False spring damage on temperate tree seedlings is amplified with winter warming

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Introduction

1. The timing of spring in temperate deciduous trees and shrubs shapes plant and animal communities and influences ecosystem services from agriculture to carbon sequestration to forest management.
   (a) With warming temperatures in the Northern Hemisphere, spring phenology (i.e., budburst and leafout) is advancing.
   (b) Budburst in trees and shrubs requires three cues: (1) over-winter cold temperatures (chilling), (2) warming spring temperatures (forcing) and (3) longer daylengths (photoperiod).
   (c) As budburst and leafout are strongly cued by temperature, deciduous woody plants provide compelling evidence of climate-induced warming.
2. And though the world is getting hotter, climate change is affecting general temperature trends but extreme weather events (e.g., polar vortexes) are still occurring.
   (a) One such weather event is known as a 'false spring', which is when temperatures drop below freezing after budburst has initiated.
   (b) Temperate plants are at risk of freezing temperatures and have evolved to minimize risk through myriad strategies, with the most effective being avoidance: plants must exhibit flexible spring phenologies in order to maximize growth and minimize spring freeze risk by timing budburst effectively.

(c) Freezing tolerance steadily decreases after budburst begins until the leaf is fully unfolded, with leafout being the most susceptible to false spring damage (Lenz *et al.*, 2016).

(d) Seedlings and saplings initiate budburst before canopy closure in order to benefit from the increased light levels (Augspurger, 2008; Vitasse *et al.*, 2013), which potentially puts understory species at greater risk to false spring damage than adult trees (Vitasse *et al.*, 2014).

(e) False springs can be very damaging, with reports of trees taking 16-38 days to refoliate after leaf loss from freezing temperatures (Augspurger, 2009, 2013; Gu *et al.*, 2008; Menzel *et al.*, 2015).

(f) Such damage can have cascading effects to pollinators (Boggs & Inouye, 2012; Pardee *et al.*, 2017), nutrient cycling and carbon uptake (Hufkens *et al.*, 2012; Klosterman *et al.*, 2018; Richardson *et al.*, 2013)

(g) False springs are predicted to increase in certain regions as climate change progresses, thus understanding the impacts of false springs on forests is essential for forest management strategies (**?**).

3. With climate change advancing, chilling is predicted to decrease as winter temperatures warm, potentially impacting phenology and, ultimately, growth.

(a) Deciduous trees and shrubs require a certain number of chilling hours in order to leave the endodormancy phase.

(b) This helps protect temperate plants against stochastic warm spells in the winter and reduce the risk of a false spring.

(c) Optimal chilling accumulates between 0°C to 4°C, which is also the optimal temperature for starch degradation to sugar accumulation (Tixier *et al.*, 2019).

(d) Decreases in chilling temperatures from climate change could affect budburst timing.

(e) And, reduced chilling—especially if there are fewer cold nights—could impact a plant's tolerance of freezing temperatures throughout the winter.

(f) As plants enter dormancy, their vulnerability to freeze damage begins to increase and their cold hardiness (i.e., freezing tolerance) increases.

(g) Cold hardiness allows plants to survive freezing temperatures through myriad mechanisms including deep supercooling, increased solute concentration, and an increase in dehydrins or other proteins (Sakai & Larcher, 1987; Strimbeck *et al.*, 2015).

4. Here, we assess the effects of climate change on temperate tree and shrub seedlings to test:

(a) (1) How reduced chilling impacts temperate plant phenology and growth?

(b) (2) How reduced chilling affects spring freezing tolerance?

(c) (3) How false springs impact seedling growth?

The actual temperatures that plants can tolerate vary strongly by species and by a tissue's degree of cold hardiness. During the cold acclimation phase — which is generally triggered by shorter photoperiods (Howe *et al.*, 2003; Charrier *et al.*, 2011; Strimbeck *et al.*, 2015; Welling *et al.*, 1997) and, in some species, cold nights (Charrier *et al.*, 2011; Heide & Prestrud, 2005) — cold hardiness increases rapidly as temperate plants begin to enter dormancy. At maximum cold hardiness, vegetative tissues can generally sustain temperatures from -25°C to -40°C (Charrier *et al.*, 2011; Körner, 2012; Vitasse *et al.*, 2014) or sometimes even lower temperatures (to -60°C in extreme cases, Körner, 2012). Freezing tolerance diminishes again during the cold deacclimation phase, when metabolism and development start to increase, and plant tissues become especially vulnerable.

Methods

We assessed the effects of three levels of over-winter chilling on seedling phenology and growth across ten temperate tree and shrub species. Once budburst was initiated, half of the individuals were exposed to freezing temperatures at -3ÂřC for three hours in a controlled growth chamber environment to mimic a false spring. Individuals were then put in a greenhouse for the remainder of the growing season to measure phenology and growth.

We found that false springs impacted growth and growing season length. Individuals exposed to the false spring treatment took longer to fully leafout at the beginning of the season and initiated dormancy earlier at the end of the season, thus reducing the length of the growing season. Additionally, across all species and chilling treatments, individuals exposed to false springs experienced more damage to the main shoot and relied more on lateral shoot growth, rendering inefficient growth patterns. However, individuals had increased growth with increased over-winter chilling. With sufficient chilling, growth and biomass were much higher—whether or not they were exposed to a false spring—suggesting chilling is more important for seedling growth than avoiding false springs. With climate change and warming temperatures, over-winter chilling is anticipated to decrease and false springs are predicted to increase in certain regions. This combination could greatly impact plant performance, survival and shape species distributions, ultimately affecting crucial processes such as carbon uptake and nutrient cycling.

Though spring phenology (e.g., budburst and leafout) is advancing with recent climate change, last freeze dates are not anticipated to advance at the same rate. This mismatch in timing could result in more intense false spring events for temperate tree and shrub species and impact some of our crops—like apples. These

events can damage buds, leaves and flowers and, in extreme cases, result in canopy dieback or damage to the xylem. Thus, false springs can have drastic economic and ecological consequences. Boston springs are confusing, temperatures can drop significantly in early February but rise again in early March, just to lead to one last snow storm at the end of March or early April. Since starting my PhD at the Arboretum, I have found myself watching the Magnolias as they are common victims of these fluctuations: they often bloom early in the season—sometimes as early as February—but then the flowers can sustain a large amount of damage from those March snow and ice storms.

Since springs can be so tricky to navigate, temperate plants have evolved to minimize false spring damage through myriad strategies, with the most effective being avoidance: plants must exhibit flexible spring phenologies in order to maximize growth and minimize false spring risk by timing budburst effectively. By having flexible phenologies, individuals can take advantage of a full growing season, without being at risk of freezing temperatures.

In an experiment I ran at the Weld Hill Research Building, I examined the effects of false springs on eight deciduous tree and shrub seedlings. I discovered that trees exposed to freezing temperatures after budburst sustained leaf damage, which ultimately led to shorter growing seasons. I also found that false springs cause damage to the shoot apical meristem (i.e., the region that allows a plant to grow straight and tall), leading to unique growth patterns. And though these changes in growth habits can be charming, they are largely inefficient and could result in seedling dieback in our forests. Additionally, I evaluated the impacts of less over-winter chilling, an essential cue in spring phenology and one that is predicted to decrease with increasing temperatures. I found that chilling not only affected budburst timing but it also determined the amount of growth an individual experienced over the course of a growing season. Individuals with less over-winter chilling had less total biomass overall.

Our forests are essential carbon sinks, they sequester carbon, mitigate the effects of climate change and work to counteract human impact. If we continue to practice poor habits that harm our environment, our trees will be at risk of having less efficient growing seasons, thus leading to smaller forests and subsequently a reduction in our carbon sinks.

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