# THE EFFECT OF THE TIMING OF EXTREME CLIMATIC EVENTS ON PLANT COMMUNITIES

By

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# ABSTRACT

In the last 100 years, the Earth's climate has warmed by approximately 1 $^{0}$C, causing extreme climatic events (ECEs) to increase in frequency, intensity, and severity worldwide. ECEs can change nutrient flows, alter organismal development, and modify population and community dynamics. As a result, ECEs have major ecological consequences that can last years after the event. Contrary to increases in mean climatic averages, ECEs are discrete events that occur at specific times during the life cycle of organisms or a community assembly. Because ECEs are characterized by extreme weather such as extreme heat or intense rain, ECEs have the potential to behave as a disturbance for many organisms and species interactions. Many studies have focused on the consequences of ECEs on phenology, ontogeny and some on population and community dynamics. Although the consequences of ECEs might be sensitive to when they occur, their timing has mostly been ignored in previous studies. In my first chapter, I explored how ECEs timing alters biological processes at the individual, population, and community scales. In my second chapter, I investigated how the timing of heat waves alters community composition and plant growth. In my third chapter, I investigated how the timing of heat waves can change plant physiology and have consequences for ecosystem services. During 2019, 2020, and 2021 I found that early- and late-season heat waves have the most potential to alter plant community compositions, stomatal conductance, and plant growth. These effects can be positive or negative depending on the plant species. Beyond these, I show that the consequences of heat waves can occur even a year after the event. Finally, certain heat waves have the potential to cascade to lower trophic levels, decreasing decomposition rates. My research provides information on the timing of ECEs and indicates that changes in community composition, plant growth, physiology, and decomposition respond to heat waves depending on when they happen.

*Esta tesis se la dedico a mis padres Margarita Elizeth Mejía Rojas y José Antonio Cinto Pérez por todo su amor y apoyo desde el otro lado del océano.*

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# TABLE OF CONTENTS

# CHAPTER 1:

## THE ECOLOGICAL CONSEQUENCES OF THE TIMING OF EXTREME CLIMATIC EVENTS

### Acknowledgment of prior publication

This chapter is a reprint of an original peer-reviewed article published in Ecology and Evolution in 2023, 13: e9661. The original article can be found at doi: 10.1002/ece3.9661.This an open-access article that allows the article to be downloaded, reused, modified, distributed, and/or copied as long as the original creators are credited via citation.

### Introduction

In the last decade, a growing number of ecological studies have focused on extreme climatic events (ECEs), which are increasing in frequency and severity across the globe (Meehl and Tebaldi 2004; Jentsch et al. 2007). ECEs, such as heat waves, drought, heavy rainfall, cold snaps, and cyclones, are characterized by short time periods of severe weather that disturb ecological systems (Smith 2011). Recent work has demonstrated that ECEs can contribute as much to the ecological consequences of climate change as changes in mean climatic conditions (Maxwell et al. 2019), making an understanding of the ecology of ECEs crucial to predicting and responding to the consequences of climate change in general. In this paper, we propose that a key piece missing from our understanding of the ecological consequences of ECEs is the role of their timing—when an ECE occurs relative to the timing of the biological processes it impacts. Resolving the role of timing will help researchers predict the consequences of ECEs and identify how, which, and when systems are most sensitive to the effects of ECEs.

Over the last few decades, an increasing number of climate change experiments have adopted temporally realistic abiotic regimes, including manipulations of the frequency, duration, and amplitude of extremes. For example, manipulating heavy rainfall events after a fire, de Luís et al. (2005) found that extreme rain reduces the survival of plant seedlings. Increased drought period events altered plant phenology delaying flowering in two Mediterranean shrublands (Llorens and Peñuelas 2005). More recent reviews (Jentsch et al. 2007, Thompson et al. 2013) call out the importance of studying climate variability and incorporating extreme values into future climate change research as well as the need to address the timing of such events. Many ECEs, like many disturbances, are discrete events that occur at specific times during the biological processes that they impact (Sergio et al. 2018), and this fact suggests that the consequences of ECEs will depend on the timing of biological and ecological events in relation to the timing of the ECE. The role of event timing has received significant attention in the ecological disturbance literature, where timing has been found to be of great importance for how disturbances affect organisms, populations, and communities. For example, physical soil disturbance can drive some plant species to extinction depending on when it occurs during community assembly (Crawley 2004). Similarly, in aquatic systems, algal communities vary in resistance to spates (flooding events) through community dynamics (Peterson and Stevenson 1992). Studies of climate change, however, have been slow to adopt the temporally explicit perspective needed to examine how the consequences of ECE depend on when they occur. Moreover, the effects of ECE timing may differ in important ways from our understanding of timing from the disturbance literature. First, many extreme climate events differ from most traditionally studied ecological disturbances. For example, events like heat waves, while stressful for many organisms, are not truly destructive (Jentsch et al. 2007). They affect ecology primarily through sublethal effects (Conradie et al. 2019, Domínguez et al. 2021) and may directly benefit some species, e.g., by increasing growth rates of heat-tolerant and temperature-limited species. Second, climate-related events often have characteristic timings, meaning that predicting their consequences requires studying these specific timings (e.g., hurricane season), rather than timing in general. Finally, some extreme climate events can have very large spatial extents, like the 2003 heat wave that affected all of Europe (García-Herrera et al. 2010), making spatial processes like recolonization potentially less important for ECEs than they are in traditional disturbance dynamics.

In this perspective, we explore how the consequences of ECEs might depend on biological timing at three scales (Figure 1.2): At the individual scale, we explore how the ecological consequences of an ECE will depend on the physiological and ontogenetic stages of organisms when an ECE occurs. At the population scale, we examine how the ecological effects of an ECE are contingent upon when the event occurs through the course of population dynamics. At the community scale, we explore how the ecological effects of an extreme climatic event vary with when an event occurs through the course of community dynamics. Finally, we show how considering differences in the timing of the ecology and biology of individuals, populations, and communities across ecosystems leads to testable predictions about when ecosystems might be susceptible to ECEs and in which ecosystems variation in timing might be more influential. Identifying how the outcomes of an ECE might vary through time and across ecosystems will improve our ability to understand the impacts of extreme weather. Throughout our paper, we use the term timing to mean when an ECE happens, in contrast to studies that focus on duration, frequency, or other aspects of timing.

Figure 1.1. Effects of ECEs at different timings during species ontogeny. A Persimmon species (Diospyros sp.) during vegetative stages (a) and a Chinese redbud (*Cersis chinensis*) during flowering stages (b) both damaged after the 2021 cold wave in Texas, USA. Photo credit: Keri Greig.

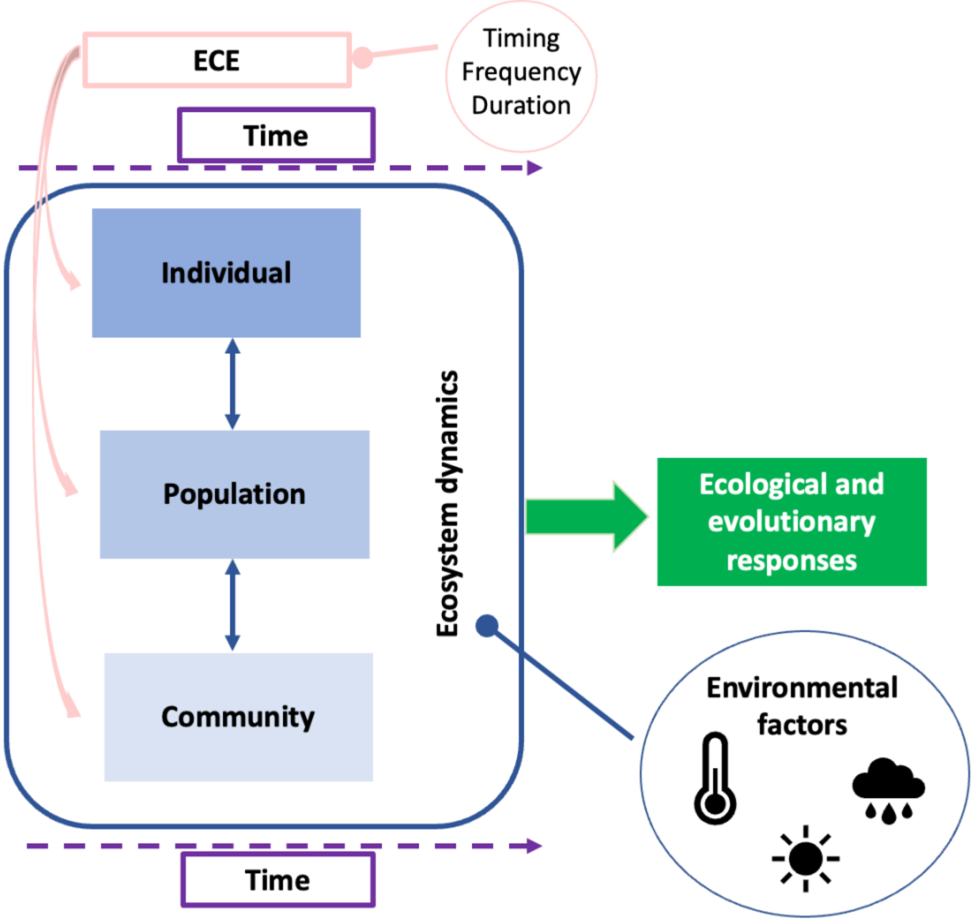


Figure 1.2. The timing (when the ECE happens), frequency, and duration of an ECE in relation to the timing of events at the individual, population, or community scale will determine future ecological and evolutionary responses, and when we might see those responses based on the ecosystem adaptation to environmental factors.

### Individual level timing

Organisms undergo biological changes through time including continuous changes in traits through growth and development and discrete changes during life history events (e.g., breeding or migration). In this section, we discuss how the ecological consequences of an ECE will depend on the current ontogenetic stages and states of the organisms present in the community when and where the ECE occurs (Figure 1.1). Extreme conditions alter physiological processes, and these effects depend on when the event happens during an organism's ontogeny. Throughout the paper, we define susceptibility or vulnerability of an organism to an ECE as the period or periods of time during organism life that due to physiological changes an ECE has a higher chance of altering the organism's response to the ECE. The susceptibility or vulnerability of an organism to an ECE is the extent to which its biological processes are perturbed by an ECE at a given point in time. For example, when considering extreme heat temperatures, all insect stages present at the time of the event will experience extreme temperatures, but the growth and survival consequences for each individual will depend on its ontogenetic stage. This stage-specific thermal response (Chun-Sen et al. 2021) governs the ontogenetic timing of susceptibility or vulnerability to the stress associated with an ECE.

Evidence from the literature suggests that the timing of ECEs predicts the physiological changes and mortality they cause. For example, the effects of heat waves on the survival of green peach aphids (*Myzus persicae*) depend on aphid age (Gillespie et al. 2012). Crucially this is also true for the nonlethal effects of an ECE on organismal performance. When cereal aphids (*Metopolophium dirhodum*) experience heat events their lifetime fecundity and longevity depend on their life stage during the event (Chun-Sen et al. 2004). Similarly, heat waves reduce the growth and development of tobacco hornworms (*Manduca sexta*) if the event happens during early stages of development but not later in ontogeny (Kingsolver et al. 2021). Even the direction of a response can vary with ECE timing. In both big bluestem (*Andropogon gerardii*) and goldenrod (*Solidago canadensis),* high heat events have opposite effects on photosynthetic rates and productivity depending on plant stage (Wang et al. 2016). In the case of marine invertebrates, Pandori and Sorte (2019) published a meta-analysis of over 250 experiments showing that while all life stages are affected by ECEs, younger stages like embryos and larvae are more sensitive to extreme heat. The bottom line is that ontogenetic variation in susceptibility to the stresses associated with ECEs can lead slight variation in the timing of an ECE to result in ecological consequences that differ quantitatively as well as qualitatively (Figure 1.3).

A key aspect of how ECE timing will interact with ontogenetic timing is the temporal pattern of trait change through ontogeny. Many traits change gradually and linearly with growth, while other traits, such as life history events, vary nonlinearly or cyclically through time (Post et al. 2001). The relationship between ontogeny and other physiological changes will vary with each trait and should be considered when examining the consequences of an ECE during growth. In marine species, such as mollusks, tolerance to salinity varies nonlinearly through development (Mann and Harding 2003). Plants like narrow leaved plantain (*Plantago lanceolata*) have a positive relationship between age and the chemical defense concentrations, and a negative relationship between age and water and nitrogen concentration (Quintero and Bowers 2018). For example, in the hypothetical case that an ECE caused herbivores to increase consumption rates or plants to produce lower defenses due to environmental stress like heat, this might have a higher impact on younger plantain plants than older ones. If we step back from the plantain example, we can hypothesize that traits that change over time can determine the effects of an ECE. We can use these relationships between traits and growth to predict when and how organisms can be susceptible to ECEs. For example, a heat event experienced by adult diamondback moths (*Plutella xylostella*) led to a 21% decrease in the number of hatched eggs produced by females with resulting population changes (Wei Zhang et al. 2013). These examples and the broader literature suggest that the timing of an ECE is likely more important for organisms that undergo rapid, discrete changes, like metamorphosis in holometabolous insects, than for organisms, like vertebrates, which change more gradually. The former organisms therefore may be more likely to pass the effects of an ECE on to community scales indirectly via species interactions.

We hypothesize that the timing of how ECE effects are transmitted to higher ecological levels will be dominated by the ontogenetic timing of organisms influential in species interactions—keystone species, foundational species, and ecosystem engineers. Paine (1966) showed how the removal of a main predator, the sea star *Pisaster ochraceus*, increased the diversity in the area by releasing mussels from predation, a foundational species that provides habitat for other species. Pike and Stiner (2007) observed that the timing of a cyclone can be detrimental to turtle populations if the cyclone happens when abundance of young turtles is high due to the mortality of these young individuals. We can expect that an ECE that occurs when a keystone species is vulnerable could lead to high mortality, and this mortality could indirectly lead to changes in species diversity. For example, sea urchins can be voracious grazers with major effects on community composition. Sea urchins can have positive effects keeping the algae populations low in coral reefs or have negative effects acting as grazers in an ecosystem (Cabanillas Terán 2009). A sea urchin (*Diadema africanum*) in Madeira, Portugal, was able to recover quickly from a mass-mortality event in part because it occurred immediately after the urchin’s spawning period (egg releasing period). While adults died in mass, the larva were resistant and contributed to a rapid population recovery.

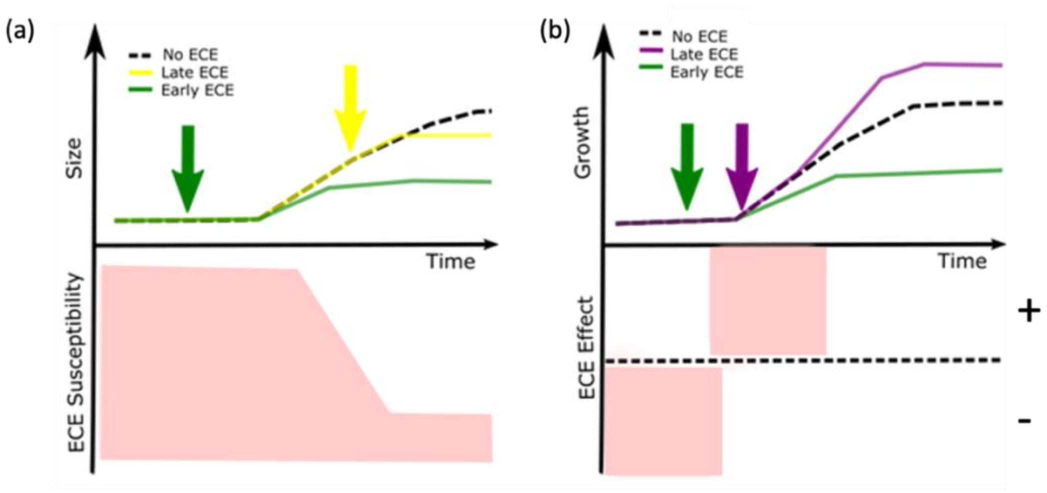


Figure 1.3. Hypothetical outcomes of an organism's growth changes depending on when an ECE happens. (a). Magnitude of the effect: An ECE happening at the early stages of growth (green arrow), when an organism's susceptibility to an ECE is high, the ECE could alter growth rate and total growth for that year. An ECE happening during the later stages of an organism (yellow arrow), when ECE susceptibility is low, might have no effects on total growth or growth rates. (b). Direction of the effect: An ECE happening when the organism's susceptibility to an ECE is high ECE, the ECE could have negative effects on growth (green arrow) due to a negative response, or positive effects on growth (purple arrow) due to a positive response. In both panels, time can be represented in different units, and it is relative to the ontogeny and phenology of organisms.

### Population level timing

We suggest that, in addition to depending on ontogenetic timing, the ecological effects of an ECE will depend upon when the event occurs through the course of population dynamics. Moreover, the role and importance of the timing of an ECE will matter differently for populations that follow different characteristic dynamical patterns: relatively steady with little change over time, cycles where abundance varies regularly through time, and chaotic or stochastic with unpredictable change through time (Tuljapurkar 2013). Additionally, age or stage distributions and genotypic frequencies change through time, and this should structure temporal variation in the consequences of ECEs.

Based on previous studies, the susceptibility to varying ECEs and the rates of growth, mortality, and behavior of individuals changing over time will drive population level responses. Climate and ecological data suggest that the ecological effects of a disturbance can range from zero to strongly negative depending on when the disturbance happens. Observational climate change data have shown that a cold wave before a population peak can reduce the population size of a Lepidoptera species (Wagenhoff and Veit 2011). By experimentally altering rain events on terrestrial ecosystems, Levine et al. (2011) found that the timing of the rain determines population dynamic patterns. Theoretical data also indicate that the consequences of altering a population depends on the life stage of the population suggesting that population vulnerability is strongly related to population phenology (Coulaud et al. 2013). For example, mathematical models found that stochastic disturbances can alter seed bank populations (Eager et al. 2013), and the season timing of animal harvesting is a major predictor of the recovery and subsequent transient population dynamics (Angulo and Villafuerte 2003). After drought events during the breeding season, the Southern pied babbler (Turdoides bicolor) recovered their population size a year after the event through compensatory breeding (Bourne et al. 2020). For the Southern pied babbler, long-term effects might depend on how many individuals remain after the ECEs to start the population recovery and how drought events affect different ages. For populations where the young are more affected than adults (increasing young mortality) by an ECE and that experience an ECE before or during the population peak, we hypothesize that the population will recover within the same breeding season or the year after due to a compensatory breeding response (Figure 1.4). While this hypothesis is within one or two breeding seasons (short time scale), the effects of an ECE can have different outcomes depending on the reproductive value of the individuals remaining (long time scale). Individuals with high reproductive value like second year individuals (Benítez Joubert and Tremblay 2003), can help the population grow long term (Bernt-Erik et al. 2007). If the ECE causes high mortality at a time when the individuals with high reproductive value are affected by the ECE, the population might not be able to recover.

The timing of an ECE will be important when considering the consequences of extreme weather on populations that cycle with another species, such as in predator-prey dynamics. In a predator-prey scenario, we may observe that the ECE will first alter the dynamics of the prey or the predator, with the magnitude of the effects depending on the timing of the populations, later cascading to consequences on predator-prey dynamics (Commander and White 2020) (Figure 1.4). Finally, in a population that has non-stationary dynamics we could observe various scenarios where the timing of ECE can have unpredictable effects or no effects. Alternatively, an ECE could act as a selection pressure depending on when it happens relative to population dynamics involving temporal variation in genotypic frequencies and eco-evolutionary dynamics. Campbell-Staton et al. (2017) found that extreme winter storms can shift eco-evolutionary dynamics in anole lizards, indicating that a one-time ECE event can alter evolutionary patterns and suggesting that the consequences of the ECE itself may depend on the timing of eco-evolutionary dynamics. Fruit flies (*Drosophila melanogaster*) show rapid phenotypic adaptation over short time scales (Bergland et al. 2014). Not many experiments explore the importance of manipulating the timing of an ECE along populations dynamics, although previous studies have indicated the importance of considering the timing of ECEs.

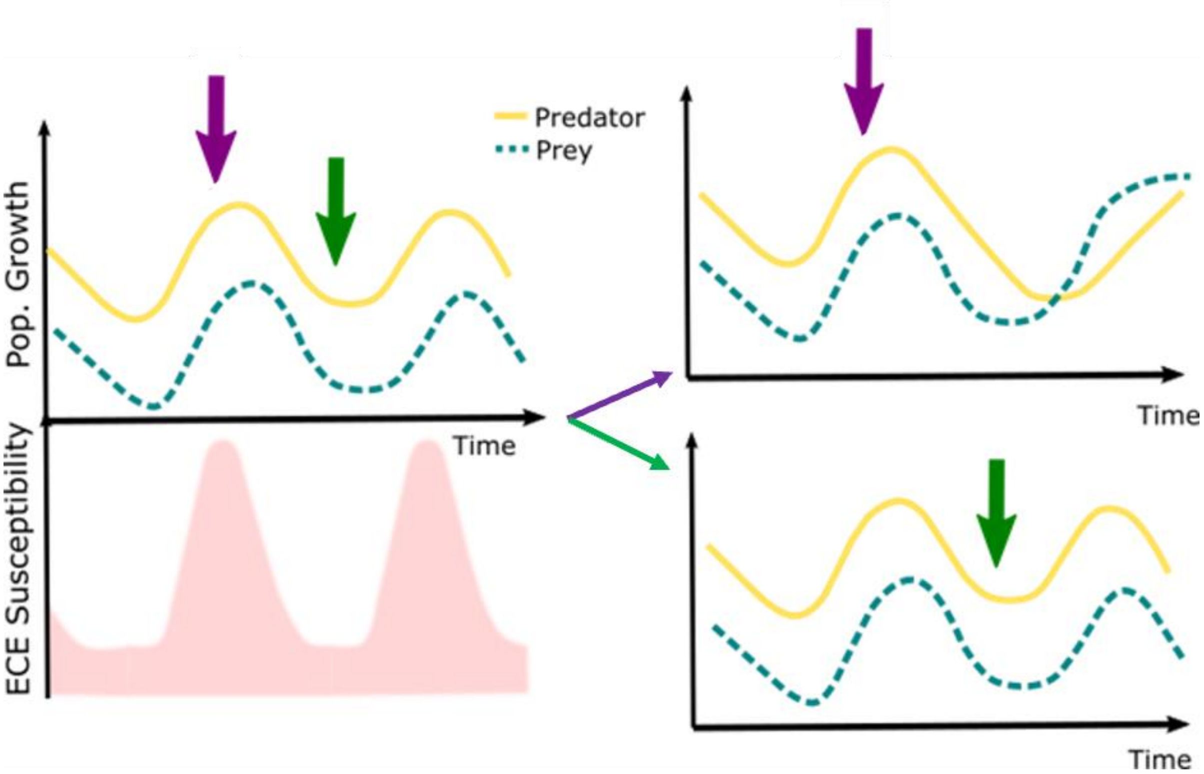


Figure 1.4. Using dynamic models, Commander and White 2019 showed the effects of various disturbances based on different predator-prey population dynamics, we hypothesized predator-prey dynamics over time after an ECE. An ECE near or at the peak of growth in populations of predator and prey (purple arrow), could result in a decrease in the predator's population growth and an increase in prey's population growth. An ECE happening near or at the valley of growth in populations of predator and prey (green arrow), could result in no changes in predator-prey dynamics.

**Community level timing**

Finally, we propose that the ecological effects of an ECE on communities are also contingent upon when the event occurs along the time scale of community dynamics. Based on past studies, the effects of the variation in ECE timing will differ across communities that have different temporal patterns of community dynamics. For example, in the disturbance literature researchers have shown that a single disturbance can alter species composition and community assemblies (Jauni et al. 2015, Collins et al. 2017) and that based on the trajectory of the community, the timing of a disturbance can determine what species can dominate a community (Turner et al. 1997, Smith 2006). Communities can be stable at an equilibrium, changing through succession or assembly, exhibiting patch dynamics, or simply varying unpredictably. We hypothesize that the timing of an ECE is less relevant for a stable community that changes slowly through time, such as a community in late stages of assembly. Of course, even if the timing of community dynamics is relatively unimportant for a given community, the timing of individual ontogeny and population dynamics within that community should still matter for the consequences of an ECE (Figure 1.5).

Communities can experience changes through time in abundance, diversity, species composition, trophic structure, and species interactions (Dornelas et al. 2018; Ushio et al. 2018), and we hypothesize that the effects of an ECE depend on the levels of these features when the event occurs. For example, tree species diversity can mitigate the impacts of a disturbance on carbon cycle (Pedro et al. 2015). Based on this study, diversity and resilience have a positive relationship where diverse ecosystems experience lower disturbance-induced variability in the ecosystem's trajectory. The synchrony between a population's phenology and seasonality will also be important when considering community dynamics. For example, flooding at different times can have no impact on some plant species that are not affected by seasonality but can alter recolonization of other species if the flooding happens late in the season (Barrat-Segretain and Bornette 2000). Species' roles in a community and when these species are part of the community can serve as a predictor of when the timing of an ECE will be important. In an ecosystem that experiences variation in species diversity through time like undergoing assembly processes, we would expect windows of time (e.g. stages of low diversity) when the ECE could have higher or lower impact vs a community where species diversity is more constant.

In addition, when an ECE happens during the course of metacommunity dynamics the timing of ECEs will matter. An ECE that happens during patch extinction or when colonization among patches is high could have less consequences on the dynamics of the metacommunity compared to when patches are experiencing higher replacement. For example, the higher dispersal could mitigate the immediate effects of an ECE that only affects a certain area.

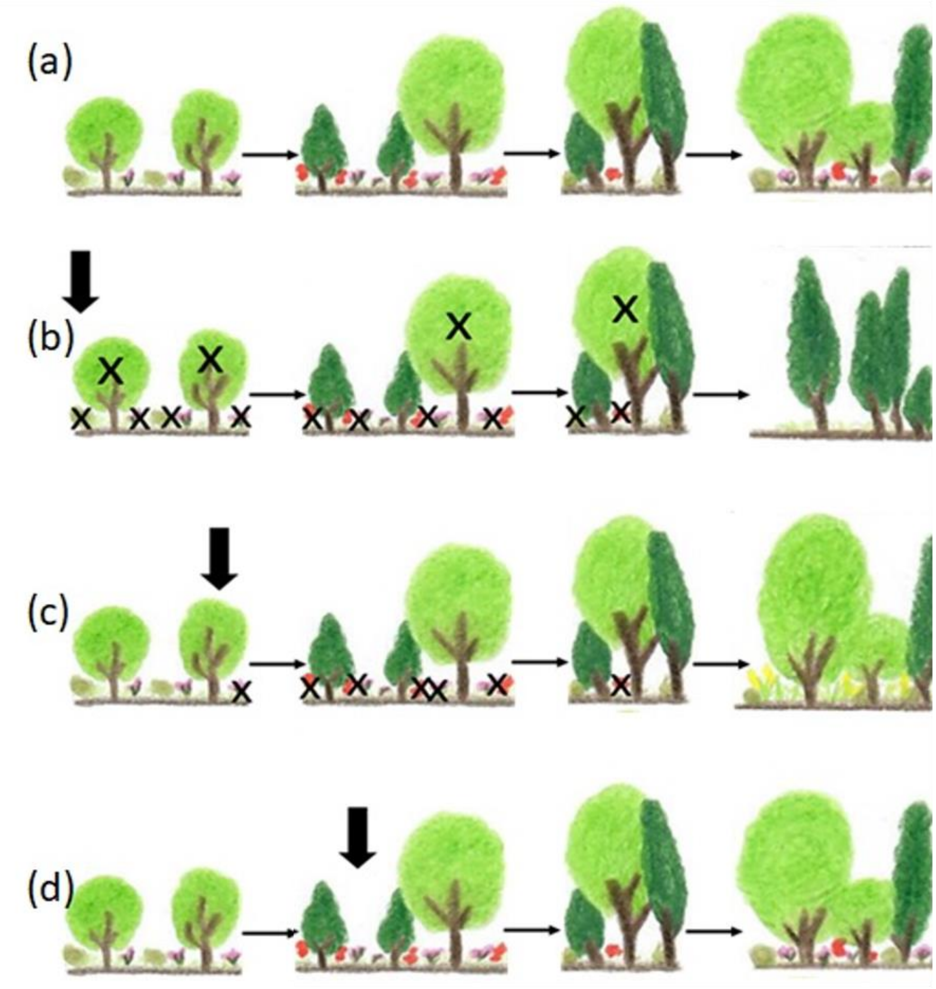


Figure 1.5. Building upon work by Suarez and Kitzberger 2008 and Anderegg et al. 2012 where due to mortality of certain species an ECE can shift the species composition in a forest and have indirect effects on habitat structure and quality, we represent this hypothetical community assembly over time. (a). There is no ECE, and the community assembly develops under the expected trajectory. (b). An ECE (black vertical arrow) that happens during early stages of the community assembly increases the mortality of understory key species (purple, red, and green), and tree species. The community becomes a different type of ecosystem with one species dominating the landscape and a decrease in diversity. (c). An ECE that happens during mid-early stages of the community assembly increases the mortality of most species (purple and red). (d). An ECE that happens during mid stages of the community assembly has no effects on the community and we do not observe high impacts on diversity and structure due to the ECE.

## Focusing on the timing of biology leads to novel predictions about the effects of ECEs across systems

Above we explored how the timing of an ECE through the progression of organismal ontogeny, population dynamics, and community assembly may influence the consequences of the ECE. In this section, we show how considering biological timing, and differences in biological timing across systems, may lead to novel insights and hypotheses about the ecology of ECEs and the vulnerability of different systems to ECEs. We illustrate how a temporally explicit approach to ECEs advances our thinking by focusing on two aspects of timing: biological synchrony and the magnitude of change in an ecosystem across time.

A major difference in biological timing across ecosystems is the level of synchrony across scales of organization (Wang et al. 2019). We predict that ecosystems with phenologies highly synchronized with the environment will be more sensitive to the timing of an ECE, and that the duration and frequency of synchronized events will interact with this ECE timing. For example, the relatively high synchrony of germination and flowering in alpine plant communities with the environment (Hall et al 2018) could lead to a strong relationship between the timing of an ECE and the strength of its effects in these systems, with strong effects during germination and flowering, which tend to be sensitive stages for many plants. In contrast, the asynchrony present in tropical plant communities could lead ECE effects to average out through time, reducing the sensitivity of the system to ECE timing. While the ECE might have high impacts on a tropical community, the timing of the ECE is likely to be less important.

Another component of biological timing is the amount of change systems exhibit within a year. Based on elevation and latitude, some ecosystems will be more variable than others in moisture, temperature, and other environmental factors. For example, in South America, the northern inner tropics receive a consistent amount of water throughout the year while in outer tropics precipitation can vary by over 90% between seasons (Sagredo et al. 2014). In a location with low weather variability, we would see less change in response to the weather, and the timing of an ECE will be less important compared to locations of high weather variability. These changes can be measured as total biomass, fitness and community metrics, or ecosystem services. In the case of a location with high weather variability, we present two possible hypotheses on how ecosystems can respond to the timing of an ECE. First, the timing of an ECE could be more important in systems that experience more change due to weather variability simply because responses to events at different times may differ more when underlying conditions also differ more through time. For example, in a high-elevation desert with high variability in the timing and amount of rain in a year, like the sagebrush steppe in western North America (Hardegree et al. 2016), heat events could be increasingly damaging with time since the last rain event. Second, and alternatively, the timing of an ECE could be less important in systems that experience more change because organisms and interactions in those systems may be more resilient to extremes in general and might have more capacity for plasticity (Climate Variability Hypothesis) (Molina-Montenegro and Naya 2012). For example, in the same sagebrush ecosystem, it is possible that organisms have ontogenetic trajectories that make them increasingly resilient to heat events with time since the last rain event. Although moisture decreases over time, resilience compensates for the possible damage, thereby actually reducing the importance of timing.

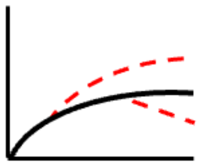
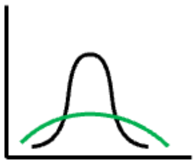
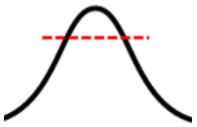
Our approach of including the timing on ECEs on future studies has limitations. First, we might not see the effects of ECEs timing until well after the event, and such lagged effects can complicate the interpretation of results. Second, every ECE happens at a certain time of growing season, species ontogeny, and year, making it difficult to divorce each variable. A way to solve the last pitfall would be with factorial experiments that include all the possible scenarios, although we acknowledge the challenge of carrying out these experiments. Although ECEs were not incorporated into their study, Yang et al. (2020) is a great example of experimental design that includes the ontogeny of an herbivore and plants to examine the survival and growth of herbivores, as well as Kharouba and Yang (2021) examining direct and indirect warming effects on interacting species.

## Conclusion

The fact that the effects of ECEs are a major part of the overall ecological consequences of climate change indicates that resolving the impacts of ECEs on ecology will be essential for understanding and responding to climate change. We have argued that understanding ECEs will require ecologists to study ECE timing and adopt a temporally explicit approach that considers not just the frequency and duration of events but also when the events occur relative to the biology of the systems they impact. Making this approach a reality will require empirical data and experiments that compare the effects of ECEs that happen at different times through biological scales.

Combining the timing of ECEs and the timing of species, populations, and communities into future analysis will increase the accuracy of our predictions on their short- and long-term consequences, identify previously overlooked groups of organisms and regions that are susceptible to ECEs, inform policy, and enable management recommendations that promote ecological resiliency to the new reality of ECEs.

Table 1.1. Example of some testable predictions based on the timing of ECEs.

| **Hypotheses** | **Possible predictions** |
|---|---|
| Based on physiological traits, organism's whose susceptibility to an ECE is variable have different responses to the ECE depending on when the ECE happens. *Ex. Organism's tolerance to cold event changing over time*.<br><br> | • The timing of the ECE will be important and the ECE will influence the organisms' phenology, physiology, behavior, or mortality if susceptibility is low at times.<br>• The timing of the ECE will not be important and there will not be a response from the organisms' phenology, physiology, behavior, or mortality if susceptibility is constant over time. |
| For organism's highly synchronized with the environment the timing of an ECE can determine the effects of the ECE depending on when the ECE happens.<br> | • The effects of timing of the ECE will depend on when the ECE happens for highly synchronized organisms.<br>• The effects of timing of the ECE will not matter for organisms not synchronized with the environment. |
| In cyclical populations, an ECE can have different effects even at the same population size depending on if the ECE happens as the population is growing vs when the population is declining.<br> | • An ECE happening at N=x as the population increases might not have as severe effects than an ECE happening as the population decreases due to population recovery and replacement. |

## Thesis objectives

The goal of this thesis was to introduce the concept of extreme climatic events timing into ecological studies and apply it to experiments at different biological levels.

***Objective I:*** Investigate the role of heat wave timing on plant communities and plant growth.

***Sub-objectives:***

***A.*** Determine how heat waves at different times can alter community composition.

**B.** Identify what plant species respond to heat waves at different times.

***Objective II:*** Investigate possible mechanisms that can explain differences in plant growth after a heat wave and possible cascading effects to other trophic levels.

***Sub-objectives:***

***A.*** Identify effects of heat wave timing on stomatal conductance of plants.

***B.*** Determine how responses to heat aboveground can alter belowground dynamics.

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# CHAPTER 2:

## TIMING OF HEAT WAVE DURING PLANT COMMUNITY ASSEMBLY ALTERS COMMUNITY COMPOSITION AND GROWTH

### Introduction

Climate change is increasing the frequency and intensity of extreme climatic events (Schär et al. 2004). Extreme climatic events are episodes of severe weather at the extremes of the historical distribution, such as heavy precipitation and droughts (Tebaldi et al. 2007). Another type of extreme climatic event—a heat wave—is a brief period of extremely high temperature (Marx et al. 2021). As the world endures human-caused climate change, heat waves are predicted to increase in maximum temperature and duration (Tebaldi et al. 2007, Meehl and Tebaldi 2004), negatively impacting economic sectors such as agriculture (Smoyer-tomic et al. 2003, Meehl and Tebaldi 2004), and contribute to higher rates of human mortality (Haines et al. 2006). They can also have profound ecological consequences (Parmesan et al. 2000, Maxwell et al. 2019) by altering function at organismal (Roitberg and Mangel 2016, Colinet et al. 2015, Vasseur et al. 2014), population (Morán-Ordóñez et al. 2018), and community scales (Seifert et al. 2015, Reyer et al. 2013).

Compared to gradual increases in average temperatures, heat waves can be sudden shocks whose impact is ontogenetically and phenologically specific (Jentsch et al. 2009). For example, a heat wave during early instars of the tobacco hornworm (*Manduca sexta*) can reduce its growth and development (Kingsolver et al. 2021). In addition, the timing of extreme heat can alter green peach aphid survival based on their ontogeny (*Myzus persicae*) (Gillespie et al. 2012). While the role of event timing in ecological disturbance has been well documented (Squiers 1989, Miller et al. 2012), climate change studies have focused less on measuring the impacts of heat waves on specific life or community stages. To our knowledge, there is a gap in climate change research where the timing of heat waves and other extreme climatic events have not been included as part of the consequences of extreme climatic events. How the timing of heat waves will interact with the stages of community dynamics and population growth remain unknown.

In plants, heat waves can reduce leaf production and photosynthetic capacity depending on the developmental stage (Filewod and Sean 2014). In some perennial plant species, heat waves can reduce the photosynthetic rate and productivity late in the growing season (Wang et al. 2016). For example, an increase in leaf area during vegetative growth can be due to an increase in transpiration to heat stress, and the decrease in growth due to a late heat wave might be detrimental to plants at a later phenology stage, like flowering. Younger plants also typically have a lower tolerance to heat (Cirillo et al. 2018). Therefore, the ecological effects of heat waves depend on phenological and ontogenetic contexts. Since the timing of a heat wave can be an important predictor of an individual organism’s metrics, these individual-level effects should scale up to how communities respond to heat waves (Cinto Mejía and Wetzel 2023).

Previous work suggests that changes initiated by a heat wave can have both short-term and long-term impacts on communities, and plant communities’ species composition and richness will determine their responses at the time of the heat wave (Dornelas et al. 2018; Ushio et al. 2018). Generally, the timing of a disturbance determines the dominant plant species in the community that then drives subsequent colonization by other species (Turner et al. 1997, Smith 2006). Another important determinant of community-level consequences of heat waves is the individuals’ thermal stress tolerance, survival, reproductive capacity, and age. Since the early community assembly often has a high rate of species turnover and greater sensitivity to disturbance, we can hypothesize that a heat wave during the early stages of community assembly should have stronger effects than if the heat wave occurs years after the community was first established. While previous research has studied the effects of droughts and other events like fires on community assembly, it is unclear when communities will be the most susceptible to heat stress. Heat waves happening at a certain time might have stronger effects than others, opposite effects, or will not cause any heat induced response. Further, ecosystems might have a delayed response to heat waves happening in a certain year or at a certain time during the growing season and there is not a single study that examines multi-year consequences based on heat wave timing. Multi-year consequences of heat wave timing remain unknown not only for a community-scale response but also for populations and individual-level responses.

In this field mesocosm study, we investigated the response of plant growth and community composition to heat waves at different times during the growing season and over the course of three years. We first selected eight plant species (focal species) commonly found in the early stages of community assembly in Michigan, USA (Broughton and Gross 2000) and later examined the colonization of our site by newly arrived species (non-focal species). We monitored species from an early developmental stage and studied the community dynamics of colonizing plants. Based on community dynamics, we hypothesized that heat waves happening early during the growing season, and in year 2 (when there are new colonizers) have the largest impact on community composition compared to controls. Based on the ontogeny of organisms, we hypothesized that heat waves happening early or in the middle of the growing season decrease plant growth compared to controls. Heat waves happening in year 1 decreased plant growth as well compared to controls that did not experience heat waves. Further, we hypothesized that heat waves display delayed effects. Heat waves happening in years 1 and 2, regardless of when during the growing season, have visible effects on communities and plant growth in year 3 compared to controls. With these sets of hypotheses, we investigated how the (1) timing of heat waves within and across seasons alters species composition in a plant community, and (2) the timing of heat waves impacts plant growth. With this approach, we can fill some of the gaps in the literature by showing that the effects of heat waves depend on the intra- and inter-annual variation of their timing and that certain heat waves have long-term effects. Given that most studies on the ecological impacts of climate change focus on extreme climatic events without considering the timing of the events, this work provides a relatively new approach to studying heat waves and other extreme climatic events and the long-term consequences of heat waves.

## Materials and Methods

To determine how heat wave timing alters plant communities, we conducted a 3-year experiment at the Kellogg Biological Station (MI, USA 42° 24’ 35”N, 85° 23’ 27”W) from 2019 to 2021. In June 2019, we selected a field site on Kalamazoo loam soil (Natural Resources Conservation Service, SSURGO SOILS, 2000) and measured the location of 148 plots (28.5 cm radius) that were 1 m apart (Figure 2.1A). On April 24, 2019, the field was treated with herbicide (1.4 l / 4046.86 m2; Roundup PowerMAX, Bayer, USA), and rototilled after the herbicide treatment. We collected the top twenty centimeters of soil from each plot and sifted it using a sand filtering machine (Lindig Soil Shredder model M8, Minnesota, USA) to minimize the number of rhizomes from previous years and to create more homogeneous soil across plots. After sifting, the soil was returned to the plots. We delimited each plot with landscape edging (12.7 cm height by 0.3 cm width; Master Mark, Minnesota, USA; Figure 2.1A). We assigned plots to 8 different treatments or a control: (1) year 1 early/mid heat wave (n=15), (2) year 1 mid-season heat wave (n=19), (3) year 1 late heat wave (n=15), (4) year 2 early heat wave (n=10), (5) year 2 early mid-season heat wave (n=10), (6) year 2 mid heat wave (n=15), (7) year 2 late heat wave (n=15), and (8) year 3 early heat wave (n=15) (Figure 2.1D). We selected these treatments based on the earliest availability of the site in 2019, and to have a gradient of heat wave times early and late during the growing season. Control plots did not receive a heat wave treatment. Each plot received only one heat treatment during the experiment to explore its effect on plant communities within a season and legacy effects on communities and plant species that were 1- or 2-years-old.

Six Michigan native and three non-native plants were planted into each plot (Table 2.1). We chose these species based on what common species have been observed in managed and abandoned fields in the area (Broughton and Gross 2000), and to encompass a wide gradient in the morphology. Seven of the nine plant species were grown from seed in a greenhouse (Prairie Moon Nursery, Winona, MN, USA; Ernst Conservation Seeds, Meadville, PA, USA; Michigan Wildflower Farm, Portland, MI, USA). Two plant species, *Solidago altissima* and *Asclepias syraca* were grown in the greenhouse from rhizomes collected from the surrounding areas near the study site. Plots were populated with the two-week-old healthy transplants between June 5 and 15, 2019. In 2019, we removed most weeds multiple times during the summer, except *Abutilon theophrasti* and *Chenopodium album* (annual weeds common in Michigan), from all plots to allow focal species to establish. While this might have affected the plant communities at the beginning of the community assembly, we wanted the plants we intentionally planted to be able to establish. In 2020 and 2021, we recorded the new colonizing plant species (non-focal species) but did not remove them. We did not apply fertilizers or pesticides during the experiment, and we only watered the plots once after transplanting them from the greenhouse. We did not do any pre- or post-experiment soil tests for fertility.

In 2019, we randomly selected 15 plots to receive an early/mid-season heat wave (July 16), 19 plots were assigned a midseason-heat wave (July 30), and 15 plots received a late-season heat wave (August 15). In 2020, 10 new plots received an early-season heat wave on June 15, 10 new plots received an early/mid-season heat wave on July 16, 15 new plots received a mid-season heat wave on July 30, and 15 new plots received a late-season heat wave on August 15. In 2021, we applied a heat wave on new 15 additional plots on June 15 (Figure 2.1D).

We applied heat waves using open top-chambers and ceramic heaters hung in the center of the chamber (300-watt, Tempco, Inc., IL) (Figure 2.1B-C). To build the open top chambers, we used wood as the frame and anti-condensate greenhouse plastic as the sides (6 mil, 91% light transmittance, Poly-Ag Corp., CA, USA). The chambers were 1.5-by-1.5 m at the base, 1.2 m tall, with a 0.6 m2 square opening at the top (Figure 2.1B). Ceramic heaters were turned on at night and if cloud cover exceeded 50% during the day. All heat waves lasted four days and four nights. For the control plots, we placed mesh chambers (with the same dimensions as the heat wave chambers) that simulated the enclosing effects of heat chambers without their heat-trapping properties. In 2019, the mean air temperature inside the warmed chambers was 29.9°C (Standard deviation (SD)=6.7°C) during the day and 21.0°C (SD=1.7°C) during the night. Controls chambers were 26.0 °C (SD=5.3°C) on average during the day and 20.2 °C (SD=2.8°C) during the night. In 2020, our chambers averaged 28.9°C (SD=7.0°C) during the day and 14.0°C (SD=2.7°C) during the night. Controls were 25.9°C (SD=6.9°C) during the day and 11.9°C (SD=2.6°C) during the night. In 2021, our chambers averaged 33.3°C (SD=6.8°C) during the day and 22.9°C (SD=1.6°C) during the night. Controls were 29.8°C (SD=6.9°C) during the day and 19.7°C (SD=1.4°C) during the night. The heating chambers would increase the ambient temperature but were not controlled for a certain temperature, thus the differences in temperature among heat wave treatments. All these temperatures were not controlled and were a result of the ambient temperature and the heaters, thus each heat wave temperature is different.

In 2019, we measured the height and visually inspected the total area of the eight focal species and two colonizing annual species (*Abutilon theophrasti* and *Chenopodium album*) in each plot. We measured area by placing a 2,500 $cm^2$ sheet of paper over the plots and estimated the number of squares to later transform it to total $cm^2$. In 2020 and 2021, we measured the area and height of all plants and identified all the species, including the non-focal species in each plot. When possible, we identified colonizing plants in 2020 and 2021 to species or genus, but some species were unidentifiable due to missing vegetative parts that were consumed by herbivores (approximately 0.5 % of the total area). We collected these response variables once per year in a period between the end of August and the beginning of September.

Table 2.1. Scientific name, family, species status in Michigan and life cycle of the focal plant species planted in year 1 (2019) in a field plot at the Kellogg Biological Station, MI.

| **Scientific name** | **Family** | **MI status** | **Life cycle** |
|---|---|---|---|
| *Achillea millefolium* | Asteraceae | native | perennial |
| *Asclepias syriaca* | Apocynaceae | native | perennial |
| *Chenopodium album* | Amaranthaceae | non-native | annual |
| *Danthonia spicata* | Poaceae | native | perennial |
| *Melilotus albus* | Fabaceae | non-native | annual |
| *Solidago altissima* | Asteraceae | native | perennial |
| *Solidago graminifolia* | Asteraceae | native | perennial |
| *Symphyotrichum pilosum* | Asteraceae | native | perennial |
| *Trifolium pratense* | Fabaceae | non-native | Perennia |
| *Abutilon theophrasti* | Malvaceae | Invasive | annual |

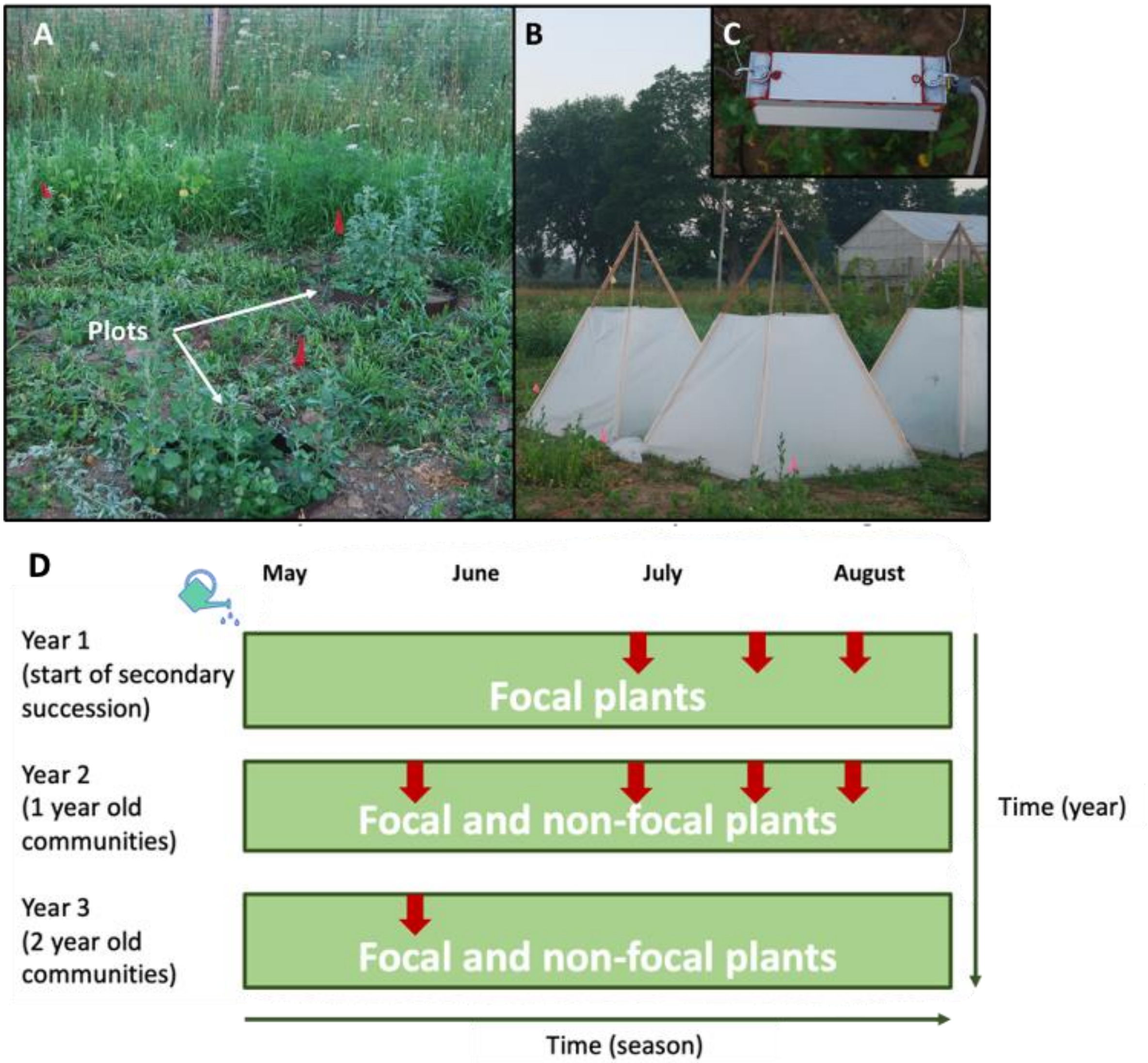

Figure 2.1. Experimental plots with plant species in year 1 (A). An example of the open-top heating chamber (B) and ceramic heating elements used in experiment (C). Simulated heat treatments were applied to plots within a year (x-axis) and over 3 years (y-axis) (D). In year 1, all non-focal plants were removed and only focal species remained in plots. In years 2 and 3 a combination of focal and non-focal species comprised plant communities in each plot. The watering can indicates the time of transplanting the focal species into the field plots. The red arrows indicate the times when heat waves were applied. During year 1 an early/mid, mid-, and late-season heat wave was applied. In year 2, early, early/mid, mid-, and late-season heat waves were applied and in year 3 a single early heat wave was applied.

## Statistical analyses

*Does the timing of heat waves alter the community composition of focal and non-focal species?*

Based on the community hypotheses stated above, we tested that early heat waves during the growing season have the strongest effects on community composition, and that community composition in year 3 of both focal and non-focal species respond to heat waves that happened the year before, year 2.

All statistical analyses were conducted in R version 4.1.2 (R Core Team 2020). We fit independent models by each of our three years of data collection. To determine the community similarity of focal species across treatments, we calculated the Jaccard index using a presence/absence species matrix. To visualize plant community similarity among treatments in 2020 we used a nonmetric multidimensional scaling (NMDS, stress=0.056, dimensions=2). To test the centroid differences among focal species in each treatment in 2020 and 2021, we conducted a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001). We also performed PERMANOVAs using Bray-Curtis dissimilarity on the species abundance calculated from the area covered by each species (stress=0.22, dimensions=2).

The first model described the inter-annual variation in species composition with the year of the experimental heat wave as a fixed effect. This model tested how the year of the heat wave, not intra-annual timing (e.g., early vs late heat wave), impacts species composition. The second model described the intra-annual variation in species composition with the heat wave season as a fixed effect (e.g., early, mid-early, mid, and late heat wave). This model tested how the timing of a heat wave during a growing season, regardless of the age of the plant community changes community composition. The third model had a fixed effect to test both intra-annual and inter-annual variation in species composition of the heat wave timing (e.g., year 2 early heat wave). This last model describes how heat waves can modify community composition depending on community age and seasonal timing. We followed these analyses with posthoc pairwise comparisons among treatments using the pairwiseAdonis R package (Arbizu 2019). To determine how the community composition of non-focal species changed depending on heat wave timing, we repeated the same analyses as above using a dataset that contained the colonizing plants (non-focal species) in 2020 and 2021.

### *Does the timing of heat waves affect plant growth?*

We hypothesized that early and mid-season heat waves regardless of year decrease plant growth. To test the effects of heat waves on the growth of individual focal and non-focal plant species at different times, we built three generalized linear models (GLMs) with height or area as dependent variables. The first model contained ‘year’ as a predictor, the second model ‘season’, and the third model ‘day,’ which had the specific date of the heat wave as a predictor (i.e., same model setup as above). We also analyzed the growth data by observation year.

## Results

We recorded 39 species in 2020 and 38 species in 2021 across all plots (Table S2.1). Due to difficulty identifying some clover species, Trifolium sp. were grouped together for analyses. During both years, the most common focal and non-focal species present in all treatments were *Symphytricum pilosum, Solidago graminifolia, Danthonia spicata, Trifolium pratense, Trifolium campestre*, and *Achillea millefolium*. These six species represented 51.3% and 52.6% of all counts in 2020 and 2021, respectively.

*Does the timing of heat waves alter the community composition of focal and non-focal species?*

The presence/absence PERMANOVA results from focal species indicated that the intra-annual heat wave variation (‘season’) and the combination of both, intra-annual and inter-annual heat variation (‘day’) altered the community composition in 2020 (Figure 2.2A) and 2021 (F>1.9, R2=0.1-0.06, p<0.05). In 2020, the Jaccard index averaged 0.16 (min-max, 0.14-0.71), and in 2021, the average was 0.17 (min-max, 0.14-0.66). The analysis of the presence/absence data of non-focal species indicated that inter-annual heat wave variation (‘year’) had a significant effect on community composition in 2021 (F=1.44, R2=0.03, p<0.05; Table S2.2). From the presence/absence data in 2021, the Jaccard index averaged 0.69 (min-max, 0.14-0.93).

For the abundance-based analysis in 2020 of focal species, the intra-annual heat wave variation (‘season’) and the combination of both, intra-annual and inter-annual heat variation (‘day’) altered community composition (F>1.5, R2=0.07-0.08, p<0.05; Figure 2.2B). From the area matrix in 2020, the Bray-Curtis index averaged 0.095 (0.07-0.55).

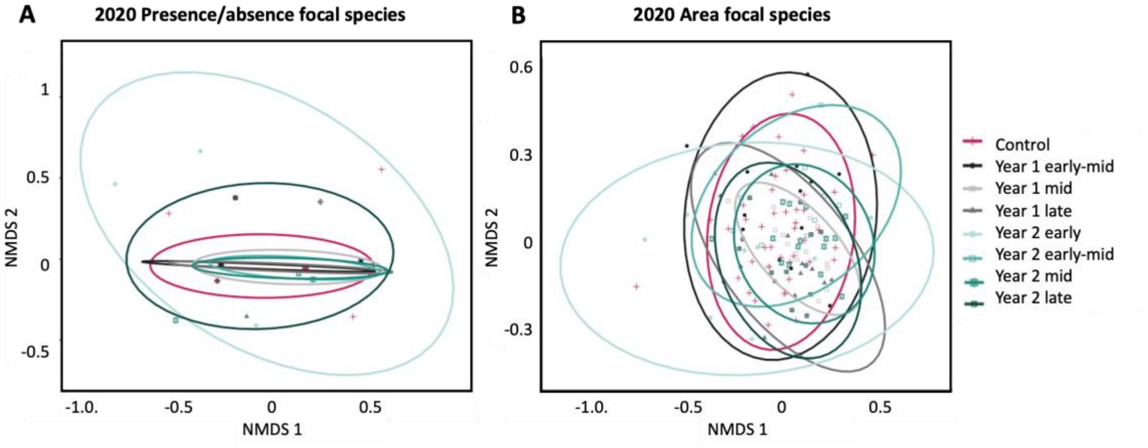

Figure 2.2. Nonmetric multidimensional scaling in two dimensions for the presence/absence of focal species (Jaccard stress=0.056) (A) and plant coverage (area) (B) of focal plant species (Bray Curtis stress=0.22) from data collected in 2020. Ellipses are the 95% confidence intervals.

*Does the timing of heat waves affect plant growth?*

Intra-annual variation in the timing of heat waves influenced both the height and the area of *S. altissima* and area of *T. pratense* in 2019 (Table 2.2). For example, the early-mid season heat wave decreased both the area and the height of *S. altissima* by ~49% compared to the control but if the heat wave occurred late in the season, the height of this species increased by 54.3% (Figure 2.3A-B).

In 2020, the intra-annual variation of heat wave timing ('season' model) and the combination of intra-annual heat wave effects and plant age ('day' model) were an indicator of plant growth for some focal species, mostly affecting the area (Table 2.2). Overall, when we observed significant effects of intra-annual heat waves, early or late heat waves were most likely to alter plant growth compared to mid-season ones (Table 2.2). Similar to 2019, a late-season heat wave increased *S. altissima* plant height by 46.7% compared to controls (Figure2. 3B). In contrast, for *S. pilosum*, early and mid-heat waves increased the area by 21.6% and early heat waves decreased the height by 16% compared to controls (Figure 2.3C-D).

In 2021, a combination of both intra-annual heat waves and plant age ('day' model) influenced plant height for *S. pilosum, D. spicata* and *S. graminifolia* (Table 2.2). Intra-annual variation of heat timing was a predictor of height only for *D. spicata* (Table 2.2). While we did not observe any changes in area for *D. spicata* (Figure 2.3E), a heat wave during mid- and late-season on one-year-old plants caused a height reduction of 19% and 24% respectively a year after the 2019 heat wave treatment (Figure 2.3F).

Our results also indicated that heat waves at different times affected the area and height of non-focal species (Table S2.3). A heat wave applied in 2020 mid-season increased the height of *P. lanceolata* by 100% compared to the control, as measured in 2021. In contrast, *P.*

*lanceolata* individuals that received heat waves in year 2 (2020) late in the season decreased in height by 38% the following year compared to the control (Figure 2.4A-B). For the common grass *P. pratense*, early heat waves decreased height by 25% the year after the heat wave compared to controls (Figure 2.4D). Results from non-focal species suggest that most heat wave events had a positive effect on growth and height, especially if the heat waves happened during the second year of the community assembly early or late in the season (Table S2.3).

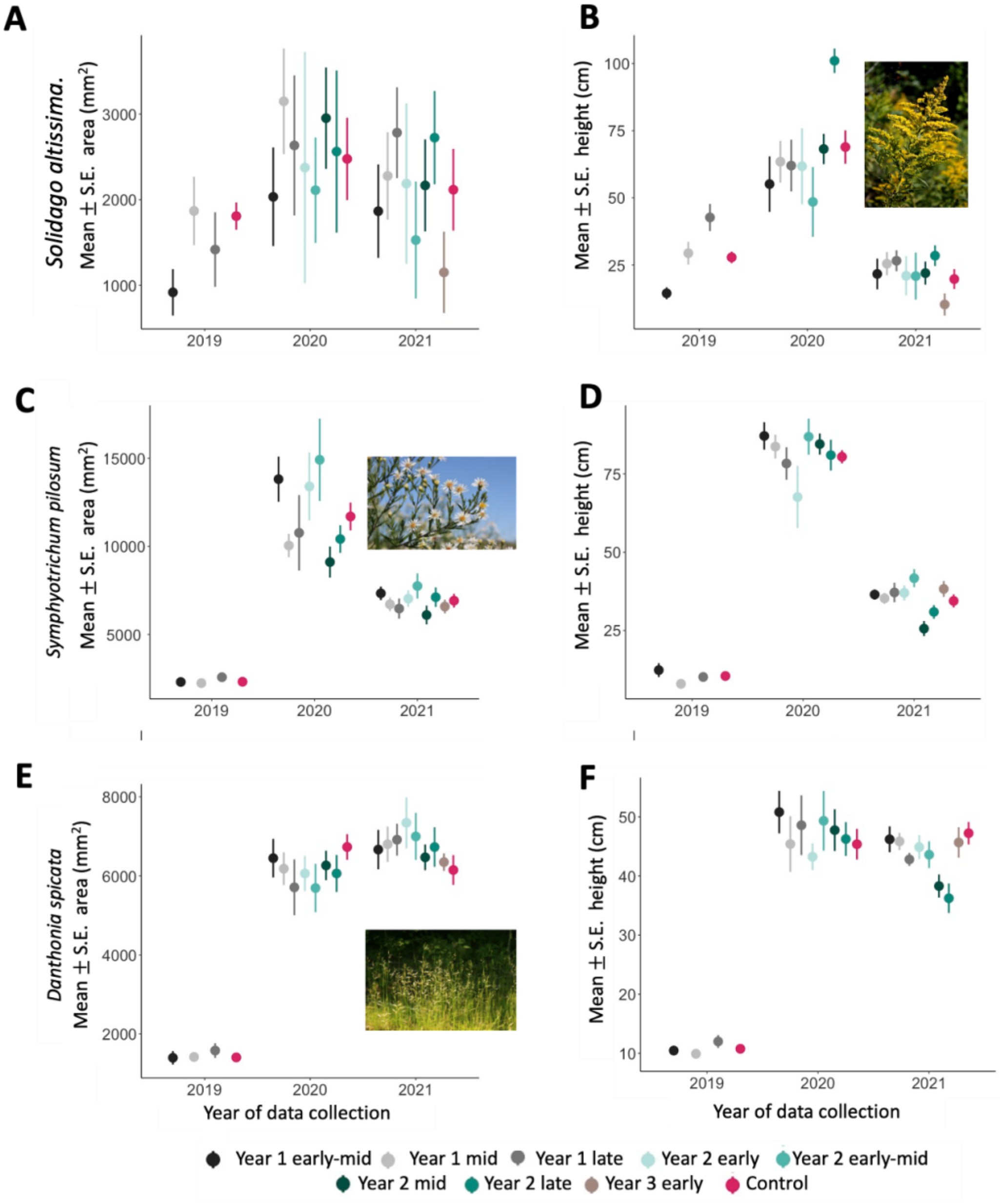

Figure 2.3. Mean ± SEM area (mm$^2$) and height (cm) of three of the focal plant species: *S. altissima* (A-B), *S. pilosum* (C-D), and *D. spicata* (E, F) in response to heat waves applied at different times during 2019-2021. Images from University of Michigan herbarium.

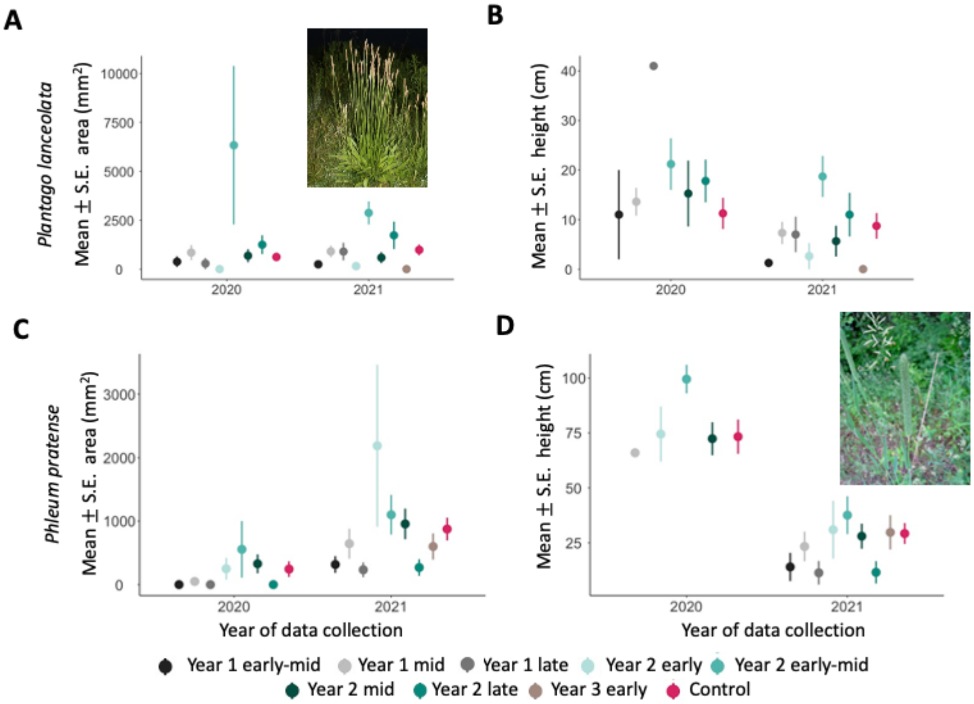

Figure 2.4. Mean ± SEM area (mm$^2$) and height (cm) of two of the non-focal species: *P. lanceolata* (A, B) and *P. pratense* (C, D) in response to heat waves applied at different times during 2020-2021.

Table 2.2. Parameter estimates, standard error (E.S.), ±95% confidence intervals (C.I.) and p-value of the generalized linear models of the focal plant species' growth area and height during 2019-2021. Year corresponds to when the measurements were taken, from end of August to beginning of September in 2019, 2020, and 2021.

| | | | | **Area** | | | | | **Height** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Year** | **Model** | **Parameter** | **Estimate** | **S.E.** | **p** | **C.I.$_U$** | **C.I.$_L$** | **Estimate** | **S.E.** | **p** | **C.I.$_U$** | **C.I.$_L$** |
| *S. altissima* | 2019 | Season | Early/mid | -13.16 | 161.14 | 0.94 | 302.67 | -328.99 | 1.88 | 1.87 | 0.32 | 5.55 | -1.80 |
| | | | Mid | -76.32 | 145.76 | 0.12 | 209.37 | -362.01 | -2.51 | 1.70 | 0.14 | 0.81 | -5.83 |
| | | | Late | 258.27 | 166.04 | 0.60 | 583.71 | -67.17 | -0.32 | 1.93 | 0.87 | 3.47 | -4.10 |
| | 2020 | Day | Early | 1708.60 | 1947.90 | 0.38 | 5526.48 | -2109.28 | -12.85 | 6.28 | 0.04 | -0.54 | -25.16 |
| | | | Early/mid | 3219.00 | 1854.40 | 0.09 | 6853.62 | -415.62 | 6.41 | 5.98 | 0.29 | 18.13 | -5.31 |
| | | | Late | -1281.00 | 1651.70 | 0.44 | 1956.33 | -4518.33 | 0.52 | 5.33 | 0.92 | 10.97 | -9.92 |
| | | | Mid | -2588.30 | 1481.50 | 0.08 | 315.44 | -5492.04 | 4.06 | 4.90 | 0.41 | 13.66 | -5.54 |
| | | | Year1 | 940.60 | 1818.20 | 0.61 | 4504.27 | -2623.07 | -0.80 | 5.95 | 0.89 | 10.85 | -12.45 |
| | | | Year1 | -2040.60 | 2802.80 | 0.47 | 3452.89 | -7534.09 | 1.04 | 9.08 | 0.91 | 18.84 | -16.76 |
| | | | Year1 | -588.10 | 2721.60 | 0.83 | 4746.24 | -5922.44 | -1.87 | 8.92 | 0.83 | 15.61 | -19.35 |
| | | Season | Early | 1709.00 | 1929.00 | 0.38 | 5489.84 | -2071.84 | -12.85 | 6.21 | 0.04 | -0.68 | -25.02 |
| | | | Early/mid | 2532.00 | 1276.00 | 0.05 | 5032.96 | 31.04 | 6.57 | 4.12 | 0.11 | 14.64 | -1.51 |
| | | | Late | -1098.00 | 1260.00 | 0.39 | 1371.60 | -3567.60 | -0.81 | 4.12 | 0.84 | 7.26 | -8.88 |
| | | | Mid | -2133.00 | 1180.00 | 0.07 | 179.80 | -4445.80 | 3.66 | 3.85 | 0.34 | 11.20 | -3.88 |
| | | Year | Year1 | -116.30 | 1128.70 | 0.92 | 2095.95 | -2328.55 | 2.93 | 3.61 | 0.42 | 10.01 | -4.15 |
| | | | Year2 | -314.30 | 1116.10 | 0.78 | 1873.26 | -2501.86 | 0.50 | 3.57 | 0.89 | 7.50 | -6.50 |
| | 2021 | Day | Early | -333.30 | 613.20 | 0.59 | 868.57 | -1535.17 | 3.83 | 3.04 | 0.21 | 9.79 | -2.12 |
| | | | Early/mid | 385.40 | 1105.50 | 0.73 | 2552.18 | -1781.38 | 8.53 | 5.48 | 0.12 | 19.27 | -2.20 |
| | | | Late | -249.20 | 1065.50 | 0.82 | 1839.18 | -2337.58 | -2.24 | 5.28 | 0.67 | 8.10 | -12.59 |
| | | | Mid | -1261.60 | 1033.10 | 0.22 | 763.28 | -3286.48 | -7.58 | 5.12 | 0.14 | 2.45 | -17.61 |
| | | | Year1 | 1055.50 | 1067.60 | 0.33 | 3148.00 | -1037.00 | 8.41 | 5.29 | 0.11 | 18.78 | -1.96 |
| | | | Year2 | 447.90 | 848.90 | 0.60 | 2111.74 | -1215.94 | -1.27 | 4.21 | 0.76 | 6.98 | -9.51 |
| | | | Year1 | -1024.30 | 1022.60 | 0.32 | 980.00 | -3028.60 | -14.91 | 5.07 | 0.00 | -4.98 | -24.84 |
| | | | Year1 | -1256.30 | 979.30 | 0.20 | 663.13 | -3175.73 | -3.47 | 4.85 | 0.48 | 6.04 | -12.97 |
| | | Season | Early | -177.50 | 533.90 | 0.74 | 868.94 | -1223.94 | 3.39 | 2.76 | 0.22 | 8.80 | -2.01 |
| | | | Early/mid | 583.30 | 521.70 | 0.27 | 1605.83 | -439.23 | 4.13 | 2.69 | 0.13 | 9.41 | -1.15 |
| | | | Late | -148.80 | 506.20 | 0.77 | 843.35 | -1140.95 | -0.18 | 2.61 | 0.94 | 4.94 | -5.31 |

Table 2.2 (cont’d)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mid | -493.10 | 476.20 | 0.30 | 440.25 | -1426.45 | -3.74 | 2.46 | 0.13 | 1.08 | -8.56 |
| | | Year | Year1 | -90.14 | 452.12 | 0.84 | 796.02 | -976.30 | 1.77 | 2.35 | 0.45 | 6.37 | -2.83 |
| | | | Year2 | -41.67 | 453.91 | 0.93 | 847.99 | -931.33 | -2.14 | 2.36 | 0.37 | 2.48 | -6.76 |
| | | | Year3 | -333.33 | 616.74 | 0.59 | 875.48 | -1542.14 | 3.83 | 3.20 | 0.23 | 10.11 | -2.44 |
| *S. graminifolia* | 2019 | Season | Early/mid | -60.80 | 196.17 | 0.76 | 323.69 | -445.29 | -1.09 | 1.91 | 0.57 | 2.65 | -4.83 |
| | | | Mid | 366.72 | 180.87 | 0.04 | 721.23 | 12.21 | 3.48 | 1.76 | 0.05 | 6.93 | 0.03 |
| | | | Late | -38.19 | 190.53 | 0.84 | 335.25 | -411.63 | -0.12 | 1.85 | 0.95 | 3.52 | -3.75 |
| | 2020 | Day | Early | -3255.81 | 1386.68 | 0.02 | -537.92 | -5973.70 | -1.77 | 11.01 | 0.87 | 19.81 | -23.36 |
| | | | Early/mid | -339.15 | 1320.13 | 0.80 | 2248.30 | -2926.60 | -2.61 | 7.15 | 0.72 | 11.41 | -16.62 |
| | | | Late | -1109.98 | 1175.78 | 0.35 | 1194.55 | -3414.51 | -5.22 | 6.82 | 0.45 | 8.14 | -18.58 |
| | | | Mid | 337.94 | 1054.63 | 0.75 | 2405.01 | -1729.13 | 1.52 | 5.49 | 0.78 | 12.27 | -9.24 |
| | | | Year1 | -77.08 | 1294.33 | 0.95 | 2459.81 | -2613.97 | 2.99 | 6.85 | 0.66 | 16.41 | -10.43 |
| | | | Year1 | 1660.42 | 1995.26 | 0.41 | 5571.13 | -2250.29 | -0.06 | 10.63 | 1.00 | 20.77 | -20.90 |
| | | | Year1 | 123.56 | 1937.47 | 0.95 | 3921.00 | -3673.88 | -4.80 | 10.60 | 0.65 | 15.98 | -25.57 |
| | | Season | Early | -3255.80 | 1376.10 | 0.02 | -558.64 | -5952.96 | -1.77 | 10.87 | 0.87 | 19.54 | -23.09 |
| | | | Early/mid | 650.40 | 910.70 | 0.48 | 2435.37 | -1134.57 | -0.74 | 4.88 | 0.88 | 8.81 | -10.30 |
| | | | Late | -1085.80 | 898.90 | 0.23 | 676.04 | -2847.64 | -6.25 | 4.95 | 0.21 | 3.45 | -15.95 |
| | | | Mid | 300.60 | 842.10 | 0.72 | 1951.12 | -1349.92 | 2.86 | 4.49 | 0.53 | 11.66 | -5.95 |
| | | | Year1 | 203.50 | 787.00 | 0.80 | 1746.02 | -1339.02 | -0.54 | 4.18 | 0.90 | 7.64 | -8.73 |
| | | Year | Year2 | -822.50 | 778.20 | 0.29 | 702.77 | -2347.77 | -1.36 | 4.26 | 0.75 | 6.99 | -9.71 |
| | 2021 | Day | Early | 533.30 | 619.30 | 0.39 | 1747.13 | -680.53 | 1.37 | 4.98 | 0.78 | 11.12 | -8.39 |
| | | | Early/mid | 908.30 | 1116.50 | 0.42 | 3096.64 | -1280.04 | 4.52 | 8.97 | 0.62 | 22.10 | -13.06 |
| | | | Late | 292.90 | 1076.10 | 0.79 | 2402.06 | -1816.26 | 1.46 | 8.65 | 0.87 | 18.41 | -15.48 |
| | | | Mid | 2246.60 | 1043.30 | 0.03 | 4291.47 | 201.73 | 11.50 | 8.38 | 0.17 | 27.93 | -4.93 |
| | | | Year1 | -2198.30 | 1078.20 | 0.04 | -85.03 | -4311.57 | -11.92 | 8.66 | 0.17 | 5.06 | -28.90 |
| | | | Year2 | -1241.70 | 857.40 | 0.15 | 438.80 | -2922.20 | -12.25 | 6.89 | 0.08 | 1.25 | -25.75 |
| | | | Year1 | 1090.00 | 1032.80 | 0.29 | 3114.29 | -934.29 | 5.51 | 8.30 | 0.51 | 21.77 | -10.76 |
| | | | Year1 | 1722.00 | 989.00 | 0.08 | 3660.44 | -216.44 | 9.03 | 7.95 | 0.26 | 24.60 | -6.55 |
| | | Season | Early | 101.40 | 545.40 | 0.85 | 1170.38 | -967.58 | -2.89 | 4.40 | 0.51 | 5.73 | -11.52 |
| | | | Early/mid | -253.30 | 532.90 | 0.64 | 791.18 | -1297.78 | -4.23 | 4.30 | 0.33 | 4.19 | -12.66 |
| | | | Late | -538.70 | 517.10 | 0.30 | 474.82 | -1552.22 | -5.78 | 4.17 | 0.17 | 2.40 | -13.95 |
| | | | Mid | 500.00 | 486.50 | 0.31 | 1453.54 | -453.54 | -0.58 | 3.92 | 0.88 | 7.11 | -8.27 |

Table 2.2 (cont’d)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Year | Year1 | -98.64 | 460.44 | 0.83 | 803.82 | -1001.10 | -1.18 | 3.63 | 0.75 | 5.94 | -8.31 |
| | | | Year2 | -88.54 | 462.25 | 0.85 | 817.47 | -994.55 | -6.61 | 3.65 | 0.07 | 0.54 | -13.77 |
| | | | Year3 | 533.33 | 628.08 | 0.40 | 1764.37 | -697.71 | 1.37 | 4.96 | 0.78 | 11.08 | -8.35 |
| *T. pratense* | 2019 | Season | Early/mid | 763.64 | 201.63 | 0.00 | 1158.84 | 368.43 | -0.36 | 0.79 | 0.65 | 1.19 | -1.91 |
| | | | Mid | 13.64 | 201.63 | 0.95 | 408.84 | -381.57 | -1.06 | 0.79 | 0.18 | 0.49 | -2.61 |
| | | | Late | 3.99 | 182.27 | 0.98 | 361.24 | -353.27 | -1.18 | 0.71 | 0.10 | 0.22 | -2.58 |
| | 2020 | Day | Early | -4585.76 | 1810.61 | 0.01 | -1036.96 | -8134.56 | 0.97 | 7.53 | 0.90 | 15.72 | -13.78 |
| | | | Early/mid | -23.26 | 1723.71 | 0.99 | 3355.21 | -3401.73 | -4.45 | 5.84 | 0.45 | 6.99 | -15.90 |
| | | | Late | -1960.76 | 1535.24 | 0.20 | 1048.31 | -4969.83 | -6.23 | 5.38 | 0.25 | 4.32 | -16.78 |
| | | | Mid | -1382.63 | 1377.05 | 0.32 | 1316.39 | -4081.65 | 0.83 | 4.78 | 0.86 | 10.20 | -8.53 |
| | | | Year1 | -440.62 | 1690.03 | 0.79 | 2871.84 | -3753.08 | -9.07 | 5.82 | 0.12 | 2.33 | -20.47 |
| | | | Year1 | 1240.62 | 2605.24 | 0.63 | 6346.89 | -3865.65 | 11.50 | 8.95 | 0.20 | 29.05 | -6.04 |
| | | | Year1 | -506.49 | 2529.79 | 0.84 | 4451.90 | -5464.88 | 10.15 | 8.83 | 0.25 | 27.46 | -7.16 |
| | | Season | Early | -4585.80 | 1792.40 | 0.01 | -1072.70 | -8098.90 | 0.97 | 7.51 | 0.90 | 15.69 | -13.76 |
| | | | Early/mid | 476.70 | 1186.10 | 0.69 | 2801.46 | -1848.06 | -2.97 | 4.11 | 0.47 | 5.08 | -11.02 |
| | | | Late | -2453.30 | 1170.80 | 0.04 | -158.53 | -4748.07 | -5.67 | 4.11 | 0.17 | 2.38 | -13.72 |
| | | | Mid | -1595.80 | 1096.80 | 0.15 | 553.93 | -3745.53 | -3.70 | 3.78 | 0.33 | 3.71 | -11.11 |
| | | | Year1 | -1244.20 | 1029.30 | 0.23 | 773.23 | -3261.63 | -5.21 | 3.44 | 0.13 | 1.54 | -11.96 |
| | | Year | Year2 | -1834.40 | 1017.80 | 0.07 | 160.49 | -3829.29 | -2.28 | 3.47 | 0.51 | 4.51 | -9.08 |
| | 2021 | Day | Early | 550.00 | 865.10 | 0.53 | 2245.60 | -1145.60 | 3.97 | 2.63 | 0.13 | 9.11 | -1.18 |
| | | | Early/mid | 3162.50 | 1559.70 | 0.04 | 6219.51 | 105.49 | 13.92 | 4.73 | 0.00 | 23.19 | 4.64 |
| | | | Late | 910.60 | 1503.30 | 0.55 | 3857.07 | -2035.87 | 7.52 | 4.56 | 0.10 | 16.46 | -1.42 |
| | | | Mid | 2046.30 | 1457.50 | 0.16 | 4903.00 | -810.40 | 6.33 | 4.42 | 0.15 | 15.00 | -2.34 |
| | | | Year1 | -2627.90 | 1506.30 | 0.08 | 324.45 | -5580.25 | -6.56 | 4.57 | 0.15 | 2.40 | -15.51 |
| | | | Year2 | -1937.50 | 1197.70 | 0.11 | 409.99 | -4284.99 | -9.65 | 3.63 | 0.01 | -2.53 | -16.77 |
| | | | Year1 | -567.90 | 1442.80 | 0.69 | 2259.99 | -3395.79 | -8.19 | 4.38 | 0.06 | 0.39 | -16.77 |
| | | | Year1 | 2434.00 | 1381.70 | 0.08 | 5142.13 | -274.13 | 1.07 | 4.19 | 0.80 | 9.28 | -7.15 |
| | | Season | Early | -123.91 | 767.27 | 0.87 | 1379.94 | -1627.76 | 0.61 | 2.37 | 0.80 | 5.25 | -4.03 |
| | | | Early/mid | 470.00 | 749.70 | 0.53 | 1939.41 | -999.41 | 1.21 | 2.32 | 0.60 | 5.74 | -3.33 |
| | | | Late | -92.86 | 727.46 | 0.90 | 1332.96 | -1518.68 | 0.10 | 2.25 | 0.96 | 4.51 | -4.30 |
| | | | Mid | -255.56 | 684.38 | 0.71 | 1085.82 | -1596.94 | -1.68 | 2.11 | 0.43 | 2.46 | -5.83 |
| | | Year | Year1 | -16.33 | 639.97 | 0.98 | 1238.01 | -1270.67 | 0.28 | 1.95 | 0.89 | 4.10 | -3.54 |

Table 2.2 (cont’d)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Year2 | -215.63 | 642.50 | 0.74 | 1043.67 | -1474.93 | -1.81 | 1.96 | 0.36 | 2.03 | -5.65 |
| | | | Year3 | 550.00 | 872.98 | 0.53 | 2261.04 | -1161.04 | 3.97 | 2.66 | 0.14 | 9.18 | -1.25 |
| *A. millefolium* | 2019 | Season | Early/mid | 1000.00 | 528.00 | 0.06 | 2034.88 | -34.88 | -1.26 | 1.30 | 0.34 | 1.30 | -3.82 |
| | | | Mid | 948.80 | 512.30 | 0.07 | 1952.91 | -55.31 | 0.77 | 1.27 | 0.54 | 3.25 | -1.71 |
| | | | Late | 613.70 | 463.20 | 0.19 | 1521.57 | -294.17 | -0.16 | 1.14 | 0.89 | 2.08 | -2.41 |
| | 2020 | Day | Early | 6987.65 | 2319.76 | 0.00 | ####### | 2440.92 | 1.47 | 4.05 | 0.72 | 9.41 | -6.47 |
| | | | Early/mid | -2307.49 | 2208.43 | 0.30 | 2021.03 | -6636.01 | -1.29 | 3.86 | 0.74 | 6.27 | -8.85 |
| | | | Late | -22.77 | 1966.95 | 0.99 | 3832.45 | -3877.99 | -4.82 | 3.44 | 0.16 | 1.92 | -11.56 |
| | | | Mid | -1246.73 | 1764.29 | 0.48 | 2211.28 | -4704.74 | -2.28 | 3.09 | 0.46 | 3.77 | -8.33 |
| | | | Year1 | 694.79 | 2165.27 | 0.75 | 4938.72 | -3549.14 | 0.14 | 3.77 | 0.97 | 7.54 | -7.26 |
| | | | Year1 | 2077.43 | 3337.85 | 0.53 | 8619.62 | -4464.76 | -0.85 | 5.82 | 0.88 | 10.55 | -12.26 |
| | | | Year1 | 1013.54 | 3276.88 | 0.76 | 7436.22 | -5409.14 | 4.44 | 5.71 | 0.44 | 15.64 | -6.75 |
| | | Season | Early | 6987.60 | 2308.40 | 0.00 | ####### | 2463.14 | 1.47 | 4.02 | 0.72 | 9.35 | -6.41 |
| | | | Early/mid | -574.90 | 1527.60 | 0.71 | 2419.20 | -3569.00 | -1.74 | 2.67 | 0.52 | 3.49 | -6.97 |
| | | | Late | 831.40 | 1527.60 | 0.59 | 3825.50 | -2162.70 | -2.53 | 2.67 | 0.35 | 2.70 | -7.76 |
| | | | Mid | -910.50 | 1412.50 | 0.52 | 1858.00 | -3679.00 | -2.21 | 2.47 | 0.37 | 2.63 | -7.05 |
| | | | Year1 | 450.40 | 1350.30 | 0.74 | 3096.99 | -2196.19 | -1.55 | 2.27 | 0.50 | 2.89 | -5.99 |
| | | Year | Year2 | 331.40 | 1327.40 | 0.80 | 2933.10 | -2270.30 | -2.09 | 2.23 | 0.35 | 2.27 | -6.46 |
| | 2021 | Day | Early | -2942.00 | 2286.00 | 0.20 | 1538.56 | -7422.56 | 6.93 | 4.09 | 0.09 | 14.95 | -1.08 |
| | | | Early/mid | -5598.00 | 4121.00 | 0.18 | 2479.16 | ####### | 8.03 | 7.37 | 0.28 | 22.49 | -6.42 |
| | | | Late | -4973.00 | 3972.00 | 0.21 | 2812.12 | ####### | 5.47 | 7.11 | 0.44 | 19.40 | -8.46 |
| | | | Mid | -4899.00 | 3851.00 | 0.21 | 2648.96 | ####### | 4.99 | 6.89 | 0.47 | 18.50 | -8.51 |
| | | | Year1 | 2396.00 | 3980.00 | 0.55 | ####### | -5404.80 | -3.21 | 7.12 | 0.65 | 10.75 | -17.16 |
| | | | Year2 | 5365.00 | 3164.00 | 0.09 | ####### | -836.44 | -1.20 | 5.66 | 0.83 | 9.90 | -12.30 |
| | | | Year1 | 3510.00 | 3812.00 | 0.36 | ####### | -3961.52 | -3.09 | 6.82 | 0.65 | 10.28 | -16.46 |
| | | | Year1 | 1635.00 | 3650.00 | 0.66 | 8789.00 | -5519.00 | 0.87 | 6.53 | 0.89 | 13.67 | -11.94 |
| | | Season | Early | -1075.72 | 2008.09 | 0.59 | 2860.14 | -5011.58 | 6.52 | 3.55 | 0.07 | 13.47 | -0.44 |
| | | | Early/mid | 91.67 | 1962.09 | 0.96 | 3937.37 | -3754.03 | 3.77 | 3.47 | 0.28 | 10.57 | -3.02 |
| | | | Late | -322.62 | 1903.90 | 0.87 | 3409.02 | -4054.26 | 3.66 | 3.37 | 0.28 | 10.26 | -2.93 |
| | | | Mid | -1101.39 | 1791.14 | 0.54 | 2409.24 | -4612.02 | 2.73 | 3.17 | 0.39 | 8.94 | -3.47 |
| | | Year | Year1 | -1164.00 | 1657.00 | 0.48 | 2083.72 | -4411.72 | 2.18 | 2.95 | 0.46 | 7.96 | -3.60 |
| | | | Year2 | 626.00 | 1664.00 | 0.71 | 3887.44 | -2635.44 | 4.88 | 2.96 | 0.10 | 10.68 | -0.92 |

Table 2.2 (cont’d)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Year3 | -2942.00 | 2260.00 | 0.20 | 1487.60 | -7371.60 | 6.93 | 4.02 | 0.09 | 14.82 | -0.95 |
| *D. spicata* | 2019 | Season | Early/mid | -9.09 | 137.81 | 0.95 | 261.01 | -279.19 | -0.30 | 0.94 | 0.75 | 1.54 | -2.14 |
| | | | Mid | 174.24 | 137.81 | 0.21 | 444.34 | -95.86 | 1.23 | 0.94 | 0.19 | 3.07 | -0.61 |
| | | | Late | 11.96 | 124.57 | 0.92 | 256.13 | -232.20 | -0.85 | 0.85 | 0.32 | 0.82 | -2.51 |
| | 2020 | Day | Early | -670.06 | 739.14 | 0.37 | 778.65 | -2118.77 | -2.12 | 5.95 | 0.72 | 9.53 | -13.78 |
| | | | Early/mid | -1038.11 | 703.66 | 0.14 | 341.06 | -2417.28 | 3.96 | 5.66 | 0.49 | 15.06 | -7.13 |
| | | | Late | -670.06 | 626.72 | 0.29 | 558.31 | -1898.43 | 0.88 | 5.04 | 0.86 | 10.76 | -9.00 |
| | | | Mid | -466.93 | 562.15 | 0.41 | 634.88 | -1568.74 | 2.38 | 4.52 | 0.60 | 11.24 | -6.49 |
| | | | Year1 | -82.29 | 689.91 | 0.91 | 1269.93 | -1434.51 | -2.35 | 5.55 | 0.67 | 8.53 | -13.23 |
| | | | Year1 | 837.85 | 1063.53 | 0.43 | 2922.37 | -1246.67 | 3.82 | 8.56 | 0.66 | 20.59 | -12.95 |
| | | | Year1 | -268.67 | 1032.73 | 0.80 | 1755.48 | -2292.82 | 4.68 | 8.40 | 0.58 | 21.15 | -11.78 |
| | | Season | Early | -670.10 | 733.50 | 0.36 | 767.56 | -2107.76 | -2.12 | 5.88 | 0.72 | 9.41 | -13.65 |
| | | | Early/mid | -565.90 | 485.40 | 0.25 | 385.48 | -1517.28 | 4.88 | 3.89 | 0.21 | 12.51 | -2.75 |
| | | | Late | -852.60 | 479.10 | 0.08 | 86.44 | -1791.64 | 2.05 | 3.89 | 0.60 | 9.68 | -5.59 |
| | | | Mid | -506.80 | 448.90 | 0.26 | 373.04 | -1386.64 | 1.24 | 3.60 | 0.73 | 8.30 | -5.82 |
| | | | Year1 | -598.80 | 408.40 | 0.15 | 201.66 | -1399.26 | 2.87 | 3.31 | 0.39 | 9.35 | -3.61 |
| | | Year | Year2 | -671.40 | 403.80 | 0.10 | 120.05 | -1462.85 | 1.50 | 3.25 | 0.65 | 7.87 | -4.88 |
| | 2021 | Day | Early | 200.00 | 556.20 | 0.72 | 1290.15 | -890.15 | -1.57 | 2.64 | 0.55 | 3.60 | -6.73 |
| | | | Early/mid | -143.80 | 1002.70 | 0.89 | 1821.49 | -2109.09 | -2.84 | 4.75 | 0.55 | 6.47 | -12.15 |
| | | | Late | -413.00 | 966.50 | 0.67 | 1481.34 | -2307.34 | -10.21 | 4.58 | 0.03 | -1.24 | -19.19 |
| | | | Mid | -673.20 | 937.00 | 0.47 | 1163.32 | -2509.72 | -8.15 | 4.44 | 0.07 | 0.55 | -16.85 |
| | | | Year1 | 1325.80 | 968.40 | 0.17 | 3223.86 | -572.26 | 6.76 | 4.59 | 0.14 | 15.75 | -2.24 |
| | | | Year2 | 993.80 | 770.00 | 0.20 | 2503.00 | -515.40 | -0.79 | 3.65 | 0.83 | 6.36 | -7.94 |
| | | | Year1 | -665.40 | 927.60 | 0.47 | 1152.70 | -2483.50 | -4.95 | 4.40 | 0.26 | 3.67 | -13.56 |
| | | | Year1 | -146.10 | 888.30 | 0.87 | 1594.97 | -1887.17 | -0.98 | 4.21 | 0.82 | 7.27 | -9.23 |
| | | Season | Early | 545.70 | 484.40 | 0.26 | 1495.12 | -403.72 | -1.84 | 2.38 | 0.44 | 2.82 | -6.50 |
| | | | Early/mid | 650.00 | 473.30 | 0.17 | 1577.67 | -277.67 | -2.07 | 2.32 | 0.37 | 2.48 | -6.63 |
| | | | Late | 680.40 | 459.30 | 0.14 | 1580.63 | -219.83 | -7.48 | 2.26 | 0.00 | -3.06 | -11.90 |
| | | | Mid | 495.80 | 432.10 | 0.25 | 1342.72 | -351.12 | -4.96 | 2.12 | 0.02 | -0.80 | -9.12 |
| | | Year | Year1 | 645.90 | 402.80 | 0.11 | 1435.39 | -143.59 | -2.21 | 1.96 | 0.26 | 1.63 | -6.06 |
| | | | Year2 | 646.90 | 404.40 | 0.11 | 1439.52 | -145.72 | -7.30 | 1.97 | 0.00 | -3.43 | -11.16 |
| | | | Year3 | 200.00 | 549.40 | 0.72 | 1276.82 | -876.82 | -1.57 | 2.68 | 0.56 | 3.68 | -6.82 |

Table 2.2 (cont’d)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. altissima* | 2019 | Season | Early/mid | -727.30 | 357.10 | 0.05 | -27.38 | -1427.22 | -13.36 | 5.50 | 0.02 | -2.58 | -24.15 |
| | | | Mid | 589.60 | 378.50 | 0.12 | 1331.46 | -152.26 | 14.85 | 5.83 | 0.01 | 26.29 | 3.42 |
| | | | Late | 512.30 | 301.30 | 0.09 | 1102.85 | -78.25 | 1.55 | 4.64 | 0.74 | 10.66 | -7.55 |
| | 2020 | Day | Year1 | -545.50 | 823.50 | 0.51 | 1068.56 | -2159.56 | -7.16 | 14.31 | 0.62 | 20.88 | -35.20 |
| | | | Year2 | -545.50 | 823.50 | 0.51 | 1068.56 | -2159.56 | -20.41 | 12.12 | 0.10 | 3.35 | -44.17 |
| | | | Early | 454.50 | 1302.10 | 0.73 | 3006.62 | -2097.62 | 32.09 | 13.04 | 0.02 | 57.65 | 6.53 |
| | | | Early2 | -1128.80 | 1131.80 | 0.32 | 1089.53 | -3347.13 | -0.73 | 9.72 | 0.94 | 18.32 | -19.78 |
| | | | Late | 1854.50 | 1202.90 | 0.13 | 4212.18 | -503.18 | -4.73 | 11.22 | 0.67 | 17.27 | -26.72 |
| | | | Year1:Early/mid | 645.80 | 1534.60 | 0.68 | 3653.62 | -2362.02 | 11.35 | 18.11 | 0.53 | 46.85 | -24.14 |
| | | | Year1:Late | -1257.10 | 1615.40 | 0.44 | 1909.08 | -4423.28 | -34.27 | 19.06 | 0.08 | 3.09 | -71.64 |
| | | Season | Early | -90.91 | 1196.43 | 0.94 | 2254.09 | -2435.91 | -7.16 | 14.69 | 0.63 | 21.64 | -35.96 |
| | | | Early/mid | -1305.19 | 752.52 | 0.09 | 169.75 | -2780.13 | -16.62 | 9.24 | 0.08 | 1.49 | -34.74 |
| | | | Late | 575.76 | 789.91 | 0.47 | 2123.98 | -972.46 | 9.34 | 9.70 | 0.34 | 28.35 | -9.67 |
| | | | Mid | -545.45 | 663.66 | 0.41 | 755.32 | -1846.22 | -3.09 | 8.15 | 0.71 | 12.88 | -19.07 |
| | | Year | Year1 | -533.20 | 650.10 | 0.42 | 741.00 | -1807.40 | -8.41 | 7.98 | 0.30 | 7.24 | -24.06 |
| | | | Year2 | -379.40 | 650.10 | 0.56 | 894.80 | -1653.60 | 0.05 | 7.98 | 1.00 | 15.70 | -15.59 |
| | 2021 | Day | Year1 | 161.11 | 657.27 | 0.81 | 1449.36 | -1127.14 | -9.47 | 5.90 | 0.11 | 2.09 | -21.02 |
| | | | Year2 | 50.00 | 697.14 | 0.94 | 1416.39 | -1316.39 | -9.58 | 10.81 | 0.38 | 11.61 | -30.76 |
| | | | Year3 | -987.50 | 1190.60 | 0.41 | 1346.08 | -3321.08 | -7.37 | 11.99 | 0.54 | 16.14 | -30.87 |
| | | | Early | 20.83 | 965.15 | 0.98 | 1912.52 | -1870.86 | -1.97 | 10.63 | 0.85 | 18.86 | -22.80 |
| | | | Early2 | -638.89 | 929.53 | 0.49 | 1182.99 | -2460.77 | -8.47 | 10.07 | 0.40 | 11.27 | -28.20 |
| | | | Late | 505.56 | 770.72 | 0.51 | 2016.17 | -1005.05 | 14.17 | 10.44 | 0.18 | 34.64 | -6.30 |
| | | | Late | 558.33 | 900.01 | 0.54 | 2322.35 | -1205.69 | 10.67 | 8.16 | 0.19 | 26.66 | -5.33 |
| | | | Year1 | 226.50 | 1227.96 | 0.85 | 2633.30 | -2180.30 | -2.70 | 10.38 | 0.80 | 17.66 | -23.05 |
| | | Season | Early | -5.76 | 5.15 | 0.27 | 4.33 | -15.84 | -5.76 | 5.15 | 0.27 | 4.33 | -15.84 |
| | | | Early2 | 1.56 | 5.21 | 0.77 | 11.78 | -8.65 | 1.56 | 5.21 | 0.77 | 11.78 | -8.65 |
| | | | Late | 6.80 | 5.87 | 0.25 | 18.31 | -4.71 | 6.80 | 5.87 | 0.25 | 18.31 | -4.71 |
| | | | Late | 8.70 | 6.78 | 0.20 | 21.99 | -4.59 | 8.70 | 6.78 | 0.20 | 21.99 | -4.59 |
| | | | Mid | 4.11 | 4.68 | 0.38 | 13.29 | -5.07 | 4.11 | 4.68 | 0.38 | 13.29 | -5.07 |
| | | Year | Year1 | 209.40 | 512.60 | 0.68 | 1214.10 | -795.30 | 4.98 | 4.32 | 0.25 | 13.45 | -3.48 |
| | | | Year2 | 50.00 | 522.10 | 0.92 | 1073.32 | -973.32 | 3.32 | 4.40 | 0.45 | 11.94 | -5.30 |
| | | | Year3 | -966.70 | 690.70 | 0.16 | 387.07 | -2320.47 | -9.47 | 5.82 | 0.11 | 1.94 | -20.87 |

Table 2.2 (cont'd)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *M. albus* | 2019 | Season | Early/mid | 41.41 | 132.72 | 0.76 | 301.54 | -218.72 | -1.47 | 3.52 | 0.68 | 5.43 | -8.38 |
| | | | Late | -108.59 | 132.72 | 0.42 | 151.54 | -368.72 | 1.93 | 3.52 | 0.59 | 8.83 | -4.98 |
| | | | Mid | -60.34 | 119.98 | 0.62 | 174.82 | -295.50 | 0.73 | 3.18 | 0.82 | 6.97 | -5.51 |
| | 2020 | Day | Early | 809.59 | 288.90 | 0.01 | 1375.83 | 243.35 | 32.00 | 20.68 | 0.22 | 72.52 | -8.52 |
| | | | Late | -44.57 | 244.96 | 0.86 | 435.55 | -524.69 | -25.00 | 20.68 | 0.31 | 15.52 | -65.52 |
| | | | Mid | 59.59 | 219.72 | 0.79 | 490.24 | -371.06 | 6.00 | 20.68 | 0.79 | 46.52 | -34.52 |
| | | Season | Early | 809.59 | 286.09 | 0.01 | 1370.33 | 248.85 | 32.00 | 20.68 | 0.22 | 72.52 | -8.52 |
| | | | Late | -87.91 | 186.87 | 0.64 | 278.36 | -454.18 | -25.00 | 20.68 | 0.31 | 15.52 | -65.52 |
| | | | Mid | -31.13 | 175.06 | 0.86 | 311.99 | -374.25 | 6.00 | 20.68 | 0.79 | 46.52 | -34.52 |
| | | Year | Year1 | -127.90 | 164.00 | 0.44 | 193.54 | -449.34 | | | | 0.00 | 0.00 |
| | | | Year2 | 127.60 | 162.10 | 0.43 | 445.32 | -190.12 | 4.33 | 17.60 | 0.82 | 38.83 | -30.16 |

## Discussion

Our results suggest that a single heat wave can have significant multi-year effects on plant community composition and growth depending on heat wave timing relative to plant ontogeny and species. For example, late-season heat waves resulted in higher *S. altissima growth*, while *D. spicata* grew shorter in these plots.

We found that intra-annual variation in heat wave timing during the establishment of a plant community, (i.e., when the heat wave occurs within a growing season), changed plant community structure even a year after the event. When we examined non-focal plants that colonized our plots, the inter-annual variation in species composition was significantly associated with community structure in year 3. Heat waves that were applied in year 1, when non-focal species were weeded out, changed the community composition of non-focal species 2 years after the heat wave. A possible explanation is that the intense heat influenced the seed bank such as changing the mortality of seeds (Ooi 2012), thus the first year's heat effects became apparent 2 years later when the non-focal species established in our plots. In a previous germination lab experiment, seeds that experienced heat waves in the spring or fall increased their germination by 30% and 50% respectively (Orsenigo et al. 2015).

Heat waves influenced focal species' growth, and in some cases, these effects were still detected more than a year after the event. Species, like *S. altissima*, reduced their growth as a seedling in response to early heat waves with a ~50% decrease in height and area after the first growing season. On the other hand, late heat waves on young and one-year-old individuals almost doubled the height compared to the control plants. An increase in growth after intense heat could be explained by an increase in photosynthesis due to heat stress. If a plant is not susceptible to damage by the heat, the heat might have provided an advantage to these species by releasing them from the competition of other species affected by the heat. A heat wave could make certain species better competitors. Even though plants often respond negatively to heat stress, some species exhibit high thermal stress tolerance (Teskey et al. 2015). A decrease in seedling growth observed after a heat wave, relative to control plants, supports our initial hypothesis. Young plants can be predisposed to growth damage caused by heat stress due to their relative sensitivity compared to older plants (Cirillo et al. 2018). In the case of *S. pilosum*, one of our focal plants, an early heat wave experienced by one-year-old individuals decreased plant height by 16%, as observed in 2020. In 2021, when focal species were two years old, *D. spicata, S. graminifolia*, and *S. pilosum* were about ~20% shorter after receiving a heat wave mid or late-season the previous year compared to control plants (Table 2.2). This finding indicates that some individuals had a lag effect due to intense heat (Niu et al. 2014). Such delayed response has been observed in subalpine forests where the mortality of *Abies lasiocarpa* increased two years after a late-season drought event (Bigler et al. 2007).

Plant height reduction could be explained by the heat damaging reproductive organs that are often located at the highest points on our focal plants (Breshears et al. 2021). Intense heat during flowering could have provoked inflorescences to abort, making the plants shorter. For example, *A. millefolium* is a species with relatively tall reproductive organs, flowers. When one-year-old individuals were exposed to heat waves at the beginning of the growing season (early-season heat waves), the heat promoted horizontal growth (area) by 5% but did not change the height (Table 2.2). This positive response indicates not only the resilience of *A. millefolium* to heat, but it also exemplifies how a relatively young (one-year-old) individual can become a good competitor for space under heat stress. On the contrary, *T. pratense* with shorter reproductive organs than *A. millefolium* reduced their area by 49% when exposed to an early heat wave in 2020 while the height did not change (Table 2.2). This plant might be less tolerant to heat than *A.*

*millefolium*, and the heat wave could have happened when the plants were more susceptible to desiccation, thus reducing the area. In our study, we examined total area per species without accounting for the number of individuals, thus an increase in area could be explained by an increase in individuals, an increase in plant size, or both.

Many species responded to certain heat wave treatments, however, the remaining species that we identified showed no response to any of the heat wave treatments like *Trifolium pratense* or *Verbascum thapsus*. Some possible explanations could be that the temperatures we applied were under the thermotolerance threshold for these species making them less susceptible to heat waves and more adapted to heat. The heat waves might not have had any effects at the time they were applied, however other potential timings could have had an impact. For example, *V. thapsus* can tolerate heat with the highest photosynthetic rates at 40°C (Willieams and Kemp 1976), making *V. thapsus* more adapted to heat. Finally, these remaining species might have changed their growth in other states that were not measured, like number of flowers or fruits, altering fitness.

Although the species I studied are common in abandoned fields and are not threatened under climate change, we still found that our one-time heat event was species specific, and that depending on the heat wave timing, heat can have various effect sizes or opposite effects on growth and alter community composition. We also observed that the effects of heat waves can be observable 2 years after the heat wave. An increase in heat wave frequency and/or intensity might have had stronger effects on the community, and weather data show that many ecosystems undergo multiple heat waves over time. If these heat wave events happen at times when ecosystems are more susceptible to change, the consequences could be significant for shaping the community's future structure. Further, we only applied heat waves on small plots (radius = 28.5

cm) in a common garden experiment where larger herbivores or insect visitors were not affected by the heat. However, plants that undergo heat stress may improve their nutritive value (Mahmood et al. 2010), having an increase in herbivory (Birkemoe et al. 2016). Further, it is possible that only the food web dynamics belowground, like soil microbial community, were altered. Heat waves can alter plant-herbivore-predator/parasitoid dynamics (Sentis et al. 2013, Gillespie et al. 2012), and modify the duration and abundance of resource availability for vertebrates (Butt et al. 2015). Since heat waves happen at larger scales compared to our plots, we can expect food web dynamics of entire ecosystems to change due to the extreme heat.

In conclusion, the intra-annual and inter-annual timing of heat waves during plant growth and community assembly was an important predictor of the consequences of heat waves. While not all heat wave timings influenced community assembly outcomes after three years new patterns may have occurred beyond the three-year experiment. With evidence that response differ by stress timing within plant ontogeny, future extreme climatic event studies should explicitly incorporate timing variation. Experimental heat wave timing should also contextualize the event within each species' unique phenology and interactions within the broader community, especially in vulnerable systems with threatened species with a narrow thermotolerance. We expect heat waves to have profound impacts on ecological communities. Resolving the mechanisms and consequences of these events will be a next major advancement in our power to predict climate changes' strongest effects on the natural world.

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# APPENDIX

Table S2.1. Scientific name, family, species status in Michigan and life cycle of all the non-focal species that occurred in our 149 plots at the Kellogg Biological Station, MI in 2020 and 2021.

| **Scientific name** | **Family** | **MI status** | **Life cycle** |
|---|---|---|---|
| *Abutilon theophrasti* | Malvaceae | invasive | annual |
| *Agropyron repens* | Poaceae | invasive | perennial |
| *Bromus inermis* | Poaceae | invasive | perennial |
| *Daucus carota* | Apiaceae | exotic | biennial |
| *Dianthus armeria* | Caryophyllaceae | exotic | annual or biennial |
| *Erigeron annuus* | Asteraeae | native | annual |
| *Erigeron canadensis* | Asteraeae | native | annual |
| *Hypericum ascyron* | Hypericaceae | native | perennial |
| *Lactuca serriola* | Asteraceae | exotic | annual |
| *Lepidium campestre* | Brassicaceae | exotic | annual |
| *Lespedeza capitata* | Fabaceae | native | perennial |
| *Leucanthemum vulgare* | Asteraceae | exotic | perennial |
| *Medicago lupulina* | Fabaceae | exotic | perennial |
| *Oxalis stricta* | Oxalidaceae | native | annual or perennial |
| *Panicum virgatum* | Poaceae | native | perennial |
| *Phleum pratense* | Poaceae | exotic | perennial |
| *Phytolacca americana* | Phytolaccaceae | native | perennial |
| *Plantago lanceolata* | Plantaginaceae | exotic | perennial |
| *Poa nemoralis* | Poaceae | native | perennial |
| *Poa pratensis* | Poaceae | invasive | perennial |
| *Potentilla recta* | Rosaceae | exotic | perennial |
| *Ranunculus acris* | Ranunculaceae | exotic | perennial |
| *Ranunculus pensylvanicus* | Ranunculaceae | native | biennial/short perennial |
| *Raphanus raphanistrum* | Brassicaceae | exotic | annual |
| *Rumex acetosella* | Polygonaceae | exotic | perennial |
| *Rumex crispus* | Polygonaceae | exotic | perennial |
| *Silene dichotoma* | Caryophyllaceae | exotic | annual |
| *Spotted knapweed* | Asteraceae | invasive | biennial/short perennial |
| *Stellaria graminea* | Caryophyllaceae | exotic | perennial |
| *Trifoium sp.* | Fabaceae | exotic | n/a |
| *Trifolum campestre* | Fabaceae | exotic | annual |
| *Verbascum thapsus* | Scrophulariaceae | exotic | biennial |
| *Veronica arvensis* | Plantaginaceae | exotic | annual |

Table S2.2. Pairwise comparisons from the significant PERMANOVA models by year of collection. ‘Day model’ contains the specific time of the heatwave (hw.), ‘season model’ refers to when the heat wave happened regardless of year (early, early/mid, mid, and late heat wave), and ‘year’ model contains the year of heat wave regardless of when within a year (year 1, year 2, and year 3).

| **Data collected in 2020: Focal species only** | | | |
|---|---|---|---|
| **Day model** | **$R^2$** | **F** | **p** |
| Year 1 mid hw. vs Year 2 early hw. | 0.23 | 6.42 | 0.012 |
| Year 1 late hw. vs Year 2 early hw. | 0.26 | 6.25 | 0.007 |
| Control vs Year 2 early hw. | 0.14 | 7.76 | 0.002 |
| Year 2 mid hw. vs Year 2 early hw. | 0.26 | 7.84 | 0.002 |
| Year 1 early/mid hw. vs Year 2 early hw. | 0.19 | 5.00 | 0.022 |
| **Season model** | | | |
| Mid vs early hw. | 0.24 | 11.45 | 0.002 |
| Late vs early hw. | 0.16 | 5.69 | 0.012 |
| Control vs early hw. | 0.14 | 7.76 | 0.004 |
| Early/mid vs early hw. | 0.20 | 7.50 | 0.003 |
| **Data collected in 2021: Focal species only** | | | |
| **Day model** | | | |
| Year 1 late hw vs year 3 early hw | 0.03 | 0.18 | 0.02 |
| Year 2 mid hw. vs Year 2 early/mid hw. | 0.13 | 3.86 | 0.041 |
| Year 2 late hw. vs Year 2 ealy/mid hw. | 0.27 | 7.73 | 0.009 |
| Year 1 late hw. vs Year 2 early/mid hw. | 0.19 | 5.32 | 0.023 |
| Control vs Year 2 late hw. | 0.10 | 4.31 | 0.046 |
| Year 3 late hw. vs Year 2 late hw. | 0.28 | 10.35 | 0.001 |
| Year 2 late hw. vs Year 1 early/mid hw. | 0.14 | 4.06 | 0.032 |
| **Season model** | | | |
| Late vs early hw. | 0.14 | 8.18 | 0.001 |
| Control vs. late hw. | 0.08 | 4.65 | 0.032 |
| Late hw. vs early/mid hw. | 0.11 | 6.56 | 0.004 |
| **Data collected in 2021: Non-focal species only** | | | |
| **Year model** | | | |
| Control vs year 1 hw. | 0.03 | 2.19 | 0.047 |

Table S2.3. Estimate, standard error (E.S.), ±95% confidence intervals (C.I.) and p-value of the significant models of focal species.

| | | | | | Area | | | | | Height | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year data collection | Species | Parameter | Estimate | S.E. | C.I. | C.I. | p | Estimate | S.E. | C.I. | C.I. | p |
| 2019 | *Chenopodium album* | Late season | | | | | | -40.28 | 9.62 | -21.42 | -59.14 | 0.000 |
| | *Melilotus albus* | Mid season | 7465.60 | 3121.60 | 13583.94 | 1347.26 | 0.018 | | | | | |
| 2020 | *Daucus carota* | Year 2 early | | | | | | 82.60 | 32.79 | 146.87 | 18.33 | 0.018 |
| | *Daucus carota* | Year 2 late | | | | | | 67.10 | 25.05 | 116.20 | 18.00 | 0.013 |
| | | Early season | | | | | | 82.60 | 35.67 | 152.51 | 12.69 | 0.028 |
| | | Year 2 | | | | | | 39.75 | 19.84 | 78.64 | 0.87 | 0.054 |
| | *Erigeron annuus* | Year 2 mid | | | | | | 19.63 | 5.62 | 30.63 | 8.62 | 0.001 |
| | | Late season | | | | | | 9.00 | 4.63 | 18.08 | -0.09 | 0.057 |
| | | Mid season | | | | | | 14.34 | 4.41 | 22.99 | 5.69 | 0.002 |
| | *Erigeron canadensis* | Year 2 late | 4257.27 | 1502.83 | 7202.82 | 1311.72 | 0.005 | | | | | |
| | | Early/mid season | | | | | | -17.14 | 7.95 | -1.56 | -32.73 | 0.043 |
| | | Mid season | | | | | | -15.81 | 7.56 | -1.00 | -30.62 | 0.049 |
| | | Year 1 | | | | | | -15.86 | 7.20 | -1.75 | -29.96 | 0.038 |
| | | Year 2 | | | | | | -13.14 | 6.51 | -0.39 | -25.90 | 0.056 |
| | *Raphanus raphanistr* | Year 1 late | 2038.91 | 807.89 | 3622.37 | 455.45 | 0.013 | | | | | |
| | *Plantago lanceolata* | Year 2 early/mid | 5711.24 | 1228.50 | 8119.10 | 3303.38 | 0.000 | | | | | |
| | | Early/mid season | 1992.50 | 904.20 | 3764.73 | 220.27 | 0.029 | | | | | |
| | | Year 1 late | | | | | | 29.75 | 10.64 | 50.61 | 8.89 | 0.010 |
| | *Potentilla recta* | Year 1 late | 4419.50 | 1587.00 | 7530.02 | 1308.98 | 0.006 | | | | | |
| | | Year 2 early | | | | | | -15.13 | 7.08 | -1.25 | -29.02 | 0.037 |
| | | Early season | | | | | | -15.13 | 7.06 | -1.30 | -28.97 | 0.036 |
| | *Dianthus armeria* | Year 1 early | -826.36 | 438.18 | 32.47 | -1685.19 | 0.062 | | | | | |
| | *Oxalis stricta* | Year 2 early | 1293.60 | 600.45 | 2470.48 | 116.72 | 0.033 | | | | | |
| | | Early season | 1293.60 | 594.18 | 2458.19 | 129.01 | 0.031 | | | | | |
| | | Year 2 late | | | | | | 10.67 | 4.38 | 19.25 | 2.09 | 0.028 |
| 2021 | *Medicago lupulina* | Year 1 late | 1291.67 | 612.60 | 2492.36 | 90.97 | 0.037 | | | | | |
| | | Mid season | | | | | | -3.07 | 1.49 | -0.14 | -5.99 | 0.042 |
| | *Phleum pratense* | Year 2 early | 1312.50 | 464.11 | 2222.16 | 402.84 | 0.005 | | | | | |
| | | Late season | -625.00 | 316.41 | -4.84 | -1245.16 | 0.050 | -17.77 | 6.94 | -4.16 | -31.37 | 0.012 |
| | | Year 1 late | | | | | | -17.87 | 8.32 | -1.56 | -34.18 | 0.034 |
| | | Year 2 late | | | | | | -17.65 | 8.74 | -0.53 | -34.78 | 0.045 |
| | | Year 1 | | | | | | -12.41 | 6.17 | -0.32 | -24.50 | 0.046 |
| | *Plantago lanceolata* | Year 2 early/mid | 1891.67 | 528.69 | 2927.90 | 855.44 | 0.000 | | | | | |
| | | Year 3 early | -983.33 | 457.86 | -85.92 | -1880.74 | 0.034 | -8.73 | 3.68 | -1.51 | -15.95 | 0.019 |
| | | Early season | -929.00 | 427.50 | -91.10 | -1766.90 | 0.032 | | | | | |
| | | Year 3 | -983.30 | 488.70 | -25.45 | -1941.15 | 0.046 | -8.73 | 3.80 | -1.29 | -16.18 | 0.023 |
| | | Year 1 early/mid | | | | | | -7.47 | 3.68 | -0.25 | -14.69 | 0.045 |
| | | Year 2 early/mid | | | | | | 9.97 | 4.25 | 18.30 | 1.63 | 0.021 |
| | | Early season | | | | | | -7.82 | 3.35 | -1.25 | -14.39 | 0.021 |
| | *Dianthus armeria* | Year 2 late | 428.80 | 198.60 | 818.06 | 39.54 | 0.036 | | | | | |
| | *Ranunculus acris* | Year 2 early/mid | 1808.33 | 582.27 | 2949.58 | 667.08 | 0.002 | 11.30 | 3.88 | 18.90 | 3.70 | 0.004 |
| | *Rumex crispus* | Year 1 | | | | | | 5.65 | 2.81 | 11.14 | 0.15 | 0.046 |
| | *Silene dichotoma* | Year 1 late | -933.33 | 418.83 | -112.42 | -1754.24 | 0.028 | -13.13 | 5.13 | -3.07 | -23.19 | 0.012 |
| | | Year 3 early | | | | | | -10.33 | 5.13 | -0.27 | -20.39 | 0.046 |
| | | Late season | | | | | | -9.43 | 4.35 | -0.91 | -17.95 | 0.032 |
| | | Year 3 | | | | | | -10.33 | 5.21 | -0.11 | -20.55 | 0.050 |

# CHAPTER 3:

## HEAT WAVE TIMING AND THE EFFECTS ON STOMATAL CONDUCTANCE AND DECOMPOSITION

### Introduction

Extreme climatic events - episodes of severe weather at the extremes of the historical distribution such as heat waves- are increasing in frequency and intensity (Schär et al. 2004). Heat waves are brief periods of extremely high temperature (Marx et al. 2021). As sudden shocks of heat, they can disturb the phenology and physiology of the organisms they impact (Roitberg and Mangel 2016, Colinet et al. 2015, Vasseur et al. 2014). Not only can heat waves alter an organisms' biology, but they can also alter species interactions. However, as mentioned in Chapter 2, there is a main gap in the literature in how the timing of heat waves interacts with changes in physiology over time.

Heat waves are more frequent events during certain times of species ontogeny and their effects may vary depending on when they happen (Cinto Mejía and Wetzel 2023). For example, a heat wave can have opposite effects on photosynthetic rates of plants depending on when it happens during ontogeny (Wang et al. 2016). Yet, most studies have ignored the potential effects of heat wave timing. Based on the variation of soil condition (water availability and nutrient cycles) throughout time, we can imply that heat waves at distinct timings will have different effects on plant nutrient and water uptake, and decomposition by microorganism in the soil.

Previous literature show that heat waves can negatively impact plant species by decreasing seed germination rates (Orsenigo et al. 2015), inhibiting photosynthesis (De Boeck et al. 2010), and causing photodamage (Larcher 2003). Previously, plant responses to heat stress have been explained by two strategies: isohydric plants closing their stomata to reduce water loss while risking carbon starvation, and anisohydric plants keeping their stomata open at the cost of hydraulic failure (Reyer et al. 2013). Previous studies have suggested that these responses can also depend on water availability. When there is water available, plants can mitigate heat stress through transpirational cooling and alleviate the stress short-term (Reichstein et al., 2007). In cases when water is not available, plants reduce growth and evaporation by closing their stomata (Padilla and Pugnaire 2007). Further, heat waves will have effects on the root system as well, leading to changes in nutrient uptake. In tomato (*Solanum lycopersicum*), severe heat waves damaged the plant roots causing a slow recovery (Anju et al. 2017). In this example, plant root damage can decrease protein concentration and nutrient uptake affecting productivity.

Organisms that interact with plants can also experience the consequences of extreme heat through plant responses (Figure 3.1). Due to changes in plant physiology, heat waves could alter plant-insect interactions (Faldyn et al. 2018) the effect of which can cascade to other trophic levels indirectly (Felton and Smith 2017). For example, if extreme heat causes plant mortality, reflection of solar radiation, infiltration of precipitation, transpiration, respiration, and decomposition rates will change leading to altered ecosystem functioning (Anderegg et al. 2013; Bragazza 2008).

However, heat waves could directly impact soil microorganisms, and soil properties where microbial communities play a crucial role in organic matter decomposition as well (Reynold et al. 2003). Depending on the temperature, heat waves can increase mortality of microorganisms through dehydration (Bérard et al. 2015) or even increase the diversity of decomposition-related bacteria (Pan et al. 2021). Because decomposition activity is dependent upon temperature, it can be accelerated with high temperatures or slowed down due to the thermal deactivation of enzymes (Barros et al. 2021). Like plants, some microorganisms can mitigate the heat through various mechanisms. Other than sporulation (formation of spores) and dormancy during periods of stress, microorganisms can synthesize heat-shock proteins and intracellular osmolytes to improve enzyme thermotolerance (Bérard et al. 2015). These physiological changes in response to heat can lead to alterations in microbial diversity and abundance, consequently changing microbial activity and decomposition.

In this study we aimed to understand how heat waves at different times during a growing season can alter stomatal conductance and soil decomposition rates. We used the same study site (Kellogg Biological Station, MI, USA) as a previous experiment (see Chapter 2) where we investigated the response of plant growth and community composition to heat waves (Cinto Mejia et al. 2023). By experimentally applying heat waves at different times, our goal was to answer two main questions: (1) does heat wave timing alter stomatal conductance during a single growing season and, (2) does inter and intra-annual variability of heat wave timing alter decomposition? For both questions, we predict that earlier heat waves will have stronger effects on stomatal conductance and decomposition due to overlap with a period of high physiological activity for both plants and microbes.

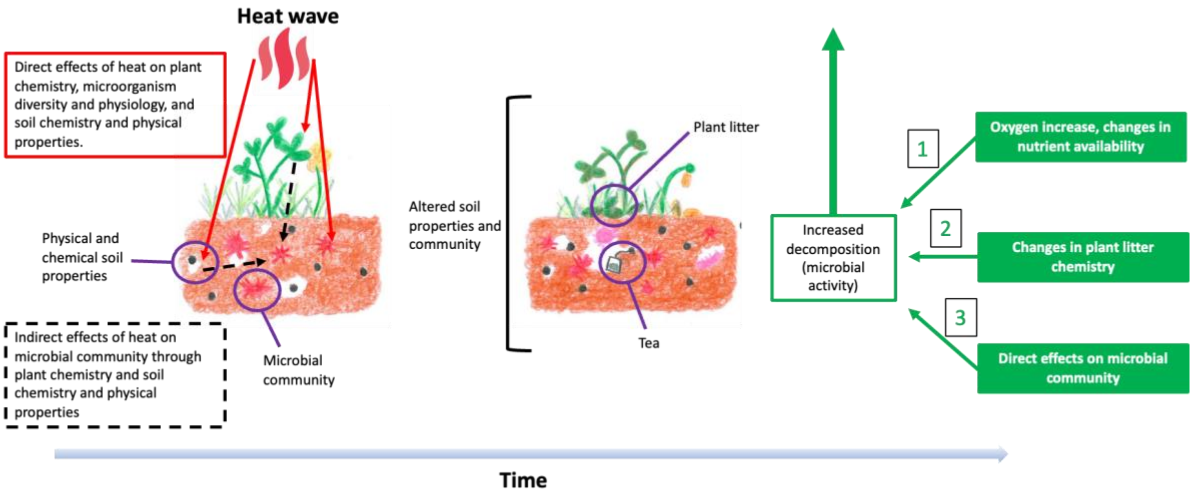

Figure 3.1. Potential effects of extreme heat on decomposition across the experimental treatment. The heat wave could have direct effects on microbial communities, plant physiology and soil properties at a certain point in time. Through these potential mechanisms, the heat can alter microbial communities indirectly. As time passes in the experiment, heated plots are altered. The experimental soil decomposition tea bag is added. Further, there will be new plant litter with potential altered chemistry and nutrient value developing naturally over time into the soil. An increase in microbial activity due to heat waves could be explained by 3 possible mechanisms: 1. Changes in soil chemistry and physical property increase the oxygen or nutrients available leading to an increase in decomposition. 2. Leaf litter produced by plants that exhibit physiological changes caused by a heat wave could have a direct effect on the microbial community. 3. Extreme heat could alter the microbial community during the time of the heat wave exerting effects weeks after the heat wave.

## Materials and Methods

To determine how heat wave timing alters plant physiology and decomposition, in 2020 we used the field site and plants described in Chapter 2. This common garden experiment contained 9 plant species that were planted in 2019. The plant community contained plant species native and non-native to Michigan: *Achillea millefolium*, *Asclepias syraca*, *Chenopodium album*, *Danthonia spicata*, *Melilotus albus*, *Solidago altissima*, *Solidago graminifolia*, *Symphyotrichum pilosum*, and *Trifolium pratense*. We experimentally applied heat waves at different timings during the summer in 2019 (year 1) and 2020 (year 2). We assigned plots to 7 different treatments and a control: (1) year 1 early heat wave, (2) year 1 mid-season heat wave,

(3) year 1 late heat wave, (4) year 2 early heat wave, (5) year 2 early mid-season heat wave, (6) year 2 mid-season heat wave, (7) year 2 late heat wave (Figure 3.1). With a total of 78 plots, in 2019, we randomly selected 15 plots to receive an early/mid-season heat wave (July 16), 19 plots were assigned a mid-season heat wave (July 30), and 15 plots received a late season heat wave (August 15). In 2020, 10 new plots received an early season heat wave on June 15, 10 new plots received an early/mid-season heat wave (July 16), 15 new plots received a mid-season heat wave (July 30), and 15 new plots received a late season heat wave (August 15). Each plot received only one heat treatment during the experiment. To mimic heat waves, we used open top-chambers and ceramic heaters (Chapter 2). Every heat wave lasted 4 days and 4 nights. We placed mesh chambers on the control plots to simulate the enclosing effects of heat chambers without their heat-trapping properties. In 2019, the mean air temperature inside the chambers was 29.9°C (SD=6.7) during the day and 21.0°C (SD=1.7) during the night. Controls chambers were 26.0 °C (SD=5.3) on average during the day and 20.2 °C (SD=2.8) during the night. In 2020, heat treated chambers averaged 28.9°C (SD=7.0) during the day and 14.0°C (SD=2.7) during the night. Controls were 25.9°C (SD=6.9) during the day and 11.9°C (SD=2.6) during the night.

### *Stomatal conductance*

In 2020, from the plants present in each plot, we selected 2 species *Trifolium pratense* and *Solidago graminifolia* for measuring stomatal conductance 2, 3, 7 and 8 days after the mid-season and late heat waves using a Li-Cor 6800 (LI-COR Biosciences, Lincoln, NE) gas exchange measuring system. Measurements were collected during the day, alternating between control and treatment plots.

To measure stomatal conductance, we took a 10-minute measurement from one leaf, having one leaf per species and plot, with the oxygen at 21%, and gas exchange at 0.5 µmol s-1. For the environmental settings, we kept the air flow rate at 500 µmol s-1, and pressure at 0.1 kPa. The reference CO2 was set to 400 µmol mol-1 and the fan speed was at 10,000 rpm. The leaf temperature set point was 25 °C and fluorometer set point was 400 µmol s-1 (r50, b50). In the field, we cut the leaf or piece of leaf used for the Li-Cor measurements and took a picture of it against a scale. Using Image J (Schneider et al. 2012), we calculated the area of each leaf used in the stomatal conductance measurement.

### *Decomposition*

To measure decomposition, we followed a modified version of the "teatime4science" protocol (Keuskamp et al. 2013). In 2020, we buried one fresh Lipton Green tea bag (EAN 87 10908 90359 5) 8 cm deep in each plot. We chose this type of methodology because plant litter (tea) decomposes at higher rates than cotton fabric, previously used in other experiments. The use of tea bags that have not been exposed to any heat treatment let us explore how a potential modified microbial community or ecosystem can alter non-treated litter. We buried all the tea bags on September 3 and retrieved them on November 29. We placed them in a drying oven for 3 days at 70 °C, then extracted the contents from each bag, weighted it and recorded the weight of the remaining dry matter (N=94). Any tea bag that was broken or had holes allowing the contents to leak out was excluded from the analysis (N=39). The decomposition measurements were collected from all the 7 different treatments described above.

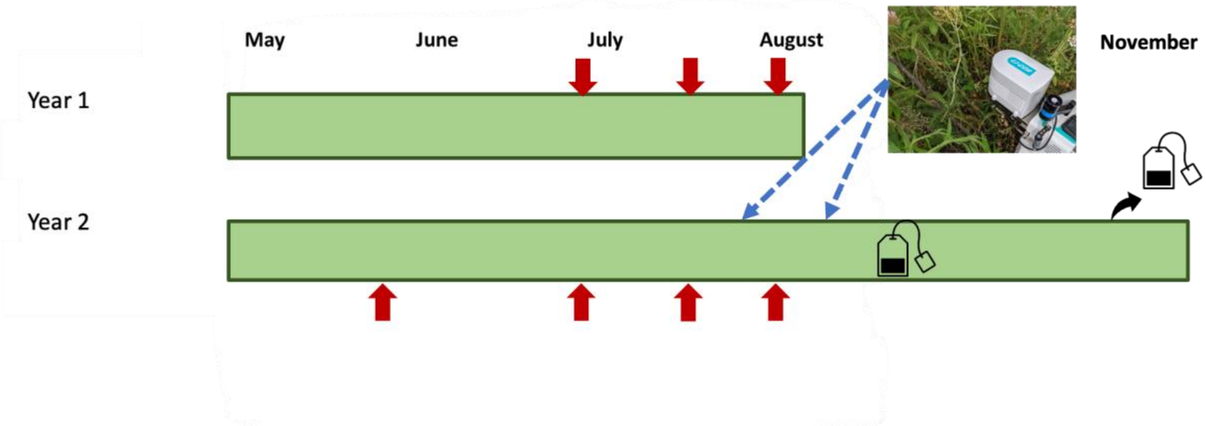

Figure 3.2. Experimental setup of heat wave experiments at the Kellogg Biological Station, MI, USA. Red arrows indicate heat wave application. During year 1 (2019), early/mid, mid-, and late-season heat waves were applied. In year 2 (2020), early, early/mid, mid-, and late-season heat waves were applied. The dotted blue arrows represent the times when stomatal conductance was measured, and the tea bags indicate when bags were buried (September 3 of 2020) and removed (November 29 of 2020).

## Statistical analysis

### *Stomatal conductance*

To test the effects of heat waves on stomatal conductance, we built a generalized mixed model (glmm) in the ‘glmmTMB’ package with stomatal conductance as the dependent variable. The model contained the interaction of treatment and days from the heat wave, and plant species as fixed effects and plot number as random effect. Heat waves, mid- and late season, were analyzed separately. If there was an effect of treatment, we built separate generalized linear models (‘glm2’ package) for each plant species. These models contained treatment and days from the heat wave as fixed effects. Because we only had one leaf per plant, we did not have to account for repeated measurements.

### *Decomposition*

To test the effects of heat wave timing on decomposition we built three generalized linear models (GLMs) in the ‘glm2’ package with weight (g) as the dependent variable. The first model ‘Season’ contained the timing of the heat wave within a year, early to late heat wave. The second model ‘Year’ contained the year of the heat wave (year 1 and year 2). The third model ‘Day’ contained the year and the time within a year of the heat wave. Because the decomposition data come from heat wave treatments in 2019 and 2020 and different times during the season, these three models let us test the intra- and inter-annual variation in heat wave timing. We conducted all statistical analysis in R version 4.1.2 (R Core Team 2020).

## Results

### *Stomatal conductance*

Only the mid-season heat wave influenced stomatal conductance of plants (Table 3.1). The general model indicated that the plant species, days from the heat wave, and heat wave were predictors of stomatal conductance (Table 3.1). When mid-season heat wave effects were examined by species, the heat wave treatment only had effects on *S. graminifolia* only (Table 3.2). *S. graminifolia* plants that received a mid-season heat wave had a 27.6% decrease in stomatal conductance compared to controls (Figure 3.2A). We did not observe any significant effects of the mid-season heat wave on *T. pratense* (Figure 3.2B).

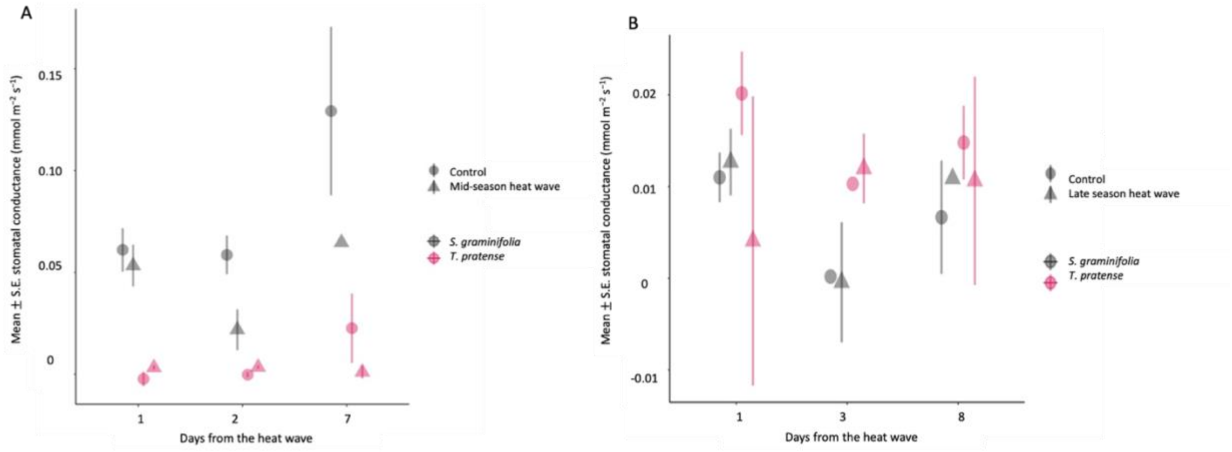

Figure 3.3. Mean ± standard error stomatal conductance (mmol $m^{-2}$ $s^{-1}$) of *S. graminifolia* and *T. pratense* at different days after the heat wave. The effects of the mid-season heat wave (A) and late heat wave (B) in 2020.

Table 3.1. Generalized linear mixed model parameter estimates, standard error (S.E.), p-value and upper and lower 95% confidence intervals from the model by heat wave (Hw) timing in 2020.

| **Heat wave timing** | **Parameter** | **Estimate** | **S.E.** | **p** | **$_{U}$C.I.** | **$_{l}$C.I.** |
|---|---|---|---|---|---|---|
| Mid-season | Intercept | 0.046 | 0.007 | <0.01 | 0.032 | 0.060 |
| | Heat wave | 0.001 | 0.010 | 0.953 | -0.018 | 0.020 |
| | Days from heat wave | 0.007 | 0.002 | <0.01 | 0.003 | 0.011 |
| | Plant species | -0.055 | 0.006 | <0.01 | -0.067 | -0.042 |
| | Heat wave*days from heat wave | -0.006 | 0.003 | 0.040 | -0.012 | 0.000 |
| Late season | Intercept | 0.012 | 0.004 | 0.003 | 0.004 | 0.019 |
| | Heat wave | -0.007 | 0.006 | 0.236 | -0.019 | 0.005 |
| | Days from heat wave | -0.001 | 0.001 | 0.364 | -0.002 | 0.001 |
| | Plant species | 0.007 | 0.003 | 0.004 | 0.002 | 0.012 |
| | Heat wave*days from heat wave | 0.001 | 0.001 | 0.593 | -0.002 | 0.003 |

Table 3.2. Generalized linear model parameter estimates, standard error (S.E.), p-value and upper and lower 95% confidence intervals from the mid-season heat wave (Hw) in 2020 by plant species.

| **Plant species** | **Parameter** | **Estimate** | **S.E.** | **p** | **uC.I.** | **lC.I.** |
|---|---|---|---|---|---|---|
| *S. graminifolia* | Intercept | 0.051 | 0.011 | **<0.01** | 0.029 | 0.074 |
| | Heat wave | -0.028 | 0.012 | **0.034** | -0.052 | -0.004 |
| | Days from heat wave | 0.008 | 0.003 | **0.018** | 0.002 | 0.015 |
| | Heat wave*Days heat | -0.01 | 0.006 | 0.13 | -0.022 | 0.002 |
| *T. pratense* | Intercept | -0.002 | 0.004 | 0.623 | -0.010 | 0.006 |
| | Heat wave | -0.001 | 0.005 | 0.900 | -0.010 | 0.009 |
| | Days from heat wave | 0.002 | 0.001 | **0.036** | 0.000 | 0.004 |
| | Heat wave*Days heat | -0.004 | 0.001 | **0.020** | -0.008 | -0.001 |

### *Decomposition*

While we did not observe significant differences across dry weight among heat wave treatments, plots that received a heat wave generally had lower weights compared to controls (Table 3.3). Plots that were exposed to a heat wave early in the season had a 7% decrease in decomposition (Figure 3.3A), and plots that underwent a heat wave in year 2 had a 4% decrease in decomposition (Figure 3.3B).

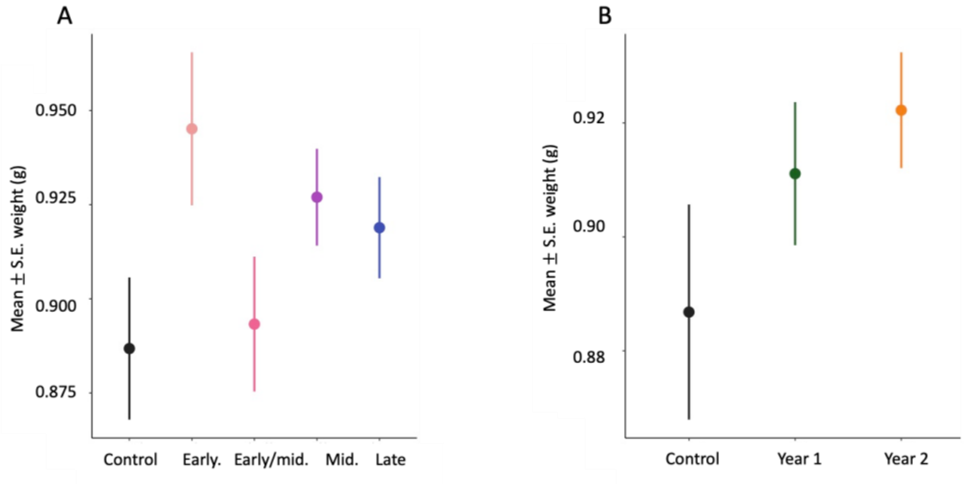

Figure 3.4. Mean ± standard error of tea weight (g) in response to heat wave during the growing season (A) and by year (B).

Table 3.3. Generalized linear model parameter estimates, standard error (S.E.), p-value and upper and lower 95% confidence intervals (C.I.) testing the effects of heat waves on decomposition in 2020. The model type corresponds to how we analyzed the timing of heat waves. The season model examines the intra-annual variation of heat wave timing (early, early-mid, mid, and late seasons). The year model examines the inter-annual variation of heat timing (year 1 vs year 2). The day model examines the inter- and intra-annual variation of heat wave timing.

| **Model** | **Parameter** | **Estimate** | **S.E.** | **p** | **uC.I.** | **lC.I.** |
|---|---|---|---|---|---|---|
| Season | Intercept | 0.887 | 0.015 | <0.01 | 0.858 | 0.916 |
| | Early | 0.058 | 0.033 | 0.084 | -0.007 | 0.124 |
| | Early-mid. | 0.006 | 0.023 | 0.779 | -0.039 | 0.052 |
| | Late | 0.032 | 0.022 | 0.143 | -0.010 | 0.075 |
| | Mid. | 0.040 | 0.022 | 0.075 | -0.004 | 0.084 |
| Year | Intercept | 0.887 | 0.015 | <0.01 | 0.858 | 0.916 |
| | Year 1 | 0.024 | 0.020 | 0.226 | -0.015 | 0.063 |
| | Year 2 | 0.035 | 0.020 | 0.073 | -0.003 | 0.074 |
| Day | Intercept | 0.887 | 0.015 | <0.01 | 0.858 | 0.916 |
| | Year 1 early-mid. | 0.012 | 0.028 | 0.659 | -0.042 | 0.067 |
| | Year 1 late | 0.020 | 0.027 | 0.469 | -0.033 | 0.072 |
| | Year 1 mid. | 0.043 | 0.029 | 0.137 | -0.013 | 0.100 |
| | Year 2 early | 0.058 | 0.034 | 0.088 | -0.008 | 0.125 |
| | Year 2 early-mid. | -0.002 | 0.032 | 0.955 | -0.064 | 0.060 |
| | Year 2 late | 0.046 | 0.028 | 0.103 | -0.009 | 0.100 |
| | Year 2 mid. | 0.037 | 0.028 | 0.184 | -0.017 | 0.092 |

## Discussion

The timing of a heat wave during the ontogeny of plants is a predictor of plant stomatal conductance. We found that when a heat wave occurred during flowering (mid-season), stomatal conductance of *S. graminifolia* increased by 27% compared to controls. Neither the mid- nor the late-season heat wave influenced stomatal conductance of *T. pratense*, indicating that it did not respond to the level or timing of heat stress in our experiment. When looking at decomposition, we observed a pattern where early heat waves decreased microbial activity compared to controls, indicating that an increase in plant material corresponds to lower decomposition activity. These results contribute to the gap in the literature where the timing of heat waves and the effects on plant physiology and decomposition has not been explored. To our knowledge, this is the first study to show the importance of the timing of extreme climatic events and ecosystem services.

Both species showed different responses to the two heat wave types. A higher trichome density in *T. pratense* could explain why we did not observe changes in stomatal conductance under heat waves. Most terrestrial plants are covered with trichomes, extensions of the epidermis that can help mitigate biotic and abiotic stressors (Gasparini et al. 2021). In addition to differences in structural trichome diversity, trichomes can vary in length and density depending on plant species. While both of our species have long trichomes (~100 µm long), *T. pratense* has a higher trichome density compared to *S. graminifolia* (Yagueddú et al. 2009; Vinogradova et al. 2017). Trichomes have the potential to reduce leaf temperatures and plant water loss (Smith and Hare 2004). The trichome layer influences heat transfer and water vapor exchange with the environment (Schreuder et al. 2001). Under stress conditions, the trichome layer can help hold the humidity around the leaves. The trichomes might have served as a buffer for *T. pratense* thus there were no differences in stomatal conductance between heat waved and control plants. On the other hand, *S. graminifolia* might have had to open its stomata to cool down the leaves.

Another mechanism that might explain the differences between the two species is their morphological structure. *Solidago graminifolia* mostly grew vertically as a single stem while *T. pratense* grew multiple stems horizontally and vertically, thus its historical use as a ground cover (Nurtjahya and Franklin 2019). The multilayer leaf growth of *T. pratense* might have served as a structure to create a microclimate with cooling effects (Zhang et al. 2013). In addition to the differences in plant structure, the two species differ in their life cycles and phenology. *Solidago graminifolia* is a perennial species that had no flowering parts at the time of the experiment and *T. pratense* is a short-lived perennial that had many inflorescences when we applied the heat waves. Although risking water lost, *S. graminifolia* may have increased the stomatal conductance during the mid-season heat wave to mitigate the hot temperature but without risking the loss of current reproductive parts, thus increasing conductance can serve as a fitness trade-off long term. Also, other species surrounding *T. pratense* providing shade to this species could have influenced the outcome. Another possibility is that *T. pratense* was stressed already with and without the treatments. For both heat wave treatments and the controls, *T. pratense* shows very low stomatal conductance (Figure 3.3), indicating stress caused by ambient heat or water availability.

Responses from *S. graminifolia* to heat stress indicated that only the mid-season heat wave and not the late-season heat wave increased stomatal conductance. A specific heat wave timing changing the stomatal conductance of *S. graminifolia* supports previous findings investigating the effects of heat wave timing during the ontogeny of an organism (Cinto Mejía and Wetzel 2023; Chapter 2). It is possible that the mid-season heat wave overlapped with peak stomatal activity during a time when the plants were most susceptible to heat stress. Furthermore, the timing of the heat wave could coincide with a time when the plants allocate more energy to growth versus later in the season when plants senescence.

Any physiological changes happening at the plant level could have cascaded to other trophic levels, like decomposers (Figure 3.1). Although we did not observe strong effects, plots that were exposed to an early heat wave had a decrease in microbial activity, measured as decomposition. Heat waves occurring pre-senescence can directly influence plant physiology and shape the final chemical composition of plant litter and root system that plays a role in decomposition (Suseela and Tharavil 2017). Plant chemical composition under stress can be altered through changes in quantity, quality, and allocation of compounds available for microbial communities (Cabane et al. 2012). A possible explanation for a decrease in microbial activity is changes in the C:N ratio of the plant litter. Plants undergoing a heat wave may alter their nutritive value due to an increase in sugar and amino acid production under stress (Suseela and Tharavil 2017). Likewise, heat waves could have altered the microbial community directly, changing future decomposition rates weeks after the heat wave. While we don’t know the mechanism behind a decrease in decomposition, extreme heat could have changed soil properties as well (Figure 3.1), modifying the microclimate and soil physical and chemical properties to accelerate decomposition. However, the tea bags were buried 8cm deep in the soil, and it is unlikely that the heat reached deep into the soil layer. Thus, the pattern we observed is likely caused by changes in plant chemistry above and below ground.

In this study, we show that heat waves can alter plant stomatal conductance and increase decomposition. The timing of heat waves within and across years can alter their effects on plant physiology and microbial activity. These relationships are important to understand because as more carbon is stored in the soil due to climate change, decomposition may increase. A potential outcome of changes in the carbon cycle is the release of more carbon into the atmosphere creating positive feedback (Davidson and Janssens 2006). With heat waves intensifying in the future and average temperatures increasing in most parts of the world, understanding how heat waves can alter decomposition is crucial for the future of ecosystem services.

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# CHAPTER 4:

## CONCLUSIONS AND FUTURE DIRECTIONS

Throughout my dissertation, I investigated how the timing of extreme climatic events, especially heat waves, is important to consider when studying the consequences of climate change. Using other evidence from the disturbance literature, I examined how the timing of extreme climatic events can alter the ontogeny of individuals, population and community dynamics depending on when the event happens. With temperatures increasing worldwide and heat waves and other extreme climatic events increasing in duration and intensity, understanding how extreme events is crucial. Chapter 1 presents various hypotheses that can be tested at various biological levels in future climate change studies. The goal of Chapter 1 is to review previous literature and present new ideas about how to investigate extreme climatic events.

In Chapter 2, I applied the theory into practice, focusing on assessing how the timing of heat waves can alter plant community composition and plant growth. Only very few community ecology studies have included the timing of extreme climatic events as a predictor of how extreme events impact ecosystems (Barrat-Segretain and Bornette 2000). I found that depending on the intra- and inter-annual variation in the timing of heat waves, heat waves can have opposite effects on plant height and area. This result suggests that heat can also have a positive response in plant growth. Plants that grew more under the extreme heat might be better competitors under stress conditions than other species. Exploring plant growth was the first step to study the effects of heat waves, however, I did not focus on possible mechanisms behind an increase or decrease in growth. To disentangle some of the responses that I observed in the field, future greenhouse studies can help answer what mechanisms are behind plant response. For example, I could individually grow the species I used in the field in growth chambers to look at the direct effects of heat timing on individual plants during ontogeny. This simple experiment would answer the direct effects of heat, without any competition or any other species interactions at different timings during the ontogeny of plants and years. New data produced by this experiment could serve as a baseline to later compare with what was observed in the field. Further, it would be interesting to examine the cost-benefits of increasing or decreasing growth and fitness. Because heat waves are becoming more prevalent, long-term data will be necessary to know what the fitness consequences are of plants growing less or growing more in response to heat. Plant species that had a positive response to heat probably invested more energy in growth and less energy in other functions like reproduction or underground growth. Under a heat wave, what is the best strategy and when?

When looking at the community composition results, I observed that the consequences of extreme heat can be observed a year after the heat wave happened. My experiment only lasted 3 years, and that is a relatively short time scale from an ecological point of view. Other research showed that a one-time extreme climatic event can change the community assembly years after the event (Suarez and Kitzberger 2008). It would be interesting to repeat the experiment using species, or a different type of community that is more threatened by climate change and monitor it for longer. This type of experiment would contribute to our understanding of how heat susceptible ecosystems might change in the future.

In Chapter 3, I focus on understanding one of the many mechanisms behind changes in plant growth after heat waves and the possible consequences at another trophic level. In the past, there have been experiments examining the physiological responses of plants to heat stressors. Future studies should consider the age and the time when the heat stress was applied, as some species might respond differently. My results showed that 7 days after the heat wave, stomatal conductance increased the most. It would be interesting to measure stomatal conductance for a more extended time after the heat wave to examine the long-term effects. More detailed data could provide insight into one of the many possible mechanisms of how heat waves alter plant growth.

Although I did not see strong effects on decomposition, my results suggest an increase in decomposition in the heat waved plots. This is a crucial finding since decomposition is a main ecosystem service and can alter the carbon cycle (Soto-Pinto and Jiménez-Ferrer 2018). Any increase in decomposition can negatively contribute to the carbon released into the atmosphere. In my study, I did not measure the cause for an increase in decomposition, whether the direct effects of the heat on microbial communities, indirect effects from the heat-altering plant chemistry and soil properties, or a combination of all resulted in changes. Future studies should focus on combining the timing of heat waves and looking at all the possibilities separately.

In my experiments, I applied heat waves that were not intense, only about 4 C° above controls. Even with this small difference, I observed major changes in community and plant growth. In the last few years, heat waves in Michigan and other places in the world have exceeded 38 C°. For certain parts of the world, these temperatures can cross the heat tolerance threshold of many species. Based on my results, I can imply that the effects of heat waves in the last few years would be stronger than the ones presented in this dissertation. In addition, my dissertation only explored the effects of a single heat wave event, however, many areas have undergone many heat waves. Only in the summer of 2022, Spain had three heat waves (Tobías et al. 2023). How species will respond to many stressors is still unknown. We do not measure if after a heat wave plant species will adapt to heat and have an ecological memory or if each heat wave will have additive/synergistic effects.

Finally, it will be crucial to learn what ecosystems will be more susceptible to multiple extreme climate events. My thesis provides a starting point to begin exploring the effects of heat waves and how their timing interacts with species responses.

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