Within-season effects of climate variability on leafhopper abundance and shoot growth in tea fields

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# Introduction

Notes:

I need to justify the focus on within-season variability 1)as being important on its own (see Baker et al 2015) and 2) as a way of getting field-realistic effects of temperature on leafhopper population dynamics. For 1) I can talk about how leafhoppers are multivoltine with a short life cycle, so warm temps earlier on could be more beneficial than warm temps later, for example. Cite Tobin and MacGregor and Bale and Berggren. Warm temps are good for insect vital rates, phenology driven by combination of temp and photoperiod predicted to result in longer/earlier growing seasons and increased range in altitude/latitude for multivoltine insects. For plants, high temps are less good. Effects of precipitation are less clear. For 2) I should introduce growth chamber studies and point out that air temps regularly go above these temps in the field—growth chambers don’t have any microclimactic variation. Not much known on importance of climate for vital rates at different life stages.

1. climate change is real

The years between 2010 and 2019 represent the warmest decade on record [CITATION]. There is consensus that this warming is caused primarily by anthropogenic release of CO2 into the atmosphere [CITATION]. We have also seen global changes in precipitation regimes over the past century [CITATION], with wet regions getting wetter and dry regions getting drier, and the frequency of extreme weather events such as droughts is increasing.

2. effects on insects

Climate change is predicted to have diverse effects on organisms and ecosystems that vary by species and geography [CITATION]. Increasing mean temperature is expected to increase the growth of many groups of insect herbivores (Bale et al., 2002), and to increase the latitudinal ranges and populations of some agricultural pests (Bebber et al., 2013; Macgregor et al., 2019; Porter et al., 1991). Warming has resulted in an increase in herbivory and crop damage over time (Deutsch et al., 2018; Meineke et al., 2018). Multivoltine insects, in particular may benefit from warming, as longer growing seasons allow for more generations and greater potential population growth (Bale et al., 2002; Tobin et al., 2008).

Changes in precipitation have less predictable effects on insect populations, partly due to limited research relative to the effects of temperature. In dry places, where desiccation may be a significant source of mortality for insects, increase precipitation may result in increases in herbivore populations (citation). In wet places, increases in precipitation may have negligible effects on plants, which are not water limited, and may increase mortality in herbivores due to infection by entomopathenogenic fungi (citation).

3. relative effects on plants, crops

4. effects on interactions (direct like insects/young leaf; indirect due to changes in plant chem, tritrophic interactions)

Temperature can act on relative growth rate of plants and insects to alter insect distribution and abundance. If host plant growth is too slow due to cold temperatures, or if leaf development is too fast due to high temperatures, there may not be enough young leaf tissue to support herbivores (Bale et al., 2002).

Climate change has the potential to alter species interactions (citations). The interactions between plants and herbivores are especially important for reasons… Alterations in herbivore—plant interactions can stem from or result in changes in plant chemistry at a population or even landscape level (Hunter). Climate change is predicted to affect plants and herbivores differently. For example, insect herbivores are predicted to have higher temperature optima for vital rates than their host plants (Berggren et al., 2009), which result in reduced growth of plant tissue and increased growth and activity of herbivores as temperature warm, compounding to increase herbivore density (e.g. insects per young leaf). Changes in precipitation can also alter the ability of plants to respond to herbivory with induced defenses (Scott et al., 2019).

In addition to the direct effects of climate change on plant chemistry, changes in herbivore density have quantitative and qualitative effects on plant defensive chemistry. For example, an increase in tea green leafhopper density resulted in complex, non-linear changes in induced tea plant secondary metabolites resulting in a change in metabolite blend in addition to overall increased secondary metabolite production (scott et al). Changes in metabolite blend can have important consequences for multiple trophic levels. For example, parasitoids (citations) and even hyperparasitoids (citation) can use plant metabolite blend to infer host density and parasitism status, altering their oviposition decisions. [landscape-scale example from Hunter]

Plant secondary metabolite blends are also important in some agricultural systems, where they are the prime determinants of crop quality. Tea quality, for example, is determined primarily by the concentrations and composition of volatiles, catechins, methylxanthines, and amino acids. In some tea cropping systems, metabolite blend can be more important than crop yield, resulting in farmers sacrificing yield to maximize quality in a number of ways (Ahmed et al., 2014; Cho et al., 2007; Saijo, 1980). One strategy unique to tea originates in northern Taiwan and involves farmers allowing and encouraging tea green leafhopper (*Empoasca onukii*) damage in order to induce secondary metabolite production (Cho et al., 2007). *E. onukii*, like other *Empoasca* species, feeds by rupturing cells and ingesting fluids (Backus et al., 2005; Jin et al., 2012). This causes chlorosis, stunting, thickening, and curling of leaves, and in severe infestations can cause necrosis at leaf margins and early leaf abscission—a set of symptoms collectively referred to as “hopperburn”. *E. onukii* is generally considered a pest and can reduce tea yields up to 20% (citation). However, some tea farmers encourage E. onukii infestations because of the volatiles induced uniquely by leafhopper damage (Zeng et al., 2019). E. onukii is highly multivoltine, having 9-15 generations per summer in the warmest parts of its range (citation). Previous lab studies have shown that development and generation time are reduced under warmer conditions in related species (citations). Within-season temperature was shown to have a greater impact on infestation severity than day of arrival in a related migratory leafhopper pest, *Empoasca fabae* (Baker et al., 2015). Therefore, there is the potential for within-season climate variablitiy to have an impact on leafhopper population. In addition, climate may affect shoot growth of tea plants. Young shoots are not only the unit of harvest, but also the preferred feeding sites for E. onukii (citation), so changes in shoot elongation must be considered together with E. onukii population in order to understand changes in functional density.

# Materials and Methods

The study was conducted at Shanfu Tea Company in Shaxian, Sanming Prefecture, Fujian Province, China (latlong, elevation ~ 200m) from June 5 to July 22, 2017. Two adjacent fields planted with the same tea cultivar (Tie Guan Yin) were used for this experiment. Tea plants in both fields were of similar age (ca. 30 years, according to the farm manager). In each field, we labeled 10 plants chosen randomly by using a random number generator to create combinations of row number and % distance into the row from the road to the edge of the field. Each day at around 6:00am, we counted tea green leafhoppers (*Empoasca onukii*) on the undersides of the second leaf from the apical meristem of haphazardly chosen shoots on these plants. At the beginning of the summer, we counted leafhoppers on 30 leaves, but switched to counting 50 leaves on June 24th. Leafhopper counts were performed by three observers and observer ID was recorded to use as a covariate. Leafhopper counts were collected every day from June 5 to July 24 on both fields. We allowed the tea farm to operate as usual in these fields and they were harvested several times during the experiment. Field A was harvested on June 28, July 8, and July 22. Field B was harvested on June 8, July 13, and July 24. Each combination of field and inter-harvest period experienced a unique weather history and is treated like a blocking factor.

Shoot growth was assessed using the same plants. Seven actively growing shoots (defined by having an expanding leaf at the meristem) per plant were labeled below the second leaf. Each day, the length of the shoot was measured from the node immediately above the label to the shoot tip. When harvested, tea pickers pluck two leaves and a bud and pluck all tea plants in the field, including the plants we labeled. Therefore, after each harvest, new shoots on the same plants were selected and measured daily as described above until the next harvest.

A temperature sensor and datalogger (model, HOBO, city) was installed between the two fields on a stake at the height of the tea canopy in a shade thingy. Datapoints were taken hourly, and later averaged to get mean daily temperatures. Precipitation was measured using a simple rain gauge (model, company, city) between (dates). Rain gauge data was not available before June 20. We compared our on-site data to local weather station data we obtained for June and July. The precipitation data was significantly correlated (Pearson’s r = 0.63, df = 32, p < 0.001), and the weather station data covered a greater time range, so we used the station data for further analyses.

## Distributed Lag Non-Linear Models

We assessed the effects of temperature and precipitation on tea shoot growth rate (daily change in shoot height in cm) and leafhopper numbers. Because the effects of weather may be delayed, we used a distributed lag non-linear model (DLNM)(Gasparrini et al., 2017). Because weather is likely to be autocorrelated through time, using lagged weather (e.g. temperature one day ago, two days ago, etc.) as independent predictor variables would result in overfitting (Teller et al., 2016). DLNMs model potentially delayed effects of predictor variables by fitting a bi-dimensional dose-lag-response association kernel where the effect of a predictor can vary non-linearly through lag time and across predictor intensity (Gasparrini et al., 2017). These bi-dimensional kernels were constructed using a cross-basis function provided by the dlnm package in R (Gasparrini, 2011) with a maximum lag effect of 15 days, the mean survival time for female *E. onukii* individuals in the field reported by Shi et al. (2015). Only data points with at least 15 days of weather history were retained (June 16 and onward). Penalized cubic regression splines were used for both dimensions with 5 knots for the response dimension and 7 knots for the lag dimension. These two-dimensional splines were then included as predictor variables in generalized additive models (GAMs) using the mgcv package in R (Wood, 2017). Preliminary analyses revealed high concurvity between the temperature and precipitation cross-basis functions. To avoid unstable estimates, we fit separate models for precipitation and temperature and compared them with AIC to determine which weather variable better explained the response. Linear shoot growth rate, *r*, was calculated as the difference between height on the day measured and height on the previous day. Growth was modeled as:

Where *a* is the intercept, *f(W, lag =* ***15****)* is the cross-basis function for either temperature or precipitation, *f(dayph)* and *f(dia.)* are a penalized cubic splines for the effect of number of days post-harvest and stem diameter, respectively, and *re(harvest)* and *re(plant)* are random effects of the harvest/field blocking factor and the plant ID within each field. We used a scaled t family error distribution because residuals followed a leptokurtic gaussian distribution when a gaussian family error distribution was used.

For leafhopper counts, we used the following model:

Where *H* is number of leafhoppers per plant with an offset of *L*, number of leaves sampled per plant. Predictor variables are the same as defined above with the addition of observer as a random effect to account for differences in detection probability among the three researchers who collected leafhopper count data. This GAM was fit using a Poisson family error distribution with a log link.

In addition to the model above using leafhopper density as a response, we also calculated a linear rate of change in leafhopper density () and used it as a response variable in a gaussian family GAM with an identity link using the same predictors as above, but without the offset.

# Results

For plant growth, the temperature model had a lower AIC than precipitation (dAIC = 8.8). Diameter had a significant, nearly linear effect on growth with wider shoots growing faster (edf = 2.6, p < 0.001)(fig 1a). Day post harvest also had a significant effect on growth with the highest growth rate at about day 10 with declining growth after that (edf = 2.8, p = 0.032)(fig1b). Lagged temperature also had a significant effect on growth (edf = 9.3, p < 0.001). Temperature effects were mostly immediate, with negligible effects of temperature lagged past 5 days (fig2). Cooler temperatures were detrimental to shoot growth with the lowest predicted growth rate of 0.26 cm/day occurring at 20.1ºC on the day of measurement. Higher temperatures resulted in increased shoot growth with the highest predicted growth rate of 0.35 cm/day occurring at 27.35ºC on the day of measurement.

A close up of a map

Description automatically generated

In the precipitation model, the diameter and day post-harvest co-variates had a similar relationship with shoot growth, although only diameter was statistically significant (diameter: edf = 2.6, p < 0.001; day post-harvest: edf = 2.5, p = 0.436). Precipitation had a negative effect on plant growth with little evidence of delayed effects (fig2). The lowest growth predicted by this model (keeping other parameters average) was 0.29 cm/day at 83.5 mm rainfall at 0 days lag. The highest growth was 0.46 cm/day at 27.9 mm rainfall at 8 days lag.

A close up of a map

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Leafhopper density

For leafhopper density, the precipitation model had a lower AIC than temperature (dAIC = 15.2). In this model, post harvest had no significant effect on leafhopper density (edf = 0, p = 0.769). Precipitation had a significant effect on leafhopper density (edf = 10.8, p < 0.001). High precipitation on the day of measurement had a positive effect on leafhopper densities (fig 3). For example, 83.5mm of precipitation at a lag of 1 day corresponded to the maximum predicted leafhopper density, 0.07 leafhoppers per leaf. On the other hand, there was a delayed effect of very low precipitation on leafhopper counts, with the strongest effects between 3 and 14 days prior to measurement. The lowest predicted density was 0.036 leafhoppers/leaf occurring at 0 mm rainfall with 15 days of lag.

A screenshot of a cell phone

Description automatically generated

The temperature model for leafhopper density also showed no significant effect of days post harvest (edf = 0, p = 0.521). Temperature had a significant effect on leafhopper density (edf = 7.0, p < 0.001). High temperatures had detrimental effects on leafhopper densities and there was evidence for delayed effects of temperature as well (fig\_\_\_). The highest leafhopper density predicted was 0.05 leafhoppers/leaf occurring at 20.15 ºC with 9 days lag (holding other parameters average). The lowest predicted density was 0.04 leafhoppers/leaf at 31.25 ºC with a 15 day lag.

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Leafhopper growth rate

If instead we used the linear rate of change in leafhopper density as a response variable, there was no significant effect of temperature, precipitation, or days post harvest (all p > 0.280).

# Discussion

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