0.11	<0.0001
April	-2.95	0.19	<0.0001
May	-1.77	0.08	0.0007
Sanguinaria canadensis **(March, April, May)**			
January	Not significant		
February	-1.11	0.08	0.001
March	-2.62	0.24	<0.0001
April	-3.49	0.20	<0.0001
May	-1.52	0.04	0.0178
Saxifraga virginiensis **(April, May)**			
January	-0.84	0.03	0.0321
February	-0.9	0.03	0.0202
March	-1.87	0.10	<0.0001
April	-2.78	0.11	<0.0001
May	-1.28	0.02	0.0425
Staphylea trifolia **(April, May)**			
January	Not significant		
February	Not significant		
March	-1.6	0.18	<0.0001
April	-2.52	0.17	<0.0001
May	Not significant		

Table 4.8. Linear regression results showing species' significant change in flowering day with monthly minimum temperatures. The months for which the species was observed in flower from 1840 to 2010 is shown in parentheses.

Month	Regression Coefficient Days/°C	R^2	*P*
Trillium cernuum **(April, May)**			
January	Not significant		
February	Not significant		
March	-1.52	0.09	0.0021
April	-2.76	0.13	0.0002
May	-1.61	0.06	0.0174
Uvularia sessilifolia **(April, May)**			
January	Not significant		
February	Not significant		
March	-2.09	0.25	<0.0001
April	-2.1	0.09	0.0228
May	Not significant		
Vaccinium corymbosum **(April, May)**			
January	Not significant		
February	-1.31	0.08	0.0301
March	-2.94	0.35	<0.0001
April	-4.49	0.34	<0.0001
May	-2.6	0.15	0.022
Viburnum acerifolium **(May, June)**			
January	-0.9	0.12	0.0016
February	Not significant		
March	-1	0.09	0.0059
April	-1.84	0.14	0.0008
May	-2.01	0.20	<0.0001
June	-1.99	0.14	0.0008

Response of Species' Flowering Day to Year and the First Six Monthly Minimum Temperatures of the Year

Multiple linear regression models of the flowering day with year and with January to May monthly minimum temperatures indicated that more recent years and rising monthly minimum temperatures are influencing the earlier flowering of all 20 species (Table 4.9 and Table 4.10). The correlation for these multiple linear regression models is stronger than for either the correlation of flowering day with year or with monthly minimum temperature for the individual species. Therefore even though some of the terms in the model were not significant they were still contributing to the higher correlation. The temperature was the more significant factor and is driving the change to earlier flowering. The species that showed the strongest correlation were woody species and were the same species that showed the strongest correlation in the individual species analysis, namely *Prunus serotina*, *Amelanchier canadensis*, *Liriodendron tulipifera*, *Vaccinium corymbosum*, *Cercis canadensis*, *Cornus alternifolia* and *Lindera benzoin* ($R^2 = 0.4 – 0.58$, $P < 0.0001$). Where monthly minimum temperatures were significant, the month prior to flowering had the strongest influence on the model. In general, the results from the multi-linear regression models support and confirm the results of the bi-variant linear regression models.

There was a significant inverse relationship between duration of flowering in days (as observed at Mt. Cuba in 2010) (Table 4.1) and correlation of flowering day with year and January to May monthly minimum temperatures (Table 4.9 and Table 4.10) ($R^2 = 0.331$, $P = 0.008$).

A student's t difference of means test showed that the correlation with year and with January to May monthly minimum temperatures was significantly higher for woody plants than for herbaceous plants ($t = 2.1$, $P = 0.005$).

Table 4.9. Multiple-linear regression results showing species correlation and significant (* $P < 0.1$, ** $P < 0.01$, *** $P < 0.001$) and not significant change in flowering day over the years 1840-2010 and with January to May monthly minimum temperatures.

Species	R^2	Year Days/yr	January Days/°C	February Days/°C	March Days/°C	April Days/°C	May Days/°C
Prunus serotina	0.578***	0.025	-0.197	0.668*	-1.264**	-2.033***	-1.523**
		t=1.10	t=-0.76	t=2.26	t=-3.34	t=-3.57	t=-3.06
Amelanchier canadensis	0.555***	-0.063	-0.365	-0.027	-2.398***	-0.495	-0.540
		t=-1.54	t=-0.73	t=-0.06	t=-3.9	t=-0.51	t=-0.78
Liriodendron tulipifera	0.484***	-0.127***	0.526	0.624	-1.264	-1.330	0.868
		t=-4.74	t=1.17	t=1.71	t=-1.73	t=-1.31	t=1.09
Vaccinium corymbosum	0.467***	0.004	-0.029	-0.702	-1.899**	-1.831	-1.154
		t=0.11	t=-0.05	t=-1.27	t=-2.95	t=-1.65	t=-1.36
Cornus alternifolia	0.430***	-0.055	-0.399	0.638	-1.00	-1.567	-1.602*
		t=-1.64	t=-0.77	t=1.03	t=-0.619	t=-1.59	t=-2.12
Cercis canadensis	0.426***	-0.027	-0.440	-0.219	-1.712**	-1.755*	-0.096
		t=-0.95	t=-1.27	t=-0.50	-3.10	t=-2.17	t=-0.16
Lindera benzoin	0.407***	0.052*	-0.314	-0.089	-2.98***	-1.191	0.584
		t=2.12	t=-1.04	t=-0.31	t=-6.9	t=-1.81	t=1.12
Mertensia virginica	0.377***	-0.044*	-0.486	-0.306	-1.387**	-1.397*	0.210
		t=-2.01	t=-1.60	t=-0.89	t=-3.08	t=-2.02	t=0.44
Dicentra cucullaria	0.343***	-0.0326	-0.614*	-0.175	-1.128**	-1.52*	-0.013
		t=-1.58	t=-2.15	t=-0.55	t=-2.67	t=-2.44	t=-0.03
Podophyllum peltatum	0.330***	-0.042*	-0.096	-0.026	-0.713	-1.335**	-0.276
		t=-2.48	t=-0.42	t=-0.10	t=-1.92	t=-2.79	t=-0.74

Table 4.10. Multiple-linear regression results showing species correlation and significant (* $P < 0.1$, ** $P < 0.01$, *** $P < 0.001$) and not significant change in flowering day over the years 1840-2010 and with January to May monthly minimum temperatures.

Species	R^2	Year Days/yr	January Days/°C	February Days/°C	March Days/°C	April Days/°C	May Days/°C
Uvularia sessilifolia	0.328**	-0.063 t=-1.85	0.706 t=1.15	-0.574 t=-1.09	-1.379* t=-2.10	0.102 t=0.10	-1.322 t=-1.27
Sanguinaria canadensis	0.303***	-0.007 t=-0.31	-0.236 t=-0.68	-0.244 t=-0.73	-1.784*** t=-3.63	-1.703* t=-2.31	-0.321 t=-0.54
Viburnum acerifolium	0.303***	-0.027 t=-1.32	-0.363 t=-1.19	0.413 t=1.29	-0.501 t=-1.18	-0.430 t=-0.65	-1.472** t=-2.97
Panax trifolius	0.275***	-0.025 t=-0.93	0.601 t=1.67	-0.763* t=-2.02	-0.906 t=-1.86	-1.065 t=-1.53	-0.221 t=-0.42
Staphylea trifolia	0.273***	-0.008 t=-0.35	0.093 t=0.29	0.530 t=1.69	-1.210** t=-2.72	-2.100** t=-2.84	0.377 t=0.71
Claytonia virginica	0.261***	-0.063 t=-1.74	-0.943 t=-1.86	-1.248* t=-2.57	-0.210 t=-0.33	-1.941* t=-2.21	-1.939* t=-2.58
Rhododendron periclymenoides	0.230***	0.018 t=0.71	-0.363 t=-1.08	0.199 t=0.64	-1.009* t=-2.27	-2.371*** t=-3.61	-0.468 t=-0.85
Erythronium americanum	0.201***	-0.036 t=-1.77	-0.064 t=-0.23	0.372 t=1.46	-0.618 t=-1.54	-1.151* t=-2.42	-0.407 t=-1.00
Saxifraga virginiensis	0.184***	-0.063* t=-2.22	-0.363 t=-0.92	0.245 t=0.58	-0.997* t=-2.03	-1.420* t=-2.03	-0.318 t=-0.51
Trillium cernuum	0.172**	-0.001 t=-0.05	-0.183 t=-0.44	-0.308 t=-0.63	-0.671 t=-1.18	-1.755 t=-1.96	-0.904 t=-1.33

Comparison of Herbarium, Field Notes and Image Data Sets

Nine species had significant R^2 values and significant regression coefficients for the correlation of flowering day with April monthly minimum temperature for herbarium specimen data points versus field notes and images data points (Table 4.11). In comparing the R^2 values, the students t-test difference of means test showed the herbarium specimen R^2 was not significantly different from the field notes and image R^2 ($\alpha = 0.01$). This indicates that both herbarium and field notes and images can produce equally accurate results. In comparing the regression coefficient, the students t-test difference of means test showed there was a significant difference between the mean slope for herbarium specimens and the mean slope for field notes and images ($\alpha = 0.01$). This indicates that the rate of change (days/°C) is significantly greater for field notes and image. Since field notes and image data represents more recent years, this indicates that in more recent years the rate of change (days/°C) is greater.

Table 4.11. Species with significant R^2 and regression coefficient pairs for the linear regression of flowering day with April monthly minimum temperature for herbarium specimen data points verses field notes and image data points. For each species, h is the number of herbarium data points and f is the number of field notes and image data points.

Species	R^2 Herbarium	R^2 Field Notes and Images	Days/°C Herbarium	Days/°C Field Notes and Images
Cornus alternifolia (h=35, f=18)	0.16	0.51	-2.038	-7.940
Dicentra cucullaria (h=88, f=58)	0.13	0.11	-2.179	-2.999
Lindera benzoin (h=67, f=42)	0.07	0.22	-2.021	-3.812
Podophyllum peltatum (h=139, f=49)	0.10	0.16	-1.520	-3.087
Prunus serotina (h=58, f=6)	0.29	0.79	-2.728	-6.956
Rhododendron periclymenoides (h=91, f=53)	0.14	0.28	-2.778	-4.032
Sanguinaria canadensis (h=89, f=53)	0.12	0.11	-3.058	-2.786
Vaccinium corymbosum (h=43, f=17)	0.15	0.50	-2.900	-7.818
Viburnum acerifolium (h=56, f=23)	0.09	0.21	-1.315	-3.948

Analysis of 28 Species Combined into a Single, Adjusted Dataset

There was a significant trend to earlier flowering over the past 170 years (1840-2010) for the 28 species combined ($R^2 = 0.13$, $P < 0.0001$) (Figure 4.1). Using an adjusted flowering day to combine all 28 species into a single data set of 2539 data points, the linear regression analysis indicated that these species are flowering 0.89 days per decade earlier ($P < 0.0001$). This value is comparable to the average of 0.94 days per decade for the 20 species analysed individually.

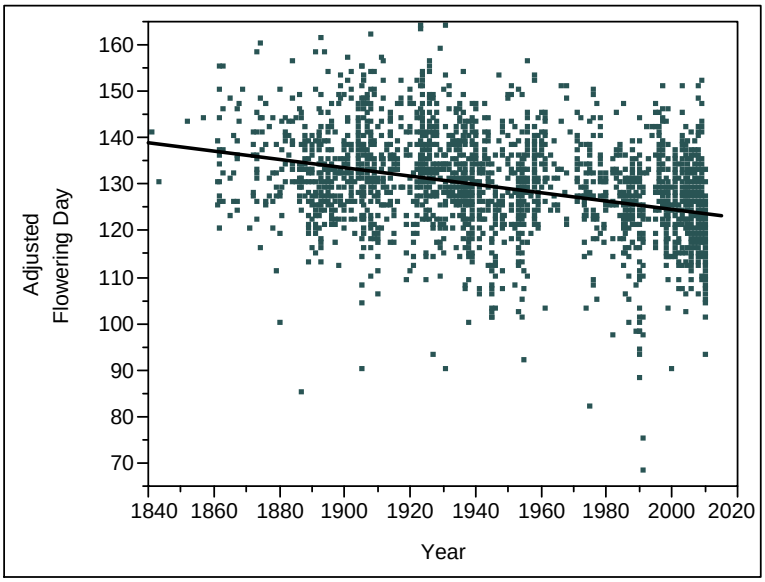

Figure 4.1. Adjusted flowering day of 28 species showing a trend towards earlier flowering time ($R^2 = 0.13$, $P < 0.0001$). From 1840 to 2010 the 28 species combined are flowering 0.89 days per decade earlier ($P < 0.0001$).

The combined analysis showed a significant trend towards earlier flowering with increased monthly minimum temperature (Table 4.12). The adjusted flowering day had the strongest correlation with March and April monthly minimum temperatures which are the months prior to flowering of the majority of the 28 species studied. The rate of change in adjusted flowering day for these two months was also the largest with 2.02 and 2.94 days per °C rise in monthly minimum temperature, respectively.

Table 4.12. Linear regression results for the combined dataset of 28 species showing the significant change in adjusted flowering day with monthly minimum temperatures.

Month	Regression Coefficient Days/°C	R^2	*P*
January	-0.81	0.04	<0.0001
February	-0.93	0.05	<0.0001
March	-2.02	0.15	<0.0001
April	-2.94	0.16	<0.0001
May	-1.67	0.06	<0.0001
June	-2.09	0.08	<0.0001

A multi-linear regression model of the combined dataset showed a significant and stronger correlation towards earlier flowering over time and monthly minimum temperatures ($R^2 = 0.24$, $P < 0.0001$). The year and the monthly minimum

temperatures for March, April and May were the most significant terms in the model (Table 4.13). February and June minimum temperatures did not contribute significantly to the model.

Table 4.13. Multi-linear regression model results for the combined dataset of 28 species showing the change in adjusted flowering day over time and monthly minimum temperatures ($R^2 = 0.24$, $P < 0.0001$). The adjusted flowering day is the flowering day plus adjustment factor where the adjustment factor is the difference between the mean flowering days for the species and the mean flowering days for all 28 species (flowering day 129).

	Regression Coefficient	*t*	*P*
Intercept	188.26084	16.88	<0.0001*
Year	-0.028 days/yr	-4.86	<0.0001*
Jan. monthly minimum temperature	-0.269 days/°C	-3.37	0.0008*
Feb. monthly minimum temperature	-0.107 days/°C	-1.30	0.1937
Mar. monthly minimum temperature	-1.045 days/°C	-9.54	<0.0001*
Apr. monthly minimum temperature	-1.353 days/°C	-8.10	<0.0001*
May. monthly minimum temperature	-0.617 days/°C	-4.69	<0.0001*
Jun. monthly minimum temperature	-0.176 days/°C	-1.07	0.2863

The mean of the adjusted flowering day for herbarium data points is significantly different from mean of the adjusted flowering day for field notes data points, which is, in turn, significantly different from mean adjusted flowering day for image data points ($\alpha = 0.05$, $P < 0.001$) (Figure 4.2). However, the mean year for herbarium specimen data points is significantly different from the mean year for field

notes data points, which is, in turn, significantly different from the mean year for image data points ($\alpha = 0.05$, $P < 0.0001$) (Figure 4.3). Hence the herbarium specimens provided flowering day data for older years while field notes and images provided flowering day data for the more recent years. This pattern was also seen for the 20 species analysed individually. These differences in means indicate that the flowering day is trending to an earlier time in more recent years.

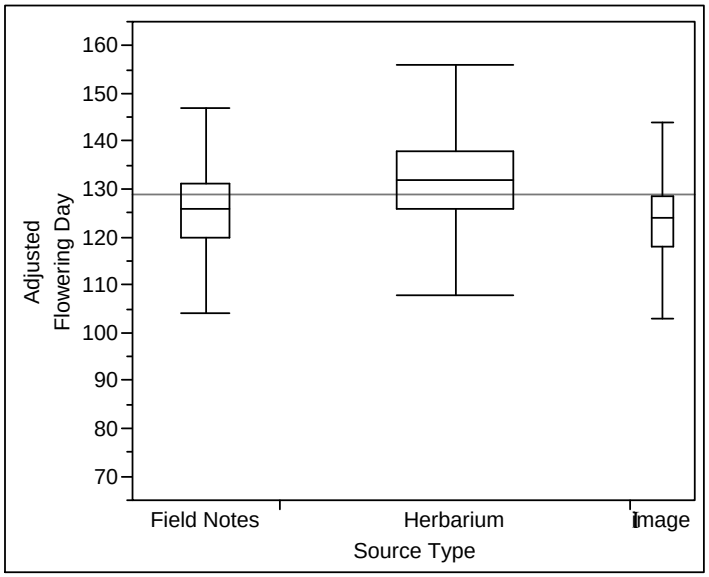

Figure 4.2. Box plots of the mean, upper and lower quartiles and range of the adjusted flowering day for field notes, herbarium and image data points. The size of the box represents the relative number of data points. The adjusted flowering day is the flowering day plus adjustment factor where the adjustment factor is the difference between the mean flowering days for the species and the mean flowering days for all 28 species (day 129).

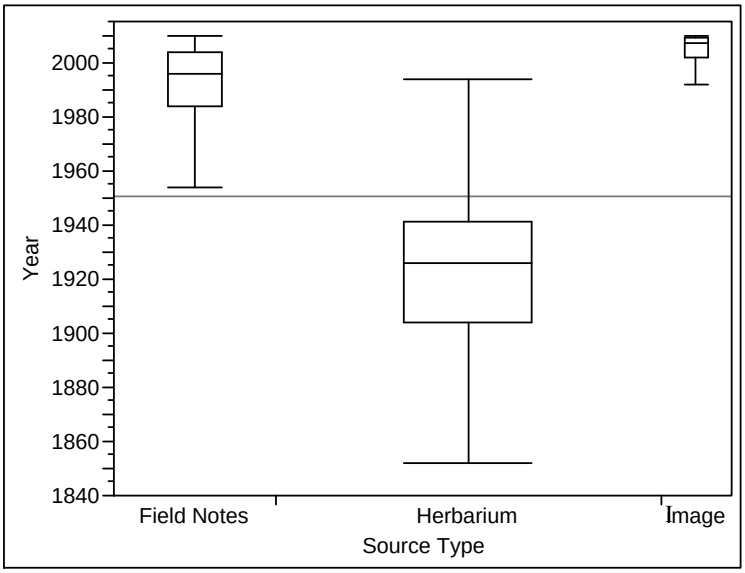

Figure 4.3. Box plots of the mean, upper and lower quartiles and range of years for field notes, herbarium specimens and image data points. The size of the box represents the relative number of data points.

Chapter 5

DISCUSSION

A wide selection of native Piedmont species in the Greater Philadelphia area are flowering significantly earlier than 170 years ago which has been driven, in part, by rising minimum temperatures. For the species studied, the order of magnitude of change in flowering day per year and flowering day per °C are comparable with other north-eastern North America studies (Bradley et al., 1999; Abu-Asab et al., 2001; Ledneva et al., 2004; Miller-Rushing and Primack, 2008), supporting the existing evidence that species in north-eastern North America are flowering earlier in response to rising temperatures. However, absolute values in this study, where an approximation to peak flowering was used, were always smaller than these studies where first flowering day was employed as the phenological event. This suggests that mid-flowering or peak flowering provides a more conservative and possibly more accurate assessment of phenological changes with climate change, concurring with evidence by Miller-Rushing et al. (2008). *Prunus serotina* was the only species in this study that showed no significant trend to earlier flowering over time, which is in agreement with earlier work (Abu-Asab et al., 2001).

The species' flowering response over time and in relation to monthly minimum temperature was quite varied, ranging from 0.43 days per decade (*Viburnum acerifolium*) to 1.69 days per decade (*Claytonia virginica*) and 1.87 days per °C (*Erythronium americanum*) to 4.49 days per °C (*Vaccinium corymbosum*) for the month for which the temperature response was greatest. Not surprisingly, species are not responding equally to the change in climate and thus a change in ecological interactions is likely. Moreover, the month for which the monthly minimum temperature has the greatest influence on the flowering day is different for different species. Since there is no uniform rise in temperature, in other words winter temperatures are rising more than summer temperatures (Hawkins et al., 2008), the uneven phenological responses through the year will compound the change in ecological interactions (Ledneva et al., 2004; Hawkins et al., 2008; Kudo et al., 2008).

An important ecological question that still remains unanswered by this and other studies is whether the flowering response to climate change is great enough to keep pace with the increased rate of climate change in the last half century (Trenberth et al., 2007). Further analysis using a non-linear model such as GAMLSS or Bayesian models (Hudson, 2010; MacGillivray et al., 2010) would be required to investigate the possibility of change points and confirm an increased response in alignment with this more rapid increase in temperature over the years.

The rising monthly minimum temperatures only explained some of the variability towards earlier flowering. Soil temperature, precipitation and ambient CO_2 concentrations might also contribute to this observed trend (Hawkins et al., 2008), but at least one study reported no significant correlation between flowering time and precipitation (Abu-Asab et al., 2001). In the present research, microclimate differences across the study area, deviation from the actual peak flowering, multiple collectors and multiple source types are all possible sources of variability. The correlation statistics from this study were, however, comparable to other phenological-climate change studies (Fitter et al., 1995; Bradley et al., 1999; Menzel et al., 2001; Ledneva et al., 2004; Lavoie and Lachance, 2006; Menzel et al., 2006; Miller-Rushing and Primack, 2008; Gallagher et al., 2009; Neil et al., 2010; Robbirt et al., 2010; Rumpff et al., 2010), indicating that this study's results are within the realm of findings from similar research. The inherent uneven distribution of historical data from herbarium, field notes or photographic sources, resulting in an imperfect time series, may also have contributed to higher correlations not being seen in this research. The ideal historic data set would therefore require a peak flowering observation from the same site and for every year of the study.

The significant negative correlation of flowering duration with the correlation (R^2) of flowering day with monthly minimum temperature indicates that shorter flowering species are better indicators of climate change. The significantly

higher correlation of flowering day with monthly minimum temperature for woody plants over herbaceous plants indicates that woody plants are better indicators of climate change. Therefore, short flowering, woody species, such as *Amelanchier canadensis*, are preferred species for phenological climate change studies and better indicators of climate change, confirming and expanding on previous research (Fitter et al., 1995; Miller-Rushing and Primack, 2008).

Provided there are sufficient data points, phenology-climate change trends can be studied with species irrespective of duration of flowering as seen by the significant trends towards earlier flowering with monthly minimum temperature of the long flowering species, *Claytonia virginica* and *Saxifraga virginiensis* and also seen in the study by Primack et al., 2004. The present study, conducted over 170 year period, suggests that using more than 100 data points for long duration flowering produces significant results while for short duration species, approximately 60 data points is sufficient.

Previous studies have shown that January (Miller-Rushing and Primack, 2008) or February (Fitter et al., 1995) temperatures are key to the timing of flowering and that the one or two months prior to flowering are most significant in the timing of flowering (Fitter et al., 1995; Cayan et al., 2001; Chmielewski and Rötzer, 2001; Primack et al., 2004; Menzel et al., 2006; Miller-Rushing and Primack, 2008; Robbirt et al., 2010). However, although the present research indicated some agreement with

the importance of January and February temperatures, it was the one or two months prior to flowering that had the most significant influence. Specifically, March and April monthly minimum temperatures had the most influence on flowering time of the spring flowering species. The data also indicated that it is not a single month's temperature that have an influence on the time of flowering but several monthly minimum temperatures prior to flowering.

The mean days per year (0.094) and mean days per °C (2.7) change in flowering day for the 20 individual species was comparable to the days per year (0.084) and days per °C (2.48) change for the combined study of 28 species. This suggests that, where there is insufficient data to study species individually, a combined study using an adjusted phenological event can produce significant results.

There was no significant difference in correlation for herbarium data compared with field notes and image data indicating that herbarium, field observations and images are equally accurate in providing phenological data, a logical result given that all three methods are an observation of a species population in flower. Given the lack of significant results comparing the rate of change of flowering day over time for herbarium versus field notes and image data, no conclusion could be drawn as to the comparable nature of different sources of data. There was a significantly more negative rate of change of flowering day with monthly minimum temperature for field notes and image data than for herbarium data. However, the field notes and image

data represents the 1970s onwards and the herbarium data represents data predominantly prior to 1950. This could indicate that species are more sensitive to temperature changes in recent years possibly due to more extreme events (Hawkins et al., 2008; Leathers, 2010) or night time temperatures not dropping as rapidly due to the greenhouse gas effect (Hawkins et al., 2008). Further study is required with data from different sources for overlapping years in order to come to a conclusion on the comparable nature of different sources of data.

No pattern was found in the difference in mean flowering day amongst the counties of the Greater Philadelphia region. In addition, although the Mt. Cuba Center and Crow's Nest Preserve field study sites were at the southern and northern most points of the study area, respectively and represented different micro-climates, there was a significant correlation between the 2010 flowering day and duration of the two sites. This confirms findings that, without temperature adjustments, phenological studies across areas of at least 80km in radius still produce significant results (Fitter et al., 1995; Abu-Asab et al., 2001). Larger areas may require the use of temperature adjustments (Lavoie and Lachance, 2006; Gallagher et al., 2009).

Many phenology studies related to climate change have used average (usually monthly) temperatures (Fitter et al., 1995; Sparks et al., 2000; Chmielewski and Rötzer, 2001; Ledneva et al., 2004; Primack et al., 2004; Wolfe et al., 2005; Menzel et al., 2006; Miller-Rushing et al., 2006; Miller-Rushing and Primack, 2008;

Gallagher et al., 2009; Robbirt et al., 2010; Rumpff et al., 2010). For this thesis, the initial intention was to use monthly average temperature data. The 1899-2010 monthly average temperatures for Pennsylvania Region 3 (The Pennsylvania State Climatologist, 2010), encompassing the counties of Lancaster, Chester, Delaware, Philadelphia, Montgomery, Bucks, Berks, Lebanon and southern Dauphin, looked appropriate for the analysis as it covered the same counties included in this thesis research plus two more northern counties. For the period from 1825-1898, the monthly average temperatures for Pennsylvania Region 3 were reconstructed from Philadelphia monthly average temperatures (Martin, 1933) using a methodology described by Leathers et al. (2008). However, regression analysis showed that there was no significant warming trend of the Pennsylvania Region 3 monthly average temperatures for either the 1899-2010 or the 1825-2010 temperature data sets. This finding concurs with observations that a warming trend is not being seen in the mid-Atlantic region (Leathers, 2010), or the change is so small that it is masked by instrument error of ~1.8^{o}C (Knight, 2010). However, the diurnal temperature range is decreasing both globally and in Pennsylvania, with minimum temperatures rising more than maximum temperatures (Easterling et al., 2000; Knight, 2010; Leathers, 2010; Menne et al., 2010) which led to the decision to utilise monthly minimum temperatures in this research. The use of monthly minimum temperatures in phenology-climate changes

studies is not unprecedented and, as was found in this research, showed correlation between flowering time and monthly minimum temperatures (Abu-Asab et al., 2001).

In light of the lack of minimum temperature data from Pennsylvania State Climatologist the switch to using monthly minimum temperature necessitated the use of the National Oceanic and Atmospheric Administration's US Historical Climatology Network's monthly minimum temperature data for West Chester, PA (Menne et al., 2010). The use of the single site West Chester temperature data, as opposed to Pennsylvania Region 3's multiple site data highlighted concerns that the single site might not be representative of the whole region and anomalies such as site moves and instrument changes may influence the data. Hence the Pennsylvania Region 3 monthly average temperatures were correlated with the West Chester monthly average, minimum and maximum temperatures. The correlations were moderately strong to strong (Table 5.1) and as expected, strongest between the two monthly average temperatures. These results indicate that the West Chester temperature data is a reasonable approximation to the Pennsylvania Region 3 temperature data and is not adversely affected by anomalies of site moves and instrument changes.

Table 5.1. The R^2 values for the correlation of Pennsylvania Region 3 monthly average temperatures with West Chester monthly minimum, average and maximum temperatures (P<0.0001*).

Pensylvannia Region 3	West Chester		
Month	**Minimum**	**Average**	**Maximum**
January	0.8647*	0.9239*	0.9109*
February	0.7346*	0.8317*	0.8305*
March	0.7301*	0.8435*	0.8404*
April	0.5842*	0.7093*	0.6723*
May	0.5713*	0.7451*	0.6954*
June	0.4352*	0.6216*	0.5841*

Observing the species through their flowering cycle at the field study sites was of tremendous help in both becoming familiar with the species but also aiding in deciding which herbarium specimens could be considered in flower and should therefore be included in the historical data. Including a field study to provide current phenological data adds value to a study and concurs with other studies that have done so (Miller-Rushing et al., 2004; Primack et al., 2004; Miller-Rushing and Primack, 2009; Robbirt et al., 2010).

Very little data gathered for this thesis was available in electronic form or online via the internet. Longwood Gardens Plant Explorer (Longwood Gardens, 2010) is available via the internet and enabled quick and easy data gathering. The Pennsylvania Flora Project database (The Pennsylvania Flora Project, 2010) was

provided in spreadsheet format and lists the number of specimens per county held at The Academy of Natural Sciences, this aided in the choice of the species studied. Swarthmore College has an online database of herbarium specimen holdings (Swarthmore College, 2010) which aided in the decision to visit that herbarium. Neither the Swarthmore College database nor the Pennsylvania Flora Project database indicated if the herbarium specimen was in flower. All the herbarium specimen data and Bowman's Hill data had to be sorted and entered manually which required many days of visiting these institutions. Individuals who provided data all provided the data in spreadsheet format. Availing herbarium specimen and phenology data electronically and via the internet would greatly enhance data access and increase the use of this data as alluded to by Gallagher et al., 2009.

Individuals, public gardens and institutions holding historic botanical data can play an important role in topical research such as climate change (Hawkins et al., 2008; BGCI, 2009; Donaldson, 2009; Primack and Miller-Rushing, 2009). Organisations and private individuals enthusiastically provided valuable historical data for this thesis indicating a willingness of the general public to provide phenological data.

In conclusion, this study illustrates that using native species and the novel approach of combining several different information sources in the form of herbarium specimens, field observations and dated photographic images can be valuable for

phenological climate change studies. The results confirm that flowering time is responding to climate change in north-eastern North America.

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Appendix A

APPENDIX A: SOURCES OF HISTORICAL FLOWERING DAY DATA

Table A1. Organisations and individuals that provided flowering day data through herbarium specimens, field notes or images with the number of Data Points and the range of Years data for each source.

Source of Data	Type of Data	Data Points	Years
Ann Rhoads	Field notes, images	110	1977 - 2010
Academy of Natural Sciences	Herbarium specimens	1397	1843 - 1998
Bowman's Hill Wildflower Preserve	Field notes	221	1935 - 2001
Dan Barringer	Images	41	2000 - 2009
Denis Machon	Images	44	2006 - 2010
F. M. Mooberry	Field notes	8	1985
Harvard Herbarium	Herbarium specimens	47	1832 - 1939
Janet Novak	Field notes	31	2006 - 2010
Joan King	Field notes	170	1985 - 2010
Karl Anderson	Field notes	4	2004
Longwood Gardens	Field notes	61	1998 - 2010
Morris Arboretum Herbarium	Herbarium specimens	74	1909 - 2010
Morris Arboretum	Field notes	110	1974 - 1988
Mt. Cuba Center	Images	30	1993 - 2003
Pennsylvania Natural Heritage	Field notes	11	1997 - 2009
Rhoda Maurer	Images	12	2005 - 2010
David Smith	Images	55	1998 - 2010
Swarthmore College Herbarium	Herbarium specimens	53	1912 - 1976
West Chester University Herbarium	Herbarium specimens	52	1843 - 1998
Zoe Panchen	Field notes	50	2010

Appendix B

APPENDIX B: FIELD STUDY WEEKLY PHOTO EXAMPLES

Photos were taken weekly of each plant species at each field study site. Photos for a selection of the species that clearly illustrated the progression of the species from flower bud to finish of flowering are included in this appendix.

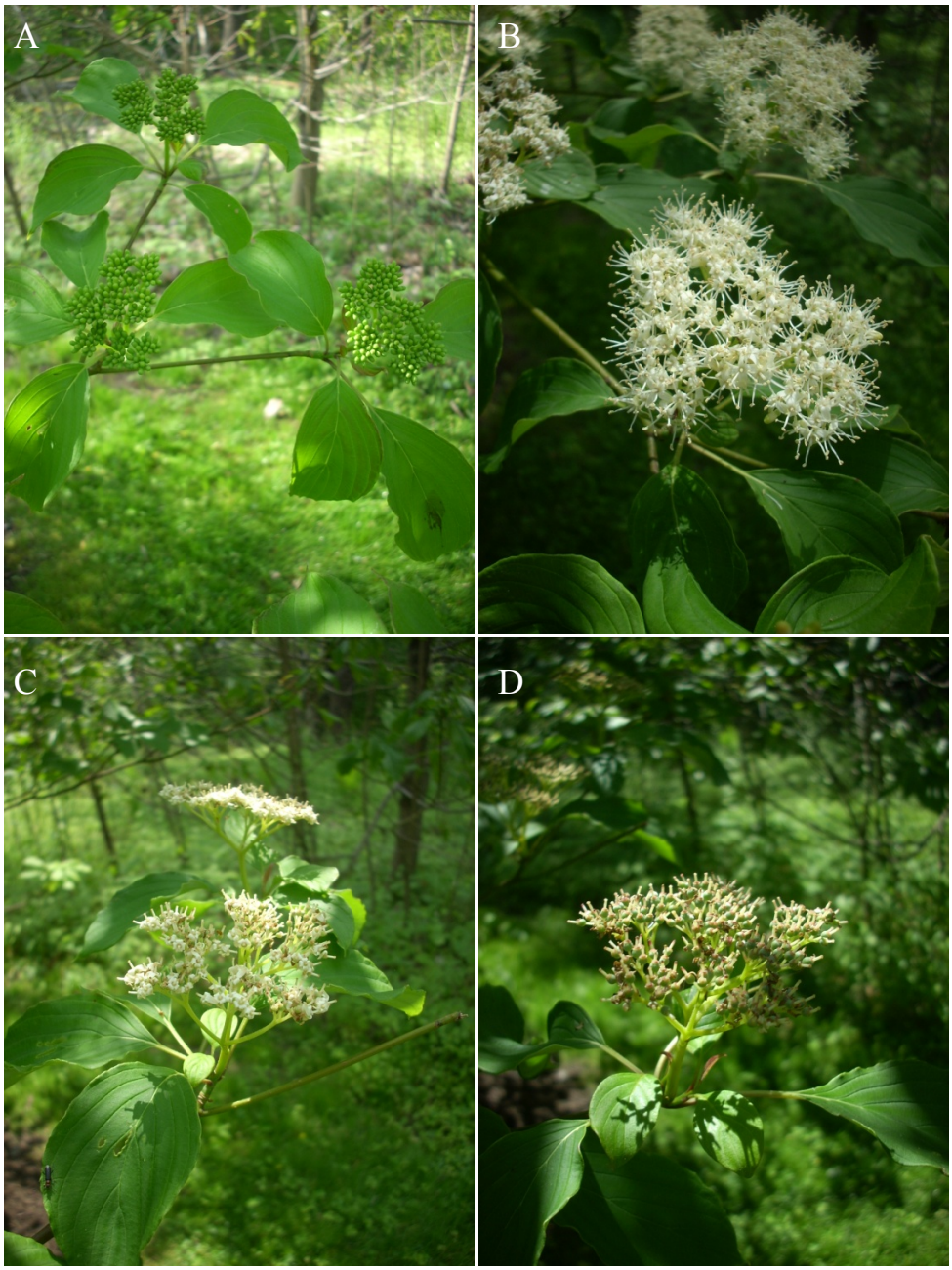

Figure A1. ***Cornus alternifolia*** **2010 flower progression at Crow's Nest Preserve. A) 1st May, B) 7th May (2 days before flowering day), C) 14th May, D) 20th May.**

Figure A2. ***Cypripedium acaule*** **2010 flower progression at Crow's Nest Preserve. A) 23rd April, B) 7th May (3 days past flowering day), C) 20th May.**

Figure A3. ***Kalmia latifolia*** **2010 flower progression at Crow's Nest Preserve. A) 14th May, B) 20th May, C) 27th May (flowering day), D) 7th June.**

Figure A4. *Kalmia latifolia* 2010 flower progression at Mt. Cuba Center. A) 14th May, B) 20th May, C) 27th May (flowering day), D) 7th June.

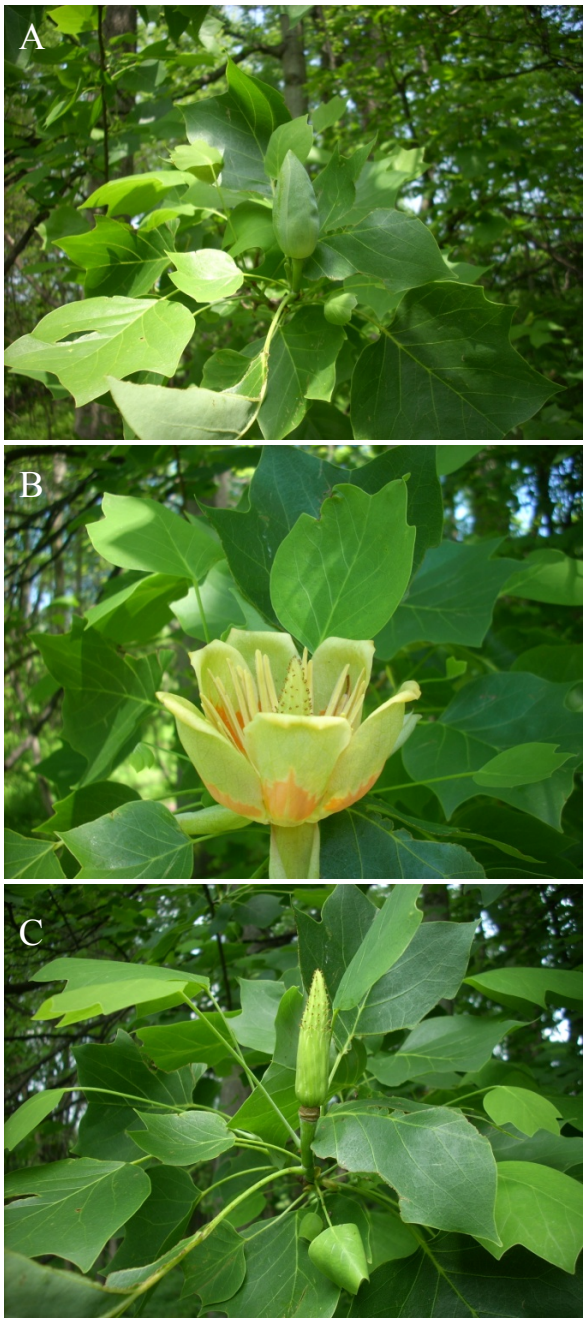

Figure A5. ***Liriodendron tulipifera*** **2010 flower progression at Crow's Nest Preserve. A) 14th May, B) 20th May (flowering day), C) 27th May.**

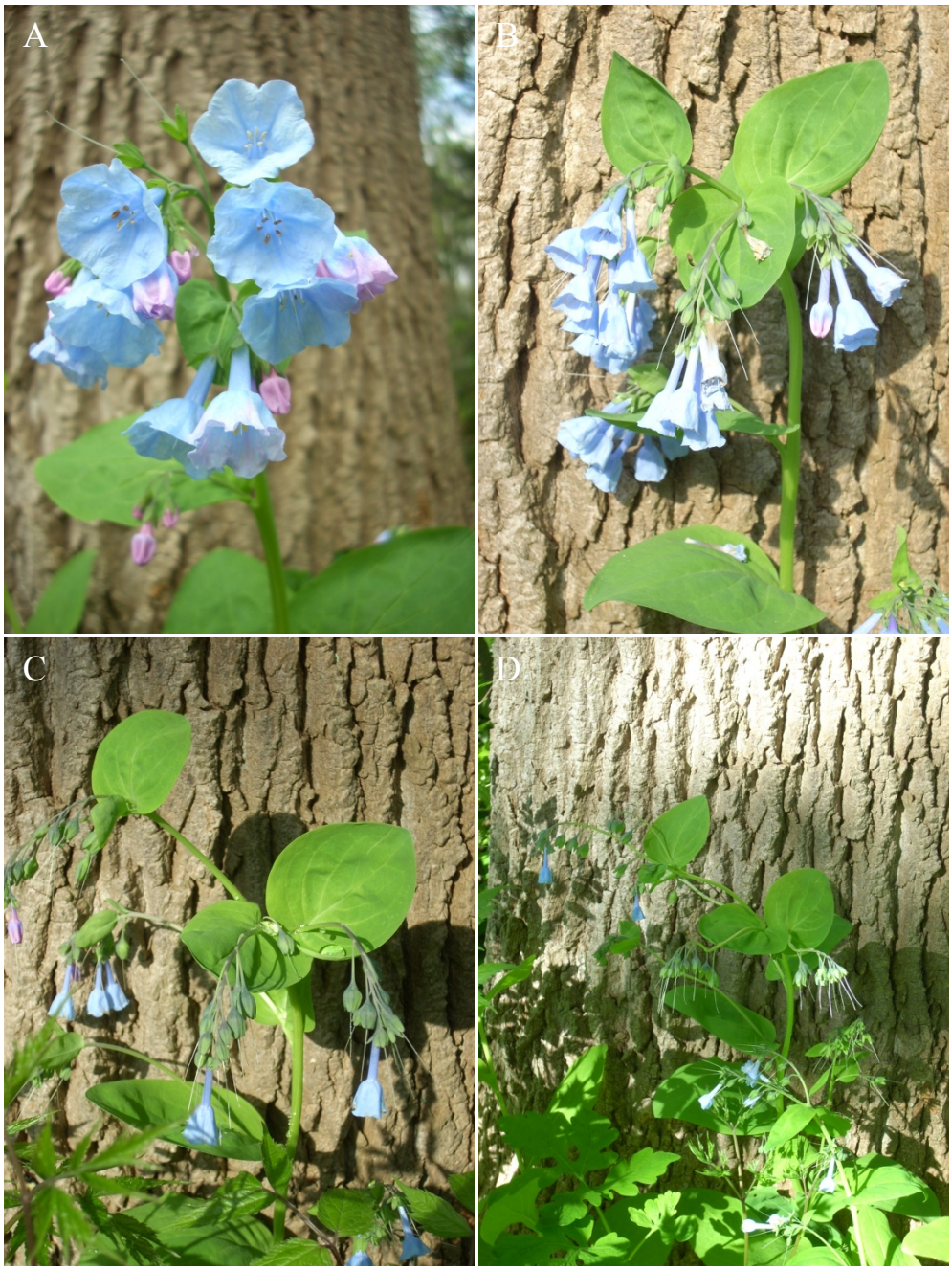

Figure A6. ***Mertensia virginica*** **2010 flower progression at Mt. Cuba Center. A) 9th April (flowering day), B) 16th April, C) 22nd April, D) 29th April.**

Figure A7. *Rhododendron periclymenoides* 2010 flower progression at Crow's Nest Preserve. A) 16th April, B) 23rd April, C) 1st May (flowering day), D) 7th May.

Figure A8. ***Rhododendron periclymenoides*** **2010 flower progression at Crow's Nest Preserve. A) 16th April, B) 23rd April, C) 1st May (flowering day), D) 7th May.**

Figure A9. ***Prunus serotina*** **2010 flower progression at Crow's Nest Preserve. A) 23rd April, B) 1st May (3 days before flowering day) C), 7th May (3 days after flowering day) D) 14th May.**

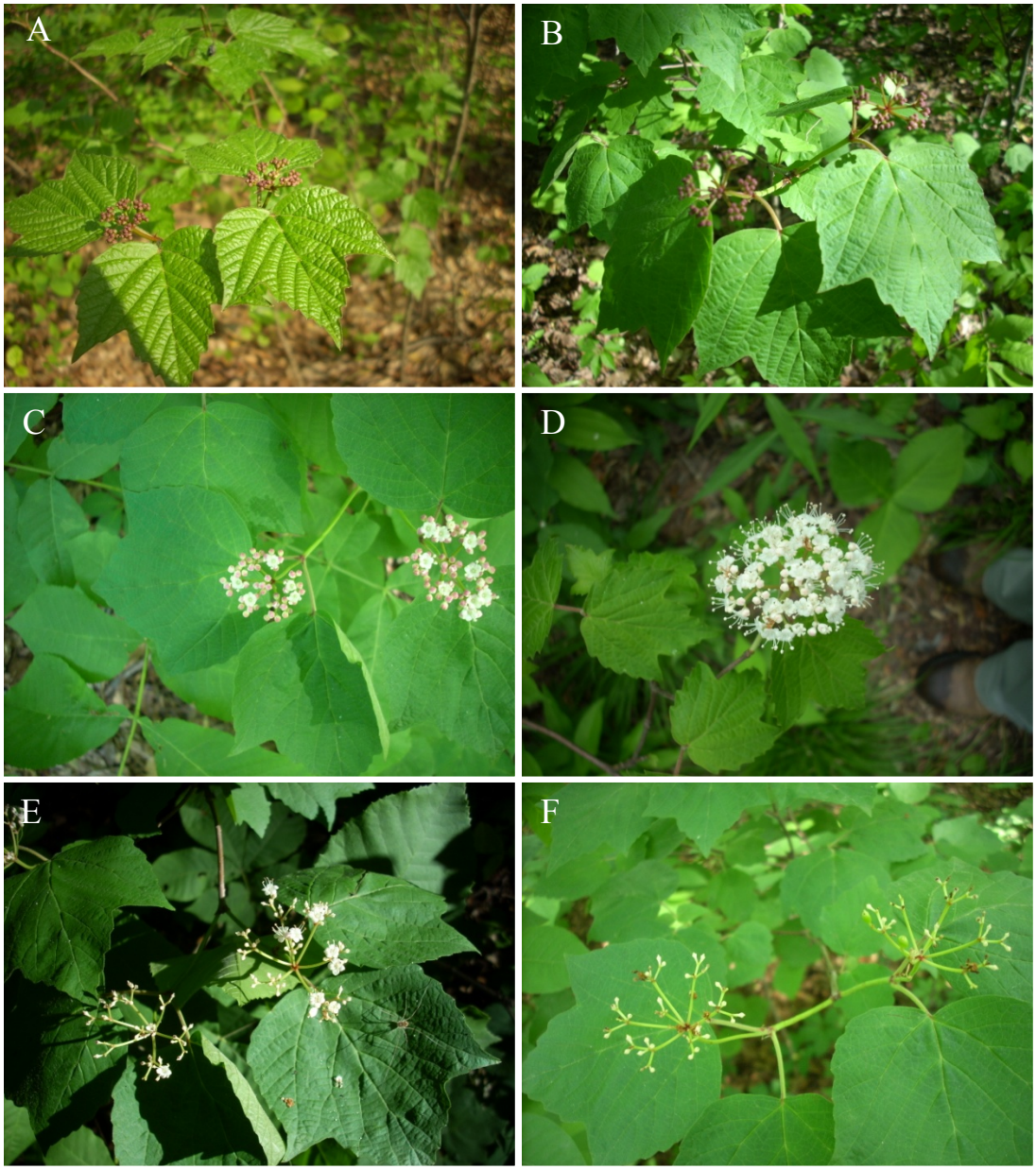

Figure A10. ***Viburnum acerifolium*** **2010 flower progression at Mt. Cuba Center. A) 16th April, B) 29th April, C) 7th May (first week in flower), D) 14th May (flowering day), E) 20th May (last week in flower), F) 27th May.**

Appendix C

APPENDIX C: GRAPHS SHOWING RESPONSE OF SPECIES' FLOWERING DAY TO YEAR

Of the 20 species analysed, 19 showed a significant trend towards earlier flowering over the past 170 years (1840-2010). Graphs showing the trend towards earlier flowering for 18 of these species are included in this appendix. The regression coefficient in days per year, R^2 and *P* are given in Table 4.3.

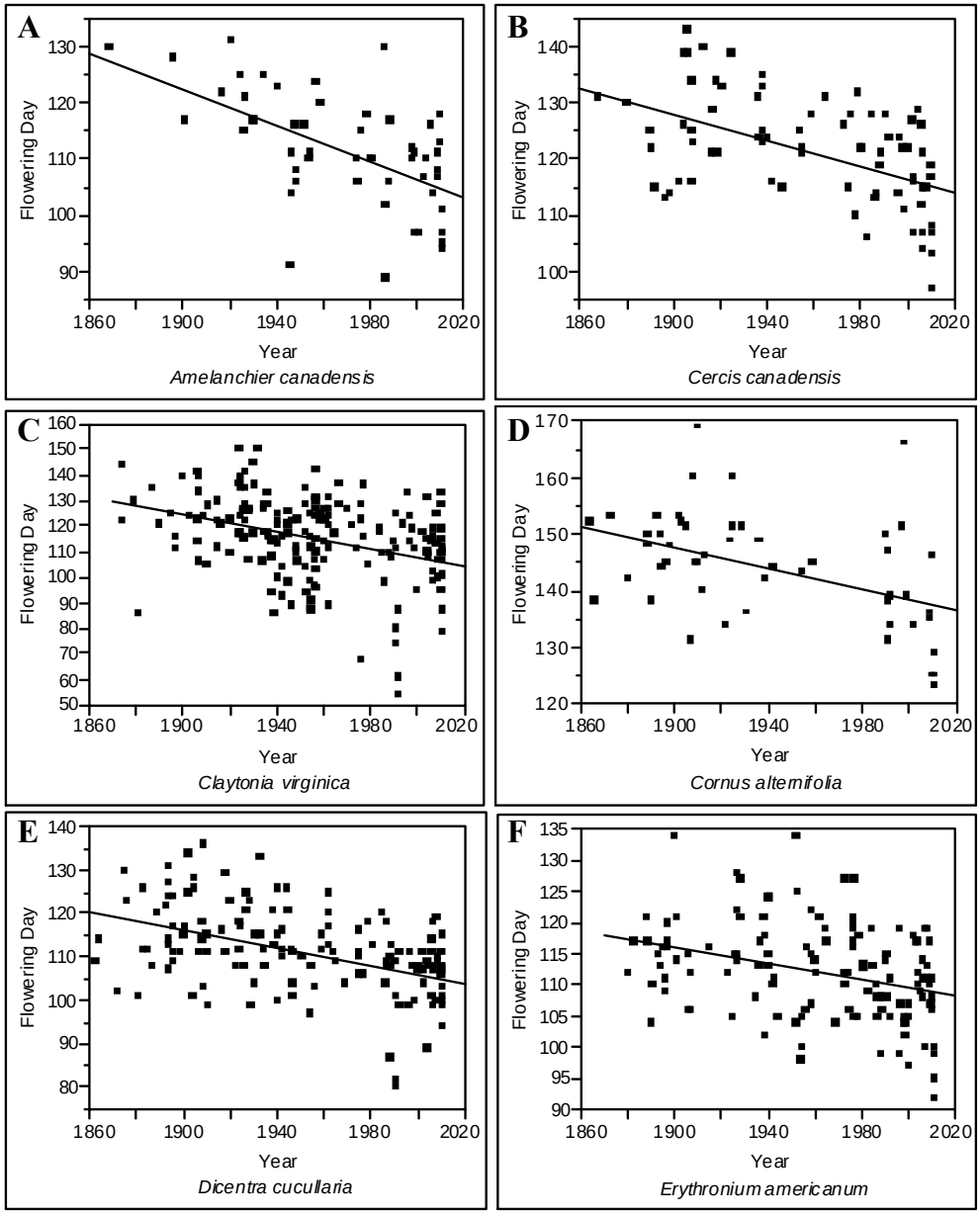

Figure A11. Species showing a significant trend towards earlier flowering. The solid line represents the best fit linear regression. (A) *Amelanchier canadensis* (B) *Cercis canadensis* (C) *Claytonia virginica* (D) *Cornus alternifolia* (E) *Dicentra cucullaria* (F) *Erythronium americanum*.

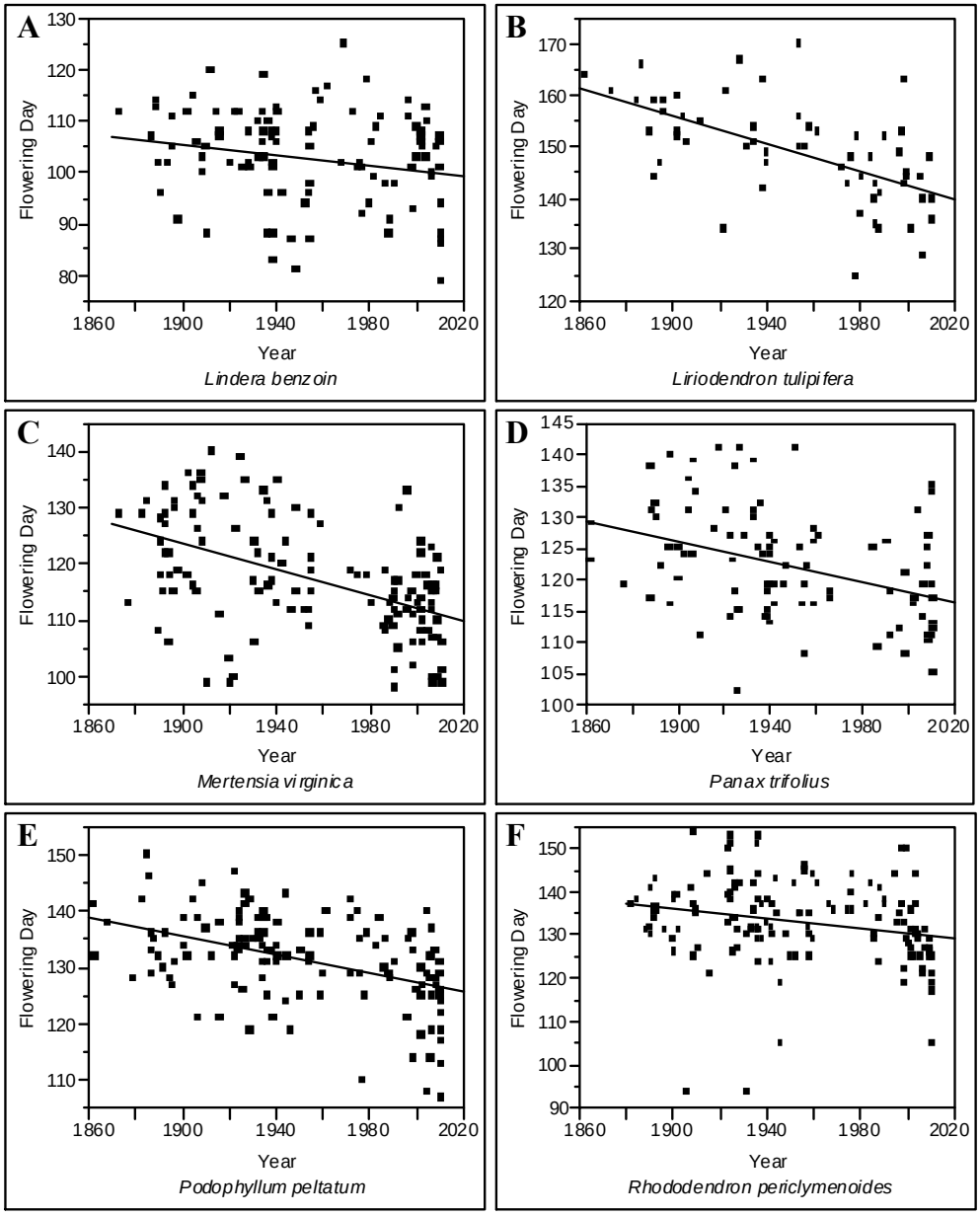

Figure A12. Species showing a significant trend towards earlier flowering. The solid line represents the best fit linear regression. (A) *Lindera benzoin* (B) *Liriodendron tulipifera* (C) *Mertensia virginica* (D) *Panax trifolius* (E) *Podophyllum peltatum* (F) *Rhododendron periclymenoides.*

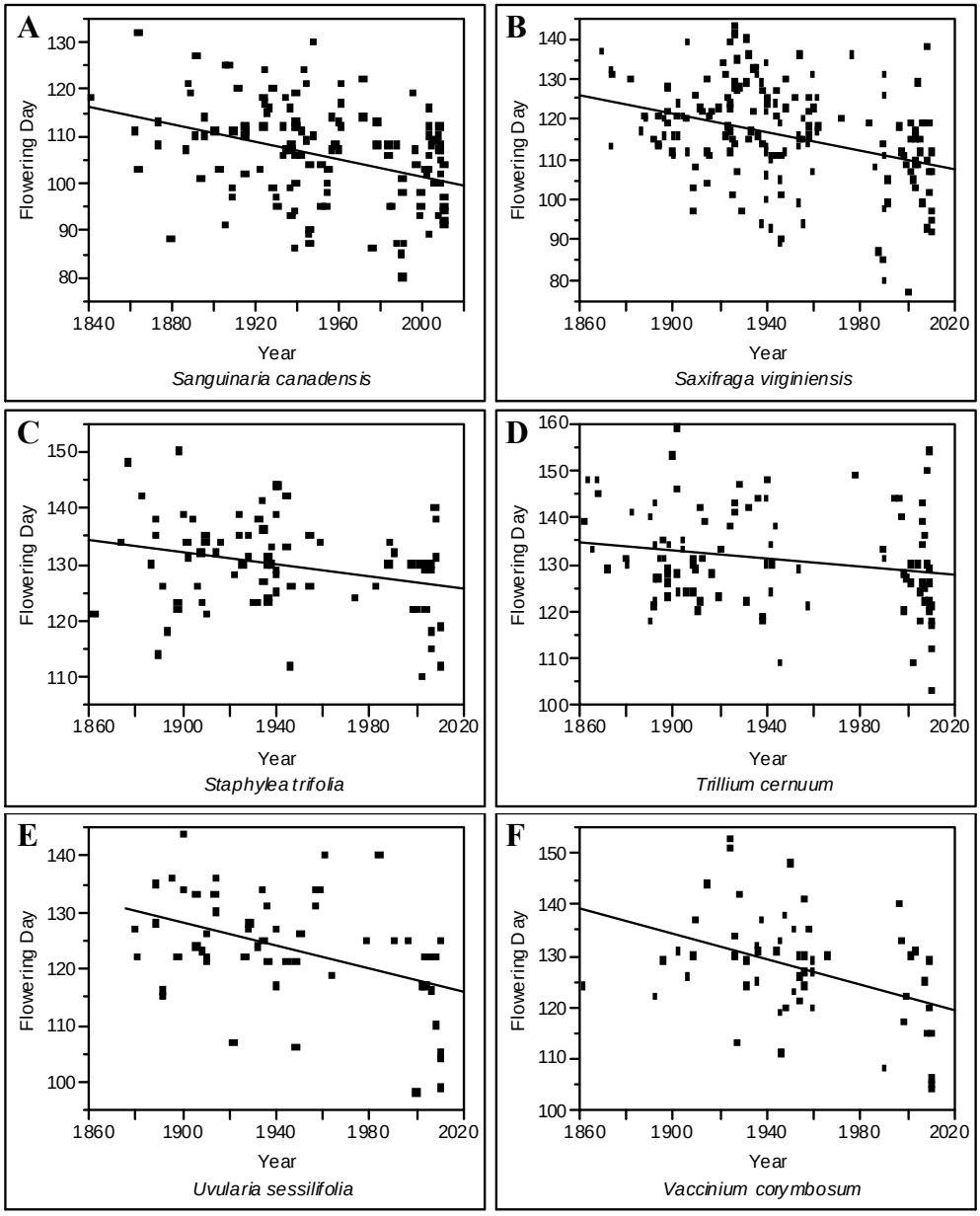

Figure A13. Species showing a significant trend towards earlier flowering. The solid line represents the best fit linear regression. (A) *Sanguinaria canadensis* (B) *Saxifraga virginiensis* (C) *Staphylea trifolia* (D) *Trillium cernuum* (E) *Uvularia sessilifolia* (F) *Vaccinium corymbosum*.