Warmer climatic conditions affect squash growth, pollination, and production

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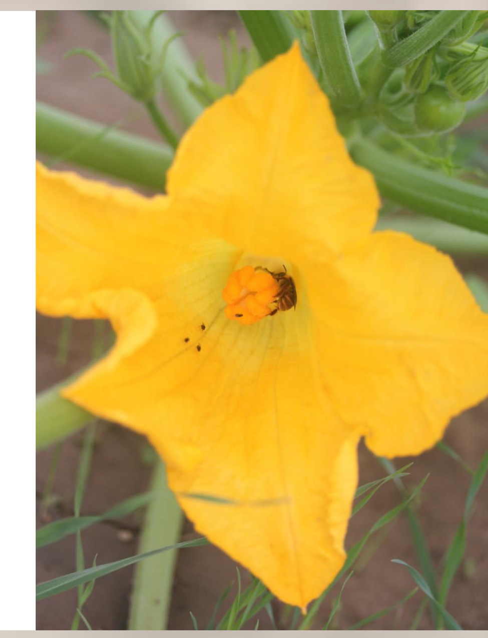

Introduction

Human-induced climate change threatens the current and future environmental stability of our planet. The first decade of the 21st century was the warmest on record (Hartmann et al. 2013). Global temperatures continue to escalate (NRC 2010), with more frequent occurrence of high temperature extremes (Collins et al. 2013).

The southwestern United States represents a hot spot for these climate effects (Diffenbaugh et al. 2015). Anthropogenic warming has increased soil moisture deficits in the California dry season, leading to an increased likelihood of intense drought throughout the 21st century (Diffenbaugh et al. 2015). What do these changes in climate suggest for important California food crops?

Although studies have investigated how modified physical conditions affect wind-pollinated plants (Lobell et al. 2011), few analyses examine similar effects in insect-pollinated crops (Rader et al. 2013). Disturbances such as colony collapse disorder and habitat fragmentation currently threaten bees, the main pollinators of the 70% of food crops pollinated by animals (Gallai et al. 2009). Human-induced climate change has the potential to escalate these issues. By modifying floral resources, warming could impact rates of pollinator visitation and outcrossing pollination. Diminished visitation subsequently increases the likelihood of pollen limitation in plants.

This study investigates how climate warming affects squash (*Cucurbita pepo*) crops. *C. pepo* is a model, bee-pollinated system because of its conspicuous floral advertisements, abundant floral resources, and obligatory pollination by bees (Figure 1).

Figure 1. A specialist pollinator, the squash bee (*Peponapis pruinosa*), as well as generalists like the honey bee (*Apis mellifera*), both visit squash (*C. pepo*). *P. pruinosa* visit flowers during the early morning hours before generalists arrive and efficiently collect the squash's heavy pollen grains, which they require for reproduction. A pollen-covered *P. pruinosa* (left) sits atop the anthers of a male squash flower. *A. mellifera* (right) sit below the female flower's stigma, gorging on nectar.

Project Goals

This study researches how climate warming affects the floral advertisements, such as flower size, and the floral resources, such as pollen mass, important to pollination in *C. pepo*. For this experiment, we determine how changes in floral traits lead to changes in bee pollination, and ultimately alter fruit production.

In order to test the effects of warming on plants, the project goals are:

- To measure differences between warmed and control plants in flower timing, flower number, flower size, and floral sex ratio.
- To measure differences between warmed and control plants in nectar volume and concentration, and pollen mass and viability.
- To measure differences between warmed and control plants in bee visitation and pollination.
- To measure differences between warmed and control plants in pollen limitation.
- To measure differences between warmed and control plants in fruit yield per plant and seed yield per plant.

Figure 2. June-September 2015 experimental set-up at the UC San Diego Biology Field Station. Control and experimental Honey Bear acorn squash (*Cucurbita pepo*) plants were interspersed in the field. Passive, open-top warming chambers surrounded experimental plants. Temperatures at individual plants were monitored using temperature loggers housed inside PVC pipes (circled in red).

Materials and Methods

We grew Honey Bear acorn squash (*C. pepo*) in the field under ambient (n=20 plants) and elevated (n=20 plants) temperatures at the University of California San Diego Biology Field Station. Plants in the elevated temperature group were grown inside passive, open-top warming chambers (Figure 2). We continually monitored plants for temperature and volumetric water content. Once flowering, we sampled plants daily for: flower number, sex, and size; nectar volume and concentration; and pollen mass and viability. Each day we monitored bee pollination of either the warmed or control plants by bagging (excluding bees) from the opposite plant group. Bee pollination surveys were conducted five times per day for 15 minutes each. We also videotaped detailed pollination behavior in open flowers. Once fruits matured, we harvested and weighed them, as well as counted and weighed their developed seeds.

Results

Warming chambers elevated mean daily temperature by 2.0˚C (two-sample *t*-test: t_{26}=11, P<<0.001) and mean maximum temperature by 5.0˚C (t_{27}=9.01, P<<0.001). However, in order to counteract potential drying effects of the chambers, warmed plants were watered more than control plants, causing a significance increase in volumetric water content in the soil surrounding warmed plants (t_{45} = 2.7, P < 0.01). Consequently, the warmed plants were actually the warmed, more irrigated plants (i.e. "warmed/wet plants"). The warmed/wet plants produced significantly more flowers (t_{28} = 6.3, P << 0.001), significantly larger flowers (t_{91} = 3.8, P < 0.001), significantly higher mean nectar volume (t_{93} = 2.3, P < 0.05), and significantly higher mean pollen mass (t_{39} = 6.2, P << 0.001) per plant. In the warmed/wet plants, the mean time spent by *A. mellifera* drinking nectar from female flowers was significantly higher than the mean time spent by *P. pruinosa* (t_{15} = -4.4, P <<0.001) (Figure 3). On the other hand, the mean time spent by *P. pruinosa* contacting female stigmas in warmed/wet plants was significantly higher than the mean time spent by *A. mellifera* (t_{11} = 2.2, P < 0.05) (Figure 4). These effects were not observed in control plants. Ultimately, the warmed/wet plants produced significantly higher mean fruit yield per plant (t_{34} = 2.8, P < 0.01) (Figures 5 and 6).

Conclusions

The warmed plants becoming the warmed/wet plants affected the results so that we cannot determine if the effects observed occurred simply because of warming, watering, or both. In any case, these results do show that imposing changing climatic conditions on the *C. pepo* system affects flower advertisements and resources. Moreover, these changes influence the visitation of specialist and generalist pollinators, but in different ways. Ultimately, these changes alter rates of fruit production in squash plants.

Figure 6. Mature fruit of Honey Bear acorn squash (*Cucurbita pepo*). Fruit took 45-55 days from stigma pollination to reach full maturity. Mature fruit were harvested and weighed, and their seeds were counted and weighed.

Future Goals

This summer, we are taking the next step of this project by conducting a fully-crossed, two-way factorial temperature x precipitation manipulation experiment on the *C. pepo* system. This experiment will investigate how the climatic forces of warming and drought interact to affect this valuable crop and its bee pollinators. This research will shed light on the agricultural effects of climate variation already occurring in Southern California and throughout the globe.

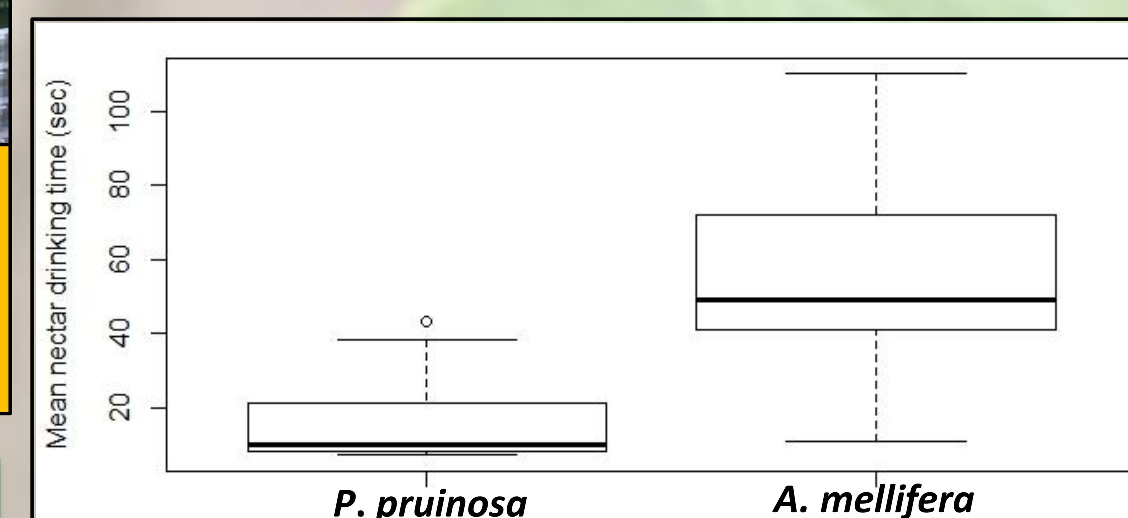

Figure 3. Mean time (seconds) per plant bees spend drinking nectar in warmed/wet female flowers. *A. mellifera* spend significantly more time (mean = 56s) drinking nectar than *P. pruinosa* (mean = 17s) (t_{15} = -4.4, P < <0.001).

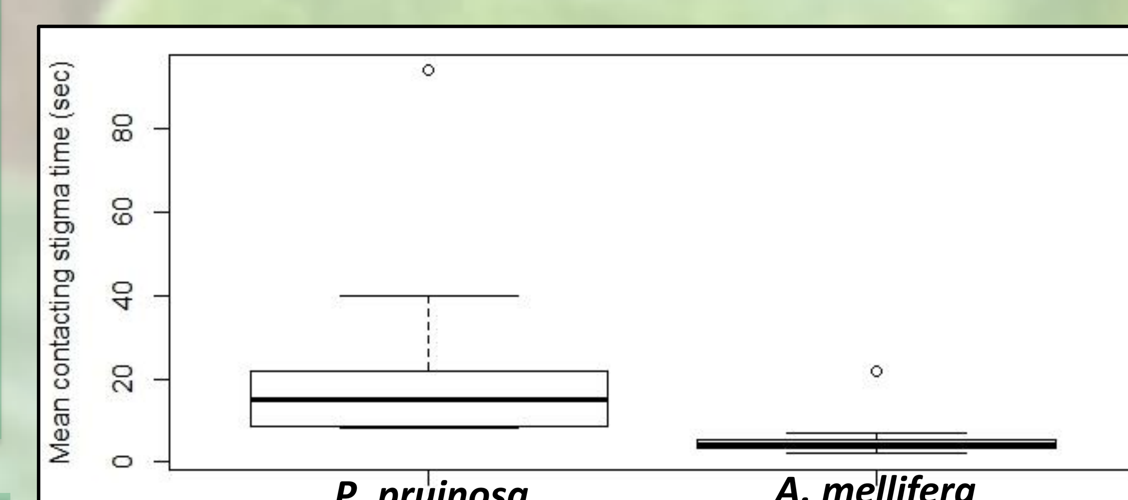

Figure 4. Mean time (seconds) per plant bees spend contacting the stigma in warmed/wet female flowers. *P. pruinosa* spend significantly more time (mean = 23s) contacting the stigma than *A. mellifera* (mean = 5.8s) (t_{11} = 2.2, P < 0.05) .

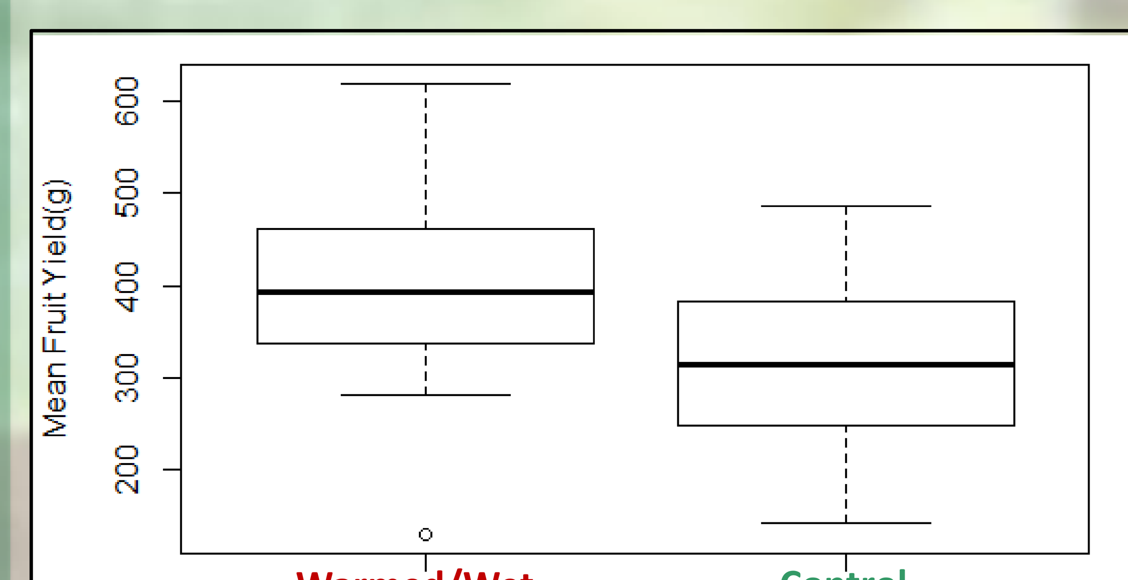

Figure 5. Mean fruit yield (grams) per plant in warmed/wet plants (mean=400g) verses control plants (mean=314g) (t_{34} = 2.8, P < 0.01).

Acknowledgements

We gratefully acknowledge the valuable advice of UCSD professors Dr. James Nieh, Dr. Josh Kohn, and Dr. Elsa Cleland. We would like to thank the rest of the Holway Lab for their support, as well as Dr. Laurie Smith and Miguel Vasquez of the UCSD Biology Field Station. This work would not have been possible without the assistance of many undergraduate researchers and volunteers: Michelle Dewey, Audrey Lunde, Jillian Schat, Taruc Alvarez, Jeremy Warner, Jocelyn Chang, Brandie White, Danielle Burner, Madie Schneider, Joseph Galm, Jaimie Choi, Kelsea Eriksen, Nicole Orsi, Elvis Salado, Alexis Cugini, and Kim Shin. This research was supported by the UC CNI Fellowship, the Messier Memorial Fund Fellowship, and the NIH CMG Training Grant.

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