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Floral traits and carbon dynamics of cucumber in response to climate change

Sarah Josina McDonald, *The University of Western Ontario*

Supervisor: Way, Danielle A., *The University of Western Ontario*

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Abstract

Pollination by animals is an important ecosystem service that contributes to the reproduction of many angiosperms. Climate change may alter this mutualism by affecting floral traits that are important to pollinators. Using *Cucumis sativus*, I tested the effects of experimentally elevated temperature and CO_2 concentration on flowering onset, flower number, flower size, and floral rewards. Additionally, to better understand plant carbon balance and investment in reproduction, I measured biomass partitioning and leaf carbon fluxes of plants under their growth conditions. Carbon dynamics were similar across treatments, and plants grown under high [CO_2] and temperature showed similar biomass production/allocation to control plants. Despite these similarities, both factors altered floral traits in ways that could affect plant-pollinator relationships. However, temperature effects were common, while CO_2 effects were not, suggesting that studies focusing on elevated [CO_2] may be less valuable than studies focusing on elevated temperature or the interaction between [CO_2] and temperature.

Keywords

Climate change, carbon dioxide, warming, carbon dynamics, *Cucumis sativus*, floral traits, floral rewards, pollen, nectar, plant-pollinator interactions

Summary for Lay Audience

Pollination is vital for the reproduction of many plants, and by supporting plant reproduction, pollination maintains food production and wild plant communities. Due to human activities, we are experiencing factors of climate change, such as increased temperature and amounts of carbon dioxide in the atmosphere. These increases in temperature and carbon dioxide concentrations may alter the ways that pollinators interact with the plants they pollinate by changing plant traits that pollinators rely on, such as the number and size of flowers, or the amount of pollinator food plants produce. To test the effects of climate change on these plant traits, and to determine if changes in plant physiology might explain changes in plant traits, I grew cucumber plants at different carbon dioxide concentrations and temperatures. I then measured flower traits that are important to pollinators (e.g., time to flowering, number of flowers, flower size, and amount of pollinator food) and aspects of plant physiology (e.g., the amount of carbon taken up by leaves and plant size) at two different plant stages. I found that increased carbon dioxide levels and temperature altered flower traits in ways that could affect how pollinators interact with plants, but these trait changes did not seem to be related to changes in plant physiology. Warming generally had negative effects on plant traits (e.g., flowers were smaller), while higher amounts of carbon dioxide reduced the negative effects of warming on floral traits, but only at very high temperatures. Interestingly, I also found that temperature affected more traits than carbon dioxide, suggesting that warming might be more important than carbon dioxide when trying to predict how plants will respond to climate change. Furthermore, male and female flowers responded differently to the treatments, and plants at later stages tended to have lower trait values and less response to the treatments. To get a better sense of plant-pollinator interactions under future climates, studies including more plant traits, and pollinator behaviour in response to these trait changes, would be useful.

Co-Authorship Statement

This work was conceptualised, analysed, and drafted with input from Dr. Danielle Way and will be made into a manuscript for publication with her collaboration.

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List of Abbreviations

AC = Ambient CO_2 (400 ppm)

Acetyl-CoA = Acetyl coenzyme A

ADP = Adenosine diphosphate

A_{net} = Net CO_2 assimilation rate

ATP = Adenosine triphosphate

BPG = 1,3-bisphosphoglycerate

C_i = Intercellular CO_2 concentration

CO_2 = Carbon dioxide

$[CO_2]$ = CO_2 concentration

Cyt b_6f = Cytochrome b_6f complex

Cyt c = Cytochrome c

C_3 = Method of photosynthesis where the Calvin-Benson cycle is used to produce a 3-carbon compound

EC = Elevated CO_2 (750 ppm)

FACE = Free-Air CO_2 Enrichment

$FADH_2$ = Flavin adenine dinucleotide

Fd = Ferredoxin

FvCB model = Farquhar-Berry-von Caemmerer model of photosynthesis

g_s = Stomatal conductance

G3P = Glyceraldehyde-3-phosphate

H^+ = Proton

IPCC = Intergovernmental Panel on Climate Change

J_{max} = Maximum rate of electron transport

NAD^+/NADH = Nicotinamide adenine dinucleotide (oxidized form/reduced form)

$NADP^+$/NADPH = Nicotinamide adenine dinucleotide phosphate (oxidized form/reduced form)

O_2 = Oxygen

PC = Plastocyanin

PG = 2-phosphoglycolate

PGA = 3-phosphoglycerate

P_i = Inorganic phosphate

PQ = Plastoquinone

PSI = Photosystem I

PSII = Photosystem II

P680/$P680^*$/$P680^+$ = First electron donor for PSII (normal form/excited state/oxidized form)

P700/$P700^*$/$P700^+$ = First electron donor for PSI (normal form/excited state/oxidized form)

Q_{10} = The change in respiration for each 10 °C temperature change

RC = Reaction center (of a photosystem)

RCP = Representative concentration pathway

R_D = Nighttime dark respiration rate

Rubisco = Ribulose-1,5-bisphosphate carboxylase/oxygenase

RuBP = Ribulose 1,5-bisphosphate

TCA cycle = Tricarboxylic acid cycle (Krebs cycle/citric acid cycle)

TL = True leaf stage

T_{opt} = Temperature optimum of net photosynthesis

UQ = Ubiquinone

UV-B = Ultraviolet type B

V_{cmax} = Maximum rate of Rubisco carboxylation

VPD = Vapour pressure deficit

0T = Ambient temperature (no warming)

4T = Ambient regime +4 °C (moderate warming)

8T = Ambient regime +8 °C (extreme warming)

1 Introduction

1.1 Climate change

Since the Industrial Revolution, anthropogenic activities, such as fossil fuel use and land use change, have dramatically increased the concentration of CO_2 ($[CO_2]$) in the atmosphere from 280 ppm to 415 ppm (IPCC, 2014; USDC, 2020). By 2100, atmospheric $[CO_2]$ could be from 750-1300 ppm without mitigation (IPCC, 2014). As a result of increases in $[CO_2]$ and other greenhouse gases, global mean annual surface temperatures could increase by 2.5 - 7.8 °C over the same time span, with the degree of warming dependent on mitigation strategies by humans to slow climate change (IPCC, 2014).

The Intergovernmental Panel on Climate Change (IPCC) assesses and synthesises published research to produce reports detailing our current knowledge of climate change, as well as the potential future impacts of, and strategies for adaptation and mitigation to, climate change. In order to make recommendations about climate change, the IPCC has designated four representative concentration pathways (RCPs). These RCPs make assumptions about the extent of future climate drivers, such as emission levels or greenhouse gas concentrations, and range from a best case/high mitigation scenario (RCP2.6), to stabilising scenarios (RCP4.5 and RCP6), to a worst case/little to no mitigation scenario (RCP8.5) (Cubasch et al., 2013). The set $[CO_2]$ used for these RCPs are 421 ppm (RCP2.6), 538 ppm (RCP4.5), 670 ppm (RCP6.0), and 936 ppm (RCP8.5) (Cubasch et al., 2013). Using information from RCP2.6, RCP4.5 and RCP8.5, the Ontario Ministry of Natural Resources and Forestry summarised IPCC findings for Ontario in 2014 (McDermid et al., 2014). Based on this report, mean annual air temperature in the Great Lakes Basin (where this research was conducted) is expected to warm between 2.4 - 4.1 °C under RCP2.6, 3.9 - 5.8 °C under RCP4.5, and between 6.7 - 9.0 °C under RCP8.5 by the end of this century (McDermid et al., 2014).

Increases in [CO_2] and temperature are not the only characteristics of climate change. We can also expect more frequent extreme weather events, rising sea levels, and increasingly melted glaciers (IPCC, 2014). However, in this thesis I focus on [CO_2] and temperature impacts for two reasons: first, because temperature and [CO_2] are driving the aforementioned events, and second, because they are pervasive across the globe. In actuality, these [CO_2] and temperature changes are already having widespread effects on biological processes, including altering plant traits that are important for plant-pollinator interactions (e.g., Parmesan, 2007).

1.2 Plant-pollinator interactions

1.2.1 Background

Pollination is the process by which male gametophytes (pollen grains) are transferred from the anthers of a plant's stamen to the stigma of a plant's pistil (Figure 1.1), this facilitates pollen germination, fertilisation, and seed production so that plants can reproduce (Willmer, 2011).

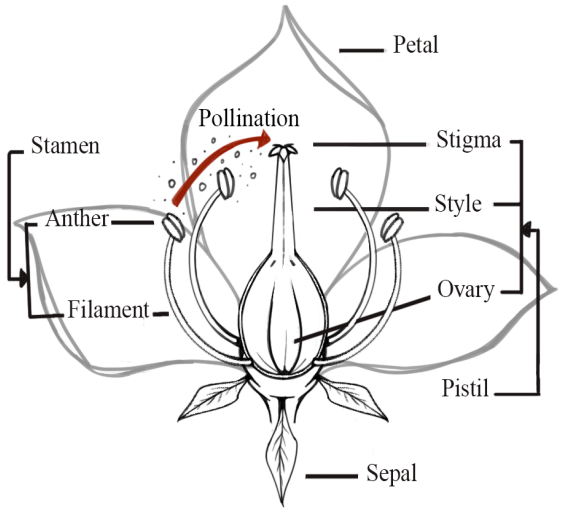

Figure 1.1. Diagram of pollination on a perfect flower (containing both male and female reproductive organs). Circles represent pollen grains and the red arrow represents pollination. Illustrated by Amy McDonald.

Pollination is an important ecosystem service given its roles in agricultural production, biodiversity maintenance, and general ecosystem function (Costanza et al., 1997; Eilers et al., 2011; Gallai et al., 2009; Klein et al., 2007; Potts et al., 2016). In terms of agricultural production, pollination precedes the development of seeds and fruits that are utilised by humans. Additionally, for biodiversity maintenance, pollination contributes to both the insurance and productivity benefits of biodiversity by allowing outcrossing within plant species and maintaining plant populations (Heal, 2001; Potts et al., 2016). Specifically, maintenance of biodiversity via pollination provides both managed and wild plant populations with increased resilience to stochastic events (e.g., disease or pest outbreaks), affording 'insurance' for ecosystem services and food production (Heal, 2001). Furthermore, more diverse systems can increase productivity via niche differentiation, such that resources are more efficiently used by a wider variety of organisms (Heal, 2001). At the same time, pollination in both anthropogenic and natural ecosystems affects habitat structure and food supplies for wildlife, which can indirectly benefit humans via recreation and esthetics (Potts et al., 2016).

As sessile organisms, plants require a vector to complete the transfer of their genetic material. Vectors of pollination can be abiotic, such as wind and water, but the majority of pollination is carried out by animals (Willmer, 2011). In fact, it is estimated that around 85% of angiosperms rely on pollination via animals to at least some extent (Ollerton et al., 2011). Animal pollination is also estimated to provide as much as $774 billion CAD annually in global food production value (Lautenbach et al., 2012; Potts et al., 2016), and this value is further increased because animal-pollinated species provide essential vitamins and nutrients to the human diet (Eilers et al., 2011). For instance, plants reliant on animal pollination produce 90% of vitamin C (Eilers et al., 2011). The most common animal pollinators are insects, such as bees or flies (Renner & Ricklefs, 1995), and within insect pollinators, managed honey bees, such as *Apis mellifera,* are perhaps the most important in terms of direct value to humans.

Animal pollinators are enticed to provide their pollination services by the promise of floral rewards, including products such as pollen and nectar (Willmer, 2011). For bees, pollen and nectar are converted into bee bread and honey, which are essential sources of

carbohydrates, proteins, and lipids that support survival and reproduction (Nicolson, 2011). Pollination also relies on a suite of cues at the whole plant and individual flower level, including characteristics such as the onset of flowering, flower number, and flower size, which can influence pollinator attraction and the efficiency of pollination (Willmer, 2011).

1.2.2 Floral traits and plant-pollinator interactions

The general ways that floral traits influence plant-pollinator interactions are related to advertisement, attraction, and efficiency. These can apply at any point along the visitation sequence including initial attraction, visitation (e.g., number of flowers visited, duration of visit), or departure of the pollinator (Willmer, 2011). In order to be able to compare my results to those of other researchers, I selected the commonly measured floral traits flowering onset, flower size, flower abundance, and floral rewards to evaluate. In the following subsections I cover the ways in which these floral traits have been found to influence plant-pollinator dynamics. Due to the importance of bee pollination (from both wild and domesticated species), and the abundance of literature on this subject, I concentrate largely on bee pollination throughout this thesis.

1.2.2.1 Onset of flowering

The timing of flowering onset is important for plant-pollinator interactions to ensure that receptive flowers are available when pollinators are foraging (Ramos–Jiliberto et al., 2018). From the plant perspective, initiating flowering when pollinators are not available could be a waste of resources, since plants risk missing pollination entirely and insufficient pollination can lead to decreased plant productivity (Kudo & Cooper, 2019). To some extent, the risk of insufficient pollination depends on a plant's reproductive strategy; for instance, an absence of pollinators can be particularly problematic if plants produce a limited number of flowers over their lifetime or if they flower for a short period of time. Furthermore, from the pollinator perspective, mismatched flowering time and insect foraging could lead to a significant lack of food resources during critical life history stages, such as larval rearing (Brodschneider & Crailsheim, 2010).

1.2.2.2 Flower abundance

The number of flowers that plants produce influences plant-pollinator interactions in two main ways. First, the number of open flowers at a given time (display size) influences a plant's advertising ability, with more flowers offering greater advertisement to pollinators; this also affects the amount of rewards available in a particular window of time (Conner & Rush, 1996). Second, the number of flowers that plants produce over their lifetime influences the amount of available floral rewards over a longer period of time, with more flowers providing more opportunities for foraging (Willmer, 2011).

1.2.2.3 Flower size

Flower size can affect both visual advertisement to pollinators and the efficiency of pollination (Conner & Rush, 1996; Galen & Newport, 1987). Larger flowers are generally more appealing to pollinators because they are bigger advertisements (Conner & Rush, 1996). At the same time, changes in whole flower size can alter the 'functional fit' between plants and pollinators (the morphological relationship between a pollinator and floral sexual organs). Altering the functional fit between plants and pollinators affects which pollinators can access resources, and also influences how much energy must be expended to forage on a particular flower (Harder, 1986). Morphological changes may also be detrimental for plants via direct effects on pollen deposition and subsequent seed set (Galen & Newport, 1987; Solís-Montero & Vallejo-Marín, 2017).

1.2.2.4 Floral rewards

Floral rewards are essential components of plant-pollinator relationships and the primary rewards produced by plants are pollen and nectar (Brodschneider & Crailsheim, 2010). For bees, pollen is an important source of protein, lipids, and micronutrients for larval growth and sexual maturation, and nectar is an essential source of water and carbohydrates for energy metabolism (Nicolson, 2011).

The dietary value of pollen and nectar depends on the amount of these rewards that is available and the concentration of nutritional components in the reward (Brodschneider

& Crailsheim, 2010; Nicolson, 2011). Both production and concentration of rewards can vary substantially between individuals and species (Pacini et al., 2003; Roulston & Cane, 2000). In fact, pollen protein levels can be anywhere between 2% and 60% (Roulston et al., 2000), while carbohydrate concentrations in nectar have been found to range from 6 to 85% (Pamminger et al., 2019). The concentration of sugars also alters nectar viscosity, and thus the rate of nectar uptake by pollinators (Pivnick & McNeil, 1985).

Pollen and nectar mainly function as pollinator attractants, but they may also manipulate pollinator behaviour during and after foraging based on nutritional information obtained from these rewards (Pyke, 2016). Pollinators may use a combination of visual, olfactory, and gustatory sensing to assess the quantity and quality of floral rewards, although there is still some debate about how, or if, some pollinators assess pollen quality (Muth et al., 2016; Nicholls & Hempel de Ibarra, 2017; Scheiner et al., 2013). In general, bumble bees show a preference for pollen that is high in protein and may prefer pollen with greater concentrations of essential amino acids (Cook et al., 2003; Hanley et al., 2008). For nectar, the preference in bees appears to be for higher sugar concentrations, with concentrations around 50-60% generally providing the fastest rate of energy uptake (Roubik & Buchmann, 1984). During foraging, the nutritional information gleaned from rewards may affect the decision of pollinators to continue feeding on the same flower (Pyke, 2016). After feeding, the nutritional value of pollen and nectar may affect the decision to forage on the same plant, another member of the same species, or a different species altogether, with corresponding impacts on plant productivity (Pyke, 2016).

Rewards can also influence plant attractiveness and pollinator behaviour to varying degrees depending on the pollinator in question. This is because pollinators vary in their sensory abilities, the floral cues they focus on, and in their nutritional requirements (Wester & Lunau, 2017). For example, honey bees have approximately 150 olfactory receptors (Robertson & Wanner, 2006), while hummingbirds are estimated to have around 50 (Steiger et al., 2008).

1.2.2.5 Other floral traits

Other floral traits can also influence plant-pollinator relationships. The complex and tightly linked evolutionary history of plants and pollinators has resulted in a multitude of traits that are important to this mutualism. As just a few examples, flower colour, scent, and shape can also play a role in plant-pollinator interactions (summarised in Willmer, 2011). Flower colour can act as an advertisement when pollinators are farther away and because pollinators see different wavelengths of light than humans, visual cues, like nectar guides, can orient pollinators during visitation (Pye, 2018). Flower scent can attract pollinators while deterring herbivores and can aid in proper pollinator entrance and orientation. Finally, flower shape affects the functional fit between plants and pollinators and pollinator visitation time. While these floral metrics were not assessed in this study, for more information on floral traits that influence plant-pollinator relationships see Willmer (2011).

1.3 Climate change impacts on plant-pollinator interactions

Climate change can directly or indirectly affect plant-pollinator interactions via both insect and plant responses (Scaven & Rafferty, 2013). Throughout this thesis I focus on the consequences of [CO_2], temperature, and their interaction from the perspective of the plant, and, consequently, insect responses are not covered here in great detail.

Plants have to invest resources in floral cues and rewards in order to attract pollinators and ensure efficient pollination; this can sometimes be costly. For instance, plant investment in nectaries can be as much as 37% of daily photosynthesis (Pyke, 1991; Southwick, 1984), and allocation of biomass to reproductive structures is estimated to be as much as 60% (Bazzaz et al., 1987). The common currency for plant growth and metabolism is carbon. In plants, photosynthesis, photorespiration, and respiration represent the major carbon fluxes, and the balance between these processes affects the resources available for plant growth and development (plant carbon balance). These fluxes have been shown to respond to changes in [CO_2] and temperature (Dusenge et al., 2019), and any [CO_2]- or temperature-induced change in carbon fluxes can cascade

throughout the plant, producing secondary effects on plant physiology, growth, and floral traits. Here I provide an overview of photosynthesis, photorespiration, and respiration. I also review the main effects of [CO_2], temperature, and their interaction on these processes, and discuss the effects of changing [CO_2] and temperature on plant growth and floral traits.

1.3.1 C3 photosynthesis

Photosynthesis is the process by which plants harvest and use energy from light in order to synthesise carbohydrates from water and CO_2 (Taiz & Zeiger, 2002). The carbohydrates produced can then be used to fuel cellular processes. For eukaryotic photosynthetic organisms, photosynthesis takes place in the chloroplasts and consists of two processes: the 'light reactions' (light harvesting and the production of chemical energy), and the 'dark reactions', aka the Calvin-Benson cycle (carbon fixation) (Taiz & Zeiger, 2002).

1.3.1.1 Light reactions

The light reactions take place in the thylakoid membranes of chloroplasts and function to generate energy in the form of adenosine triphosphate (ATP), and reducing power in the form of nicotinamide adenine dinucleotide phosphate (NADPH) (Johnson, 2016; Taiz and Zeiger, 2002) (Figure 1.2). The first step in the light reactions is the absorption of light by chlorophyll pigments. Within the thylakoid membrane, there are two pigment-protein complexes that harvest incoming solar radiation: photosystem II (PSII), and photosystem I (PSI) (Taiz & Zeiger, 2002). PSII and PSI each consist of several light harvesting complexes (aggregates of pigments and membrane-embedded proteins), which act as antenna complexes to transfer energy from photons towards the reaction centers (RCs) of the photosystems, and towards the 'special pair' of chlorophyll molecules contained therein (Johnson, 2016). The RCs of each photosystem reach peak absorption at different wavelengths of light. The RC of PSII peaks at 680 nm (red light), while the RC of PSI peaks at 700 nm (far-red light), thus, the initial electron donors for each photosystem are referred to as P680 and P700, respectively (Johnson, 2016).

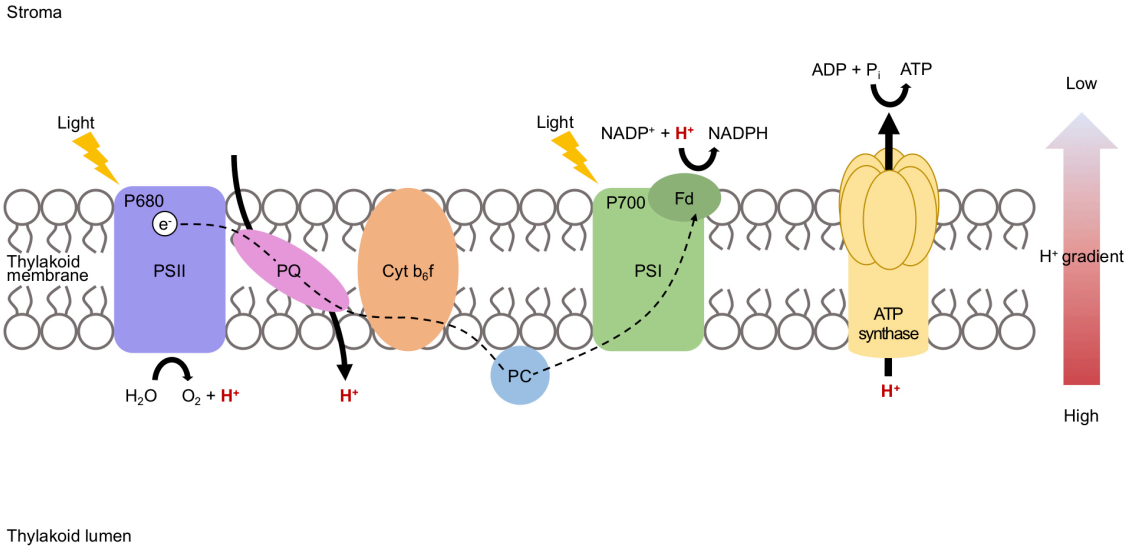

Figure 1.2. Schematic representation of the light reactions of photosynthesis. Light energy excites the specialized chlorophyll (P680) in the reaction center of photosystem II (PSII). This excites an electron (e^-), which travels along an electron transport chain through a series of redox reactions. The movement of the electron generates a proton gradient across the thylakoid membrane and allows the production of NADPH and ATP, which can be used in the Calvin-Benson cycle. H^+ = proton, PQ = plastoquinone, Cyt b_6f = cytochrome b_6f, PC = plastocyanin, PSI = photosystem I, P700 = specialized chlorophyll in PSI, Fd = ferredoxin, $NADP^+$/NADPH = nicotinamide adenine dinucleotide phosphate, ADP = adenosine diphosphate, P_i = inorganic phosphate, ATP = adenosine triphosphate. Based on information from Taiz and Zeiger (2002).

Light energy funnelled to the RC of PSII excites an electron within P680 producing $P680^*$ (excited state of the first electron donor of PSII) (Johnson, 2016). The energy of the excited electron can then be dissipated in one of three ways: it can be released as heat, emitted via fluorescence, or used in photochemistry (Taiz & Zeiger, 2002). In photochemistry, redox reactions pass the electron down an electron transport chain to PSI, generating $P680^+$ (oxidized form of the first electron donor of PSII) in the process. First, the excited electron from P680* is passed to plastoquinone (PQ) via pheophytin, then it is passed from PQ to the cytochrome b_6f complex (cyt b_6f). From cyt b_6f the

electron is passed to plastocyanin (PC), and on to PSI where another photon is absorbed to re-excite the electron (Johnson, 2016; Taiz & Zeiger, 2002). At PSI, ferredoxin (Fd) then reduces $NADP^+$ to NADPH. At PSII, the oxygen evolving complex oxidizes water, producing O_2 and an electron from water is passed to $P680^+$ to generate P680 (Johnson, 2016). The oxidation of water and PQ, and the corresponding deposition of protons in the thylakoid lumen, contribute to the establishment of a proton gradient across the thylakoid membrane (Taiz & Zeiger, 2002). The protons then move down their concentration gradient to the stroma via ATP-synthase, thus generating ATP from adenosine diphosphate (ADP) (Taiz & Zeiger, 2002).

1.3.1.2 Calvin-Benson cycle

The Calvin-Benson cycle takes place in the chloroplast stroma and utilises the ATP and NADPH generated from the light reactions to fix CO_2 into carbohydrates (Johnson, 2016; Taiz & Zeiger, 2002) (Figure 1.3). In the initial step of the Calvin-Benson cycle, ribulose 1,5-bisphosphate (RuBP) is combined with CO_2 to produce two molecules of 3-phosphoglycerate (PGA), and this reaction is catalysed by the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Taiz & Zeiger, 2002). The PGA is then converted stepwise to 1,3-bisphosphoglycerate (BPG) using ATP, and glyceraldehyde-3-phosphate (G3P) using NADPH (Taiz & Zeiger, 2002). Most of the produced G3P is directed back into the Calvin-Benson cycle to regenerate RuBP using ATP, while the rest is processed into sucrose or starch (Taiz & Zeiger, 2002)

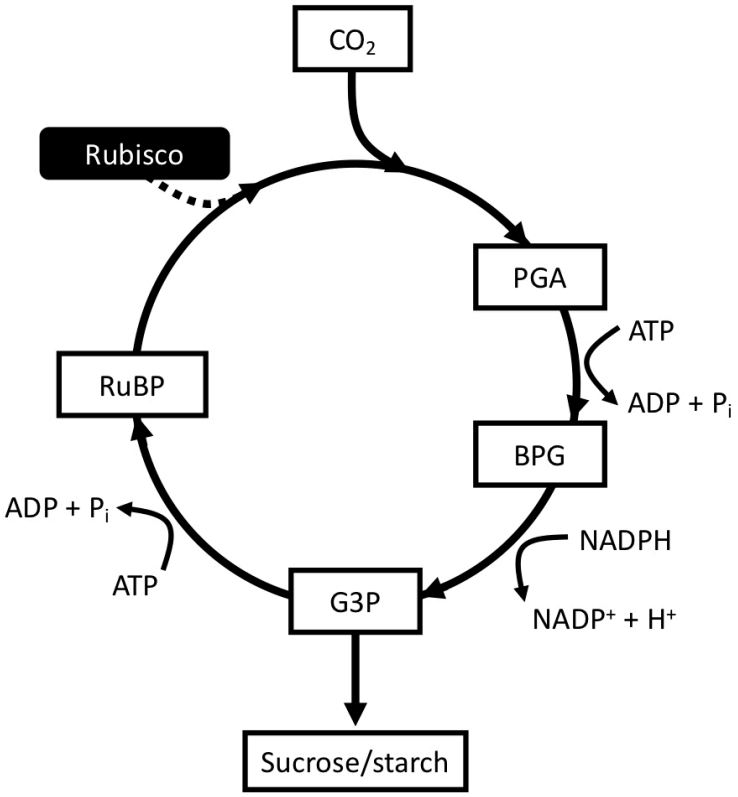

Figure 1.3. Schematic representation of the Calvin-Benson Cycle. In the chloroplast stroma, Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) catalyzes the production of 3-phosphoglycerate (PGA) from carbon dioxide and Ribulose 1,5-bisphosphate (RuBP). PGA is then converted to 1,3-bisphosphoglycerate (BPG) and glyceraldehyde-3-phosphate (G3P) using products from the light reactions. Some G3P is used to produce sucrose and starch and some is used to regenerate RuBP. Redrawn and modified from Taiz and Zeiger (2002). $NADP^+$/NADPH = nicotinamide adenine dinucleotide phosphate, ADP = adenosine diphosphate, ATP = adenosine triphosphate, P_i = inorganic phosphate. Based on information from Taiz and Zeiger (2002).

1.3.1.3 Modelling photosynthesis

In the literature, photosynthesis is often reported in terms of A_{net} (the net rate of CO_2 assimilation), which is the difference between the rate of total CO_2 assimilation (i.e., the rate of gross photosynthesis) and the rate of CO_2 release in photorespiration and respiration. Farquhar et al. (1980) proposed a biochemical model of photosynthesis that is still commonly used today (the FvCB model). This model outlines two main processes that underlie the responses of A_{net} to intercellular [CO_2] (C_i): Rubisco carboxylation capacity and RuBP regeneration capacity. Under low [CO_2] Rubisco carboxylation capacity is often limiting for photosynthesis based on the low availability of CO_2 as a substrate. However, when [CO_2] increases, the ability of the Calvin-Benson cycle to regenerate RuBP becomes limiting for A_{net}, as this regeneration depends on the availability of NADPH and ATP produced by the electron transport chain. Ultimately, the FvCB model characterises photosynthetic net CO_2 uptake as the lowest rate between these two processes, and these are the most common biochemical limitations to net photosynthesis seen under natural conditions.

When A_{net} is measured as a function of C_i, producing an A/C_i curve, the aforementioned model can be fit to the measurements and two parameters of photosynthetic capacity can then be estimated: the maximum rate of Rubisco carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) (Farquhar et al., 1980). For an example of an A/C_i curve using my own data see Figure 1.4.

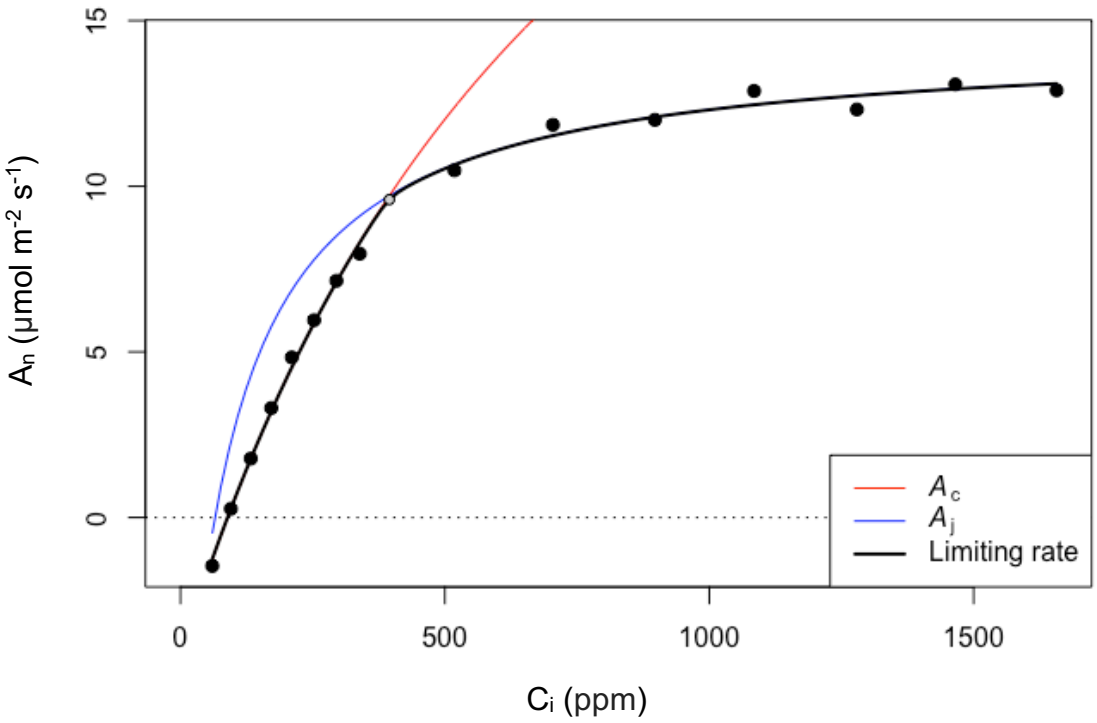

Figure 1.4. Example A/C_i curve (net CO_2 assimilation rate vs. intercellular CO_2 concentration). The red line (A_c) represents the Rubisco carboxylation-limited region of the curve and the blue line (A_j) represents the RuBP regeneration-limited region of the curve. The black line shows the lowest rate of these two limitations across a range of intercellular [CO_2]. Black circles are data from *Cucumis sativus* modelled in R using the Plantecophys package (Duursma 2015).

1.3.1.4 Effects of CO_2 on photosynthesis

Short term

Rubisco is a dual function enzyme that can catalyze both the carboxylation of RuBP using CO_2, and the oxygenation of RuBP using O_2 (Peterhansel et al., 2010). The oxygenation of RuBP is the first step in the process of photorespiration. In contrast to photosynthesis, photorespiration produces one PGA molecule and one molecule of toxic 2-phosphoglycolate (PG). The generation of PGA from PG requires the utilisation of ATP and NADPH, and releases previously fixed CO_2 (Taiz & Zeiger, 2002). This has led to the conjecture that photorespiration is 'wasteful' compared to the use of CO_2 in

photosynthesis. However, photorespiration also provides photoprotection and is involved in plant nitrogen cycling (Peterhansel et al., 2010).

In response to elevated [CO_2] alone, plants generally show increased A_{net}, which may, in turn, increase the carbon available for growth and reproduction. This is brought about via two main mechanisms: first, elevated [CO_2] provides more substrate to Rubisco, thus allowing increased carboxylation rates, and second, elevated [CO_2] reduces the occurrence of the oxygenation reaction of Rubisco, which decreases carbon and energy consumed in photorespiration (Long et al., 2004). As one example of the effects of elevated [CO_2] on photosynthesis, Ainsworth and Rogers (2007) found that across a suite of Free-Air CO_2 Enrichment (FACE) studies, C_3 plants displayed a 31% stimulation in A_{net} compared to control plants.

Long term

Initial stimulation of A_{net} under higher [CO_2] is not constant over time (Drake et al., 1997). With increased photosynthesis, the carbohydrate concentration of leaves also increases (Drake et al., 1997), and in the absence of adequate sink capacity, these carbohydrates can accumulate (Long et al., 2004). Accumulated leaf carbohydrates can then negatively feed back onto the expression of genes related to photosynthesis, resulting in lower investment in Rubisco and reduced photosynthetic capacity (Long et al., 2004). However, although photosynthesis is not continually stimulated to the same extent under elevated [CO_2], plants reared in high CO_2 conditions do still tend to show greater A_{net} than their low CO_2 counterparts when measured at their respective growth conditions, potentially meaning great greater availability of photosynthate to invest in plant processes (Leakey et al., 2009).

1.3.1.5 Effects of temperature on photosynthesis

Short term

In response to elevated temperatures, A_{net} tends to increase up to a temperature optimum (T_{opt}), but declines at temperatures beyond this point (Taiz & Zeiger, 2002). Initial increases in A_{net} in response to warmer temperature can be explained by accelerated

enzymatic activity under higher temperatures (Arcus et al., 2016). Temperature effects on the enzyme Rubisco activase may also explain photosynthetic declines above T_{opt}. Rubisco activase 'primes' Rubisco to produce PGA and has been shown to be thermally labile at moderately high leaf temperatures (Salvucci et al., 2001). As such, under high temperatures, Rubisco activase may not be able to maintain an adequate Rubisco activation state (Salvucci et al., 2001). On the other hand, photosynthetic declines above the T_{opt} might also be explained by declines in the rate of electron transport, and thus declines in the production of chemical energy (Yamori et al., 2008).

Temperature also affects the occurrence of photorespiration by influencing both Rubisco specificity and the relative amounts of substrate. Under higher temperatures, Rubisco has a higher affinity for O_2, thus resulting in more oxygenation reactions (Jordan & Ogren, 1984; Ku & Edwards, 1977a). At the same time, elevated temperatures result in a greater amount of O_2 in the chloroplast than CO_2 due to the solubility of O_2 decreasing more slowly with temperature than the solubility of CO_2 (Ku & Edwards, 1977b). By stimulating photorespiration, high temperatures negatively affect plant carbon balance.

Long term

Plants acclimate their photosynthetic processes to changes in growth temperature, with greater V_{cmax} and shifts to a higher T_{opt} when plants are grown under higher temperature conditions allowing plants to maintain their performance (reviewed by Dusenge et al., 2019). However, the degree of photosynthetic acclimation varies across species and environmental conditions.

1.3.1.6 Interactive effects of CO_2 and temperature on photosynthesis

Stomatal conductance (g_s) also influences the ability of plants to photosynthesize and both [CO_2] and temperature affect stomatal function (summarised in Taiz & Zeiger, 2002). In general, plants experience trade-offs between maintaining photosynthetic rates by opening their stomata and limiting water loss by stomatal closure (Medlyn et al., 2001). Stomatal conductance responds to vapour pressure deficit (VPD) (the difference between the maximum moisture holding capacity of the air and the current moisture in

the air), which tends to increase with temperature (Taiz & Zeiger, 2002). When VPD is high, plants may experience increased water loss via transpiration (Taiz & Zeiger, 2002). However, when under elevated [CO_2], plants are able to take up the carbon necessary for photosynthesis while maintaining lower stomatal conductance, and therefore can limit transpirational water losses (Taiz & Zeiger, 2002). This may improve plant responses to drought conditions. As one example of the effects of elevated [CO_2] on stomatal conductance, Ainsworth and Rogers (2007) found that C_3 plants exhibited 22% lower stomatal conductance at high [CO_2] than at current [CO_2] across a set of FACE studies. Conversely, at the same time as reduced water loss, low stomatal conductance limits the ability of plants to take up CO_2 (Franks & Farquhar, 1999). This limitation on CO_2 uptake may offset some of the photosynthetic gains obtained from increased carboxylation discussed previously and may reduce the photosynthate available for investment in plant tissues, such as flowers (Franks & Farquhar, 1999). Moreover, reduced stomatal conductance may lead to increased leaf temperatures, which then stimulates photorespiration (Kimball & Bernacchi, 2006).

As mentioned previously, photorespiration is affected by both [CO_2] and temperature. More specifically, higher [CO_2] reduces the occurrence of photorespiration by favouring Rubisco carboxylation, while higher temperatures favour the oxygenase function of Rubisco (Taiz & Zeiger, 2002). In future conditions of higher [CO_2] and temperature, elevated [CO_2] is expected to repress photorespiration, counteracting temperature-induced stimulations of photorespiration (Jordan & Ogren, 1984; Long, 1991). In fact, studies show that elevated [CO_2] stimulates photosynthesis more when temperatures are high (Long, 1991). Elevated [CO_2] also shifts the thermal optimum of photosynthesis to higher temperatures by reducing the occurrence of photorespiration (Sage & Kubien, 2007; Way et al., 2015). This might mean that with elevated [CO_2], plants could experience greater photosynthetic gains under temperature conditions that would be detrimental if [CO_2] were at ambient levels (Way et al., 2015). Thus, warmed plants might have comparatively more photosynthate to invest in growth and reproduction when grown at elevated [CO_2].

1.3.2 Cellular respiration

Aerobic respiration is the process by which the stored chemical energy of a substrate (usually glucose) is released in the form of ATP (Taiz & Zeiger, 2002). The energy released by respiration is essential for plant growth and maintenance, and CO_2 is released as a by-product (Taiz & Zeiger, 2002). Respiration consists of three main processes: glycolysis (in the cytosol), the tri-carboxylic acid (TCA) cycle (in the mitochondrial matrix) (Figure 1.5), and oxidative phosphorylation (in the inner mitochondrial membrane) (Figure 1.6) (Taiz & Zeiger, 2002).

Glycolysis functions to convert glucose into pyruvate, producing ATP and nicotinamide adenine dinucleotide (NADH) in the process (Taiz & Zeiger, 2002). Pyruvate is then converted into Acetyl coenzyme A (Acetyl-CoA) to be used in the TCA cycle, and through this conversion NADH and CO_2 are produced (Taiz & Zeiger, 2002). In the TCA cycle, Acetyl-CoA is combined with oxaloacetate to produce citrate and, through several other steps, oxaloacetate is eventually regenerated so the cycle can repeat (Taiz & Zeiger, 2002). Throughout this stepwise series, CO_2, NADH, flavin adenine dinucleotide ($FADH_2$), and some ATP are released (Taiz & Zeiger, 2002). Finally, to produce greater amounts of ATP to power cellular processes, the reducing power generated through glycolysis and the TCA cycle is used in oxidative phosphorylation (Taiz & Zeiger, 2002). Oxidative phosphorylation takes place in the inner mitochondrial membrane, and the chemical energy from glycolysis and the TCA cycle is used to produce ATP via an electron transport chain (Taiz & Zeiger, 2002). The components of the electron transport chain, in order, are NADH dehydrogenase, succinate dehydrogenase, cytochrome $b6_1$, cytochrome oxidase, and ATP synthase (Taiz & Zeiger, 2002).

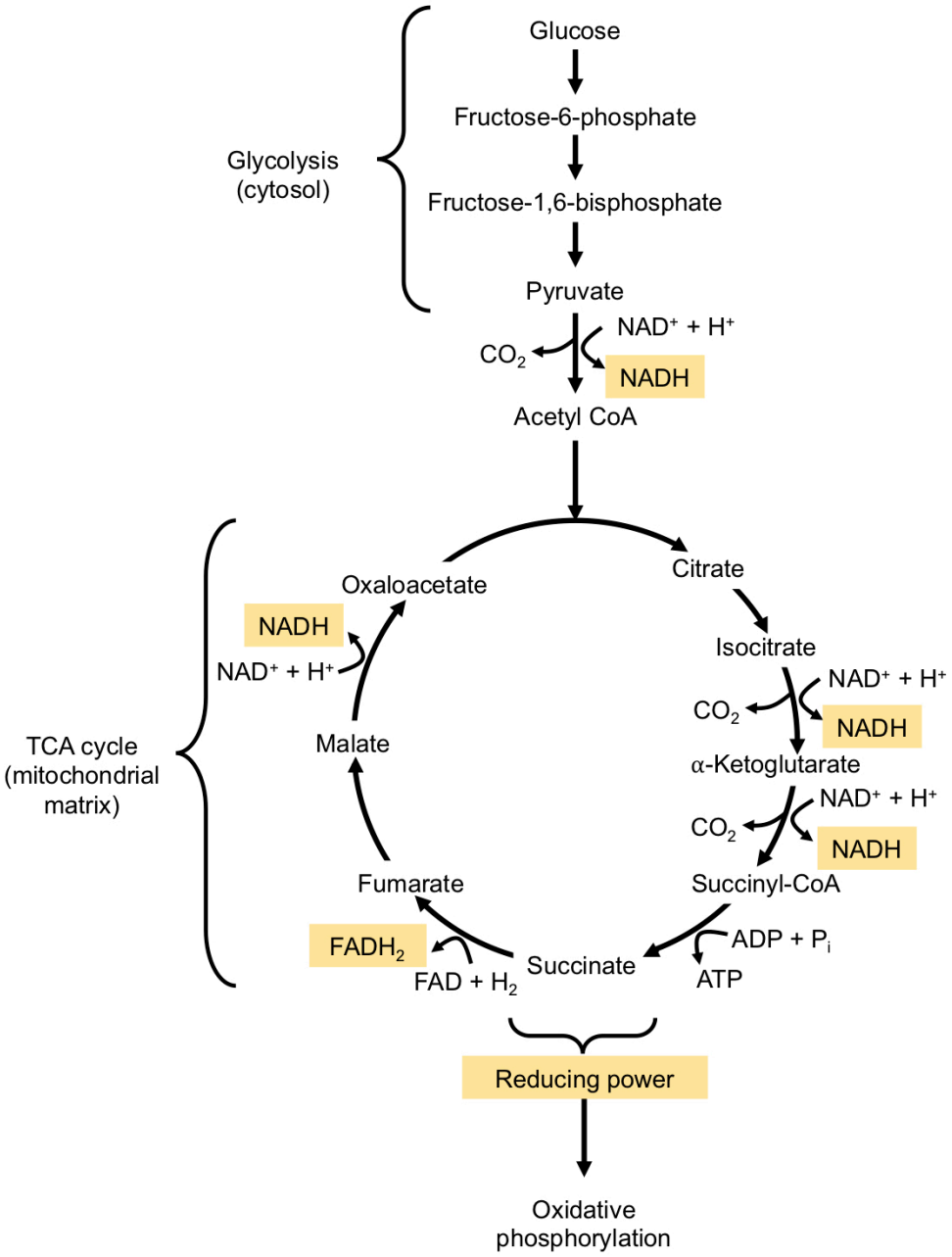

Figure 1.5. Schematic representation of glycolysis and the tricarboxylic acid (TCA) cycle. Glycolysis converts glucose to pyruvate. Pyruvate then is converted into Acetyl CoA, which is used in the TCA cycle to generate reducing power in the form of NADH and $FADH_2$ (highlighted in yellow). Acetyl CoA = Acetyl Coenzyme A, NAD^+/NADH = nicotinamide adenine dinucleotide, FAD/$FADH_2$ = flavin adenine dinucleotide, ADP = adenosine diphosphate, P_i = inorganic phosphate, ATP = adenosine triphosphate. Based on information from Taiz and Zeiger (2002).

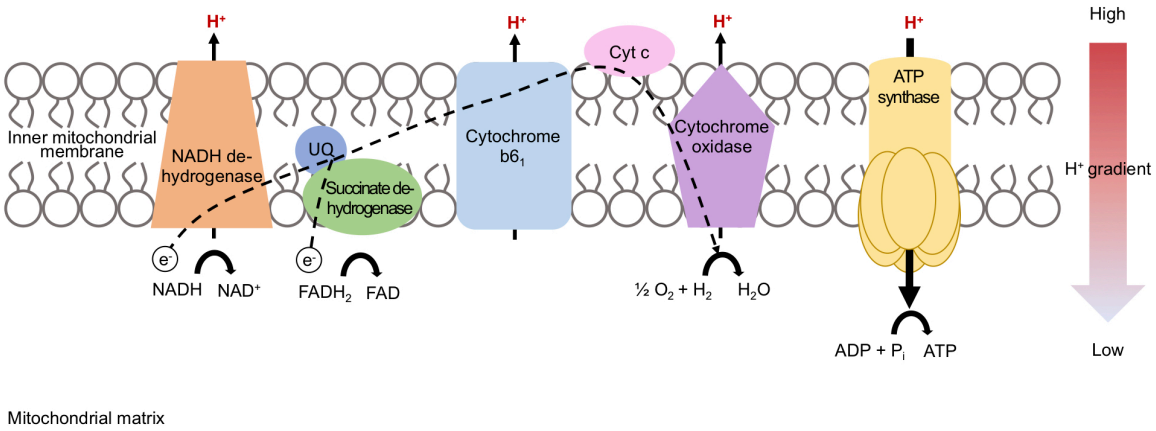

Figure 1.6. Schematic representation of oxidative phosphorylation. Reducing power from glycolysis and the tricarboxylic acid cycle is used in oxidative phosphorylation to support production of adenosine triphosphate (ATP) by ATP synthase by moving an electron down an electron transport chain and generating a proton gradient across the inner mitochondrial membrane. H^+ = proton, NAD^+/NADH = nicotinamide adenine dinucleotide, UQ = ubiquinone, FAD/$FADH_2$ = flavin adenine dinucleotide, Cyt c = cytochrome c, ADP = adenosine diphosphate, P_i = inorganic phosphate, ATP = adenosine triphosphate. Based on information from Taiz and Zeiger (2002).

1.3.2.1 Effects of CO_2 on respiration

Short term

In general, elevated [CO_2] has little effect on dark respiration (R_D) in the short term (i.e., seconds to hours) (Amthor, 2000).

Long term

In contrast to short-term effects on respiration, over the long term, the effects of [CO_2] are variable (reviewed by Way et al., 2015). Several studies show increased R_D when plants were grown at higher [CO_2] (Davey et al., 2004; Markelz et al., 2014; Shapiro et

al., 2004), potentially mediated by increased leaf carbohydrate content (substrate for respiration), or greater numbers of mitochondria (Griffin et al., 2001). However, several studies have also shown no change in rates of respiration in response to high [CO_2] (Ayub et al., 2011, 2014; Crous et al., 2012), and some show reduced respiration rates (Gifford et al., 1985), possibly linked to lower leaf nitrogen concentrations, and thus lower metabolic rates (Ainsworth & Long, 2005).

1.3.2.2 Effects of temperature on respiration

Short term

Temperature has a greater effect on respiration than does [CO_2]. In the short-term, higher temperatures increase respiration rates by stimulating enzyme function. Thus, plants may be expected to burn through their carbon supplies more quickly in warmed conditions, with less available for plant processes, such as growth and reproduction. However, these temperature-driven exponential increases in respiration occur up to a temperature optimum of ~50 °C (reviewed by Way et al., 2015).

Long term

Over longer periods of time, plants acclimate their respiratory processes to increased temperatures. This may be due to reductions in the temperature sensitivity of respiration (i.e., Q_{10}, the change in the rate of respiration for a 10 °C increase in temperature), or reduced respiration rates at low temperatures (Atkin & Tjoelker, 2003; Dusenge et al., 2019). Acclimation often helps maintain homeostasis, whereby plants grown under different thermal conditions have the same respiration rate at their respective growth temperatures (Slot & Kitajima, 2015), thus improving the plant carbon balance in a warmer environment. So far, the mechanisms underlying respiratory acclimation to temperature are unclear (Dusenge et al., 2019).

1.3.2.3 Interactive effects of CO_2 and temperature on respiration

Temperature effects tend to dictate respiratory changes when plants are grown at both elevated [CO_2] and temperature (Dusenge et al., 2019). For instance, Tjoelker et al.

(1999) found that trees grown under elevated [CO_2] and temperature had few [CO_2]-mediated effects on respiration, while higher temperature treatments tended to decrease respiration rates (i.e., induce acclimation).

1.3.3 Development and biomass production

Plant carbon balance, the initiation of plant organs, and the expansion of plant organs are the main factors influencing plant biomass production and allocation to different tissues (Morison & Lawlor, 1999). More available carbon associated with an increasingly positive plant carbon balance allows increased production of ATP, which can be used in plant growth and development and can stimulate plant growth rates or biomass production, as well as providing greater C availability for building material (Morison & Lawlor, 1999). In addition, the rate of organ initiation influences the number of organs that are produced, while the rate and duration of organ expansion influence the final size of plant organs (Morison & Lawlor, 1999).

1.3.3.1 Effects of CO_2 on development and biomass production

A common outcome from increased photosynthetic rates at elevated [CO_2] is greater biomass production, or the so-called 'CO_2 fertilisation effect'. So far, there is evidence of enhanced biomass production under elevated [CO_2] in both wild plants and crop species. With elevated [CO_2], wheat aboveground biomass increased 25% (Broberg et al., 2019), rice biomass increased 21% (Ainsworth, 2008), and soybean shoot biomass increased 25% (Kimball, 2016). Similarly, biomass in natural systems has increased with higher [CO_2] as well. Elevated [CO_2] enhanced grassland biomass production by 30% when nutrients and water were not limiting (Reich et al., 2014) and aboveground biomass of trees at the Duke FACE site increased 21-27% when exposed to elevated [CO_2] from 1996 to 2010 (Kim et al., 2020).

Elevated [CO_2] has also been shown to affect individual plant organs. Leaves under high [CO_2] tend to be larger, which can be attributed to greater cell production or cell expansion (Gray & Brady, 2016). Elevated [CO_2] may also increase total leaf area via the total number of leaves, individual leaf size, or the duration of leaf expansion (Morison &

Lawlor, 1999). For roots, elevated [CO_2] tends to increase biomass production, which may be attributed to longer, or more branched roots (Gray & Brady, 2016). Elevated [CO_2] may also affect the rate of organ expansion in plants, with higher [CO_2] generally increasing expansion rates (Morison & Lawlor, 1999). As one example, *Populus* spp. grown under elevated [CO_2] had faster leaf expansion rates than their counterparts grown under ambient [CO_2] (Taylor et al., 2001). Additionally, in *Arabidopsis,* elevated [CO_2] resulted in greater root expansion rates (Crookshanks et al., 1998).

1.3.3.2 Effects of temperature on development and biomass production

While responses of overall biomass to [CO_2] are relatively well-established and consistent, the effect of temperature increases on biomass production varies with both geographic location and species (Gray & Brady, 2016). As discussed previously, in the short-term, high temperatures will likely reduce stomatal conductance, prevent the maintenance of Rubisco in an active state, favour photorespiration, and stimulate respiration via greater enzymatic rates, thus decreasing a plant's carbon balance (Arcus et al., 2016; Salvucci et al., 2001; Taiz & Zeiger, 2002). In addition, accelerated initiation and expansion of organs, but a shorter duration of development in response to higher temperatures, can decrease biomass production (Morison & Lawlor, 1999). This is attributed to shorter development times leading to less biomass accumulation time for plants (Hatfield & Prueger, 2015; Morison & Lawlor, 1999). Some general effects are also observed for particular plant organs. For leaves, higher temperatures tend to increase rates of production in terms of both initiation and expansion (Gray & Brady, 2016). Similarly, in roots, higher temperatures accelerate rates of growth (up to a point) and can also influence root architecture (Gray & Brady, 2016). For instance, Nagel et al. (2009) found that when plants were exposed to a gradient of soil temperatures along their root depth, they tended to produce more roots at depths near their temperature optima.

1.3.3.3 Interactive effects of CO_2 and temperature on development and biomass production

Temperature and [CO_2] effects on biomass production may 'balance each other out' in some cases (Way et al., 2015). This is because some aspects of plant carbon fluxes respond more strongly to [CO_2], while others respond more strongly to temperature, potentially leading to similar carbon fluxes in plants grown under varied temperatures and CO_2 concentrations (Way et al., 2015). For example, Benlloch-Gonzalez et al. (2014) found that higher [CO_2] increased the aboveground and belowground growth of wheat, but under both higher temperatures and [CO_2] these benefits were reduced. Similarly, *Oryza sativa* grown under 664 μmol mol^{-1} [CO_2] produced greater biomass than plants under ambient [CO_2], but this effect was weakened under elevated temperatures (Ziska et al., 1996). In terms of development, there are not yet clear interactions between [CO_2] and temperature on either the initiation or expansion of organs in plants (Morison & Lawlor, 1999).

1.3.4 Floral traits

1.3.4.1 Onset of flowering

Many species have shown altered phenologies in response to climate change. In plants, increased [CO_2] can accelerate phenological events such as flowering time and bud break, while delaying other events, such as senescence (Piao et al., 2019). For flowering time, Springer and Ward (2007) conducted a meta-analysis on crop responses to elevated [CO_2] and found that almost half of the studies recorded evidence of accelerated flowering time when [CO_2] was increased. However, when flowering time was evaluated in more naturally representative FACE experiments, there were few effects of [CO_2] on floral phenology (Springer & Ward, 2007), and another study actually found flowering delays in grasses in response to elevated [CO_2] (Cleland et al., 2006).

Similar to the effects of elevated [CO_2], increased temperature and resultant changes in spring snowmelt time have accelerated the onset of flowering in many species. Primack et al., (2004) found that flowering times noted on herbarium specimens from 1980-2002

were 8 days earlier compared to 1900-1920 records. Fitter and Fitter (2002) found that flowering time across 385 British plants was around 5 days earlier from 1990-2000 than the previous 40 years, and Miller-Rushing and Primack (2008) combined historical and more current observations of flowering time, and found that the average date of flowering was 7 days earlier from 2004-2006 than it was in 1852-1858.

Interacting species (i.e., those in symbioses) may respond differently to environmental cues in either the direction or extent of their phenological response (Fitter & Fitter, 2002). For instance, insect pollinators and plants may both advance their emergence times in response to warming, but insect pollinators tend to advance their phenologies to a greater extent than plants (Parmesan, 2007). Variation in the phenological responses of interacting species can lead to temporal mismatches in the symbiosis, potentially disrupting some species' interactions entirely (Gérard et al., 2020). For instance, in a meta-analysis, Parmesan (2007) found that butterfly emergence advanced three times more than the start of flowering for plants in the Northern Hemisphere. Gordo & Sanz (2005) found that insects and plants in a Mediterranean ecosystem had different degrees of phenological change over approximately 50 years, with insects advancing their phenologies more. Likewise, Burkle et al. (2013) found that forbs in Illinois bloomed 9.5 days sooner over 120 years, while bees displayed an 11 day acceleration in their peak activity. On the other hand, some studies have found greater phenological shifts for plants. For instance, Kehrberger and Holzschuh (2019) showed that the endangered plant *Pulsatilla vulgaris* was more responsive to warming than two co-occurring bee species, and Kudo and Cooper (2019) found that 19 years of warming led *Corydalis ambigua* to flower up to one week before bumblebee emergence. Furthermore, in contrast to evidence supporting temporal mismatches, a meta-analysis by Bartomeus et al. (2011) found no distinguishable differences in plant and pollinator phenologies using reports spanning 130 years.

1.3.4.2 Flower abundance

In response to high [CO_2] conditions, flower abundance often increases. *Gerbera jamesonii* grown under high [CO_2] produced significantly more flowers than plants at 400

μmol mol^{-1} [CO_2] (Xu et al., 2014), as did *Vicia faba* (Osborne et al., 1997)*, Parthenium hysterophorus* (Bajwa et al., 2019*),* and *Solanum lycopersicum* (Pazzagli et al., 2016). On the other hand, in a different study *Solanum lycopersicum* had no flowering response to high [CO_2], and when *Capiscum annuum* plants were grown under elevated [CO_2], they produced fewer flowers (Lopez-Cubillos & Hughes, 2016).

Similar to the effects of elevated [CO_2], several studies have found that plants increase the number of flowers they produce under warming. Zheng et al. (2002) found that *Glycine max* grown under higher nighttime temperatures had increased flower production, and Descamps et al. (2020) found the same result in *Echium plantagineum*. Similarly, in two different tropical forests, Pau et al. (2013) showed that years with higher temperatures resulted in greater flower production, and when *Betula ermanii* saplings were grown under higher aboveground temperatures the number of male flowers per shoot increased (Nakamura et al., 2016). However, there is variation in these results and when warming is more extreme, or applied in shorter bursts, it may lead to flower abortion. For instance, *Arachis hypogaea* exposed to short bouts of daytime heat stress produced fewer flowers than plants at ambient temperatures (Vara Prasad et al., 2000), and *Tanacetum cinerariifolium* exposed to high temperature bursts exhibited reduced flower production compared to un-warmed plants (Suraweera et al., 2020). Furthermore, Warner & Erwin (2005) found that five different herbaceous species produced fewer buds per plant under higher temperatures, and Descamps et al. (2018) found decreased flower production for *Borago officinalis* when growth temperatures increased.

There are few studies focusing on flower production in response to both elevated [CO_2] and temperature, and the results from these studies are inconsistent. Palacios et al. (2019) found that *Glycine max* flower production increased when both [CO_2] and temperature were elevated (800 μmol mol^{-1} CO_2 and 4 °C of warming). However, Hoover et al. (2012) found that elevated [CO_2] slightly reduced the positive effects of higher temperature on flower production in *Cucurbita maxima* (700 ppm CO_2 and 4 °C of warming). Moreover, Balasooriya et al. (2018) found that the stimulatory effects of high [CO_2] dominated the effects on flower production when *Fragaria* × *ananassa* plants were grown under

different combinations of [CO_2] and temperature (400, 650 or 900 µmol mol^{-1} CO_2 and 25 or 30 °C of warming).

1.3.4.3 Flower size

Flower size generally increases in response to elevated [CO_2]. As one example, *Brassica napus* grown under high [CO_2] (740 µmol mol^{-1} CO_2) produced flowers with larger petals compared to control plants (Qaderi & Reid, 2005). Additionally, compared to plants grown under current CO_2 levels, *Gerbera jamesonii* produced larger flowers under 800 µmol mol^{-1} CO_2 (Xu et al., 2014), a *Rosa* hybrid grown under 1500-3000 ppm CO_2 produced larger buds (Biran et al., 1973), *Heterotheca villosa* produced flowers with greater petal area under 800 ppm CO_2 (Glenny et al., 2018), and *Betula papyrifera* had increased catkin size under 560 ppm CO_2 (Darbah et al., 2007).

In contrast to CO_2 effects, increased temperature tends to decrease flower size. One study found that higher growth temperatures reduced the flower size of roses (Shin et al., 2001). Similarly, *Viola x wittrockiana* plants produced smaller flowers as temperatures increased (Pearson et al., 2015), as did *Aster* spp. (Oren-Shamir et al., 2000), *Borago officinalis* (Descamps et al., 2018), *Echium plantagineum*, *Echium vulgare* (Descamps et al., 2020), *Calendula officinalis*, *Impatiens wallerana*, *Mimulua x hybridus*, *Torenia fournieri* (Warner & Erwin, 2005), and *Chrysanthemum morifolium* (Carvalho et al., 2005). However, the flower size response of *C. morifolium* varied with the phase at which treatment was applied, with earlier phases showing more negative temperature effects on floral size (Carvalho et al., 2005).

When both high temperatures and [CO_2] are applied, the effects of temperature seem to dominate, and flowers are usually smaller. Hoover et al. (2012) found that *Cucurbita maxima* plants produced smaller flowers when grown at higher temperatures and elevated [CO_2]. Similarly, *Campanula carpatica* flowers were smaller with increasing growth temperature regardless of [CO_2] (Niu et al., 2001).

1.3.4.4 Rewards

Under elevated [CO_2], pollen quantity has been found to increase. For example, three studies conducted on *Ambrosia artemisiifolia* found increased pollen production under high [CO_2] (Kelish et al., 2014; Wayne et al., 2002; Ziska & Caulfield, 2000) and stands of *Pinus taeda* exposed to free-air CO_2 enrichment displayed similar increases in pollen at elevated [CO_2] (Ladeau & Clark, 2006). Additionally, *Phleum pretense* grown at high [CO_2] produced more pollen per flower (Albertine et al., 2014).

Similar to pollen production, nectar quantity shows fairly consistent increases under elevated [CO_2]. In high [CO_2] conditions, increased nectar quantity was found in *Tropaeolum majus* (Lake & Hughes, 1999), *Epilobium angustifolium* (Erhardt et al., 2005), *Capsicum chinense* (Garruña-Hernandez et al., 2012), and *Cucumis melo* (Dag & Eisikowitch, 2000) compared to those grown at ambient [CO_2]. However, *Vicia faba* exposed to high [CO_2] showed no significant differences in nectar production compared to control-grown plants (Osborne et al., 1997), and *Trifolium pratense* and *Lotus corniculatus* exhibited little effect on nectar production as well (Rusterholz & Erhardt, 1998), suggesting that leguminous species may not respond as strongly to elevated [CO_2]. In addition, *Scabiosa columbaria*, and *Centaurea jacea* produced significantly less nectar per flower under [CO_2] (Rusterholz & Erhardt, 1998).

In response to elevated temperature, there is some evidence that pollen production decreases. For example, in *Arachis hypogaea* plants grown under elevated temperatures pollen production decreased compared to control treatments (Vara Prasad et al., 1999). Pollen production also decreased in *Lycopersicon esculentum* (El Ahmadi & Stevens, 1979), *Cicer arietinum* (Devasirvatham et al., 2012), and *Oryza sativa* (Prasad et al., 2006) under high temperature. On the other hand, *Helianthus annuus* displayed a unimodal response of pollen production per flower to growth temperature (Astiz & Hernández, 2013). Pollen development requires carbohydrate investment and there is some indication that decreased pollen production under high temperatures is related to a reduced ability of the anthers to utilise carbohydrates under temperature stress (Pressman et al., 2002).

The effects of temperature on nectar quantity have been proposed to follow a unimodal relationship (Petanidou & Smets, 1996). Consistent with this, when temperature increases were moderate, nectar production was stimulated in *Teucrium divaricatum,* and *Ballota acetabulosa,* but at higher temperatures, nectar production declined (Takkis et al., 2015). Similar results were seen in other studies (Jakobsen & Kritjánsson, 1994; Petanidou & Smets, 1996; Takkis et al., 2018). However, some studies have found different results. Garruña-Hernandez et al. (2012) found no significant temperature effect on nectar production in *Capsicum chinense*, nor did Descamps et al. (2020) in *Echium vulgare.* Furthermore, other studies found declines in nectar production with warming (Descamps et al., 2018; 2020; Mu et al., 2015). Nectar volume may decline under extreme temperatures due to increased transpiration and evaporation.

Few studies have examined the effects of both elevated [CO_2] and temperature on nectar and pollen, although both climate change factors change concurrently in nature. For pollen, one group explored the effects of UV-B radiation, [CO_2], and temperature on *Glycine max*, and found that elevated [CO_2] (720 μmol mol^{-1}) increased pollen production. However, when temperature was increased with elevated [CO_2], pollen production was similar to control plants from ambient [CO_2] and temperatures (Koti et al., 2005). Similarly, elevated [CO_2] did not significantly affect the number of pollen grains per anther under either ambient or elevated temperature regimes (28/22 °C or 32/26 °C day/night) for *Capsicum annuum* plants (Aloni et al., 2001). On the other hand, for *Sorghum bicolor* plants, high temperatures decreased pollen production under both current and future [CO_2] levels (Vara Prasad et al., 2006), and pollen production was also reduced for *Phaseolus vulgaris* with no significant effect of growth [CO_2] (Vara Prasad et al., 2002).

For nectar volume, I am aware of only one study that has looked at the combined effects of [CO_2] and temperature. Hoover et al. (2012) found that high [CO_2] decreased nectar produced per flower, while higher temperatures increased nectar production; there were no significant interactions observed between [CO_2] and temperature.

1.4 Study species

1.4.1 Overview

Cucumis sativus, or cucumber, was used in this experiment because of its reliance on pollination, its high nectar and pollen production, its geographical distribution within the study region, and its economic importance. *Cucumis sativus* is an herbaceous annual in the family Cucurbitaceae. Plants grow as a branched, hairy vine and produce numerous small, yellow flowers (Pessarakli, 2016). Male flowers produce pollen, while both male and female flowers produce nectar. From their flowers, cucumber plants produce long, cylindrical fruits that are typically harvested when immature and then eaten.

1.4.2 Importance

Cucumbers originated in Nepal, but have been cultivated for thousands of years and can now be found across the majority of the world, excluding Antarctica, Greenland, and parts of South America and Africa (FAOSTAT, 2016). Estimates for global annual production are around 29 million tonnes, with China, Iran, and Turkey listed as the top producers (FAOSTAT, 2016).

In 2017, Canada produced 206,227 metric tonnes of cucumbers via greenhouse production, and the estimated farm gate value was $396 million CAD (AAFC, 2019). In the same year, cucumber production from field grown varieties was another 61,064 metric tonnes, with a value of approximately $35 million CAD (AAFC, 2019). The majority of cucumber production in Canada takes place in Ontario (AAFC, 2019).

1.4.3 Biology

Cucumis sativus is a warm-adapted species and thrives at day temperatures between 20 – 25 °C (Backlund, 2009), and night temperatures between 18 – 21 °C (Pessarakli, 2016). Cucumbers are historically monoecious, having separate male and female flowers on the same plant (Pessarakli, 2016). Male flowers generally develop before female flowers and in greater numbers to ensure that the pollen supply is adequate and available when female

flowers emerge (Pessarakli, 2016). The ratio of male to female flowers is typically around 10:1 and male flowers can be distinguished from females by their lack of an ovary (Figure 1.7) (McCormack, 2005). In general, flowers last for about one day (Barber et al., 2011) and male flowers produce less nectar than their female counterparts. One study found that average nectar production for male flowers was 0.69 mg, while females produced 1.29 mg nectar (Nemirovich-Danchenko, 1964), and another found that males produced between 0.9 - 1.6 mg while females produced between 1.1 - 2.4 mg of nectar (Kaziev & Seidova, 1965).

Monoecious varieties are beneficial for their prolonged production over the growing season, and several monoecious varieties are still cultivated today, such as Marketmore 76, and Straight 8 (Badgery-Parker et al., 2019). However, new gynoecious cucumber varieties are often favoured today due to their increased fruit production (Badgery-Parker et al., 2019). This is because gynoecious cucumber plants produce all female flowers and can yield many fruits in a short period of time (Badgery-Parker et al., 2019). Other available cultivars include parthenocarpic, or seedless, gynoecious varieties, which can have decreased fruit quality if pollinated (Pessarakli, 2016).

Figure 1.7. Male and female *C. sativus* flowers. Female flowers (right) can be distinguished from male flowers (left) by their inferior ovary (red arrow).

Despite increased popularity of gynoecious varieties, monoecious varieties are still essential as pollen sources for gynoecious plants (Badgery-Parker et al., 2019). In fact, Klein et al. (2007) listed the benefit of animal pollination to *C. sativus* as ‘great,’

indicating a 40 – < 90% reduction in cucumber value without animal pollination. In addition, Stanghellini et al., (1997) found that when pollinators were excluded the abortion of cucumber fruits was as much as 100%. Bees, and honey bees in particular, are the most common pollinators for cucumbers, and honey bee hives are recommended in field at approximately 1 – 2 hives per acre to ensure adequate pollination (McCormack, 2005). While honey bees typically visit cucumbers to obtain nectar, pollen is also collected as a food source, and both pollen and nectar from cucumbers are listed as attractive to bees (USDA, 2017).

1.5 Objectives

Objective 1: Determine if high [CO_2] and/or temperature induces changes in carbon fluxes or biomass.

Predictions:

1. High [CO_2] will increase plant biomass and A_{net}.
2. Moderate warming will reduce plant biomass, increase A_{net} and stimulate R_D, while extreme warming will reduce plant biomass, suppress A_{net} and stimulate R_D.
3. When combined, high [CO_2] and moderate warming will increase plant biomass and improve leaf carbon balance, but high [CO_2] and extreme warming will produce no change in biomass or leaf carbon fluxes compared to control plants.

Objective 2: Test the effects of elevated [CO_2] and/or temperature on floral traits that are important to plant-pollinator interactions at multiple time points.

Predictions:

1. High [CO_2] will promote greater floral trait values, such as flower size, flower number, and reward quantity.
2. High growth temperatures, particularly the highest temperature treatment, will negatively affect floral trait values, such as reward quantity, and flower size.
3. Floral trait responses to combined high [CO_2] and temperature will be additive.

Objective 3: Investigate if floral trait changes are related to changes in carbon fluxes and biomass.

Predictions:

1. A greater ratio of A_{net}:R_D will result in increased available resources for investment in floral traits.
2. A reduced ratio of A_{net}:R_D will result in fewer available resources for investment in floral traits.
3. Plants will experience trade-offs between aspects of floral traits (e.g., flower number and size).

2 Materials and Methods

2.1 Plant material and growth conditions

On May 24th, 2019, 78 10-cm diameter pots (0.5 L) were filled with general purpose Pro-Mix HP growth medium with mycorrhizae (Premier Tech Home and Garden, Rivière-du-Loup, Quebec, Canada). Prior to potting, Miracle-Gro Shake-N-Feed general purpose slow release fertiliser (12-4-8) was mixed with the growth medium according to manufacturer's instructions (The Scotts Miracle Gro Company, Marysville, Ohio, USA). After pots were filled, three seeds of *C. sativus* (Spacemaster trailing variety) were planted equidistant from one another in each pot (McKenzie Seeds, Brandon, Manitoba, Canada).

After seeding, pots were haphazardly assigned to one of six experimental glasshouses at the University of Western Ontario's Biotron Centre for Experimental Climate Change Research so that each glasshouse contained 13 pots. Glasshouses were subject to natural variation in light intensity and photoperiod, while air temperature, CO_2 concentration, and relative humidity were controlled and measured every minute.

The treatments in each glasshouse consisted of either current, ambient [CO_2] (400 ppm, AC), or elevated [CO_2] (750 ppm, EC), and temperatures of either an ambient regime (0T), 0T+4 °C (4T), or 0T+8 °C (8T). Treatments were applied in a full-factorial design, resulting in six climatic regimes: AC0T, AC4T, AC8T, EC0T, EC4T, and EC8T. For CO_2, the EC regime was based on the IPCC's 'business as usual' projections for atmospheric [CO_2] in 2100 (IPCC, 2014). For temperature, the 0T regime was based on a 5-year average (2013-2018) of hourly temperatures taken at the London airport meteorological station (ECCC, 2019), and the 4T and 8T treatments were based on predicted warming for 2100 under 'stabilising' and 'business as usual' emission scenarios, respectively (IPCC, 2014).

Across the 14 weeks of the experiment, the mean [CO_2] in the AC treatment was 404.52 ± 7.11 ppm (values are means ±SD) and the median value was 403.33 ppm. For the EC

treatment, the mean [CO_2] was 746.48 ± 1.77 ppm and the median value was 746.33 ppm over the experiment. In the temperature treatments, the mean difference from 0T to 4T was 4.12 ± 0.56 °C and the median temperature difference was 3.88 °C. Additionally, from 4T to 8T, the mean difference in temperature was 4.21 ± 0.53 °C, and the median difference was 4.01 °C.

Each day soil moisture was checked in three haphazardly selected pots per treatment using a Delta-T HH2 soil moisture meter, and ML2x probe (Delta-T Devices, Burwell, Cambridgeshire, UK). All pots were watered as needed to maintain soil volumetric water content between 25-30%. When plants had developed two true leaves (TL), they were transplanted to 30 cm diameter (11.35 L) pots containing the same growth medium and slow release fertiliser.

One week after transplanting seedlings to the larger pots, they were thinned to one plant per pot. When plants began to flower, 1 L of Growmore 20-20-20 fertiliser was applied per plant at a rate of 1.8 g/L each week (Grow More Inc, Gardena, California, USA).

Higher temperatures can accelerate the development of plants. Therefore, in order to prevent the effects of developmental stage from confounding the effects of [CO_2] and temperature on the measured parameters, I measured variables within specific developmental windows from 15-20 true leaves (15-20TL), and 25-30 true leaves (25-30TL), where applicable. True leaf stage was assessed by counting the number of mature, fully expanded leaves. Measuring variables within two developmental windows also allowed me to determine how climate change may alter floral metrics at different stages, since at 15-20TL plants had just begun to flower, and at 25-30TL plants were well into their flowering period.

2.2 Floral metrics

Plants were monitored daily for signs of flowering. Each day following the start of flowering, true leaf stage and the number of newly opened male and female flowers on each plant was recorded until the experimental end date, August 26th. To determine mean daily display size for 15-20TL and 25-30TL stages, the number of open flowers per day

(male and female summed) was averaged for each plant in each treatment, but separately for the two developmental windows. To determine mean lifetime flower production, all measures of male and female flower production were summed for each plant in each treatment. Flower production was then averaged within each treatment.

Between 15-20TL and 25-30TL, the length and width of three male flowers and one female flower were measured on each plant (Figure 2.1), with the sampling reflecting the higher male to female ratio of flower production in monoecious cucumber varieties. The geometric mean of these two measurements was used to estimate overall flower size while accounting for variations in flower shape (Williams & Conner, 2001).

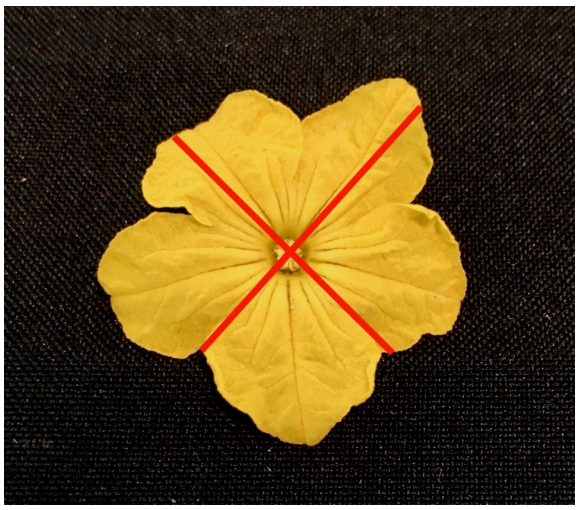

Figure 2.1. Measurements of floral size for *C. sativus* flowers. Measurements were made as indicated by the red lines**.**

2.3 Nectar

2.3.1 Nectar collection

At both the 15-20 and the 25-30TL stage, the nectar from three male flowers and one female flower per plant was harvested using 5 μL microcapillary tubes, again reflecting the greater production of male flowers. Nectar was collected between 12:00 and 15:00

each day to minimise the effect of diurnal variation in nectar production (Nicolson et al., 2007). For each flower, I used as many microcapillary tubes as needed until no more nectar was taken up.

2.3.2 Nectar quantity

Directly after harvesting, the volume of nectar in each microcapillary tube was calculated by measuring the length of the nectar column with calipers. Where multiple microcapillary tubes were used to harvest nectar from an individual flower, the nectar column values from the same flower were summed. Nectar volume in μL was calculated by using equation [1]:

$$nectar\ volume\ (\mu L) = \frac{microcapillary\ volume\ (5\mu L)}{microcapillary\ tube\ length\ (mm)} * length\ of\ nectar\ column\ (mm) \quad [1]$$

Nectar production was also scaled up to the whole plant level according to equation [2]. This was done for each plant in each treatment and 'mean nectar' in equation [2] represents nectar per flower averaged across the two developmental stages.

$$\frac{nectar}{plant} = [\#\ male\ flowers * \frac{mean\ male\ nectar}{flower}] + \left[\#\ female\ flowers * \frac{mean\ female\ nectar}{flower}\right] \quad [2]$$

2.4 Pollen

2.4.1 Pollen collection

Stamens were harvested from three male flowers per plant between 15-20TL, and again between 25-30TL. Stamens from each flower were stored in separate glass vials at -6 °C until mounting.

2.4.2 Pollen quantity

To visualise pollen grains for counting, basic fuchsin jelly was prepared and stamens were semi-permanently mounted in the jelly according to Kearns & Inouye (1993). Pollen grains on prepared slides were counted using a modified protocol based on Costa & Yang (2009). Where resolution between grains was good, ImageJ was used to

automate counts using the 'Analyze Particles' function and the parameters 'pixel 20-800' and 'circularity 0.5-1' (Rasband, 2020). Where grains were closer together, counts were supplemented by hand using a Leica S4E stereo microscope and a hand clicker. ImageJ counts and hand counts were added together for each set of stamens. The number of pollen grains per plant was determined using equation [3].

$$\frac{pollen}{plant} = [\#\ male\ flowers * \frac{mean\ number\ of\ pollen\ grains}{flower}] \quad [3]$$

2.5 Leaf gas exchange measurements

2.5.1 Light response curves

Before measuring leaf gas exchange, saturating light values for plants between 25-30TL (plants at the same developmental stage) were determined by measuring light response curves using a portable LI-6400XT system (Li-Cor Bioscience, Lincoln, Nebraska, USA). Plants were exposed to 100, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, 2000 μmol photons m^{-2} s^{-1} and net CO_2 assimilation rate (A_{net}) was measured at each value. Saturating light was determined to be 1600 μmol photons m^{-2} s^{-1}.

2.5.2 Net CO_2 assimilation rate and conductance

Between August 7th and 9th, gas exchange was measured on the second, fully expanded leaf from the top of each of five plants from each treatment. Measured plants were all between 25-30TL to minimize the effects of developmental stage on gas exchange, and due to logistics only this developmental stage was evaluated. Gas exchange was measured to assess how A_{net} varies with intercellular [CO_2] (C_i), thus generating A/C_i curves. The A_{net} was measured at CO_2 concentrations of 50, 100, 150, 200, 250, 300, 350, 400, 600, 800, 1000, 1200, 1400, 1600, and 1800 ppm. Cuvette conditions were 1600 μmol photons m^{-2} s^{-1}, 500 μmol s^{-1} flow, and leaf temperature was set to 23 °C, 27 °C, or 31 °C (for the 0T, 4T, and 8T treatments, respectively) to assess A/C_i curves at plant growth temperatures. Leaf temperature settings were based on midday air temperature values in each treatment on August 6th. Cuvette relative humidity was maintained between 40 and 70% as needed to prevent stomatal closure.

To assess photosynthetic performance under the different growing conditions, A_{net} values at either 400 ppm or 800 ppm CO_2 (for AC and EC plants, respectively) were extracted from the CO_2 response curve data.

2.5.3 V_{cmax} and J_{max}

The A/C_i curves were fit with R version 4.0.0 and the Plantecophys package to obtain the maximum rate of carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) for each measured plant (Duursma, 2015; Farquhar et al., 1980; R core team, 2020)

2.5.4 Dark respiration

Between August 13th and 14th, nighttime dark respiration was measured on the same leaves used to measure A_{net}. Plants were left in the dark for one hour after sunset, and then point measurements of dark respiration (R_D) were recorded using an LI-6400XT portable photosynthesis system. All measurements were taken under growth conditions: measurement parameters were 0 μmol photons m^{-2} s^{-1}, 500 μmol s^{-1} flow, 400 ppm or 800 ppm reference [CO_2] (for AC and EC treatments, respectively), and leaf temperatures of 22 °C, 26 °C, and 30 °C in each treatment (0T, 4T, and 8T, respectively). Leaf temperatures were based on air temperature values in each treatment one hour after sunset on August 6th.

2.6 Biomass production and allocation

Five random plants from each treatment were selected for biomass measurements. After other measurements were completed, the selected plants were separated into leaf, stem, and root components, and the roots were carefully washed to remove attached soil. Leaf, stem and root components were then dried at 60 °C and weighed.

2.7 Statistical analysis

Means, standard deviations, and standard errors were calculated using the summarySE function in the package Rmisc (Hope, 2013). The effects of growth temperature and [CO_2] were analysed using two-way analyses of

variance (ANOVA) with [CO_2] and temperature treatment as main effects ($\alpha = 0.05$) and using type III sum of squares where sample sizes of groups were unequal. Prior to running ANOVAs, Levene's test was used to verify homogeneity of variance, and the Shapiro-Wilk test was used to verify normality. Tukey's HSD post-hoc test was used to test for pairwise differences. All statistics were run in RStudio (version 1.2.5042) using R version 4.0.0 and the packages car and lsmeans (Fox & Weisberg, 2020; Lenth, 2018; RStudio team, 2020; R core team, 2020).

3 Results

3.1 Carbon dynamics

3.1.1 Net CO_2 assimilation and nighttime respiration rates

There were no significant main effects on A_{net}. However, the A_{net} in EC4T plants was double that of AC4T plants (Table 3.1; Figure 3.1a). For nighttime dark respiration rates there was an interaction between [CO_2] and temperature, but no significant effect of [CO_2] or temperature alone (Table 3.1). The AC plants had similar R_D across all the temperature treatments, whereas EC plants had declining respiration rates with warming (Figure 3.1b).

Table 3.1. Summary statistics (F and p-value) of ANOVAs for floral traits, floral rewards, plant biomass, and gas exchange parameters measured on *C. sativus* plants. Plants were grown under six climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Bold values are significant ($\alpha = 0.05$). A_{net} = net rate of CO_2 assimilation, R_D = dark respiration rate, g_s = stomatal conductance, V_{cmax} = maximum rate of Rubisco carboxylation, J_{max} = maximum rate of electron transport.

	CO_2		Temperature		CO_2×Temperature	
Gas exchange	p-value	F-value	p-value	F-value	p-value	F-value
A_{net}	0.67	0.19	0.40	0.94	0.08	2.77
R_D	0.35	0.92	0.42	0.91	**<0.05**	**3.87**
A_{net}:R_D	0.82	0.05	0.37	1.06	0.44	0.84
g_s	0.79	0.07	0.06	3.28	0.14	2.13
V_{cmax}	0.35	0.91	0.36	1.06	0.63	0.47
J_{max}	0.77	0.09	0.55	0.62	0.35	1.09
Plant biomass traits						
Leaf biomass	0.15	2.23	**<0.01**	**6.26**	0.44	0.85
Stem biomass	0.77	0.09	**<0.001**	**12.43**	0.08	2.81
Root biomass	0.34	0.97	**<0.05**	**4.71**	0.36	1.07
Total biomass	**<0.0001**	**24.54**	**<0.001**	**9.90**	0.19	1.78
% allocation to leaves	0.92	0.01	0.40	0.94	0.68	0.39
% allocation to stems	0.10	2.93	0.37	1.05	0.89	0.12
% allocation to roots	0.69	0.16	0.06	3.08	0.50	0.72

Floral metrics						
Flowering onset	**<0.0001**	**31.13**	**<0.0001**	**109.14**	**<0.001**	**8.07**
Daily display size (15-20TL)	0.94	0.0060	**<0.01**	**7.37**	0.83	0.19
Daily display size (25-30TL)	0.08	3.10	0.23	1.50	**<0.001**	**10.15**
Male flower production	0.27	1.25	**<0.05**	**4.53**	**<0.05**	**3.70**
Female flower production	0.78	0.08	**<0.0001**	**13.93**	0.23	1.51
Male flower size (15-20TL)	0.60	0.28	**<0.0001**	**40.88**	0.82	0.20
Male flower size (25-30TL)	0.38	0.79	**<0.0001**	**30.77**	**<0.01**	**6.31**
Female flower size (15-20TL)	0.23	1.46	**<0.001**	**8.34**	0.15	1.92
Female flower size (25-30TL)	0.65	0.20	**<0.01**	**6.19**	0.21	1.61
Floral rewards						
Male nectar/flower (15-20TL)	0.87	0.03	**<0.01**	**6.52**	0.86	0.15
Male nectar/flower (25-30TL)	0.22	1.55	**<0.05**	**4.29**	0.72	0.33
Female nectar/flower (15-20TL)	0.35	0.90	0.05	3.15	0.12	2.21
Female nectar/flower (25-30TL)	0.56	3.79	**<0.01**	**6.24**	0.16	1.86
Nectar/plant	0.95	0.0032	**<0.0001**	**11.59**	**<0.0001**	**15.81**
Pollen/flower (15-20TL)	0.26	1.34	**<0.05**	**5.34**	0.23	1.56
Pollen/flower (25-30TL)	**<0.05**	**4.45**	**<0.01**	**6.72**	**<0.05**	**4.67**
Pollen/plant	0.61	0.26	0.42	0.90	0.45	0.81

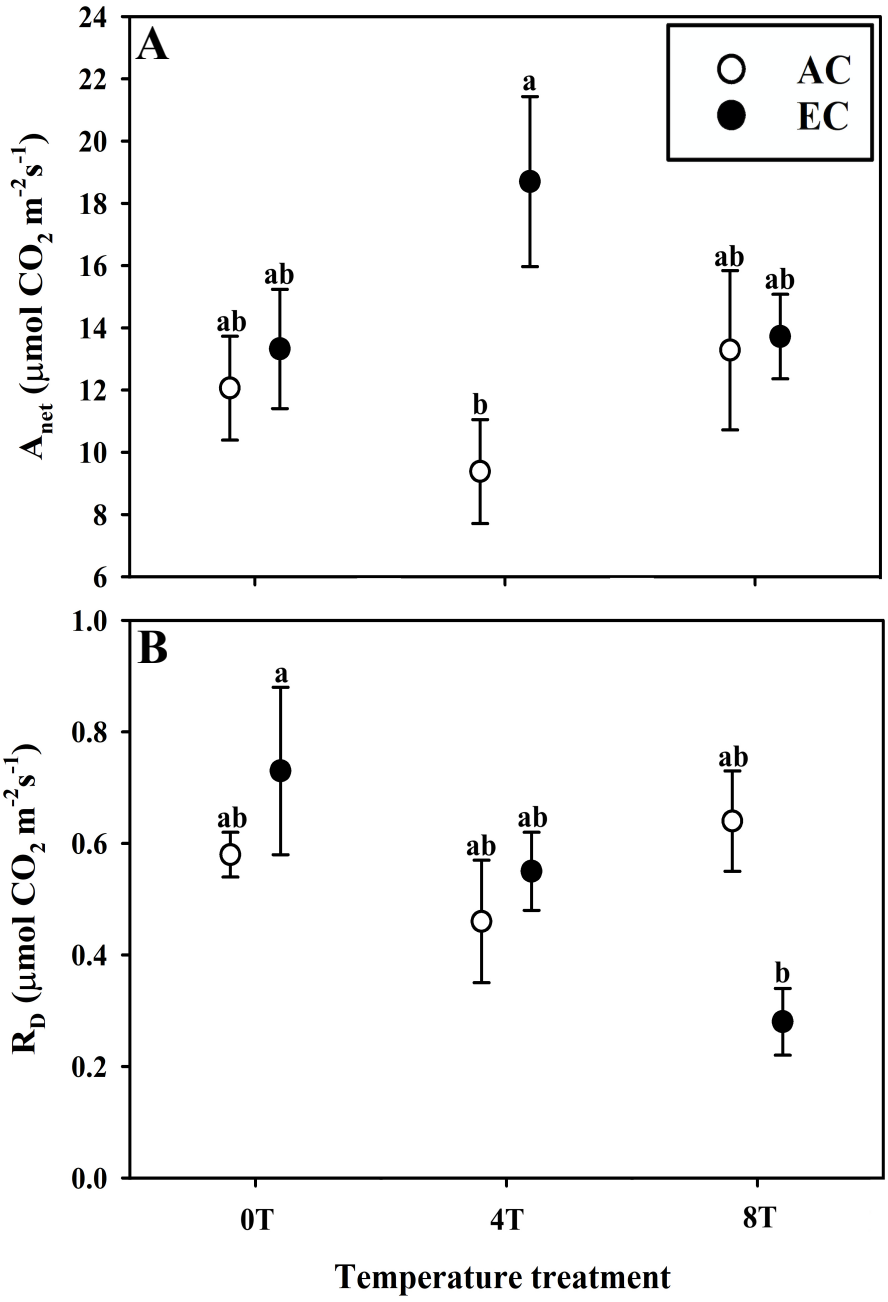

Figure 3.1. Mean net CO_2 assimilation rate (A_{net}) (±1 SE) (a); and mean nighttime respiration rate (R_D) (±1 SE) (b) measured on *C. sativus* plants between 25-30 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 4-5).

I also compared the ratio of A_{net} to R_D across the treatments as an index of leaf carbon balance (Figure 3.2). Despite the treatment effects seen in R_D, there were no significant differences in the ratio of A_{net} to R_D across the treatments (Table 3.1).

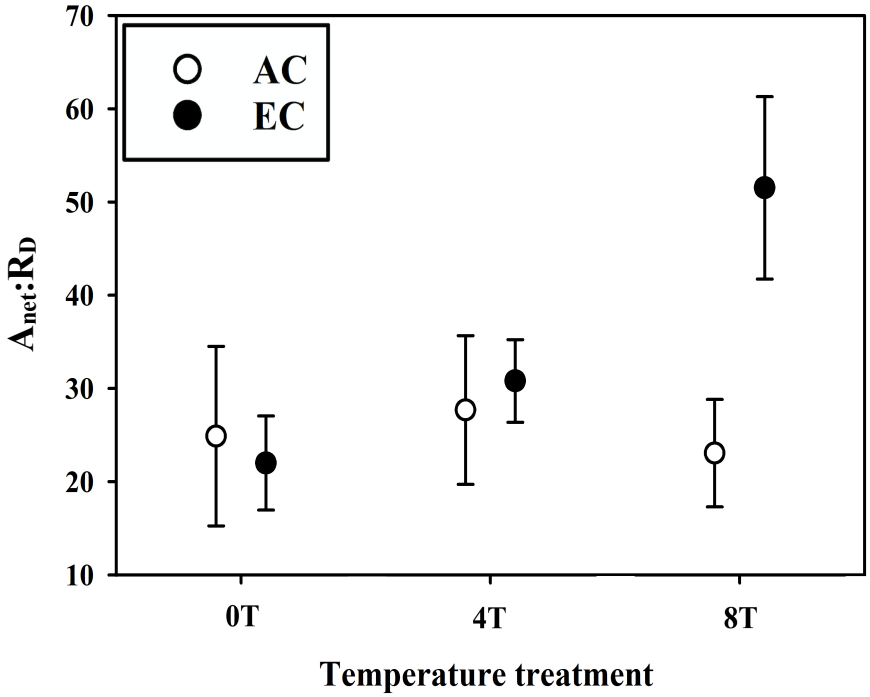

Figure 3.2. Mean ratio of net CO_2 assimilation rates (A_{net}) to nighttime respiration rates (R_D) (±1 SE) measured on *C. sativus* plant between 25-30 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C ($\alpha = 0.05$, n = 4-5)**.**

3.1.2 Stomatal conductance

There were no significant differences in g_s between plants grown in different treatments (Table 3.1; Figure 3.3).

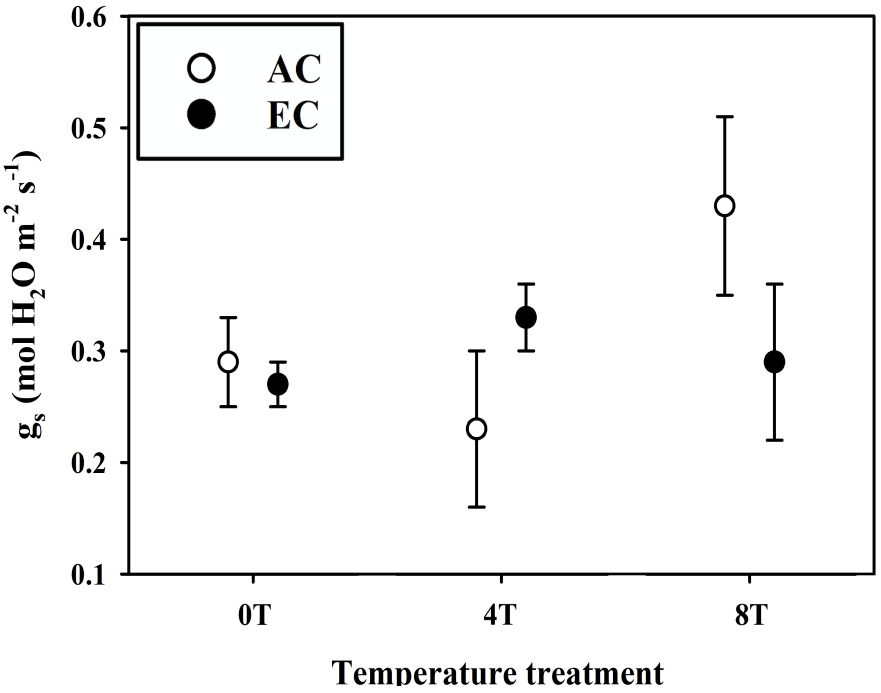

Figure 3.3. Mean stomatal conductance (g_s) (±1 SE) of *C. sativus* plants between 25-30 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C (α = 0.05, n = 4-5)**.**

3.1.3 V_{cmax} and J_{max}

There were no significant differences in photosynthetic capacity (V_{cmax} or J_{max}) between plants grown under different treatments (Table 3.1; Figure 3.4).

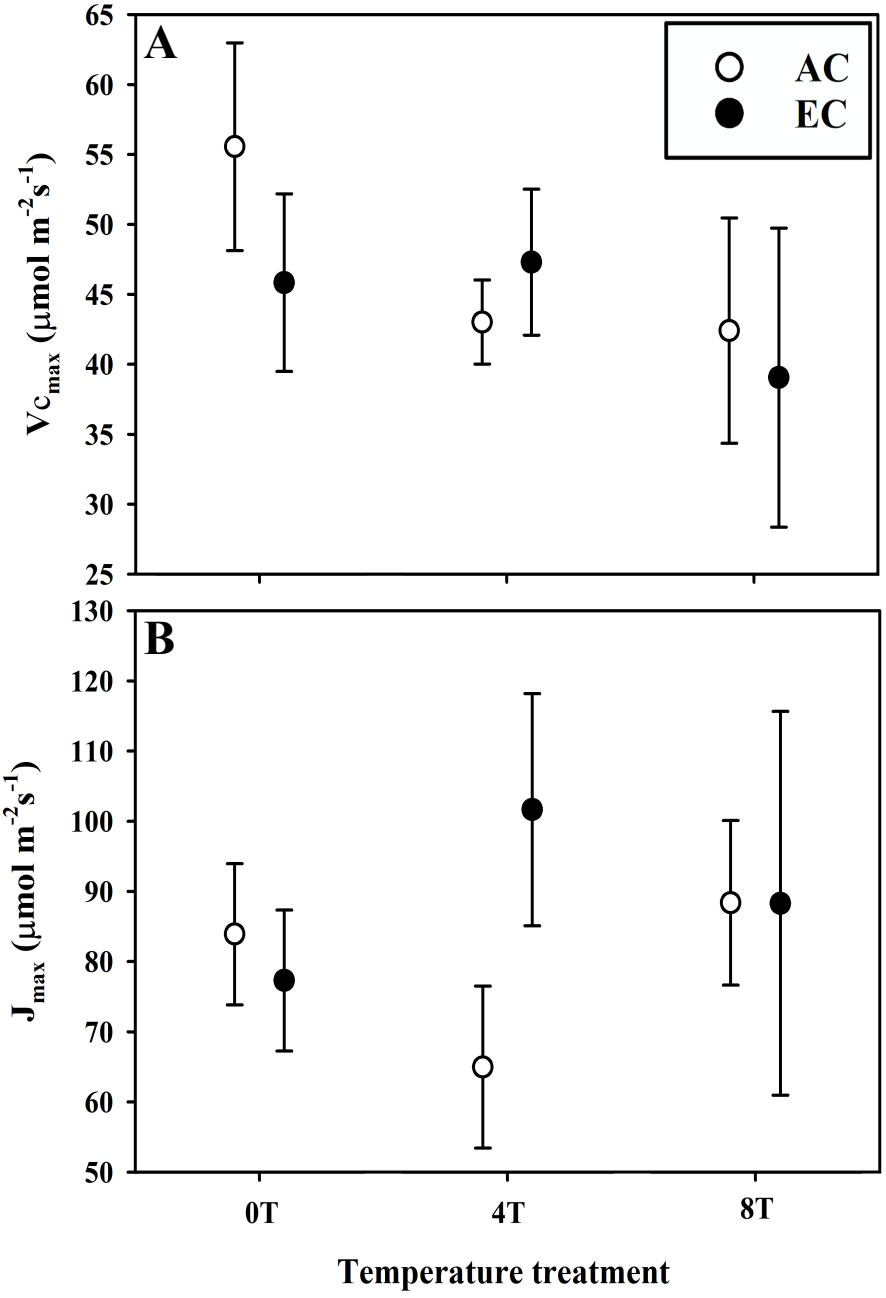

Figure 3.4. Mean maximum rates of (a) Rubisco carboxylation (V_{cmax}) (±1 SE) and (b) electron transport (J_{max}) (±1 SE) for *C. sativus* plants between 25-30 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C (α = 0.05, n = 4-5).

3.2 Biomass production and allocation

Both temperature and [CO_2] had significant effects on total biomass production, but there was no significant interaction between the two (Table 3.1). In contrast, for each biomass component (leaf, stem, and root), the effect of temperature was significant but there was no effect of [CO_2] and no interaction between [CO_2] and temperature (Table 3.1).

In general, plants produced less biomass in the warming treatments and greater biomass in elevated [CO_2], but did not alter their percent allocation to leaf, stem, and root components (Table 3.1). The EC treatment increased total biomass in all temperature treatments, and plants exhibited a 14% increase in total biomass at 0T, a 41% increase at 4T, and a 69% increase at 8T compared to AC-grown plants (Figure 3.5). However, elevated [CO_2] did not affect measurements of leaf, stem or root biomass. In contrast, warming reduced total biomass, and also reduced leaf, stem and root biomass (Figure 3.5). Interestingly, these CO_2 and warming effects counterbalanced each other, so that the total biomass (Figure 3.5) and biomass allocation patterns (Figure 3.6) of the AC0T and EC8T plants were similar.

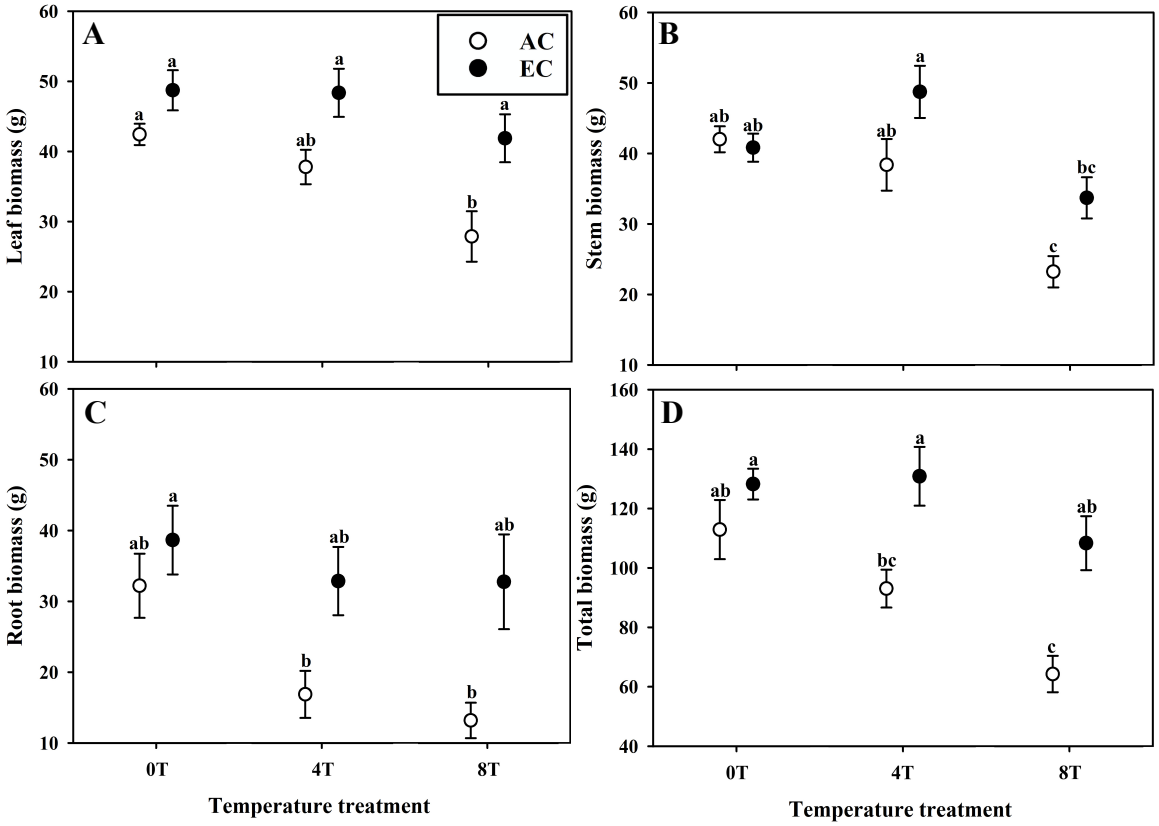

Figure 3.5. Mean biomass (±1 SE) of (a) leaves, (b) stems, (c) roots, and (d) whole *C. sativus* plants. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 5).

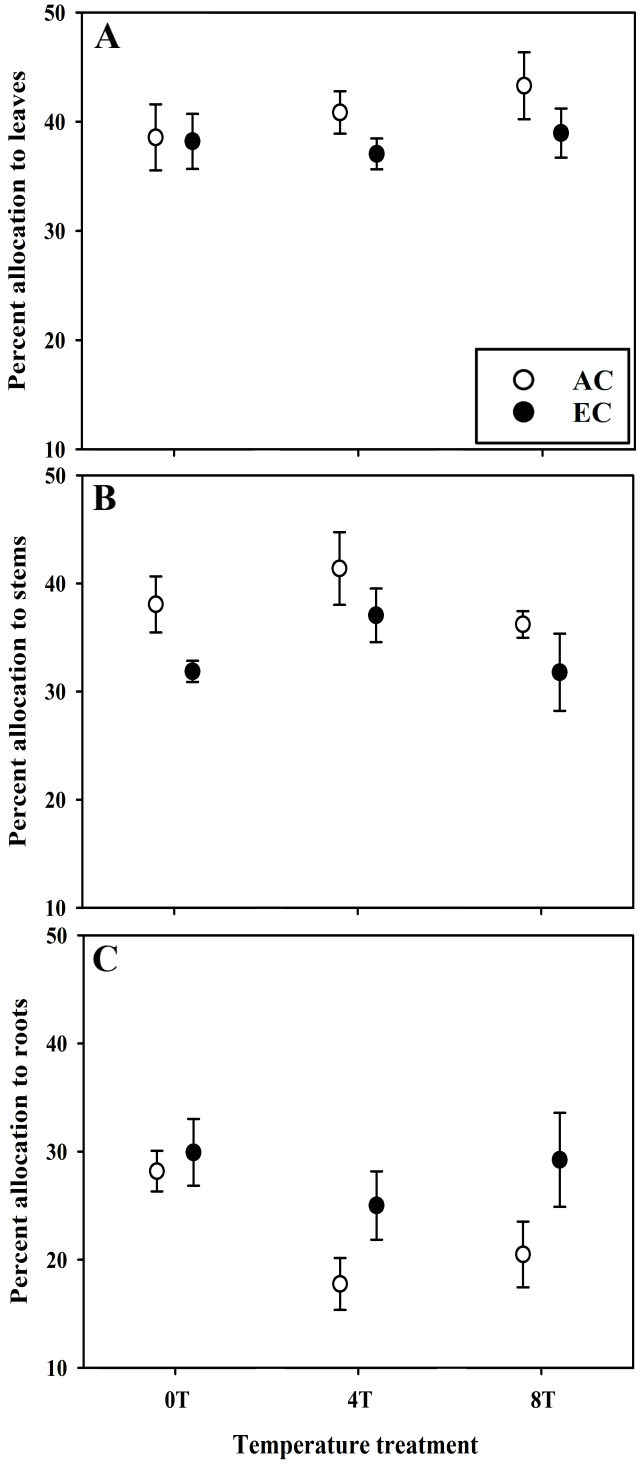

Figure 3.6. Mean percent biomass (±1 SE) allocated to (a) leaves, (b) stems, and (c) roots of *C. sativus* plants. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C ($\alpha = 0.05$, n = 5)**.**

3.3 Floral metrics

3.3.1 Flowering onset

There was a significant interaction between temperature and [CO_2] on flowering onset, as well as a significant effect of temperature and [CO_2] (Table 3.1). In general, warming reduced the time to flowering onset (Figure 3.7). The AC4T plants flowered 14% earlier than AC0T plants, and the AC8T plants flowered 19% earlier than those from the AC0T treatment. Similarly, EC4T plants flowered 8% earlier than EC0T plants, and EC8T plants flowered 14% earlier than the EC0T plants (Figure 3.7). In addition, elevated [CO_2] accelerated flowering onset by 8% in the 0T treatment, though it had little effect on flowering onset in the other temperature treatments (Figure 3.7).

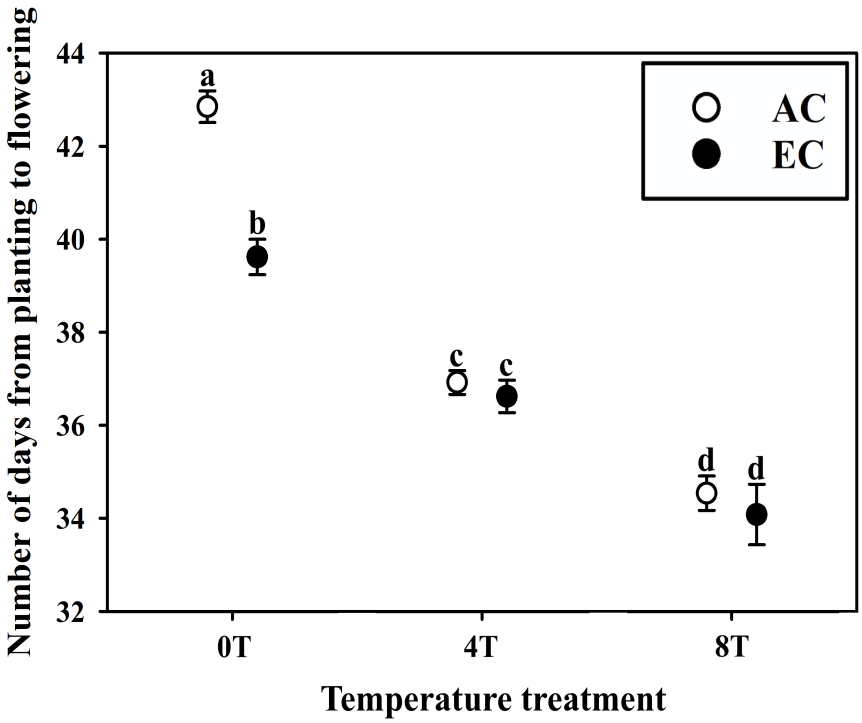

Figure 3.7. Mean number of days from planting to first flowering (±1 SE) for *C. sativus* plants. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 13).

3.3.2 Flower production

3.3.2.1 Daily display size

For plants between 15-20TL, increasing temperature reduced the daily display size (number of open flowers on each plant per day), but there was no effect of [CO_2] and no interaction between [CO_2] and temperature (Table 3.1; Figure 3.8). Display size was similar between AC- and EC-grown plants at all temperature treatments (Figure 3.8). Display size was also similar between 0T and 4T treatments but decreased by approximately 50% compared to control temperatures when plants were grown at 8T (Figure 3.8).

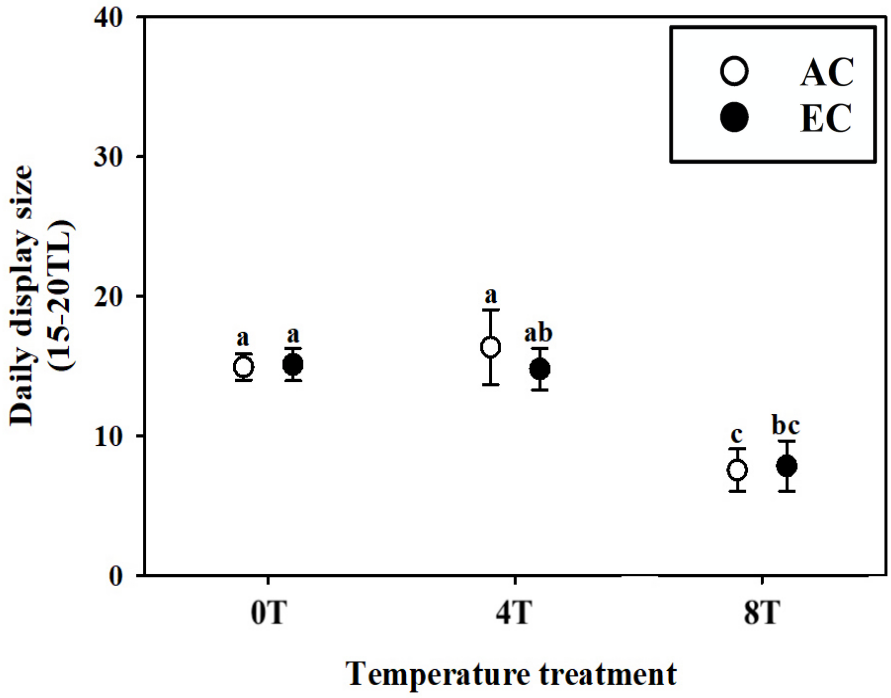

Figure 3.8. Average daily display size (±1 SE) produced by *C. sativus* plants between 15-20 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 13).

Between 25-30TL, there was no effect of either [CO_2] or temperature, but there was a significant interaction between temperature and [CO_2] on daily display size (Table 3.1). AC plants showed similar display sizes across the temperature treatments, whereas EC plants produced more open flowers as temperatures increased (Figure 3.9). From 0T to 4T, EC plants produced 82% more open flowers and from 0T to 8T EC plants produced 138% more open flowers (Figure 3.9).

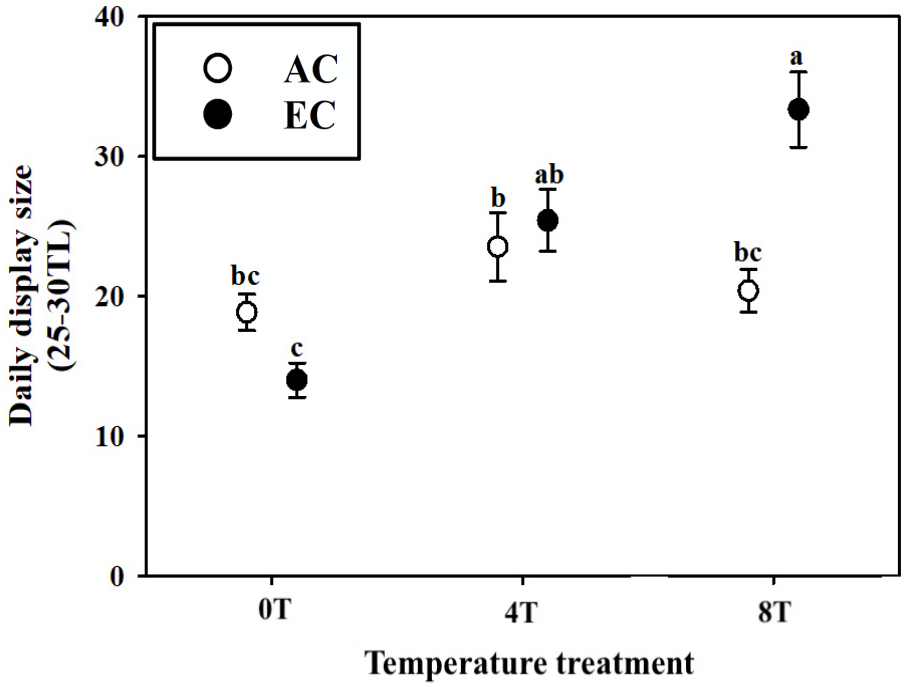

Figure 3.9. Average daily display size (±1 SE) produced by *C. sativus* plants between 15-20 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 13).

3.3.2.2 Lifetime flower production

There was a significant temperature effect and a significant interaction between temperature and [CO_2] on the number of male flowers produced, however, the effect of

[CO_2] was not significant (Table 3.1). Both AC and EC plants produced similar numbers of male flowers at 0T (Figure 3.10a). Compared to the number male of flowers produced at 0T, male flower production in the EC treatment increased by 98% with 4T warming, and by 120% with 8T warming (Figure 3.10a). However, in the AC-grown plants, male flower production peaked at 4T, with an increase of 57% compared to 0T, and male flower production at 8T was similar to both the 0T and 4T values (Figure 3.10a).

Growth temperature also significantly affected female flower production, but there was no effect of [CO_2], and no interaction between [CO_2] and temperature (Table 3.1). Female flower production was similar in the 0T and 4T treatments for both CO_2 treatments, but decreased in the 8T plants by approximately 41% (Figure 3.10b).

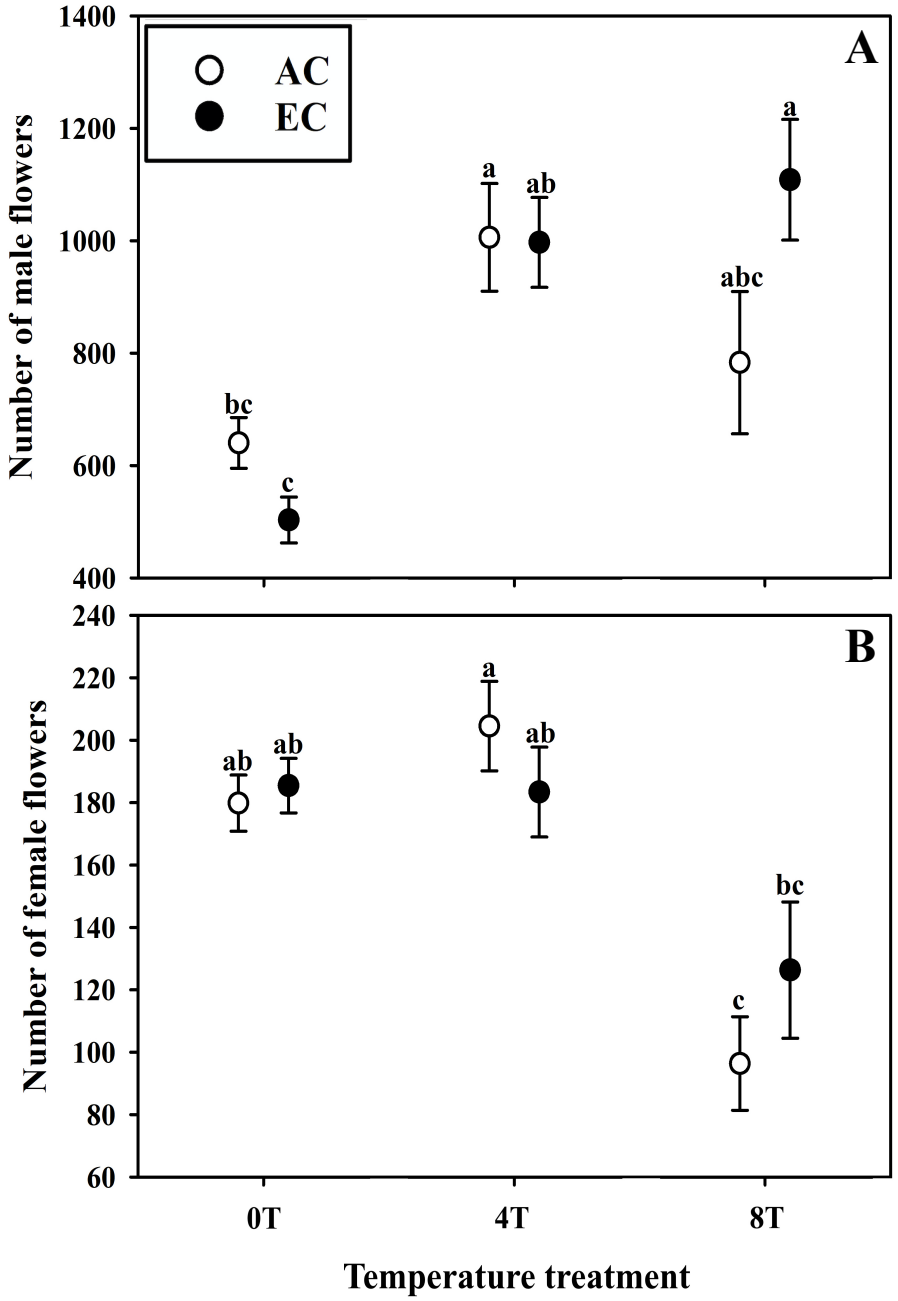

Figure 3.10. Mean lifetime number of: (a) male and (b) female flowers (±1 SE) produced by *C. sativus* plants. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 13).

3.3.3 Flower size

In 15-20TL plants, both male and female flower size decreased with warming, but there was no effect of either growth [CO_2] or the interaction between [CO_2] and temperature on flower size (Table 3.1; Figure 3.11). Compared to 0T flowers, male flower size decreased by 11% when grown at 4T and by 25% when grown at 8T (Figure 3.11a). For female flowers, flower size was similar for AC4T plants, but decreased by 13% for EC4T plants when compared to 0T flowers (Figure 3.11b). Female flower size also decreased by 20% and 18% for the AC8T and EC8T plants, respectively when compared to the 0T flowers (Figure 3.11b).

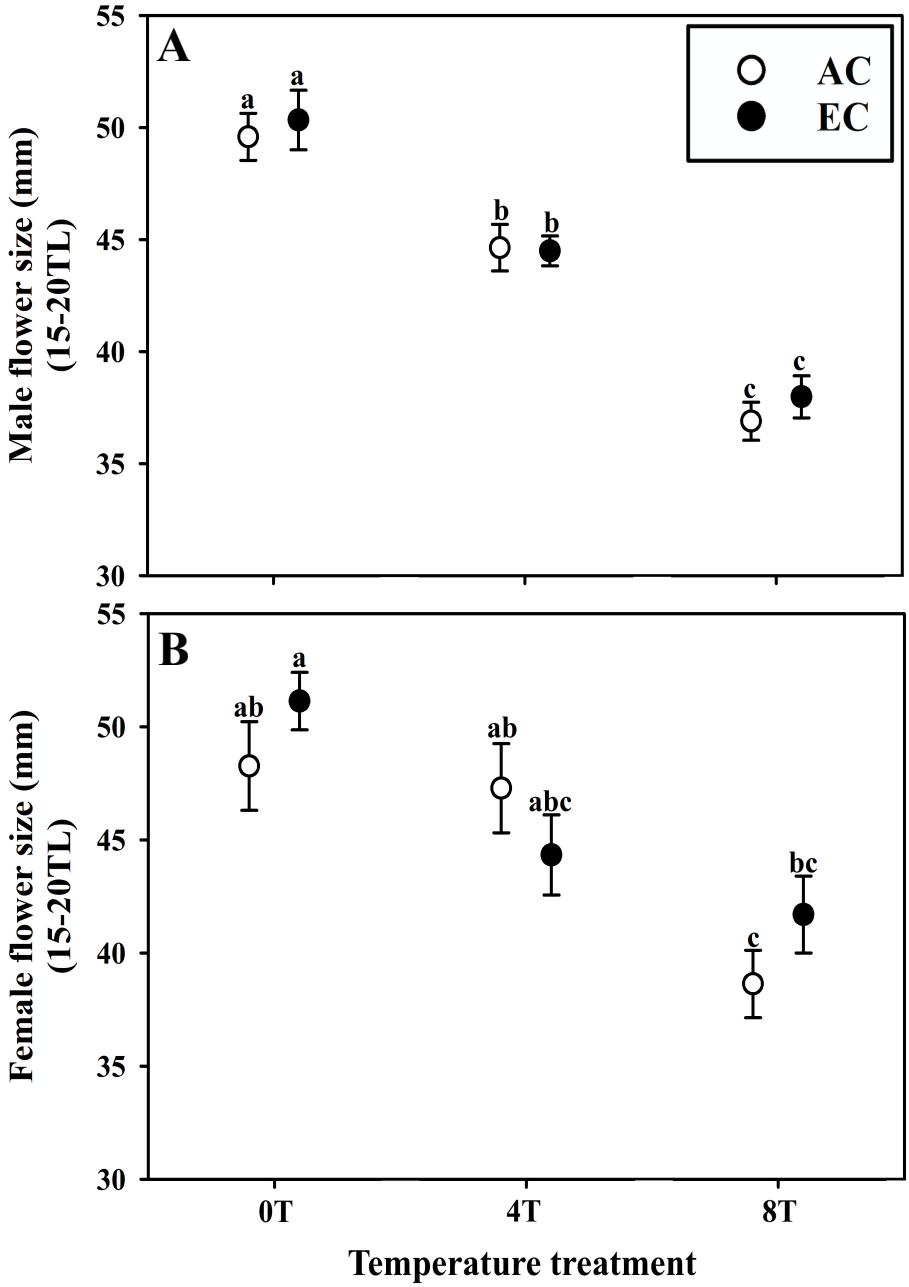

Figure 3.11. Mean size (mm) of: (a) male; and (b) female flowers (±1 SE) produced by *C. sativus* plants between 15-20 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C. Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, $n_{male} = 13$, $n_{female} = 10\text{-}13$).

In 25-30TL plants, both male and female flower size decreased with warming and there was a significant interaction between [CO_2] and temperature on the size of male flowers, but the effect of [CO_2] alone was not significant (Table 3.1; Figure 3.12a). Average male flower size was similar between the 0T and 4T treatments (Figure 3.12a). However, when plants were grown at 8T, male flower size decreased by 19% and 8% compared to 0T flowers (for the AC and EC plants, respectively) (Figure 3.12a). Average female flower size also decreased with warming (Table 3.1; Figure 3.12b). At 4T, AC-grown female flowers were similar in size to 0T flowers, but EC-grown flowers were 8% smaller than 0T flowers. At 8T, female flowers were 17% and 10% smaller compared to those under control temperature conditions (for the AC and EC plants, respectively) (Figure 3.12b).

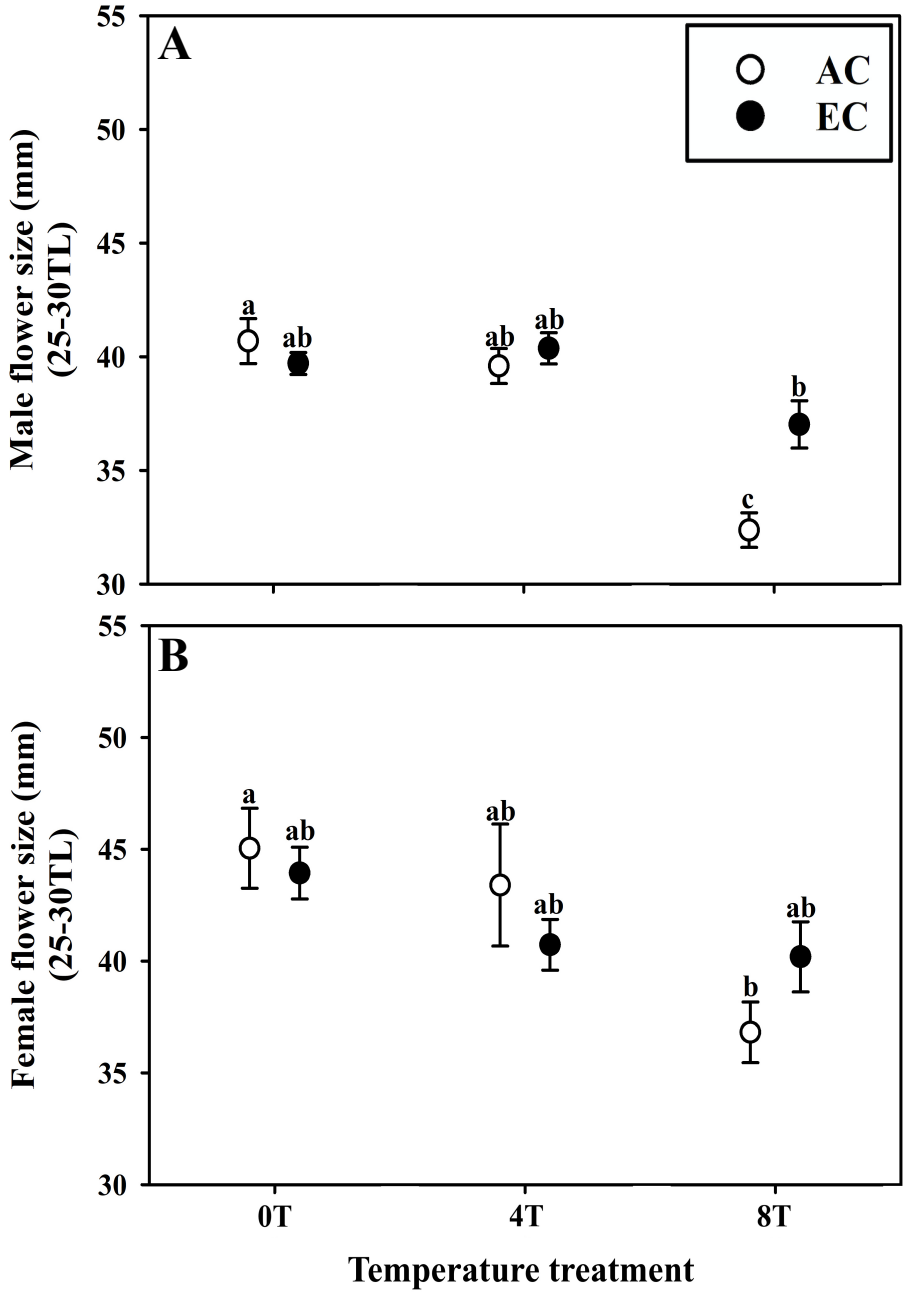

Figure 3.12. Mean size (mm) of: (a) male; and (b) female flowers (±1 SE) produced by *C. sativus* plants between 25-30 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 12-13).

3.4 Nectar production

3.4.1 Nectar produced per flower

For male flowers produced by plants between 15-20TL, there was a temperature effect but no effect of [CO_2] and no interaction between [CO_2] and temperature. In general, male nectar produced per flower declined with warming but was similar between [CO_2] treatments (Table 3.1). Mean nectar produced per male flower declined by 35% at 4T, and by 65% at 8T, compared to the 0T flowers (Figure 3.13a). Female nectar production in 15-20TL plants was not affected by temperature, [CO_2], or the interaction between the two factors (Figure 3.13b).

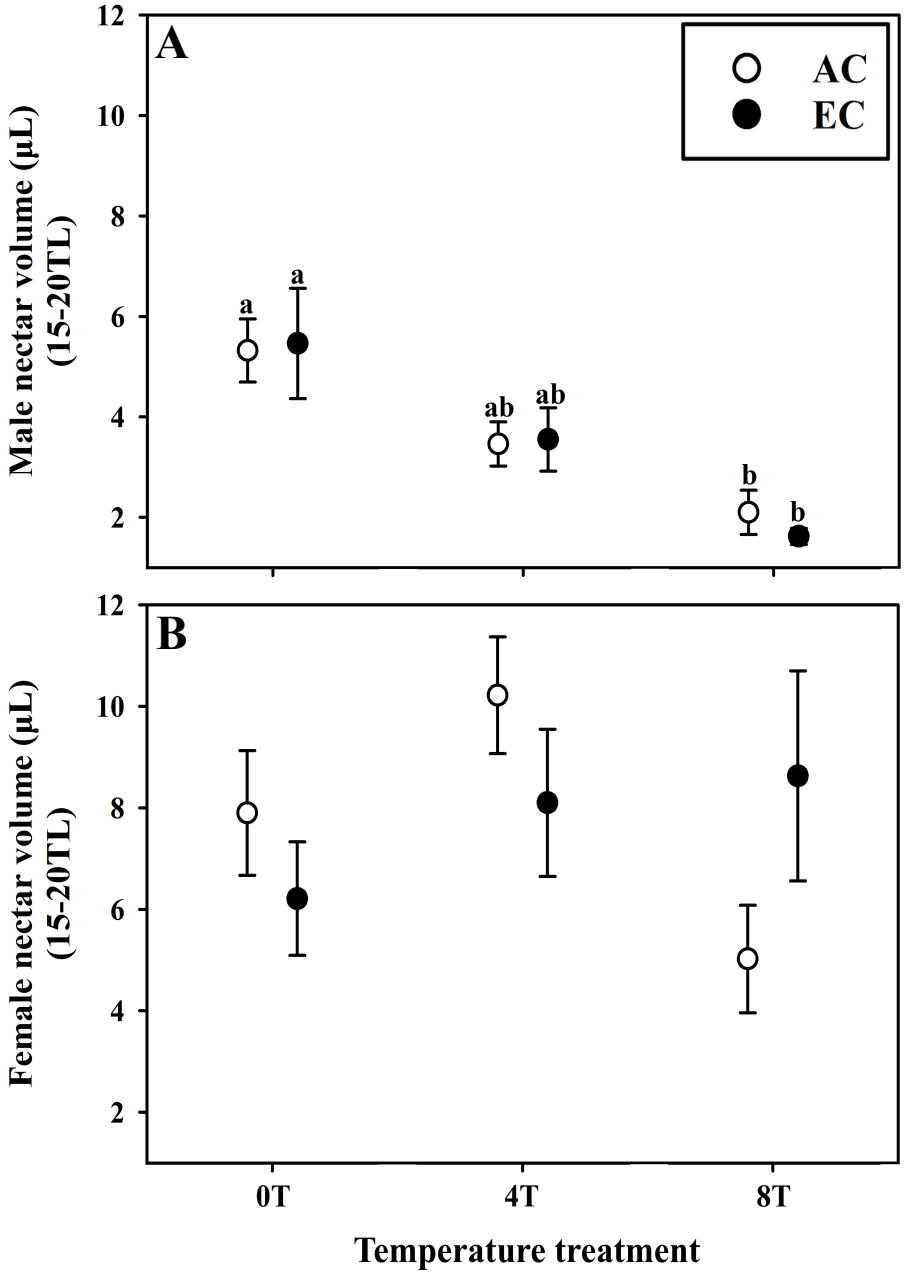

Figure 3.13. Mean nectar volume per flower for (a) male; and (b) female *C. sativus* flowers (±1 SE) between 15-20 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, $n_{male} = 8\text{-}13$, $n_{female} = 7\text{-}13$).

For 25-30TL plants, both male and female nectar production per flower increased with warming, but there was no interaction between [CO_2] and temperature and no significant effect of [CO_2] (Table 3.1; Figure 3.14). Compared to 0T flowers, mean nectar produced per male flower increased by 87% and 38% at 4T, and by 67% and 41% at 8T (AC and EC respectively) (Figure 3.14a). For female flowers, mean nectar production increased by 215% and 37% at 4T compared to the 0T plants (AC and EC, respectively). At 8T, female nectar production remained similar for AC plants, while nectar production increased by 87% for EC plants compared to those at 0T (Figure 3.14b).

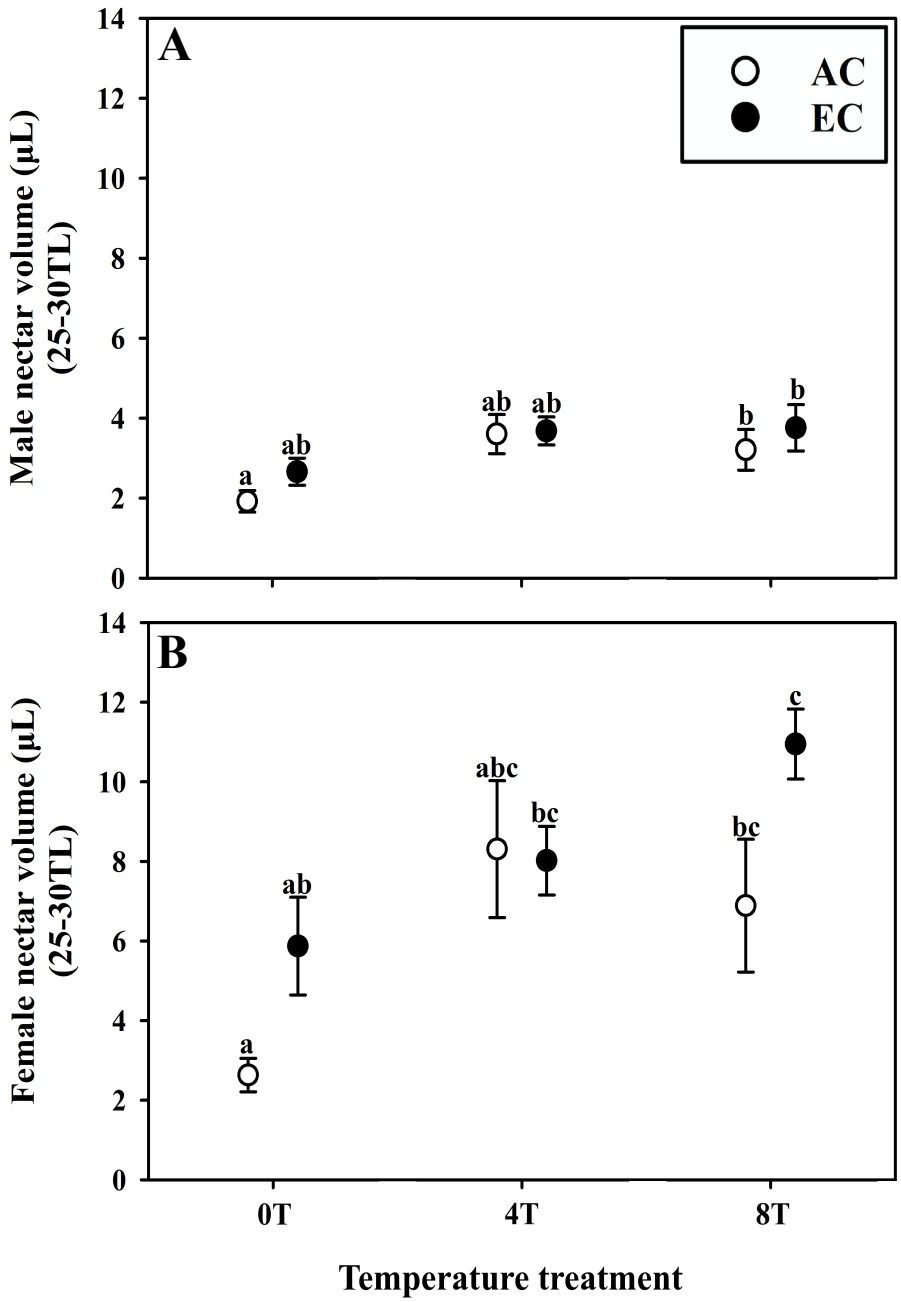

Figure 3.14. Mean nectar volume per flower for (a) male; and (b) female *C. sativus* flowers (±1 SE) between 25-30 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4 °C, and 8T = 0T+8 °C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, $n_{male} = 12\text{-}13$, $n_{female} = 11\text{-}13$).

3.4.2 Nectar produced per plant

There was a significant interaction between [CO_2] and temperature and a significant effect of temperature on whole plant nectar production; however, the effect of [CO_2] was not significant (Table 3.1). Under AC, nectar production per plant was similar in the 0T and 8T treatments but was 73% greater than this at 4T. In contrast, in EC plants, nectar production per plant increased 71% from 0T to 4T and increased 113% from 0T to 8T. Thus, when comparing control plants and the most extreme future climate scenario-grown plants (i.e., AC0T and EC8T), nectar production per plant approximately doubled (Figure 3.15).

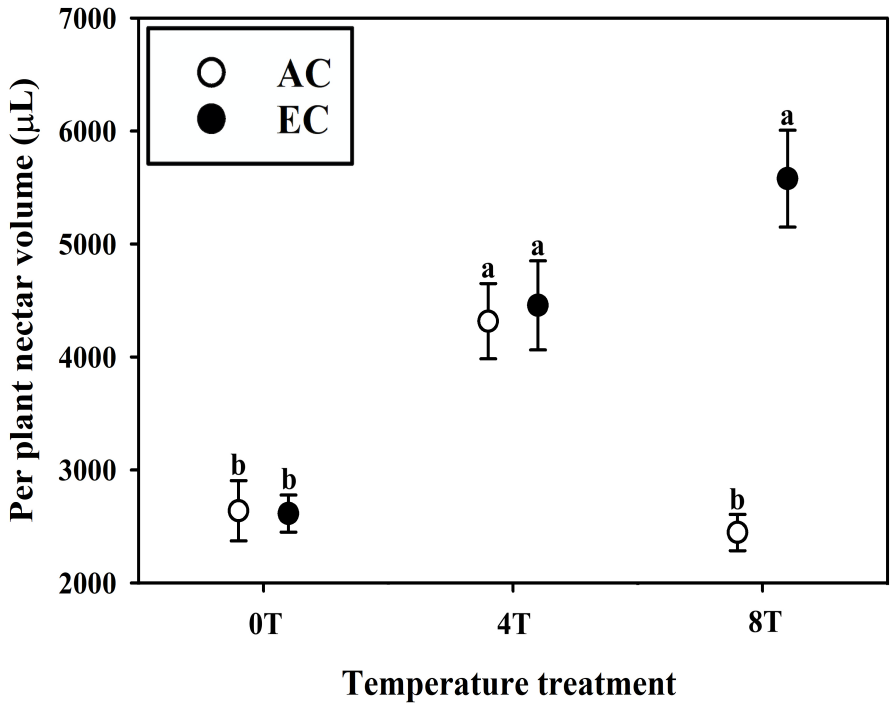

Figure 3.15. Mean nectar produced per *C. sativus* plant (±1 SE). Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C**.** Different letters above the points indicate significant differences between the six treatments (α = 0.05, n = 11-13).

3.5 Pollen production

3.5.1 Pollen produced per flower

Temperature significantly affected the number of pollen grains that 15-20TL flowers produced, but there was no interaction between [CO_2] and temperature and no effect of [CO_2] (Table 3.1). At current temperatures (0T), both AC- and EC-grown plants had similar pollen production per flower (Figure 3.16). From 0T to 4T, EC pollen production was similar, but AC pollen production decreased by approximately 30%. From 0T to 8T, EC pollen production remained similar, and AC pollen production returned to that of the control (AC0T) plants (Figure 3.16).

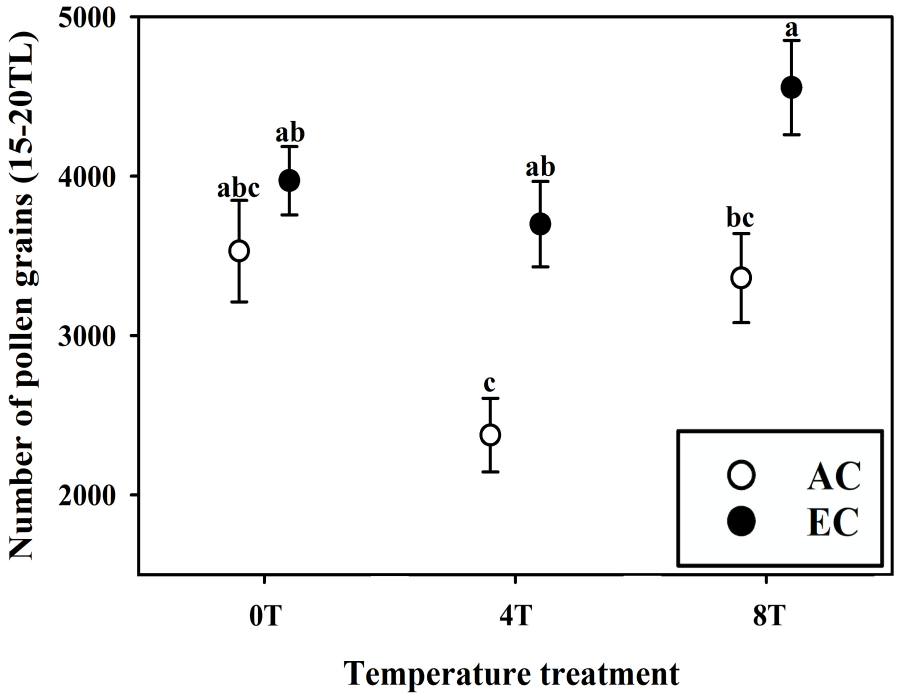

Figure 3.16. Average number of pollen grains (±1 SE) per flower produced by *C. sativus* plants between 15-20 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 6).

In 25-30TL plants, there was a significant effect of [CO_2], temperature, and a significant interaction between [CO_2] and temperature when looking at pollen production per flower (Table 3.1). EC plants showed no significant differences in per flower pollen production across the temperature treatments, while AC flowers had similar pollen production in 0T and 4T treatments but produced 60% less pollen under 8T compared to control plants (Figure 3.17).

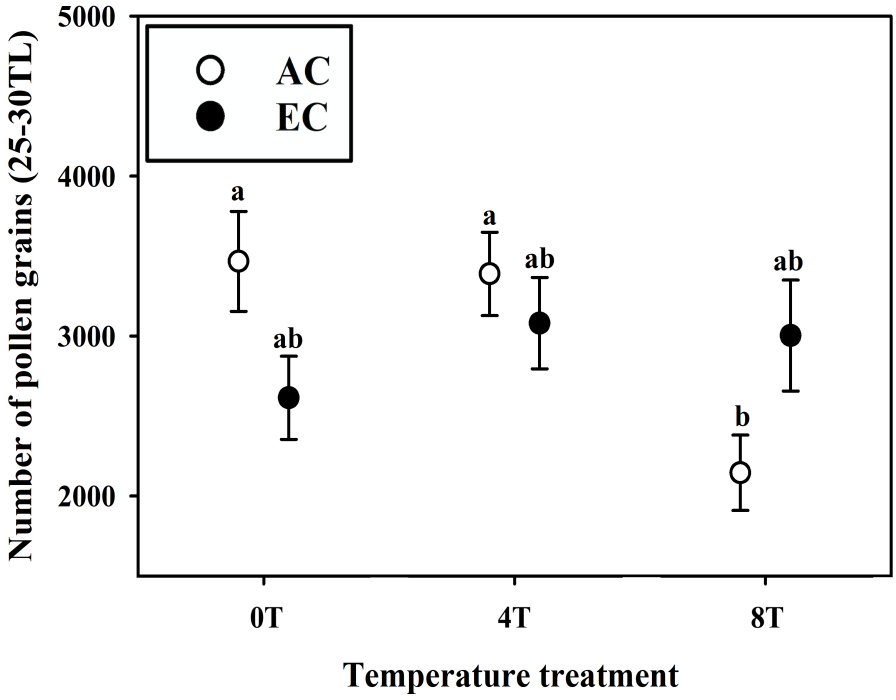

Figure 3.17. Average number of pollen grains (±1 SE) per flower produced by *C. sativus* plants between 25-30 true leaves. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C**.** Different letters above the points indicate significant differences between the six treatments ($\alpha = 0.05$, n = 6).

3.5.2 Pollen produced per plant

Despite the observed effects on the pollen production of individual flowers, when pollen production was scaled up to the whole plant level, there were no significant main effects and no differences in pollen production between the treatments (Table 3.1; Figure 3.18).

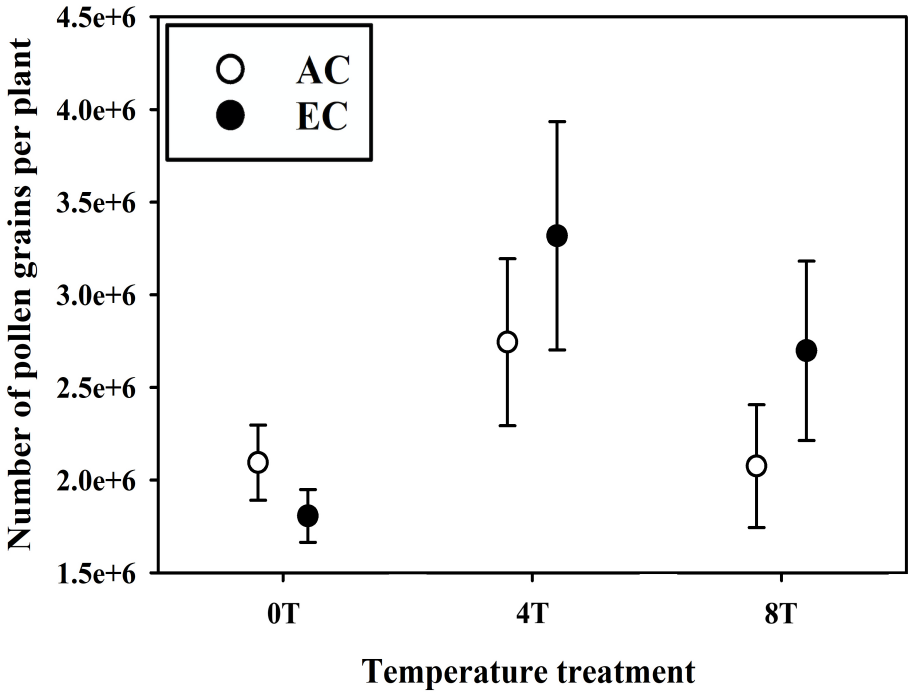

Figure 3.18. Average number of pollen grains (±1 SE) produced by *C. sativus* plants. Plants were grown under six different climatic treatments: AC0T, EC0T, AC4T, EC4T, AC8T, and EC8T. AC = 400 ppm CO_2, EC = 750 ppm CO_2, 0T = ambient temperature regime, 4T = 0T+4°C, and 8T = 0T+8°C ($\alpha = 0.05$, n = 6).

4 Discussion

4.1 Temperature effects

Temperature had little effect on gas exchange parameters or biomass allocation patterns in cucumber. But in response to warmer growth temperatures, *C. sativus* plants produced less biomass, and warming also negatively affected floral trait values (Figure 4.1). Specifically, high growth temperatures accelerated flowering onset, decreased flower size, reduced female flower production, reduced daily display size (for 15-20TL plants), reduced nectar per male flower (in 15-20TL plants), and reduced pollen per flower (in 25-30TL plants). Thus, overall, elevated growth temperatures reduced plant size and many reproduction-related traits, but in a manner that appears to be unrelated to measured carbon fluxes.

The effects of high temperature I saw on floral traits of *C. sativus* are consistent with results of other studies. Hoover et al. (2012) also found accelerated flowering time and reduced flower size for *Curcurbita maxima* plants exposed to high temperature (comparing plants grown at 19 or 23 °C). Additionally, Descamps et al. (2018 and 2020) found that increased temperatures (ranging from 21, 24 and 27 °C) reduced corolla surface area, corolla diameter, flower production, and nectar volume for *Borago officinalis* and *Echium plantagium*.

High temperatures reduce the duration of the initiation and/or expansion of floral organs (reviewed by Morison & Lawlor, 1999). This leaves less time for biomass accumulation and ultimately results in smaller plant size (reviewed by Hatfield & Prueger, 2015; Morison & Lawlor, 1999). Accelerated development with warming, as evidenced by earlier flowering in the warmed treatments, likely underlies the declines in biomass I observed in the warm-grown plants in this study and could also explain reduced flower sizes. In response to increasing temperature, many species also show augmented growth responses up to a species-specific thermal optimum, and above this temperature, growth declines rapidly (reviewed by Hatfield & Prueger, 2015). For cucumbers, the optimum range of growth

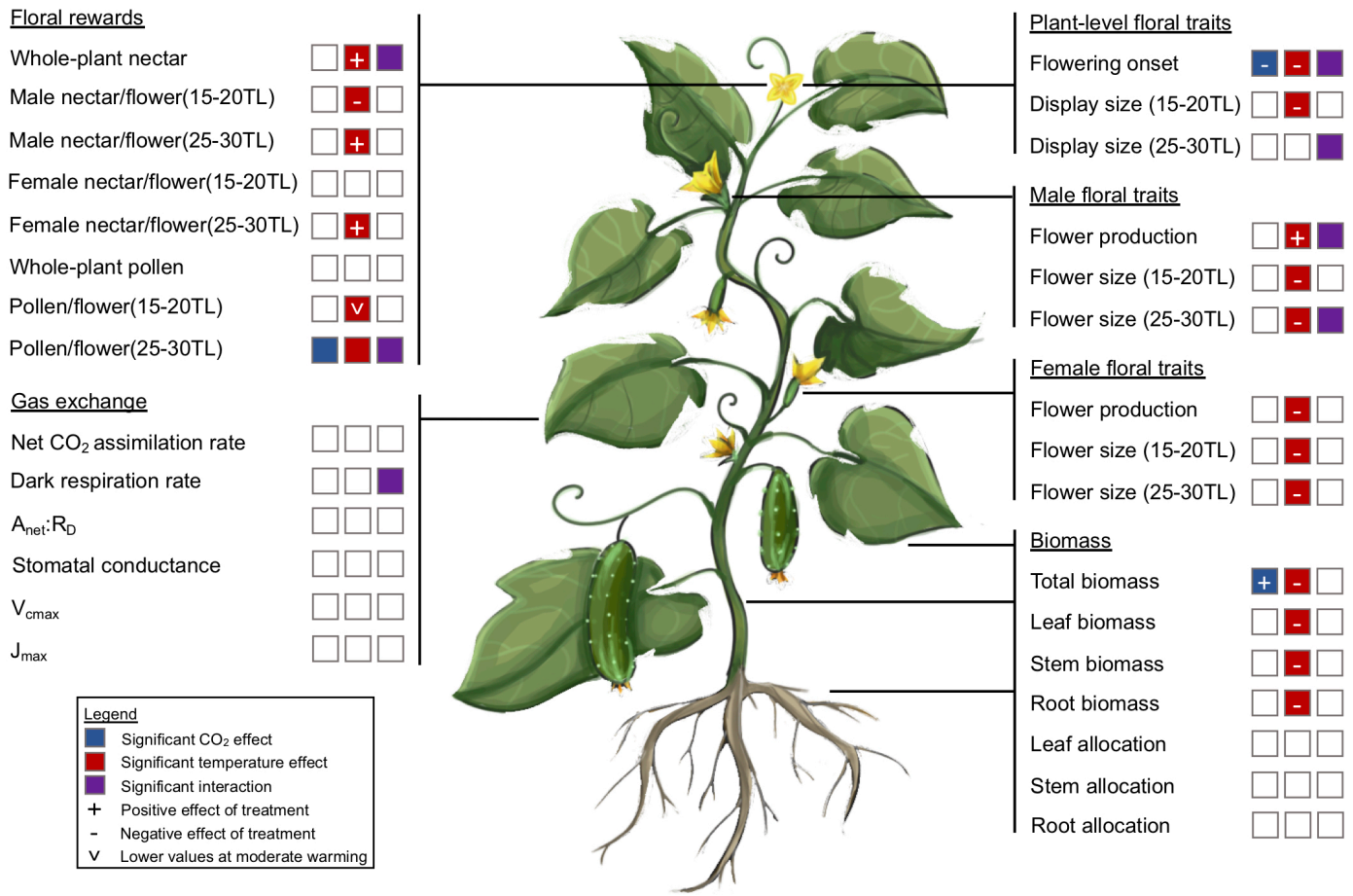

Figure 4.1. Summary of the effects of temperature, [CO_2], and their interaction on floral traits, gas exchange, and biomass of *C. sativus*. Blue squares = significant [CO_2] effect, red squares = significant temperature effect, purple squares = significant CO_2 x temperature interaction, (+) = positive effect, (-) = negative effect, and (v) = lower at moderate temperature, A_{net} = net rate of CO_2 assimilation, R_D = dark respiration rate, V_{cmax}= maximum rate of Rubisco carboxylation, J_{max}= maximum rate of electron transport. Illustrated by Amy McDonald.

temperatures is between 20-25 °C, and temperatures around 35 °C, like those in the 8T treatment, can induce heat stress (Backlund, 2009). Plant reproduction is especially susceptible to high temperature stress (Sage et al., 2015; Zinn et al., 2010), which could explain the declines in reward and flower production with warming.

High temperatures also affected some traits of male and female flowers differently. With warming, the number of male flowers increased while nectar per flower (15-20TL) and pollen per flower (25-30TL) tended to decline. In contrast, female flower production decreased with warming, while nectar per female flower increased in warm-grown plants (25-30TL). Temperature stress has previously been found to affect male and female function differently (Herrero, 2003). In stressful conditions, such as low moisture or high altitude, studies have observed increased production of male flowers, while less stressful conditions (e.g., adequate moisture or lower altitude) tended to favour female flower production (Freeman et al., 1981; Pickering & Hill, 2002). Female flowers can be more costly than male flowers, since females invest resources in petals, nectar, fruits, and seeds, while males invest resources in petals, nectar, and pollen (Obeso, 1997). Thus, lower male costs may promote male flower production under stressful conditions and the differential responses of floral sexes to stress may be mediated by their respective costs.

4.2 CO_2 effects

In response to elevated [CO_2], *C. sativus* plants produced more biomass, but had similar patterns of biomass allocation, A_{net}, R_D, photosynthetic capacity, and stomatal conductance to 0T plants when measured at their respective growth conditions. For floral traits, plants tended to exhibit similar trait values at both ambient and elevated [CO_2] when temperature treatments were less extreme (i.e., 0T and 4T). However, when plants were grown under more extreme warming (i.e., 8T), those exposed to elevated [CO_2] showed increased floral trait values in several instances when compared to their ambient [CO_2]-grown counterparts at the same temperature. Specifically, at 8T, elevated [CO_2] promoted greater female flower production, greater daily floral display size (25-30TL), larger male flower size (25-30TL), more pollen grains per flower, and more nectar per

plant compared to ambient [CO_2]-grown plants. Hence, the benefits of elevated [CO_2] were strongest when growth temperatures were high, and elevated [CO_2] alleviated some of the negative effects of high temperatures on *C. sativus*.

Other studies have also found mitigating effects of elevated [CO_2] at high temperatures, though most studies to date focus on growth and carbon fluxes, with few evaluating floral traits. For example, Song et al. (2014) exposed *Poa pratensis* to a range of growth temperatures (15, 20, 25, 30, and 35 °C) and either 400 or 800 µmol mol^{-1} [CO_2] and measured aspects of carbon balance. Higher [CO_2] stimulated root growth, shoot growth, and A_{net} in each temperature treatment, and also reduced the negative effects of very high temperatures (30 and 35 °C). As a result, plants grown at higher [CO_2] generally displayed greater trait values, such as root and shoot growth, under very high temperatures compared to ambient [CO_2]-grown plants. Furthermore, a meta-analysis by Wang et al. (2012) studied the effects of elevated [CO_2] on plant physiology and growth over a range of temperatures. They found that the effects of elevated [CO_2] varied with plant functional type and photosynthetic pathway, but C_3 species in particular had greater photosynthesis across a range of temperatures when grown at elevated [CO_2]. In addition, this beneficial effect of high [CO_2] was particularly noticeable when C_3 plants were grown at very high temperatures or were heat stressed. In this case, the slight recovery in trait values observed under elevated [CO_2] might be attributed to higher antioxidant activity in response to elevated [CO_2]. While antioxidant concentrations were not assessed in this thesis, high [CO_2] might improve the antioxidant defence capacity of plants by supplying more carbon for the production of antioxidant molecules (reviewed by AbdElgawad et al., 2016), thus improving growth and reproduction under heat stress.

4.3 The relative importance of climate change drivers

Across all measured variables, [CO_2] significantly affected only total biomass production, flowering onset timing, and pollen production from 25-30TL plants (Figure 4.1). On the other hand, temperature, or the interaction between [CO_2] and temperature, significantly affected the majority of variables measured (Figure 4.1). Consistent with these findings, Sallas et al. (2003) found that temperature had a greater effect on *Pinus sylvestris* and

Picea abies growth, physiology, and secondary metabolites than [CO_2]. Other studies have also found that temperature effects were stronger than [CO_2] effects (e.g., Dusenge et al., 2020; Kroner & Way, 2016). Furthermore, in their recent review, Dusenge et al. (2019) highlighted that temperature effects tend to dictate respiratory responses under future climate scenarios, and while photosynthetic responses to high [CO_2] are fairly consistent, photosynthetic responses to temperature are more variable, suggesting that temperature effects may be more important than [CO_2] when trying to predict plant responses to climate change. Similarly, my results suggest that studies focusing on the effects of elevated [CO_2] alone may not represent climate change impacts as accurately as studies considering temperature alone or those incorporating both temperature *and* [CO_2] effects.

4.4 Carbon dynamics

I expected that changes in [CO_2] and temperature would lead to changes in leaf gas exchange parameters. Instead, I found that leaf carbon dynamics (measured at growth conditions) were largely similar across the different climatic treatments. In fact, the only significant treatment effect I found on gas exchange parameters was an interaction between [CO_2] and temperature on leaf dark respiration (Table 3.1, Figure 4.1). Similar gas exchange parameter values in the different climate treatments suggest that these plants acclimated both photosynthetic and respiratory processes to changes in [CO_2] and temperature to maintain homeostasis. Although I did not explicitly measure acclimation in this study (which would involve measuring all the plants under common conditions), acclimation is very likely considering that the ratios of A_{net}:R_D were not different across the treatments despite the well-established effects of [CO_2] and temperature on photosynthesis and respiration.

Despite similarities in carbon balance, elevated [CO_2], elevated temperature, and their interaction did affect plant biomass and floral traits. This is similar to the results of Wookey et al. (1994), who found no difference in A_{net} in response to warming, but showed that *Polygonum viviparum* plants had greater reproductive investment (e.g., greater bulb weight, spike length) at higher temperatures. While this disparity could be

due to my small sample size for gas exchange, other studies on cucumbers have found significant differences in their gas exchange data with similar sample sizes to my study (e.g., Ibarra-Jiménez et al., 2008; Xiaotao et al., 2013; Zhou et al., 2011). Another possibility is that photosynthesis is not always tightly coupled with plant growth. While carbon is the primary resource that plants must allocate to maximise survival and reproduction, it is not the only resource that requires tradeoffs: water and nutrient balance also influence plant growth and reproduction (Coskun et al., 2016; Flexas et al., 2006). Changes in water or nutrient relations may, in turn, uncouple photosynthesis and growth relations. For example, Muller et al. (2011) reviewed literature on water deficits and plant carbon balance and found that water deficits often lead to swift declines in plant growth, while photosynthesis is maintained over a longer period of time, implying a mismatch in the response rates of carbon supply and demand to water stress. Similarly, in the absence of adequate nutrients, plant growth may be stunted while photosynthesis may respond more slowly (Kirschbaum, 2011). Although my plants were grown under ample water and nutrient regimes, those in the 8T treatment likely experienced greater variation in soil moisture levels due to high evaporative demand, which could have uncoupled the responses of photosynthesis/respiration and growth.

Another possible explanation for the incongruent responses between leaf carbon dynamics and floral traits is that whole plant carbon dynamics may not reflect leaf carbon dynamics, such that minor differences in carbon dynamics at the leaf level can scale up to produce detectable differences in plant traits (Way et al., 2011). In this experiment, I measured leaf net CO_2 assimilation rates and respiration rates because the majority of carbon uptake takes place in the leaves. However, other plant organs substantially influence carbon dynamics as well. Other organs may contribute to carbon fixation, for instance, reproductive structures can supply between 2 – 65% of their own photosynthetic carbon costs (Aschan & Pfanz, 2003; Bazzaz et al., 1979), and other organs contribute to respiration; for instance, stems and roots also respire (Atkin et al., 2007). Ultimately, whole plant respiration and photosynthesis are better indicators of plant carbon balance than leaf-level measurements alone.

4.5 Developmental stage

Floral traits were measured at two developmental stages to get a more representative sense of trait values at different time points. In general, trait values were reduced at the later developmental stages and traits appeared less responsive to climatic treatments later in development. For instance, at 15-20TL, the largest male flowers had a geometric mean size of 50 mm and high growth temperatures reduced this to 37 mm, a 25% decrease. However, at 25-30TL, the largest male flowers had a geometric mean size of 41 mm and high temperatures reduced this to 35 mm (average of AC and EC values at 8T), which is only a 15% decrease in flower size (Figures 5a and 6a, respectively). Other studies have also found declining floral trait values with plant age. Williams and Conner (2001) found that flower size of *Raphanus raphanistrum* in the field declined with increasing plant age and Devlin et al. (1987) found that nectar production in field-grown *Lobelia cardinalis* decreased as plants got older.

Over a plant's lifetime, environmental conditions, such as resource availability or temperature, will change, as will patterns of resource allocation and source/sink dynamics (Marshall et al., 2010). Changes in these factors could explain changes in floral traits as plants mature (Ehlers & Olesen, 2004). For example, as plants grow and use resources in their environment, reduced resource availability and corresponding effects on floral traits might be expected (Marshall et al., 2010). This effect likely explains reductions in nectar production for *Lobelia cardenalis* (Devlin et al., 1987) and the smaller flowers produced by *Raphanus raphanistrum* (Williams and Conner, 2001) at later ages when measured in the field. However, since the plants in my experiment were reared under similar nutrient regimes throughout their lifetimes, this is unlikely to explain my results. On the other hand, as plants mature, allocation to fruits and seeds (and the sink strength of these organs), as well as the cost of maintenance, may increase relative to allocation of resources to flowers (Marshall et al., 2010). As allocation to flowers declines, one might expect fewer flowers to be produced or to see a reduction in overall flower size/rewards, which is consistent with what I observed for flower size and male nectar production.

One exception to reduced trait values with plant age was display size, where 25-30TL plants produced more open flowers per day than plants at 15-20TL (Figures 3.3 and 3.2, respectively). Others have also found increased reproductive investment with aging. For example, Ehlers and Olesen (2004) found that older *Corydalis intermedia* plants produced more flowers than those that were younger under field conditions, and Carroll et al. (2001) found that *Epilobium angustifolium* produced slightly more nectar as plant age increased in the field. Generally, mature plants are more likely to have successfully reproduced than younger plants, and if a plant has been successful in setting seed, it may abort later flowers or fruits. For instance, *Vaccinium macrocarpon* produces 5-7 flowers sequentially, but only 1-3 fruits are ultimately produced (Brown & McNeil, 2006). The opposite can also be true, where plants that have not yet been successful in reproducing may invest more in reproduction later in life than they typically would. Brown and McNeil (2006) conducted an experiment using *V. macrocarpon* and found that later flowers only produced fruit when earlier flowers were unsuccessful/removed, despite ensuring adequate pollination for all flowers. In my experiment, *C. sativus* plants were grown in glasshouses without pollinators, so there was little to no chance for successful fruit production throughout the growing season, which could explain larger display size at 25-30TL. While developmental stage considerations were not a principal driver of this thesis, my results suggest that plant developmental stage may play a larger part in plant-pollinator interactions, and potentially plant carbon dynamics, than is generally considered.

4.6 Future directions

I found that the majority of floral traits measured were affected by future climate scenarios in ways that could influence plant-pollinator relationships. Compared to plants grown under current conditions (AC0T), plants grown under future climate conditions (EC8T) started to flower about one week earlier, which could affect the synchrony between *C. sativus* and their pollinators (Settele et al., 2016). The EC8T plants also produced smaller flowers and less nectar per male flower (15-20TL) than the AC0T plants, both of which are likely to increase the energetic costs of foraging for pollinators (Harder, 1986). Flower size can also alter the efficiency of pollination via the functional

fit between plants and their pollinators with resulting consequences for plant fitness (Willmer, 2011), and smaller flowers are generally less attractive to pollinators (Martin, 2004). On the other hand, I found that the number of male flowers increased with warming, which could enhance pollinator attraction, since there is some evidence that bee pollinators prefer to forage on male flowers (Huang et al., 2006). Moreover, daily display size increased when comparing current and future climatic treatments, which would likely increase plant attractiveness to pollinators as well (Hernández-Villa et al., 2020; Nattero et al., 2011).

As previously mentioned, there are many floral traits that can affect plant-pollinator relationships. This experiment tested a subset of important traits; however, plant pollinator interactions are ultimately determined by assemblages of plant-level and flower-level characteristics (Willmer, 2011). If some trait values are enhanced under climate change, while others are diminished, the consequences for pollination may be complex. For example, I found that whole plant nectar production doubled in response to climate change drivers (Figure 3.15), which, theoretically, would be beneficial for pollinators. However, if increases in nectar volume are accompanied by unfavourable changes in nectar concentration or composition, then pollinators may experience adverse effects (Shackleton et al., 2016). To better understand how climate change will influence plant-pollinator relationships, a more comprehensive approach to floral trait sampling is needed. In particular, there are few studies in the context of climate change that include nectar guides, flower colour, floral volatile organic compounds, or flower temperature in their sampled floral traits (but see Glenny et al., 2018; Koski & Ashman, 2015; Shrestha et al., 2018).

In addition to quantifying the effects of climate change on a more comprehensive set of floral traits, quantifying pollinator behaviour and survival in response to trait changes will improve our understanding of the ecological consequences of these floral shifts (Scaven & Rafferty, 2013). This is especially true because pollinators may not always respond to floral trait changes in the way we might expect. As one example, Hoover et al. (2012) looked at the response of *Bombus terrestris* to nectar produced under nitrogen enrichment, elevated [CO_2], and high temperature. They found that *B. terrestris*

individuals consumed more nectar from artificial flowers simulating the nectar collected from the high nitrogen treatments, and they also tended to visit these flowers more frequently. However, the simulated nectar from the high nitrogen treatments reduced bee lifespan (Hoover et al., 2012). In addition, despite observed changes in plant size, mean petal area, and floral display size, Glenny et al. (2018) found no significant changes in pollinator visitation rates for three out of four plant species exposed to increased [CO_2] and drought.

Several studies have assessed the effects of [CO_2] or temperature on nectar independently of pollen (e.g., Dag & Eisikowitch, 2000; Erhardt et al., 2005; Hoover et al., 2012; Jakobsen & Kritjánsson, 1994; Lake & Hughes, 1999; Mu et al., 2015; Takkis et al., 2015, 2018). However, thus far, I am aware of only one other study that has looked at *both* pollen and nectar resources from the same species in the context of climate change, and these researchers focused on temperature and drought effects rather than temperature and [CO_2] (Descamps et al., 2018). Social pollinators often specialize on a particular task and, in the case of bees, an individual may specialize on foraging for pollen *or* nectar during a particular foraging bout (Russell et al., 2017). As a result, an individual bee may not need to evaluate both pollen and nectar in the same foraging bout. However, pollen and nectar may still be collected from the same plant, or different plants of the same species. Since notable pollinators, like bees, require adequate quantities and quality of *both* pollen and nectar to grow and reproduce (Nicolson, 2011), considering changes in both pollen and nectar in response to climate change may be more critical than evaluating changes in either resource alone.

The consequences of climate change are expected to be pervasive and numerous. In addition to [CO_2] and temperature changes, models predict rising sea levels, ocean acidification, and increased frequency of extreme weather events (Cubasch et al., 2013). While this thesis addressed the consequences of elevated [CO_2] and temperature, which are widespread climate change drivers, plant exposure to extreme events, such as heatwaves, could prove to be more important in shaping plant-pollinator interactions than sustained growth under higher temperatures or [CO_2]. For instance, based on the results of this study and previous work, flower production increases when plants are grown at

higher temperatures (Nakamura et al., 2016; Pau et al., 2013; Zheng et al., 2002). However, when plants are exposed to short-term bursts of heat mimicking heatwave conditions, flower production is reduced (Orsenigo et al., 2014; Suraweera et al., 2020). Thus, evaluating floral trait responses to sustained elevated [CO_2] and temperature, in addition to extreme events, could prevent underestimating climate change impacts on flowers.

While I did not evaluate the effects of increased [CO_2] and temperature on *C. sativus* yield, I did find that high temperatures reduced female flower production (Figure 7b). In addition, I did not find that elevated [CO_2] counteracted these female flower declines. Since female flowers are fruit producers, declining female flower numbers with warming could mean that cucumber yields will be reduced with climate change, which would be detrimental for producers. However, considering that the variety used in this experiment is monoecious, and that fruit weight and quality were not evaluated, these results should be interpreted with caution. A 2018 review on the effects of climate change on vegetable production highlighted that there are surprisingly few studies focusing on this area of research, although the independent effects of temperature and [CO_2] have received attention (Bisbis et al., 2018). Thus, this is a promising area for future exploration.

4.7 Conclusions

Leaf carbon dynamics were largely homeostatic across an 8 °C growth temperature range and a 350 ppm difference in [CO_2], and these carbon dynamics were uncoupled from growth and floral trait measurements, potentially due to different rates of response between photosynthesis and growth (Muller et al., 2011). Despite this, future climate scenarios still affected floral traits of *C. sativus* in ways that could alter their relationship with pollinators. Specifically, temperature generally produced negative effects on floral traits, including smaller flowers, less nectar per flower (males 15-20TL), and accelerated flowering onset. This suggests that higher temperatures may be detrimental to plant-pollinator interactions in the future. For instance, smaller flower size reduces plant advertisement to pollinators, and also has the potential to alter the efficiency of pollination and the cost of foraging (Willmer, 2011). On the other hand, higher [CO_2]

facilitated a recovery of some trait values, which might be beneficial for pollinators and alleviate some of the negative effects of warming. For instance, whole plant nectar production doubled in the EC8T treatment compared to AC0T. However, the beneficial effects of [CO_2] only occurred when warming was extreme and were not consistent across the measured traits, suggesting more work is needed to evaluate these [CO_2] effects.

Additionally, temperature (or the interaction between [CO_2] and temperature) had greater consequences for plant traits and physiological parameters than [CO_2] alone, suggesting that temperature effects may dominate plant responses to climate change. The treatments also affected male and female flowers differently, potentially due to the distinctive costs of male and female function, with females typically requiring increased resource investment (Obeso, 1997). In addition, plant developmental stage influenced floral trait values and responses to the treatments, with more mature plants generally showing lower trait values, and less response to the climatic treatments. These results indicate a need for increased sampling over the lifetime of plants to get a better sense of variation in floral traits and carbon dynamics as plants age.

Future studies focusing on a wider range of floral traits, as well as pollinator responses to these traits under climate change, are needed to allow researchers to make more informed predictions about the effects of climate change on plant-pollinator interactions. In particular, more studies evaluating the effects of climate change on the quantity and quality of *both* pollen and nectar resources from the same species are needed to determine how these resources change in tandem, since both are important food source for bee pollinators, and they may be gathered from the same species. Finally, considering the effects of extreme climatic events, such as heatwaves, in addition to chronic climatic changes will be important for developing a more complete picture of crop floral responses to climate change, since plant responses to prolonged climatic changes likely differ from short-term responses.

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Curriculum Vitae

Name:	Sarah Josina McDonald
Post-secondary Education and Degrees:	University of Guelph Guelph, Ontario, Canada 2014 – 2018 Hons. BSc. With distinction.
Honours and Awards:	NSERC Alexander Graham Bell Canada Graduate Scholarship 2019 – 2020 Dr. Joy Dickson-Clark Ontario Graduate Scholarship 2020 Queen Elizabeth II Graduate Scholarship for Science and Technology 2018 – 2019 (offered 2019 – 2020) Botanical Society of America Young Botanist Award 2018 Monroe Landon Memorial Scholarship (for interest in native flora and field biology) 2018 Dean's Honours List 2014 – 2018 NSERC Undergraduate Research Award 2017 University of Guelph Entrance Scholarship 2014
Related Work Experience:	Teaching Assistant University of Western Ontario 2018 – 2020 Undergraduate Research Assistant University of Guelph 2017 Research Assistant

Ontario Ministry of Agriculture, Food, and Rural Affairs
2015, 2016

Presentations:

McDonald, S., & Way, D. A. Climate change effects on floral traits and carbon dynamics of cucumber: Potential consequences for a plant-pollinator mutualism. (Presentation) *Canadian Botanical Association Meeting*, Online, Canada, 2020

McDonald, S., & Way, D. A. Climate change effects on floral traits and carbon dynamics of cucumber: Potential consequences for a plant-pollinator mutualism (Poster) *Canadian Society of Plant Biologists Eastern Regional Meeting*, St. Catherine's, Ontario, Canada, 2019

McDonald, S., & Way, D. A. How will climate change affect nectar and pollen quantity and quality in an economically important crop? (Poster) *Plant Cell and Environment 40th Anniversary Symposium*, Glasgow, Scotland, 2019. *Biology Graduate Research Forum*, London, Ontario, Canada, 2019. *Canadian Society of Plant Biologists Eastern Regional Meeting,* London, Ontario, Canada, 2018.

Publications:

Duarte A. G., Dusenge, M. E., McDonald, S., Bennett, K., Lemon, K., Radford, J., & Way. D. A. (In press). Photosynthetic acclimation to temperature and CO_2: The role of leaf nitrogen. In *Photosynthesis, Respiration, and Climate Change*. Springer.

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