2009

The Impacts of Global Warming on Appalachian Wildflower Phenologies

Rachel D. Wigginton
Western Kentucky University

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THE IMPACTS OF GLOBAL WARMING ON APPALACHIAN WILDFLOWER

PHENOLOGIES

by

Rachel D. Wigginton

A Capstone Experience/Thesis

submitted in partial fulfillment of the requirements of

University Honors College at

Western Kentucky University

Approved by:

Albert J. Meier

Scott A. Grubbs

Ouida W. Meier
IMPACTS OF GLOBAL WARMING ON APPALACHIAN WILDFLOWER PHENOLOGIES

by:

RACHEL D. WIGGINTON

Under the Direction of Albert Meier

ABSTRACT

Public and private interest in global warming has prompted exploration of the impacts this phenomenon may impart on ecosystem functions. Flowering phenology has been one of the areas many scientists believe is particularly susceptible to the impacts of anthropogenic warming. Over three weekends in spring of 2008, the vernal herb community was surveyed at five sites within the Great Smoky Mountains regions of the southern Appalachian Mountains. The intent was to capture the naturally occurring elevational gradient and determine if the temperature cue for blooming was the same for all co-flowering species in the study. This information would allow for conjecture on the impacts of climate change on co-flowering communities. Initial findings were inconclusive because low sample size prevented statistical analysis.

INDEX WORDS: Global Warming, Phenology, Southern Appalachians, Elevation gradients
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Committee Chair: Albert Meier

Committee: Ouida Meier
Scott Grubbs

Electronic Version Approved:

Honors College
Western Kentucky University
May 2009
ACKNOWLEDGEMENTS

I would like to take this opportunity to thank everyone that helped me begin and complete this project. Specifically, I would like to thank Dr. Albert Meier. Without his tireless dedication and belief in my abilities, I would not have seen the finish line. Also, thank you to Dr. Ouida Meier and Dr. Scott Grubbs for serving on my committee. Your help and advice was greatly appreciated. A big thank you to Great Smoky Mountains National Park who allowed me to work in their ecological playground. Thank you to the BESURE Summer Research Grant which funded this project. A special thank you to my family and friends who helped me through this stressful but rewarding process. Finally, thank you to all my field hands: Dr. Albert Meier, Mary Penick, David Kem, Mark Wigginton, Ryan Pennington, Cabrina Hamilton, Landon Baker, Meridith Bartley, John Dale VanSlyke, and Cornelius Lee.
# TABLE OF CONTENTS

ACKNOWLEDGEMENTS iv

LIST OF TABLES vii

LIST OF FIGURES viii

LIST OF IMAGES x

CHAPTER

1 INTRODUCTION 1

2 METHODS 8

   Study Sites 8

   Study Species 9

   Field Methods 10

   Methods of Data Analysis 11

3 RESULTS 12

   Presence vs. Absence 12

   Bloom Results 14

   Elevation (meters) vs. Blooms/Stem 14
LIST OF TABLES

Table 1: Presence and Absence of Stems 13
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>S. pubera</em>’s blooming pattern in relation to elevation</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td><em>P. fimbriata</em>’s blooming pattern in relation to elevation</td>
<td>16</td>
</tr>
<tr>
<td>3</td>
<td><em>C. caroliniana</em>’s blooming pattern in relation to elevation</td>
<td>16</td>
</tr>
<tr>
<td>4</td>
<td><em>P. fimbriata</em>’s bloom presence for each elevation</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>compared to time in days.</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td><em>S. pubera</em>’s bloom presence for each elevation compared</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>to time in days.</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td><em>C. caroliniana</em>’s bloom presence for each elevation compared</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>to time in days.</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Blooms/Stem across time in <em>S. pubera</em>, <em>P. fimbriata</em>, <em>and C. caroliniana</em> at 588m</td>
<td>20</td>
</tr>
<tr>
<td>8</td>
<td>Blooms/Stem across time in <em>S. pubera</em>, <em>P. fimbriata</em>, <em>and C. caroliniana</em> at 701m</td>
<td>21</td>
</tr>
<tr>
<td>9</td>
<td>Blooms/Stem across time in <em>S. pubera</em>, <em>P. fimbriata</em>, <em>and C. caroliniana</em> at 823 m</td>
<td>22</td>
</tr>
<tr>
<td>10</td>
<td>Blooms/Stem across time in <em>S. pubera</em>, <em>P. fimbriata</em>, <em>and C. caroliniana</em> at 1442 m</td>
<td>23</td>
</tr>
<tr>
<td>11</td>
<td>Blooms/Stem across time in <em>S. pubera</em>, <em>P. fimbriata</em>, <em>and C. caroliniana</em> at 1487 m</td>
<td>24</td>
</tr>
<tr>
<td>12</td>
<td>Blooms/Stem graphed against soil temperature for <em>P. fimbriata.</em></td>
<td>25</td>
</tr>
<tr>
<td>13</td>
<td>Blooms/Stem graphed against soil temperature for <em>S. pubera.</em></td>
<td>26</td>
</tr>
<tr>
<td>14</td>
<td>Blooms/Stem graphed against soil temperature for <em>C. caroliniana.</em></td>
<td>27</td>
</tr>
<tr>
<td>15</td>
<td>Maximum daily temperatures for the Gatlinburg, <em>Tennessee</em> area for March-June of 2008</td>
<td>29</td>
</tr>
</tbody>
</table>
Figure 16: Minimum daily temperatures for the Gatlinburg, Tennessee area for March-June of 2008.

Figure 17: Mean daily temperatures for the Gatlinburg, Tennessee area for March-June of 2008.
<table>
<thead>
<tr>
<th>Image</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Image 1</td>
<td>Lower Porter’s Creek Site</td>
<td>40</td>
</tr>
<tr>
<td>Image 2</td>
<td>Upper Porter’s Creek Site</td>
<td>40</td>
</tr>
<tr>
<td>Image 3</td>
<td>Chimney Tops Site</td>
<td>41</td>
</tr>
<tr>
<td>Image 4</td>
<td>Lower New Found Gap Site</td>
<td>41</td>
</tr>
<tr>
<td>Image 5</td>
<td>Upper New Found Gap Site</td>
<td>42</td>
</tr>
</tbody>
</table>
INTRODUCTION

Great variability in daily or seasonal temperature patterns occurs naturally in many ecosystems, with air and soil temperatures undergoing up to 20ºC changes seasonally or diurnally (Atkin et al. 2000). Due to human induced climate change, global surface temperatures by 2090-2099 are projected to have increase an average of (low scenario) 1.8°C to (high scenario) 4.0°C (IPCC 2007). This global temperature shift stands to impact natural temperature patterns. Climate change would have complex impacts on seasonal temperature patterns, including storms, fire, precipitation, air humidity, snow cover, and severity and timing of extreme events (e.g., hurricanes and tropical storms; Michener et al. 1997; IPCC 2007). The United Nations Intergovernmental Panel on Climate Change (IPCC) (2007) indicated that for tropical storms specifically, an increase in storms reaching categories 4 and 5 have been observed since the 1970’s. This increase was most notable in the Indian Ocean and the northern and southwestern regions of the Pacific Oceans. Five separate global atmospheric circulation models (GCM) have been developed, and though their results vary slightly, Long and Hutchin (1991) summarized their findings and the current IPCC (2007) report mirrors many of these previous findings. The GCMs predicted the mean temperature differences between summer and winter will be less pronounced. Increased temperature will be most apparent at high latitudes. Impacted latitudes were projected to be those between 60º and 75º by the GCMs (Long and Hutchin 1991) but have been expanded to include latitudes between 30º and 85º (IPCC 2007). During the summer months at these
latitudes, and in general at lower latitudes, average surface temperature will increase 0°-4°C. Soil moisture will also be impacted, with decreased moisture in the tropics and, at high latitudes, decreased moisture in the summer and increased moisture in the winter. In some situations, these changes may positively impact overall biomass production. But increases in production could negatively impact the availability of nutrients such as nitrogen. Conversely, increased temperature, impacting both soil moisture and temperature, could increase rates of decomposition which could offset negative impacts (Long and Hutchin 1991).

While these projections appear reliable, they do not fully address specific systems and their responses to these changes. As a result, projections such as these have provoked public and private interests in anthropogenic climate change resulting in numerous studies examining the outcomes of this change on our planet’s ecology. As the topic of global climate change becomes more pressing, increasing numbers of scientists will continue the effort to project its impacts.

Numerous studies pay special attention to the issue of phenology, or the study of the timing of reoccurring biological events, biotic and abiotic forces controlling these events, and how phases are interrelated on the species and community level (Walther et al 2002), as current yearly variations in climate are known to impact these seasonal events (Badeck et al. 2004). In natural ecosystems, metabolic rates are greatly influenced by variations in temperature (O’Hara 1967). Atkin et al. (2000) found that increased temperature resulted in increased root respiratory acclimation. Root respiration in plants accounts for 33-60% of the total soil respiration and represents a major site of CO₂ loss in
plants. Thus, increases in global temperature could result in increased rates of natural processes on the organism level, leading to widespread consequences for ecosystems. Based on such information, researchers have hypothesized that plant phenology will be particularly responsive to climate change (Badeck et al. 2004; Walther et al. 2002; Root et al. 2003). Changes in timing on the species level could have far reaching impacts on the community level, especially the changes observed in primary producers. Shifts in phenology have already been observed for various plant species. For example, *Pinus sylvestris* was found to migrate a few degrees southward with increased temperature (Saxe et al. 2001). While these changes in phenology could be influenced by natural yearly climate variation and environmental variables unrelated to climate change, the most parsimonious explanation appears to be human driven shifts in climatic and atmospheric conditions (Hughes 2000). These impacts are expected to be amplified at high latitudes and elevations (Dunne et al. 2003).

Further, global warming could alter forest dwelling herbaceous species more than other groups from other habitats (Gilliam and Roberts 2003). Several key factors are linked to timing of flowering phenology, including temperature, moisture, circadian rhythmicity, and photoperiod (Rathcke and Lacey 1985). Here, I will examine the impacts of circadian rhythms and temperature. Circadian rhythms were defined by Bradshaw et al. (2003) as a natural, internally maintained rhythm with the duration of about a day that repeat continually. Circadian rhythms are usually highly temperature compensated. Because these rhythms are predictable and consistent with the seasons, many plants, vertebrates, and arthropods use them as indicators for biological patterns.
(Bradshaw et al. 2003). Marshall and Bowman (1978) observed that there was increased synchrony in development as they traveled up an elevational gradient which could most likely be attributed to the compression of the spring light phase. While photoperiodic control has been reported for some short-lived herbs, very little literature exists on the subject of photoperiodic cues and circadian rhythms in forest herbs.

Conversely, it has been widely reported for vernal herbs that flowering phenology is deeply linked to temperature. Most species occurring in temperate climates flower in response to cumulative degree sums above a threshold temperature (Rathcke and Lacey 1985). Vernal herbs flower early in the season before canopy closure, foul weather, or lack of pollinators have the chance to impact reproductive success (Schemske et al. 1978). Many studies have shown that species flowering early in the seasons will do so as soon as temperatures reach an appropriate level (Lindsey and Newman 1956; Jackson 1966; Schemske et al. 1978; Motten 1986). Lindsey and Newman (1956) developed a statistical-graphical method for determining how long a flower needed to develop before bloom and found temperature was a controlling factor in this timing. Specifically, they found that herbs that bloomed for a short period of time had a lower threshold of temperature than did individuals with persistent flowering patterns. Lindsey and Newman determined that temperature, not sunlight, was the dominant abiotic factor controlling flowering phenology. Schemske (1978) supported this finding, showing that most flowering activity in vernal herbs began as soon as temperature was suitable and ended before daylight hours reached their maximum. His paper also revealed that seasonal variation in degree-days caused a shift in flowering phenology, in most cases,
causing the whole community of vernal herbs to reach peak flower at an earlier date. As more daylight is comparable with more time for pollinator visitations, these findings further suggest that temperature, and not necessarily daylight hours, has a major impact on flowering phonologies. Schemske (1978), however, expressed concern that simple degree-day observations are not sufficient when examining shifts in phenology, noting that soil temperature is also extremely important.

As the impacts of temperature on phenology have been widely documented, I chose to use this variable to guide my investigation. Pollination, however, further complicates the issue of shifting phenology for the plant community and must be addressed. Motten (1986) found that fecundity in a community of co-flowering forest, vernal wildflowers was not significantly impacted by competition for pollinators. Conversely, other studies have shown that co-flowering results in competition for pollinators impacting flowering phenology (Ishii and Higashi 2001; Pleasants 1980; Campbell and Motten 1985). Even when flowering groups increased the number of pollinator visits within associated species, it sometimes led to intraspecific pollination (Rathcke and Lacey 1985). Flowering times are now thought to be adapted to reduce competition between co-flowering species. However these two schools of thought aren’t necessarily mutually exclusive. Competition resulting in specific flowering time might alleviate pressures associated with decreased numbers of pollination events. Furthermore, because many vernal herbs flower in large aggregates, attract generalist pollinators (Campbell and Motten 1985), and require very few pollinator visits for reproductive
success (Motten 1986), co-flowering might be advantageous for such species as it attracts numerous pollinators to the site.

When applying this information to global climate change, note that phases in phenology are cued by environmental variables (e.g., circadian rhythms, moisture, temperature, et cetera), but these environmental conditions are not likely to be the same for organisms at differing trophic levels (e.g., plants, invertebrates, or vertebrates; Visser and Booth 2005). As a result, phenologies cued by temperature (most vernal herbs for example) could fall out of synchrony with those cued by other factors as a result of increased global temperature, resulting in mismatching phenotypic patterns (Stenseth and Mysterud 2002). Climate change may result in altering of pollination and food webs if community members respond differently to the changing environment. These impacts may prove especially apparent in environments where seasons result in very short growing periods for target species (Senseth and Mysterud 2002). Visser (2004) warns “such trophic decoupling of food web phenology may have severe consequences, including biodiversity loss.”

Whittaker (1956) examines the distribution of plant populations along naturally occurring elevational gradients in the Great Smoky Mountains. He found that plant community composition varied along the gradient based on several factors that changed consistently with increases in elevation, one of which was temperature. In the northeastern United States, adiabatic lapse rate increases 0.6°C with every 100 m rise in elevation (Marchland 1987). Because the southern Appalachians house a unique climate for the region, Iverson et al. (1999) predicted that the community composition of tree
species would shift to favor the lower elevation community as global surface
temperatures increased. Ibanez et al. (2006) agreed with this prediction, but further
hypothesized that the area would undergo climate, soil, and land cover changes that may
best suit species not yet present in the region

Thus, I sought to use preexisting elevational gradients in Great Smoky Mountains
National Park as a natural indicator of how climate change might impact Appalachian
wildflower phenologies. As the temperature along this gradient change predictably with
elevation, observations concerning co-flowering species can be used to assess the impacts
of temperature on flowering phenology.

My study seeks to address a few basic questions:

1. Along the elevation gradient and, thus, the adiabatic temperature gradient
   (Whittaker 1956a, Whittaker 1956b) in Great Smoky Mountains National
   Park, are co-flowering patterns consistent at different elevations?

2. If co-flowering patterns are not consistent, are increases in temperature
   significant factors in cuing flowering phenologies in study species (Lindsey
   and Newman 1956; Jackson 1966; Schemske et al. 1978; Motten 1986)?

3. Finally, what conclusions can be drawn about the impacts that anthropogenic
   global warming might have on co-flowering species and their plant-pollinator
   phenologies (Gilliam and Roberts 2003; Stenseth and Mysterud 2002)?

I hypothesized the following:
1. Not all flowering phenologies would be cued by the same temperature threshold resulting in differing co-flowering communities at different elevations.

2. Such findings are significant when considering the future impacts of global climate change and the potential for the decoupling of pollination webs.

METHODS

Study Sites

The Great Smoky Mountains National Park in eastern Tennessee and western North Carolina captures some of the highest elevations east of the Rockies, with elevations ranging from 460 m at the base to 2,025 m at Clingman’s Dome (Whittaker 1966). I chose five study sites within the park in an attempt to represent capture the naturally occurring elevational gradient and habitat types present.

1. The lowest elevation site, in the Porter’s Creek area, is 588 meters in elevation. This stand has been logged. Second growth stands in Great Smoky Mountains National Park are characterized by a loss of herbaceous understory up to 50 – 85 years following deforestation (Duffy and Meier 1992). Despite this, at peak flower, numerous species still occur in this site.

2. The Upper Porter’s Creek site, occurring at 701 meters in elevation, is an old growth stand. The understory community, unaffected by the impacts of
logging and clear cutting, remains intact. Duffy and Meier (1992) found that old growth forests had a significantly higher number of vernal herbs in a meter-squared quadrat than comparable stands of logged forest.

3. The next site along the elevation gradient occurs near Chimney Tops at about 823 m. This study site was smaller in area, compared to the rest, and was also second growth. As previously stated, logging results in overall lower alpha-diversity (Meier et al. 1995).

4. Near New Found Gap, at approximately 1442 meters, I chose a beech gap site. Russell (1953) explains the term “beech gap” refers to a small forest of young beeches (Fagus grandifolia) occurring around 5000 feet in elevation (or roughly 1524 meters). These forests usually occur where spruce previously stood. Russell further explains that the herbaceous cover is great in these “gaps” as compared to the surrounding spruce forest.

5. At about 1487 meters, within a few miles of my first New Found Gap site, I chose a second beech gap. The same characteristics apply to this site as to the previous; expect that the elevation is increased.

Study Species

These sites characterize the habitat range for my study species. I chose to follow the bloom of Phacelia fimbriata (Fringed Phacelia) as its bloom is pervasive in much of the park and has a plethora of co-flowering species. A subset of frequently co-flowering species was chosen to include in the study. These species are as follows: Stellaria
pubera (Star Chickweed), Trillium erectum (White Wake-robin), T. luteum (Yellow-flowered Trillium), T. grandiflorum (Large-flowered Trillium), Podophyllum peltatum (May-apple), Dicentra cucullaria (Dutchman’s-breeches), D. canadensis (Squirrel-corn), Cardamine diphylla (Five-parted Toothwart), Claytonia caroliniana (Spring Beauty), and Erythronium americanum (Trout Lilly). These species vary in their phenological timing and duration, but all occur alongside P. fimbriata at some point during their respective flowering seasons.

Field Methods

On three weekends, April 12, 2008, May 15, 2008, and May 30, 2008, each elevational site was surveyed. Each site was marked by GPS to allow a cross reference between elevations recorded on topographic maps of the area. For each location, a grid approximately 900 m² was established. This excludes the site at Chimney Tops where the grid was only approximately 450 m². Within each grid, I positioned seven 1 m² quadrats using a random number generator.

Several types of data were gathered at each quadrat. Most importantly, within each square meter quadrat total stem and total bloom counts were recorded for each study species. Because the number of blooms and stems present within a single quadrat could be very high, a one quarter subsampling method was employed for ease and increased observation accuracy. For each species, stem and bloom counts were recorded for the entire quadrat unless there were more than 100 blooms or stems. In this case, the quadrat was divided into quarters and one quarter was randomly selected and the totals were
recorded. At the peak of the bloom, some quarters contained more than 100 blooms or stems. For this instance, the same method was applied, but to a randomly selected quarter of the chosen quarter, or $\frac{1}{16}$th of the quadrat.

Soil temperature was quantified at the quadrat scale using a digital thermometer to the 0.1°C. The thermometer was inserted into the ground approximately two cm below the surface. This was allowed to remain in the soil until the temperature reading equilibrated, usually about 45 seconds. Atmospheric temperature was measured at the site scale using the same device employed to determine soil temperature. Finally, elevation for each site was attained using the GPS system cross-referenced with topographic maps of the study area.

**Methods of Data Analysis**

Due to small sample size, my ability to perform statistical analysis was limited. Simple presence verses absence of all study species was examined. In addition, graphical representations were employed to make predictions about trends and relationships. For each quadrat the height of bloom was determined by calculating the blooms per stem (total blooms/total stems). On the site level, I determined the mean blooms per stem. In this way, average blooms per stem for each site and date were calculated. Only three of the study species, *Phacelia fimbriata*, *Stellaria pubera*, and *Claytonia caroliniana*, were in bloom consistently along the elevational gradient, thus, the graphical analysis focused on these three species. These values were then employed when examining trends and
relationships between bloom and various other factors such as elevation, date, and soil temperature.

To fully understand the impacts of temperature, a better understanding of the overall temperature of the area was required. Daily highs, lows, and means were obtained for the Gatlinburg, Tennessee area for March through July of 2008 from the National Oceanic and Atmospheric Administration (NOAA 2008). These values were graphed and used to more fully explore blooming trends.

RESULTS

Presence vs. Absence

When looking at simple presence or absence of the 11 study species, we can see that on the first weekend (April 12-13th, 2008) Phacelia fimbriata, Stellaria pubera, Cardamine diphylla, and Claytonia caroliniana had leafed out at all elevations. Trillium luteum and Podophyllum peltatum had shown leaf out only at the three highest elevations. Dicentra canadensis and Erythronium americanum had emerged at all but the lowest site, while T. erectum, T. grandiflorum and D. cucullaria were found intermittently among the five elevations.

The second weekend (May 11-12th, 2008), only P. fimbriata leafed out at all five sites, while S. pubera plants were recorded at all but the highest elevation site. Trillium erectum was observed at the mid-elevation sites (701 m and 823 m), while T. grandiflorum absent only at the highest and lowest elevations. Podophyllum peltatum
was found only at the 823 m and 1442 m sites. *Trillium luteum* was present only at the lowest elevation while *D. cucullaria* leafed out only at the highest elevation. *Dicentra canadensis, C. diphylla,* and *E. americanum* had interrupted presences along the elevational gradient. *Claytonia caroliniana* occurred at the three highest elevation sites.

The final weekend (May 30, 2008-June 1, 2008), both *P. fimbriata* and *S. pubera* were, again, found leafed out at all elevation. *Dicentra cucullaria* and *E. americanum* were absent at all sites. _Trillium erectum_ occurred only at the two highest elevations. *T. luteum* was found only at the lowest elevation. *Trillium grandiflorum* and *P. peltatum* were found only at the 1442 m site. *Dicentra canadensis* was found only at the mid-elevation (823 m) site. *Cardamine diphylla* and *C. caroliniana* showed inconsistency in flowering along the elevational gradient. A summary of the presence and absence of species for each of the three weekends can be found in Table1. This table does not represent which species were flowering, just which ones has exhibited leaf out.

Table 1: Presence and Absence of Stems

<table>
<thead>
<tr>
<th>Study Species</th>
<th>588 m</th>
<th>701 m</th>
<th>823 m</th>
<th>1442 m</th>
<th>1487 m</th>
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<tbody>
<tr>
<td>Week</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><em>P. fimbriata</em></td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td><em>S. pubera</em></td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td><em>T. erectum</em></td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>P</td>
</tr>
<tr>
<td>Species</td>
<td>Week 1</td>
<td>Week 2</td>
<td>Week 3</td>
<td>Week 4</td>
<td>Week 5</td>
</tr>
<tr>
<td>-----------------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
</tr>
<tr>
<td>T. luteum</td>
<td>P P P</td>
<td>P A A</td>
<td>A A A</td>
<td>A A A</td>
<td>A A A</td>
</tr>
<tr>
<td>T. grandiflorum</td>
<td>A A A</td>
<td>P P A</td>
<td>P P A</td>
<td>A P P</td>
<td>A A A</td>
</tr>
<tr>
<td>P. peltatum</td>
<td>A A A</td>
<td>A A A</td>
<td>P P A</td>
<td>P P P</td>
<td>P A A</td>
</tr>
<tr>
<td>D. cucullaria</td>
<td>A A A</td>
<td>P A A</td>
<td>A A A</td>
<td>A A A</td>
<td>A A A</td>
</tr>
<tr>
<td>D. canadensis</td>
<td>A A A</td>
<td>P A A</td>
<td>P P P</td>
<td>P P A</td>
<td>P A A</td>
</tr>
<tr>
<td>C. diphylla</td>
<td>P P P</td>
<td>P A A</td>
<td>P P A</td>
<td>P P P</td>
<td>P P A</td>
</tr>
<tr>
<td>C. caroliniana</td>
<td>A A A</td>
<td>P A A</td>
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<td>P P P</td>
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<tr>
<td>E. americanum</td>
<td>A P A</td>
<td>P A A</td>
<td>P A A</td>
<td>P P A</td>
<td>P P A</td>
</tr>
</tbody>
</table>

Presence (P) verses absence (A) of study species for all three weeks.

_Bloom Results_

*Elevation (meters) vs. Blooms/Stem*

For the three focus species, graphs revealed several trends. When examining blooms per stem in relation to elevation, *S. pubera* and *P. fimbriata* both peaked in flower around 800 m and showed a relatively normal distribution of blooms in relation to elevation for all three weekends (Fig. 1, Fig. 2, and Fig. 3). For the first week, the curve is the most robust in both species. For the later two weeks, the curves reach about the same peak in *S. pubera* and for *P. fimbriata* the curve is most depressed in the last weekend and only slightly less so in the middle weekend. In *S. pubera* there is a dip in
the curve around the 701 m site where there were no blooms observed. *Claytonia caroliniana* lacked a similar bell shaped pattern, instead it lacked abundance in the middle elevations during the first weekend of the study and only began to occur in the higher elevations in weeks two and three (Fig. 3).

**S. pubera blooms/stem vs. Elevation (m)**

![Graph](image)

Fig 1. *S. pubera*’s blooming pattern in relation to elevation
**P. fimbriata** blooms/stem vs. Elevation (m)

![Graph showing the blooming pattern of P. fimbriata in relation to elevation.](image)

Fig 2. *P. fimbriata’s* blooming pattern in relation to elevation

**C. caroliniana** blooms/stem vs. Elevation (m)

![Graph showing the blooming pattern of C. caroliniana in relation to elevation.](image)

Fig 3. *C. caroliniana’s* blooming pattern in relation to elevation
**Time(days) vs. Blooms/Stem for Individual Species**

When examining blooms per stem over time (in days) results are similar. For *P. fimbriata* the three lowest elevation (588, 701, and 823 meters) exhibited low blooms per stem in the first week, then declined to zero throughout the rest of the study. For these elevations, the least blooms per stem count occurred at the lowest elevation, followed by the second lowest blooms per stem count at the second lowest, with the most blooms per stem counted in the first week occurring at 823 meters. At the two highest elevations *P. fimbriata* shows a normal distribution with the zenith at the middle date of the study for the two highest elevations. In *S. pubera* few or no blooms per stem were found at the 701 meters and 1487 meters sites. At the 588 and 823 meter sites the blooms per stem count was heighest during the first weekend of study and declined steadily to zero. Most notably, the second highest elevation shows the beginning of what could be another bell shaped curve (Fig. 4 and Fig. 5). *Claytonia caroliniana* shows a completely different flowering pattern when compared to time. For all elevations where *C. caroliniana* was observed, the blooms per stem count starts out higher, then steadily declines to zero throughout the course of the study (Fig. 6).
Figure 4: *P. fimbriata*’s bloom presence for each elevation compared to time in days.

Figure 5: *S. pubera*’s bloom presence for each elevation compared to time in days.
Next, I examined the relationships of the three species to one another when blooms per stem was graphed against time in days. At 588 meters all three species hit their peak observed bloom on the first study weekend (Fig. 7). At 701 meters only *P. fimbriata* was observed in bloom, and it’s observed peak occurred during the first weekend (Fig. 8). The site occurring at 823 meters showed a peak bloom of *P. fimbriata* and *S. pubera* during the first weekend of the study. *Claytonia caroliniana* was not observed blooming at this elevation (Fig. 9). At 1442 meters *C. caroliniana* peaked during the first weekend and *P. fimbriata* and *S. pubera* most likely hit peak bloom.
shortly after the second study weekend (Fig. 10). Lastly, the site at 1487 meters showed *C. caroliniana* in peak bloom on the first weekend and *P. fimbriata* hitting its peak around the second study period. *S. pubera* was never observed in bloom at this elevation (Fig. 11).

**Figure 7:** Blooms/Stem across time in *S. pubera*, *P. fimbriata*, and *C. caroliniana* at 588 m.
Figure 8: Blooms/Stem across time in *S. pubera*, *P. fimbriata*, and *C. caroliniana* at 701 m.
Figure 9: Blooms/Stem across time in *S. pubera*, *P. fimbriata*, and *C. caroliniana* at 823 m.
Figure 10: Blooms/Stem across time in *S. pubera*, *P. fimbriata*, and *C. caroliniana* at 1442 m.
Figure 11: Blooms/Stem across time in *S. pubera*, *P. fimбриата*, and *C. caroliniana* at 1487 m.

*Soil temperature vs. Blooms/Stem for each Species*

Finally, I sought to graphically represent the soil temperature cue for each of the three selected species by plotting blooms per stem against soil temperature. For *P. fimбриата* the temperature at which peak bloom was reach was not consistent along the elevational gradient. The lowest temperature of peak bloom occurred at the highest elevation (1487 m) site at approximately 7.5 °C (Fig. 12) and the highest temperature of peak bloom occurred at lowest elevation site (588 m) at approximately 14.75 °C.
Figure 12: Blooms/Stem graphed against soil temperature for *P. fimbrata*. The peak of each line represents the peak bloom temperature at the respective elevation.

When examining *S. pubera*, I found that temperature of peak bloom was not the same at differing elevations. The lowest temperature of peak bloom occurred at the highest elevation (1487 m) site at approximately 7.5 °C (Fig. 13) and the highest temperature of peak bloom occurred at lowest elevation site (588 m) at approximately 14.75 °C.
Figure 13: Blooms/Stem graphed against soil temperature for *S. pubera*. The peak of each line represents the peak bloom temperature at the respective elevation.

Like the other two species *C. caroliniana* reached peak bloom at different temperatures based on location on the elevational gradient. The lowest temperature of peak bloom occurred at the second highest elevation (1442) site at approximately 5 °C (Fig. 14) and the highest temperature of peak bloom occurred at lowest elevation site (588 m) at approximately 14.75 °C.
Figure 14: Blooms/Stem graphed against soil temperature for *C. caroliniana*. The peak of each line represents the peak bloom temperature at the respective elevation.

With the exception of *C. caroliniana* at the 1442 meters elevation site, soil temperature of peak bloom was consistent between species at each point on the elevational gradient. At 588 meters all three species reached peak bloom at about 14.75 °C. For the second site at 701 meters, peak bloom was reached at approximately 12.5 °C, with the exception of *S. pubera* which was never observed blooming at 701 meters. At 823 meters, all three species hit peak bloom when soil temperatures were approximately 8.8°C. For *P. fimbriata* and *S. pubera* peak bloom at 1442 meters occurred at approximately 11.3°C. For *C. caroliniana*, this peak occurred at about 5°C. Finally, at 1487 meters, peak bloom for all three species occurred at about 7.5°C.
National Oceanic and Atmospheric Administration Temperature Results

It is interesting to note that for the two lowest elevation sites, soil temperatures were lower the second weekend of study than they were the first. In March, the area was experiencing some relatively low temperatures (Fig. 16), but these patterns did not persist. Near the date of the beginning of my study, the area was experiencing some of the highest temperatures of the month (Fig. 15), but these highs quickly tapered off after our data collection, reaching the average low of the month around the 15\textsuperscript{th}. Around the date of the second field weekend in May (11\textsuperscript{th}-12\textsuperscript{th}) temperatures were relatively stable, but were on average, lower than they had been around the same time in April (Fig. 17). Finally, around the end of May and into early June, the date of our last study weekend, temperatures were increasing steadily, consistent with the end of the spring growing season for vernal herbs.
Figure 15: Maximum daily temperatures for the Gatlinburg, Tennessee area for March-June of 2008.
Figure 16: Minimum daily temperatures for the Gatlinburg, Tennessee area for March-June of 2008.
DISCUSSION

When examining simple presence versus absence of leaf out in the study species, several trends can be observed. *Phacelia fimbriata* is present at all elevations each of the weeks of the study. In addition, *Stellaria pubera* was present at all elevations on all dates aside from the highest elevation on the weekend of May 11, 2008 thru May 12, 2008. As numbers for this site in the other two weeks were extremely low, it’s most likely that *S. pubera* was present and the sample size was simply not large enough to consistently observe its presence at these low levels. *Claytonia caroliniana* appears to be leafing out along the elevations as time passes, implying that as temperature increases, this species is leafing out at higher elevations. This assumption is contradicted by the presence of the
species at the 701 meter site. Again, the most parsimonious explanation for this is a sample size that was not large enough to fully capture the species diversity at each site on each date.

The three trillium species have similar inconsistent findings. Problems of sample size might explain the disrupted flowering pattern observed in *Trillium erectum*. The first and last sampling events suggest that *T. erectum* had already senesced in the lower elevations and is leafing out at higher elevation sites along elevational gradient. However, at the midpoint of the study, it was observed at the 701 meter elevational site. Never observing this species at the lowest elevation does suggest that the species was present at the mid elevation in the first week, and we simply did not observe it. *Trillium luteum* was never observed above the 701 meter site. This suggests that either the herb had not yet emerged at upper elevations, does not occur at the highest elevations, or I simply did not observe it. Lastly, *Trillium grandiflorum* never reached the highest elevation, but it did show a consistent progression through the mid-elevation sites. When examining the different trillium species, it is important to remember that this is a long-lived genus and, though pervasive at other locations within Great Smoky Mountains National Park, my sites were chosen based on the presence of *P. fimbriata*, not Trillium. Jules and Rathcke (1999) encountered similar problems when studying *Trillium ovatum* in Oregon. They were concerned that the timing and duration of their sampling events impacted their findings significantly. Despite this, all plants in the population they studied bloomed within three weeks of one another, indicating that the gaps between some of our sampling
periods might also impact our findings in addition to the poor choice of study site for Trillium.

The remaining five study species, *Podophyllum peltatum, Dicentra cucullaria, Dicentra canadensis, Cardamine diphylla,* and *Erythronium americanum,* all exhibit problems similar to those shown above. There was inconsistency in the progression up the elevational gradient with species present in the first and last study events but absent in the middle weekend; these findings are inconsistent with phenology cued by either photoperiod or temperature. *E. americanum*’s progression is almost consistent with a climb up the gradient, but it appears in the lowest elevation only in the middle field weekend. These kinds of inconsistencies are prevalent in all the remaining study species, making analysis of trends based on simple presence and absence problematic.

There are several possible explanations for these inconsistencies we observed in presence of absence of leaf out along the elevational gradient. As previously stated, sample size could impact findings. I did observe leaf out in all the species at some point, implying that for a measure of overall species diversity, our sample size was sufficient. However, the growing season of vernal herbs is greatly restricted by the speed of canopy closure in the spring (Giliam and Roberts 2003). This means that a species leafing out at a single elevation one month, senescing during the next month, then having a second wave of leaf out is extremely unlikely as fully exploiting the growing season is of paramount importance. In addition, aside from the three species that appeared most often (*P. fimbriata, S. pubera,* and *C. caroliniana*), the other species were rarely observed blooming. Many senesced bloomed were observed in the first and second weekends, but,
for the purpose of our study, only flowers capable of being pollinated were counted. This information coupled with low sample size might lead to the hypothesis that for many of the study species peak bloom occurred before the beginning of the study or during the month period between the first and second sampling events.

When examining phenology, a simply study of presence and absence of leaf out is not extremely telling. As the first three species detailed showed pervasive blooming and were observed in bloom at several elevations, they were appropriate to examine blooming patterns along the elevational gradient. When graphing elevation versus blooms per stem, a blooming pattern cued by temperature would be portrayed by a normal curve for each field weekend. The peak of this curve should migrate to the right along the x-axis for each successive study date if the full blooming phenology was captured by the study. This move along the x-axis would be seen as an indication that the bloom is occurring at successively higher elevations as the growing season progresses. In addition, the curve would be compressed vertically if the peak bloom had not yet occurred or had already occurred, reflecting low blooms per stem count.

For *P. fimbriata* and *S. pubera* the graphs of elevation in meters versus blooms per stem reflected such normal distributions and, in some cases, the hypothesized right shift. The robust curves in the first week imply that this is the peak bloom of the species at the mid-elevation. The two subsequent sampling events imply that the bloom has ended at the lower elevation and has not reached its peak in the highest elevation. In *S. pubera*, the dip in the curve where no blooms were observed at 701 meters is most likely explained by low sample size. For *C. caroliniana*, the blooming pattern is less consistent
with a phenology cued by temperature. The erratic occurrence of blooms in the first week could be due to small sample size. Despite this, the highest concentrations of blooms observed were in the lowest elevations this first week; this is somewhat consistent with our hypothesis. The bloom of this species was only observed in the highest elevation in the last two weekends, implying that the peak bloom of this species had passed by the time the second field weekend commenced.

Normal curves, similar to those resulting from graphs of elevation verses blooms per stem, were expected when graphing time versus blooms per stem if phenology is cued by temperature. Again, the graphs of *P. fimbriata* for time versus blooms per stem give support to the hypothesis that this species phenology is cued by temperature. The shape of the curve for the three lowest elevations may reflect that I missed the peak bloom for these elevations. The 1442 meter curve is not as robust as the 1487 meter site. This could show that I did not fully capture the bloom at this elevation or that the elevation was simply not as populated, in general, as the highest elevation. If temperature is cuing *P. fimbriata* to bloom, and I came in midway through the bloom in the lower elevations, the shape of the curves at the higher elevations is especially telling as I would expect to fully capture the bloom at these elevations.

I drew similar conclusions about the graph of time versus blooms per stem in *S. pubera*. No blooms were observed at 701 and 1487 meters. As previously discussed, the density of blooms in this species was never high. So in the mid-elevation, I attribute this to small sample size. In the highest elevation, it is more likely that the bloom had not yet reached this altitude. Again, I assume that the reasons for the shapes of the curves in the
lower elevations are a result of not capturing the full bloom. The 1442 meter site shows a less robust bell-shape consistent with temperature cued phenology and a less pervasive bloom.

In *C. caroliniana* the peak bloom occurred for all elevations in the first week of the study. This suggests that the peak bloom for this species had already passed before the beginning of the study, essentially cutting the graph off at or after the apex of the curve. If the phenology of this species were cued by temperature, I would expect the elevations to fall in a different order in respect to the y-axis, with the elevation experiencing peak bloom at the top, with the elevations above and below falling next, and the lowest elevations where peak bloom had passed approaching zero. However, as I could not observe the shape of the full bloom, no reliable assumptions can be made based on this particular graph.

It is best to discuss the analysis of time versus blooms per stem at each elevation and blooms per stem versus soil temperature simultaneously. The analysis of time versus blooms per stem for each elevation reveals that these are co-flowering species at numerous points along the elevational gradient (588m and 1442 m specifically). I believe that all three species are co-flowering at some time at each point on the gradient and my sample size and observational timing failed to capture this. With the exception of *C. caroliniana* at 1442 meters and *S. pubera*’s lack of observed bloom at 701 meters, all three species reach peak bloom at approximately the same soil temperature at each point along the elevational gradient. Peak bloom for the three species was not reached at the same time at each elevational site, implying that photoperiod was not the cue for bloom
time. The fact that temperature of peak bloom was consistent between species at different elevations but not the same for individual species at all elevations is an additional complication. If temperature were the controlling abiotic factor for bloom time, I expected this temperature to be consistent within a particular species across the elevational gradient. When examining the overall atmospheric temperatures of the area during the time of the study, no major highs or lows were persistent enough to cause a large change in soil temperature. And even if this were the case, the fact that peak bloom was not always the same in regard to time would negate this as a reason for the coinciding temperatures.

When returning to my hypothesis that not all flowering phenologies would be cued by the same temperature threshold resulting in differing co-flowering communities at different elevations, I find that my study was insufficient to either reject or fail to reject the hypothesis. Alternatively, my findings seem to indicate that, for at least *P. fimbriata*, *S. pubera*, and *C. caroliniana* the temperature of peak bloom is consistent along the elevational gradient but not within species. I have several alternative hypotheses to explain these findings.

First, such patterns could be the simple impact of acclimation to available sunlight. Rothstein and Zak (2001) showed that *Viola* had a high ability to acclimate and alter the rates or biological processes based on periods of direct irradiance. Routhier and Lapointe (2002) found evidence that *T. erectum* exhibited acclimation of carbon allocation patterns, overall plant size, and fruit characteristics due to differences in speed of canopy closure. As my sites encompassed a large variety of canopy types, light intensity and speed of
canopy closure are factors that could impact bloom time. Images 1-5 demonstrate the extent of canopy cover at each study site on May 30, 2008 thru June 1, 2008. We can see that at 588 meters (Image 1; a second growth site), 1442 meters (Image 4; a beech gap site), and the 1487 meters (Image 5; another beech gap) there are many more sun spots. Alternatively, at the old growth site (Image 2; 701 meters) the canopy is much more complete in its cover. This could lend support to the hypothesis that light availability cues blooms as we rarely observed in the three target species at this site (Figure 8). These images also indicate the density of other understory plants could also impact shading to small vernal herb species. The 823 meter site (Image 3) and the 1442 meter site differing digress of relatively sparse understory cover, whereas the 701 meter site (Image 2) and the 1442 meter site (Image 4) show more pervasive understory shading. The site at 701 meters couples the two levels of shading. Obviously, as no measures of light intensity were taken during the study, this is pure conjecture. Future studies should fully examine the impacts of light intensity in relation to bloom time and total bloom counts.

Alternatively, it is possible that the long lived nature of vernal herbs (Gilliam and Roberts 2003) lends these species to acclimate temperature of bloom based upon location, perhaps resulting in ecotypic differentiation. Ecotypes can develop when populations of a species persist in differing environmental conditions such as elevation, latitude, salinity, water availability, or heavy metals (Clary 1975; Bennington and McGraw 1995; Gauthier and Bedecarrats 1998). As co-flowering might prove advantageous for vernal herbs
(Campbell and Motten 1985), the fact that different species might acclimate to bloom at the same time at different elevations is not surprising.

Numerous additions to the study could be made to fully capture the phenotypic trends in the study species of Appalachian wildflowers. First, sample size and the duration of the study should be increased. The study should begin before the start of flowering (mid March) and continue until no blooms were observed at any elevation. This could be achieved by either having someone in the field at all times or setting up field cameras at each site that would take high enough quality photographs to allow for the counting of blooms. Most likely, a combination of these two approaches would work most effectively. Second, measures of light intensity should be taken. This would help to control for a major abiotic factor that was unaccounted for in this study. Finally, to fully understand phenotypic cues, studies must persist for several years. This adds power to the findings by showing consistency through time. Larger sample size would also allow the statistical analysis which is much more telling than graphical representation. I would also control more on the site level. Having different habitat types, initially, seemed wise. However, having the same sort of habitat could eliminate some of the confounding factors, such as light intensity and community composition, existing within the study. When examining ecotypic differentiation, transplanting specimens and growing in the greenhouse could reveal if specific populations bloom at differing elevations. Future studies should also examine the merits of genetic analysis of isolated populations such as those found in high altitude vernal herbs. If temperature is
controlling phenology and this temperature is, in fact, specific to location, genetic analysis could illuminate possible speciation.

Image 1: Lower Porter’s Creek Site; June 6, 2008 (588m)
Showing sun spots indicating incomplete canopy closure
Image 2: Upper Porter’s Creek Site; June 6, 2008 (701m)
No sun spots and complete canopy closure. Dense shading by other understory plants.

Image 3: Chimney Tops Site; May 30, 2008 (823m)
No visible sun spots, but much available light. Mild amount of shading by other understory plants
Image 4: Lower New Found Gap site; May 30, 2008 (1442m)
Large sun spots and sparse understory.

Image 5: Upper New Found Gap site; May 30, 2008 (1487m)
Showing canopy closure and dense understory shading.
What does all this tell us about the future impacts of global warming on the vernal herb communities in the Great Smoky Mountains region of the Southern Appalachian Mountains? If my alternative hypothesis of ecotypic differentiation is considered, impacts could be significant, but not in regard to co-flowering. As temperatures increase co-flowering will not be impacted as species are cued around the same temperature at each distinct elevation. However, the alteration of bloom date (resulting from higher temperatures earlier in the growing season) could still lead to decoupling of pollination webs. If pollinators were cued by the same temperatures as the study species, distinct pollinator communities acclimated to such specific temperature parameters would have to exist. My time in and around the study site leads me to reject this idea based on simple observation. If light intensity is the explanation, studies that examine the impacts of increased temperature on canopy closure would be appropriate to appraise the impacts of global warming. Based on my sites, I believe that the 701 meter site experienced canopy closer first, while the 588 meter and 1487 meter were more open and may have never experienced full canopy closure. This could explain some of the patterns we saw, especially at the 701 meter site. However, because an actual measure of light intensity was never taken, this is speculatory.

Lastly, future research should seek to better utilize naturally occurring elevation gradients in their studies of global warming. More extensive studies of this nature could tell us a great deal about the nature of phenology in response to changing climactic conditions while avoiding expensive manipulative techniques.
LITERATURE CITED


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