Severe frost but not shade could limit the future growing season of *Erythronium americanum*

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Severe frost but not shade could limit the future growing season of *Erythronium americanum*

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Abstract

Changes in climate are leading to modifications in the timing of seasonal events such as migrations and flowering. *Erythronium americanum* (trout lily) can break bud early in response to warming, but changes to its growing season may be limited by early shade from canopy trees and frost. I experimentally assessed the impact of shade and frost on senescence in *E. americanum* and descriptively monitored the response of *E. americanum* to vernal air and soil temperatures in a garden setting. Early shade did not affect the timing of senescence. Experimental exposure to frost resulted in increased leaf damage, earlier senescence, and greater corm death than in control plants. Despite ten days in which the air temperature dropped below freezing, there was no evidence of leaf damage in the field. These results suggest that early shade from canopy trees will not hasten the end of the future growing season for *E. americanum*, but that late frost could bring about early senescence if that frost is sufficiently hard.

Keywords

climate change, forest ecosystem, forest understory, freezing, leaf lifespan, Liliaceae, senescence, spring ephemeral, trout lily, deciduous forest

Introduction

Global climate change is causing modifications to patterns of temperature and precipitation around the world (e.g., Di Cecco and Gouhier, 2018; Konapala et al., 2020). In particular, these changes are affecting the timing of transitions between seasons, with spring temperatures arriving earlier than typical in some areas (Monahan et al., 2016; Christiansen, Markstrom and Hay, 2011). As a result, some species have altered the timing of their migrations (Gill et al., 2014; Somveille et al., 2020), flowering (CaraDonna, Iler, and Inouye, 2014; Bertin,

2015), bud break (Sivadasan et al., 2017; Ladwig et al., 2019), and leaf senescence (Gallinat, Primack and Wagner, 2015; Wu et al., 2018).

One species that is capable of adjusting its timing of bud break is *Erythronium americanum* Ker. Gawl. (Werier, 2017). This species is native to the northeast United States (Siccama, Bormann and Likens, 1970; Stokes, Philpott and Culley, 2019) and is a spring ephemeral, with leaves emerging shortly after snowmelt and senescing after canopy leaf out (Muller, 1978; Tessier, 2008). This early activity makes this species valuable to wildlife as a source of pollen (Thomson, 1986; Austen, Lin and Forrest, 2018). Vernal activity in *E. americanum* also makes this species important to nutrient cycling and retention (Muller, 1978; Lerat et al., 2002). When exposed to early warming, *E. americanum* can hasten its leaf out, suggesting that early spring warming could expand its growing season (Tessier, 2019). What is not clear is what ecological factors could limit the expansion of the growing season for *E. americanum*.

This study addressed the question: if *E. americanum* can emerge early in response to early spring warming, will other factors prevent it from extending its growing season? I hypothesized that early shade from canopy trees and late spring frost could shorten the duration of the growing season for leaves of *E. americanum* that emerge early (Inouye 2000, 2008). This hypothesis led to two predictions. First, shaded leaves will senesce earlier than those in full sun. Second, leaves that emerge early will suffer death if exposed to extended freezing temperatures.

Materials and methods

I assessed the effect of early shade on leaf senescence experimentally. Thirty subpopulations of *E. americanum* were identified in a second growth hardwood forest in Delhi, NY (42° 16' 33" N, 74° 55' 98" W) on April 19, 2020. A different field site was used for the

shade component of this project than the frost component due to logistical constraints during the COVID-19 Pandemic (Korbel and Stegle, 2020; Myers et al., 2020). Each subpopulation was at least 1 m from its neighbor to ensure different genets. Cube-shaped shade structures (15 cm on all sides) were constructed of PVC tubing and greenhouse shade cloth. At least 10 leaves of each subpopulation were covered by a shade structure and at least 10 other leaves of each subpopulation were left uncovered. I measured light intensity on cloudless days between 10 AM and 2 PM with a LI-COR LI-250 Light Meter (LI-COR Biosciences, Lincoln, NE, USA) inside (shade) and outside (control) of the shade structures on April 28, 2020 and after the tree canopy closed in both background light (forest floor in the shade of the tree canopy) and sunflecks (small areas of high light intensity where the tree canopy does not provide background levels of shade) on June 8, 2020. Twice per week, I assessed the subpopulations for senescence, documenting when it began and was complete for each treatment and replicate. Beginning of senescence was recognized as yellowing or browning of the leaf and end of senescence was recognized as the leaves being brown and no longer upright.

I also assessed the response of *E. americanum* to frost experimentally. On November 21, 2019, I collected 120 corms from a second growth hardwood forest near Delhi, NY (42° 14' 33" N, 74° 56' 03" W). These corms were planted in seed starting trays in forest soil collected from the O_a layer (where corms usually are found, within the bottom 10 cm of the organic soil horizons) of the same forest. The trays were placed in a refrigerator at 5°C and watered when the soil surface appeared dry (approximately weekly). Corms were assigned to a treatment in a systematic design within the trays (Hurlbert, 1984). On February 20, 2020 the trays were removed from the refrigerator and placed on a lab bench (18°C) under a fluorescent lamp. Eight plants were already emerging from the soil at that time. By March 6, 117 plants had emerged

and no others did so after that time. On March 10, all plants were moved back to the refrigerator under the lamp for cold acclimation. On March 11, 30 plants for each treatment were placed on a shelf in a freezer (to provide airflow on all sides) at -3°C for 0 (control), 1, 8, or 24 hours. While the air temperature of the freezer was -3°C , the soil may not have reached that temperature, particularly in the 1-hour treatment. When their time in the freezer was over, the plants were moved back to the lab bench. On March 13, leaves were categorized based on their leaf area of damage (undamaged leaves were upright and medium green while damaged areas were flaccid and dark green) where 0 = no damage, 1 = 1-25% damaged, 2 = 26-50% damaged, 3 = 51-75% damaged, and 4 = 76-100% damaged. Leaves were monitored daily to document date of senescence. On April 10, (after all leaves had senesced) corms were excised and assessed for survival where 0 = dead and 1 = alive. Live corms were solid with a tan husk and dead corms were soft and dark or decomposed leaving only the outer husk.

To document frost damage outside of the lab, I used a descriptive study with a population of *E. americanum* growing in a garden setting in the Village of Delhi, NY for logistical feasibility ($42^{\circ} 16' 39'' \text{N}$, $74^{\circ} 55' 25'' \text{W}$). From snowmelt (March 2, 2020) until senescence of the plants (June 9, 2020), air (at ground level) and soil temperature (5 cm depth) were measured where the plants were growing in the morning (daily low) and afternoon (daily high) with a soil temperature probe (HBE International, South Wayne, NJ, USA). The intention was to note the temperature when any leaf damage appeared, but none did despite a study-wide low of -3°C air temperature after leaf out.

All data analyses were conducted using Minitab version 19 (Minitab, Inc., State College, PA, USA) at $\alpha = 0.05$. Light measurements from the shade experiment were compared with Analysis of Variance followed by a Tukey's means comparison test. The day of year for both

the start and end of senescence were compared between the shade and control plants using a paired t-test. In the frost experiment, the amount of damage, day of year of senescence, and corm survivorship were each compared among the different durations of freezing with Analysis of Variance and a Tukey's means comparison test. Finally, the temperature data from the field were used to regress air temperature against soil temperature to determine the air temperature at which the soil would reach the experimental -3°C during an overnight period.

Results

In the shade experiment, each light intensity was significantly different from the others ($F_{119,3} = 404.90$, $P < 0.0001$). The light intensity was 1245.9 ± 32.2 (mean $\pm$ standard error) $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the control, 411.2 ± 32.0 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the shade treatment, 281.3 ± 26.1 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the sunflecks, and 24.49 ± 3.41 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the background, closed canopy. The greatest absolute difference in mean light intensity was between the control and the other three conditions. Given that the shade treatment had more light than the sunflecks and background during the fully closed canopy condition, it is representative of mid-canopy closure when *E. americanum* typically begins senescing. There was no significant difference between the control and shade treatment in start date of senescence ($T = 0.000$, $df = 29$, $P = 1.000$) nor end date of senescence ($T = 0.44$, $df = 29$, $P = 0.662$; Figure 1). In both the control and the shade treatment, senescence began in late May and ended in mid-June (Figure 1).

There was significantly more leaf damage in the plants experimentally exposed to freezing than those in the control group, but no difference in the amount of leaf damage among those plants exposed to freezing for 1, 8, and 24 hours ($F_{115,3} = 187.37$, $P < 0.0001$; Figure 2A). On average, control plants had less than 25% of their leaves damaged while those that experienced any freezing had more than 75% of their leaves damaged (Figure 2A). Leaves in the

control senesced significantly later than those that experienced freezing, but there was not a significant difference in the time of senescence of leaves that experienced freezing ($F_{115,3} = 153.68$, $P < 0.0001$; Figure 2B). Control leaves senesced in early April and those in the 1, 8, and 24 hours of freezing treatments senesced in mid-March, within days of the freezing conditions. Likewise, the control plants had a higher corm survival rate than those that experienced freezing, but there was no difference in survivorship among the 1, 8, and 24 hour freezing treatments ($F_{119,3} = 99.23$, $P < 0.0001$; Figure 2C). Four corms died in the control, 27 corms died in the 1 hour treatment, and all thirty corms died in both the 8 hour and 24 hour treatments (Figure 2C).

In the descriptive field study, there was no evidence of frost damage on any of the *E. americanum* leaves. There was only one morning after the *E. americanum* leaves emerged from the soil that the air was -3°C or lower. On 10 days, the air temperature at ground level was at or below freezing. Ice crystals were visible on the leaves on four mornings. The lowest soil temperature was -1°C , which occurred on three mornings. All three of those mornings were before the leaves emerged. In this field study, the air temperature would have to be -8°C for the soil and corms to reach -3°C , based on the relationship between air and soil temperature (Figure 3).

Discussion

Early exposure to shade did not result in early senescence in *E. americanum* (Figure 1), which rejects part of the hypothesis. Senescence in this experiment occurred at a typical time for the species (Muller, 1978; Tessier, 2008), when the canopy leaves were expanding. In contrast, Taylor and Pearcy (1976) noted earlier senescence in *E. americanum* plants growing under tree species that leaf out early, though they did not show data for this observation. Also, Kim et al. (2015) found that shade hastened senescence in the congener *E. japonicum*, but their light levels

were considerably lower than those of this study, with their control being around $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and their shade treatment being around $50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The results of this study suggest that if canopy trees leaf out earlier than currently the norm with a warming climate (Richardson et al., 2006; Polgar and Primack, 2011), they will not cause a significantly early end to the growing season for *E. americanum*. However, the shade from canopy leaves may reduce the total photosynthetic capacity during that growing season (Taylor and Percy, 1976; Percy, 1988; Chazdon and Percy, 1991). Like other spring ephemerals, *E. americanum* exploits the leaf-free period to conduct photosynthesis at a high rate to compensate for its relatively short growing season (Eickmeier and Schussler, 1993; Hull, 2002). Most sun-adapted species and leaves are not successful in adapting to shaded environments (Groninger et al., 1996; Kubiske and Pregitzer, 1996; Lombardini, Restrepo-Diaz and Volder, 2009; Mathur, Jain and Jajoo, 2018). If the high light intensity in the understory disappears early due to canopy leaf out (see Results; Kato and Komiyama, 2002; Dreiss and Volin, 2013), the photosynthetic benefit of extending the late end of the growing season in *E. americanum* may be reduced. Therefore, while early shade from canopy trees should not shorten the physical growing season, it may shorten the functional growing season.

At first glance, the results of the experimental freezing and the field descriptive study appear contradictory, with the experimental results supporting the hypothesis and the descriptive results rejecting the hypothesis. However, they together tell a more complete story. It is clear from the experiment that if the leaves and corm reach -3°C , there is significant frost damage and corm death (Figure 2). Similarly, Loik et al. (2004) saw such susceptibility to frost in *Erythronium grandiflorum*. Importantly, reaching this level of frost (-8°C air temperature) during the growing season for *E. americanum* is probably rare under the current climate. Based on data

from the nearest weather station to the field site from the National Oceanic and Atmospheric Administration (NOAA, 2020), such temperatures have been reached during the above ground season for *E. americanum* in two of the last four years and nine total times. Weather stations that produce these data are typically in open areas to get data for temperature and precipitation that lack interference by trees and other aboveground structures, making these stations more likely to experience colder temperatures than the more sheltered microclimates where *E. americanum* grows (Beatty, 1984; Vanwallegghem and Meenemeyer, 2019; Zellweger et al., 2020). Collectively, if *E. americanum* starts its growing season early as the climate warms (Ladwig et al., 2019; Tessier, 2019), it may suffer frost damage and potentially corm death from severe, late frosts in some years (Figure 2, Gu et al., 2008; Hufkens et al., 2012). This pattern may further drive the species into more sheltered and warmer microclimates in the forest (Beatty, 1984; Vanwallegghem and Meenemeyer, 2019; Zellweger et al., 2020), thereby reducing its abundance across gradients (Van Der Veken, Bossuyt and Hermy, 2004; Gracia et al., 2007). However, the frost would have to be severe to bring about any damage to the plants and repeated across years before affecting the demography of the population.

Barring repeated and heavy late frost, *E. americanum* could experience an extended growing season with future climate warming. Early spring warmth causes plants of this species to break bud and emerge early (Tessier, 2019) and potentially early shade from canopy trees will not cause an advanced end to the growing season (Figure 1). This extension provides greater opportunity for photosynthesis under high light, spring conditions (Lapointe, 2001; Kato and Komiyama, 2002) and could lead to greater energy resources for reproduction, both vegetative and sexual (Muller, 1978; Weiner et al., 2009), pending risk of frost damage to reproductive structures (Thomson, 2010). Such an extension of the growing season in *E. americanum* would

be consistent with patterns in other plant species (Christiansen, Markstron and Hay, 2011; Haggerty and Galloway, 2011; Piao et al., 2019).

The results of this study lead to new questions about changes in the growing season caused by climate change. First, are other spring ephemerals capable of responding to early warming in the way that *E. americanum* can? In the northeast United States, *Claytonia caroliniana*, and *Allium tricoccum* are common spring ephemerals and candidates for such study (Rock, Beckage and Gross, 2004; Parker and Thomson, 2018). Second, can wintergreen species (such as *Dryopteris intermedia*, *D. marginalis*, and *Polystichum acrostichoides*; Noodén and Wagner, 1997; Tessier, 2014) break bud early with warming, withstand late frost, and extend their access to high light conditions in the spring? Third, how much does canopy leaf out reduce the photosynthetic rate in *E. americanum* and other understory species (Brach, McNaughton and Raynal, 1993; Hull, 2002). Significant reductions would minimize the functional utility of keeping leaves in the shade. Fourth, what determines timing of senescence in *E. americanum*? If shade does not hasten senescence, other ecological and physiological factors could play a role (Lim, Kim and Gil Nam, 2007; Gutjahr and Lapointe, 2008; Gandin et al., 2011; Liu et al., 2020)

In summary, late frost could limit the expansion of the growing season for *E. americanum* in a warming climate if those frosts are hard enough and frequent enough to injure the plants. Shade from early canopy leaves will not cause early senescence. New questions tie to related species and species groups in regard to their capacity to expand their growing season and functional changes in *E. americanum* once canopy leaves open.

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233 **Data availability statement**

234 Data are available from figshare in August 2022: 10.6084/m9.figshare.16435584. Data can be
235 reused with permission of the author.

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Draft

438 **Figure 1.** Timing of senescence in *Erythronium americanum* for control plants and those
439 exposed to experimental early shade in a second growth hardwood forest in Delhi, NY USA. (A)
440 Start date of senescence. (B) End date of senescence. Statistical results are for a paired t-test.
441 Error bars indicate one standard error.

442 **Figure 2.** Effect of experimental exposure to frost in *Erythronium americanum* under laboratory
443 conditions for plants exposed to 0, 1, 8, and 24 hours of -3°C temperatures. (A) Leaf damage
444 where scores are 0 = no damage, 1 = 1-25% damaged, 2 = 26-50% damaged, 3 = 51-75%
445 damaged, and 4 = 76-100% damaged. (B) Day of year of leaf senescence. (C) Percent corm
446 survivorship. Statistical results are for Analysis of Variance and Tukey's means comparison test.
447 Error bars indicate one standard error.

448 **Figure 3.** Relationship between air (at ground level) and soil (5 cm depth) temperature during
449 the spring of 2020 in a garden setting with *Erythronium americanum* in Delhi, NY USA.
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