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

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# Abstract

(to write)

# Introduction

The years between 2010 and 2019 represent the warmest decade on record (NOAA, 2020). There is consensus that this warming is caused primarily by anthropogenic release of CO2 into the atmosphere (Cook et al., 2016). ﻿In addition to elevated mean temperatures, the variability of climate within years has increased. For example, the frequency of extreme events such as heat waves and precipitation anomalies have increased over the last century (IPCC, 2007). These changes are predicted to have diverse effects on organisms that vary by species and geography (Bale et al., 2002). Because insects are poikilotherms, changes in temperature are particularly likely to affect insects directly by altering metabolic rates (Bale et al., 2002). For example, an increase in 10 ºC results in roughly a doubling of insect metabolic rates across the range of regularly experienced temperatures (Bale et al., 2002; Berggren et al., 2009). Therefore, increasing mean temperature is expected to increase the vital rates and populations of many groups of insect herbivores (Bale et al., 2002; Berggren et al., 2009; Porter et al., 1991), 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 a documented increase in herbivory on herbarium specimens (Meineke et al., 2018) and crop damage (Deutsch et al., 2018) over time.

Changes in precipitation, on the other hand, are less uniform across the globe, with some regions seeing increases in precipitation and others seeing relative decreases (IPCC, 2007). In addition, the predicted effects on insect populations are less clear, partly due to limited research relative to the effects of temperature (Bale et al., 2002). Precipitation may moderate the impacts of temperature through changing humidity. Dry conditions can lead to increases in insect mortality due to desiccation, so in dry habitats, increased precipitation may result in increases in herbivore populations (Beirne, 1970). Espeset et al 2016 found that monarch butterflies benefitted from warm, humid springs in California However, precipitation and increased humidity can also favor the spread of entomopathogenic fungi, which could reduce insect herbivore densities (Goettel and Glare, 2010).

[paragraph on increased variability in weather]

The temperature optima of insect herbivores and their host plants can differ (Berggren et al., 2009). Although some degree of warming may improve plant growth, insect populations are predicted to benefit more from high temperatures than their host plants. At high temperatures that are beneficial to herbivores, plants are likely to experience increased respiration and decreased photosynthetic efficiency due to photorespiration, thus decreasing their growth rate relative to their insect herbivores (Berggren et al., 2009). Because many herbivores feed exclusively on developing plant tissue, high temperatures may increase herbivory as a combined function of increased herbivore densities and either increased rates of leaf maturation or decreased plant growth, both of which would reduce availability of young leaves (Bale et al., 2002; Berggren et al., 2009)..

For many organisms it is difficult to study effects of climate change on abundance because they have long lifespans. However, multivoltine insects may offer an opportunity to study the effects of changes in temperature and precipitation over a shorter time scale. Multivoltine insects complete multiple generations per season, with each generation experiencing a unique climate history. Multivoltine insects are predicted to benefit from climate change because of the potential to add additional generations due to advancing phenology (Bale et al., 2002; Kerr et al., 2019; Macgregor et al., 2019; Tobin et al., 2008). However, weather conditions within a year may affect the abundance of multivoltine insects independently from mean yearly trends in temperature and precipitation. For example, infestation severity on crops by the migratory, multivoltine, polyphagous crop pest, the potato leafhopper (*Empoasca fabae*) is less affected by advancing phenology caused by yearly warming than by within season temperatures(Baker et al., 2015). [DIRECTION OF EFFECT? HIGH TEMPS = MORE HOPPERS?]. By aggregating measures across a growing season (and therefore multiple generations) we lose information on responses to weather at a time scale more appropriate to multivoltine insects.

[Different life stages effected differently? Why are we looking for lagged effects?]

[sentences about how insect herbivory not only effects plants through consumptive effects, but also through induced changes in metabolite profiles]. 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 valuable 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 damage by the tea green leafhopper (*Empoasca onukii*) 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% (Fu et al., 2014). However, in late summer when tea quality generally declines, *E. onukii* infestations can be beneficial to some tea farmers because of the volatiles induced uniquely by leafhopper damage (Zeng et al., 2019). One such tea produced from leafhopper attacked plants is known as Eastern Beauty oolong (东方美人, dongfang meiren) (Scott and Orians, 2018). Eastern Beauty oolong originated in Taiwan but is now produced in some other tea-growing regions of Asia where *E. onukii* is a common pest. This type of tea is produced in the late summer when leafhoppers are abundant and tea quality would otherwise be low, offering farmers a way to increase their income while reducing insecticide inputs. *Empoasca onukii* is highly multivoltine, having 9-15 generations per summer in the warmest parts of its range (Fu et al., 2014), and leafhopper vital rates are influenced by temperature (Reineke and Hauck, 2012). Therefore, there is the potential for within-season climate variability 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.

Here we present an observational study performed at a tea farm in Fujian Province, China that produces Eastern Beauty oolong when leafhopper herbivory is high enough in the late summer. We tracked leafhopper population density and tea shoot growth in tea fields and modeled their responses to recent temperature and precipitation.

# Materials and Methods

The study was conducted at Shanfu Tea Company in Shaxian, Sanming Prefecture, Fujian Province, China (26°25'04.1"N 117°44'56.8"E, elevation ~ 200m) from June 5 to July 22, 2017. Two adjacent fields (hereafter A and B) planted with the same tea cultivar (铁观音, 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). Field A was on a slope facing north-east and Field B faced south and south-west. In each field, we labeled 10 randomly chosen plants. Each day at 6:00am, we counted tea green leafhoppers (*Empoasca onukii*) on the undersides of the second leaf from the apical meristem of 30 or 50 haphazardly chosen shoots on these plants. *E. onukii* is the only common leafhopper pest on tea (Mao et al., 2014). At the beginning of the summer, we counted leafhoppers on 30 leaves per plant, but increased our search effort to 50 leaves per plant on June 24th. Leafhopper counts were performed by three observers and observer ID was recorded along with the count data. Leafhopper counts were collected every day from June 5 to July 24 on both fields. The tea farm operated 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 (hereafter “harvest”) experienced a unique weather history and is treated as a blocking factor.

Shoot growth was assessed using the same plants. Seven actively growing shoots per plant were labeled below the second leaf. “Actively growing” was defined as having an expanding leaf at the apical meristem. Each day, the length of the shoot was measured from the node immediately above the label to the shoot tip. When fields are harvested, young shoots are plucked from all 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. Shoot diameter was measured at the beginning of each harvest period to use as a covariate. Because our study began only three days before the first harvest of Field B, we excluded this first inter-harvest period from analyses of shoot growth.

A temperature sensor and datalogger (HOBO 8k Pendant® temperature data logger, Onset Computer Corporation, Bourne, MA, USA) was installed between the two fields on a stake at the height of the tea canopy in a solar radiation shield (Onset Computer Corporation). Air temperature was logged hourly, and later averaged to get mean daily temperatures. Precipitation was measured using a simple 500 mm rain gauge (model, company, city) between June 20 and July 23. 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 counts per leaf. We were interested in accounting for potentially delayed effects of weather, but 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. Furthermore, the choice of how to discretize lag (days, weeks, etc.) is arbitrary. Instead of including parameters for every unit of lag as an independent predictor, we can model the delayed effects of weather with fewer parameters by fitting a curve. The effects of weather may decay linearly over time, so rather than choosing a kernel (e.g. exponential or gaussian) a priori, we can model the effects of lag as a spline (Gasparrini, 2011; Teller et al., 2016). Distributed lag non-linear models (DLNMs) model potentially delayed effects of predictor variables by fitting a bi-dimensional dose-lag-response association spline where the effect of a predictor can vary non-linearly through lag time and across predictor intensity (Gasparrini, 2011; 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 (Wood, 2008, 2017) (Figure S1). To avoid unstable estimates resulting from this concurvity, we fit separate models for precipitation and temperature. We report results of both models and compared them with AIC to determine which weather variable better explained the response.

Penalized cubic regression splines were used for modeling the cross-basis functions for weather as well as covariates. Penalization favors more linear shapes such that unless the data supports non-linearity, the resulting fitted relationship will be linear. Effective degrees of freedom (edf) represent the degree of non-linearity of the penalized spline and are reported for each predictor. For example, edf = 0 is equivalent an intercept only, edf = 1 is a linear relationship, and edf = 2 is a quadratic relationship.

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 ln(*L*), number of leaves sampled per plant, to account for variation in sampling effort and to put the expected values in units of leafhoppers per leaf. 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.

# Results

Mean precipitation (± standard deviation) was 7.37 ± 12.29 mm with 68% of the days having some rain (Figure 1A). The mean temperature over the experiment was 26.9 ± 2.5 ºC (Figure 1B). Leafhopper density averaged 0.056 ± 0.046 leafhoppers per young leaf. Leafhopper densities were higher in field A on all but three dates (Figure 1C).

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Figure 1. Weather patterns and leafhopper densities over the course of this study (June 5 through July 26, 2017). (A) Precipitation data from weather station in Shaxian, Fujian Province, China. (B) Mean (solid line), minimum, and maximum (dashed lines) temperatures from data logger on site. (C) Mean number of leafhoppers per young leaf on two fields. Harvest of each field are marked by changes in line color.

For shoot growth, the precipitation model had a lower AIC than the temperature model (dAIC = 4.7). Precipitation had a significant effect on plant growth (edf = 10.4, p < 0.001) with little evidence of delayed effects (Fig 2C). At 1 day lag, the optimum precipitation for growth is 13.85 mm (growth rate = 0.42 cm/day) with a modest decrease in growth at the low end of observed precipitation (0.39 cm/day at 0 mm) and substantial decreases at the high end of observed precipitation (0.21 cm/day at 83.5 mm).

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Figure 2. Partial effects plots for the effects of weather from the model including (A) lagged precipitation as a predictor and (B) lagged temperature as a predictor. Plots show predicted shoot growth from a two-dimensional cross-basis smooth and can be interpreted as as the predicted effects of precipitation or temperature at lag times of 1–15 days, all else being equal. For example, in panel B, temperature has a non-linear relationship with shoot growth at 0 days of lag (the day the measurements were taken) with the highest growth rates occurring around 27 ºC. In contrast, temperature at lag times greater than 5 days has little effect on shoot growth.

Lagged temperature 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 (Fig. 2B). At one day of lag, the optimum temperature for growth was 26.5 ºC (growth rate = 0.34 cm/day) with substantially lower growth at temperatures at the low end of observed values (20.1 ºC, growth rate = 0.28 cm/day) and modest decreases at the upper end (30.1 ºC, growth rate = 0.32 cm/day). The relationship between temperature and shoot growth shows little effect of temperature above 26 ºC and beyond 5 days of lag (Figure 2B).

Stem diameter had a significant, nearly linear effect on growth with wider shoots growing faster in both models (edf = 2.6, p < 0.001)(Fig. 3A). Number of days post-harvest had a non-monotonic relationship with growth with the highest growth rate at about day 10 with declining growth after that, although this relationship was not statistically (temperature model: edf = 2.6, p = 0.452, precipitation model: edf = 2.4, p = 0.425)(Fig. 3B).

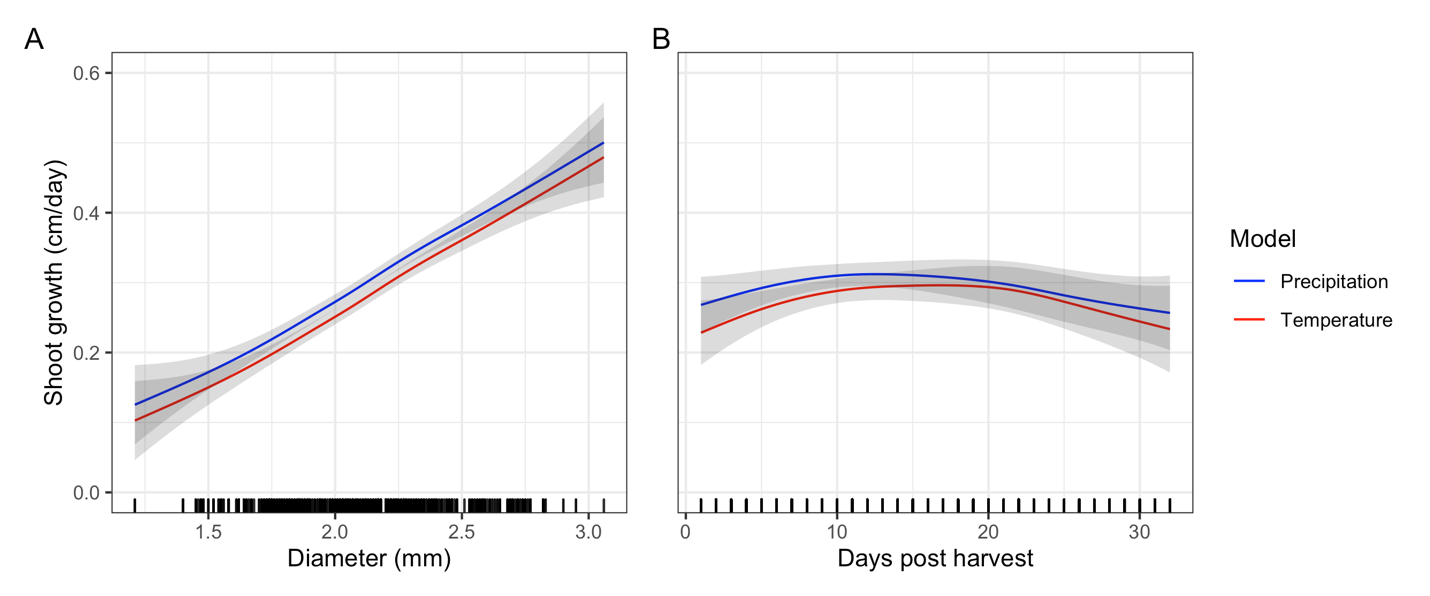


Figure 3. Predicted effects of covariates from models including either lagged temperature or precipitation as predictors. Plots show the effect of stem diameter (A) and number of days post-harvest (B) on shoot growth (cm/day). Predicted effects of co-variates differed only slightly between the two models. The effect of days post-harvest is not statistically significant.

For leafhopper densities, the precipitation model had the lower AIC than the temperature model (dAIC = 16.9). Lagged precipitation had a significant effect on leafhopper density (edf = 10.3, p < 0.001). High precipitation had a positive effect on leafhopper densities (Figure 4A). The relationship between precipitation and leafhopper densities was essentially monotonic regardless of lag time with highest predicted densities at the highest observed precipitation (83.5 mm) and lower predicted densities at 0 mm precipitation. Unlike the effects of precipitation on shoot growth, the effects of precipitation on leafhopper densities remained strong between 1 and 14 days of lag indicating delayed effects of precipitation on leafhopper densities (Figure 4A).

Lagged temperature also had a significant effect on leafhopper density (edf = 6.6, p < 0.001). High temperatures had detrimental effects on leafhopper densities especially at lag times of 5–13 days (Fig. 4B). Temperature had the strongest effects at 9 days of lag with the lowest recorded temperatures resulting in the highest predicted leafhopper density (0.05 leafhoppers/leaf at 20.15 ºC). At 9 days lag, predicted leafhopper density declines up to about 24 ºC, after which there is little effect of termperature (Fig. 4B). In contrast to precipitation, there was little effect of temperature on leafhopper density with 1 day of lag.

Number of days post-harvest had no significant effect on leafhopper density in both the temperature and precipitation models (edf = 0, p > 0.5).

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Figure 4. Partial effects plot for the lagged effect of weather on leafhopper density from models including (A) lagged precipitation as a predictor and (B) lagged temperature as a predictor. The highest leafhopper densities occurred when there were cool temperatures 9 days previous and higher temperatures (at any lag) resulted in lower leafhopper densities. The temperature on the day of measurement had only a weak effect on leafhopper densities.

# Discussion

TO READ:

(Hoffman et al., 1990)

(Hogg, 1985) (requested on ILL)

We found contrasting effects of weather on tea shoot growth and leafhopper density Tea shoot growth was highest in warm dry periods and leafhopper density was reduced under warm dry conditions. Responses of tea shoot growth to temperature and precipitation were essentially immediate, while temperature had a delayed effect on leafhopper densities, and the effects of precipitation were both immediate and delayed.

Warmer temperatures and low precipitation resulted in the fastest tea shoot growth. These two variables had high concurvity (Figure S1), as rainy days on average had cooler temperatures. While we did not measure photosynthetic activity or water stress in this experiment, these results suggest that tea plants in this experiment were not water limited. Here, precipitation is likely a proxy for sunlight and photosynthetic activity since high precipitation resulted in slower shoot growth. Responses to changes in temperature and precipitation by tea shoot growth were mostly immediate, as the relationship between growth and weather is strongest on the day of measurement

Leafhopper density, on the other hand, increased in wet and cool conditions. This suggests that desiccation may be an important source of mortality for *E. onukii* in the field. Our results agree with previous studies. For example, Mao et al. (2014) found that higher maximum daily temperatures corresponded to lower *E. onukii* densities in a field study in Shaanxi Province, although they also found that higher minimum temperatures increased densities. They also found that higher humidity and precipitation was beneficial to leafhopper population densities, although this finding did not reach statistical significance.

The negative effects of warm and dry conditions on leafhopper densities were delayed, having the strongest effect 8–10 days prior to measurement. One possible explanation for this is that earlier life stages, which are less conspicuous, are more susceptible to these warm, dry conditions than later life stages which are more conspicuous. For example, eggs are unaccounted for in this study and 1st instar nymphs may be underestimated because they are very small and colorless and likely less detectible than later instars. Reineke and Hauck (2012) investigated development of a related leafhopper, *Empoasca vitis*, under laboratory conditions and found an average development time of 5.9 days from egg to second instar and 8.7 days from egg to third instar. Mortality in these early life stages would therefore not be detected in leafhopper counts immediately, but as the cohort matured and became more detectible, the effects of that mortality on population densities would become noticeable. Reineke and Hauck (2012) also showed that first and second instar nymphs have lower optimum temperatures for development (17.55 and 15.55 ºC, respectively) than later instars which thrived at temperatures between 22.35 and 26.8 ºC (Reineke and Hauck, 2012). In addition, they found a strong decrease in egg hatching at temperatures above 18 ºC at night and 28 ºC in the day. The mean temperature in our study was 26.9º, although maximum daily temperatures were often above 28 ºC (Figure 1). Although Reineke and Hauck (2012) may overestimate the effects of temperature on leafhoppers because their study does not account for microclimatic variation in the crop canopy, our results suggest the possibility for similar patterns in mortality and hatching rates in the field. In addition, our methods are likely to be biased toward nymphs and underestimate adult population size (Shi et al., 2015). It is possible that adverse weather conditions affect the oviposition rates of adult female leafhoppers resulting in a delayed effect on nymph densities.

Alternatively, the negative impact of high temperatures could be due to indirect effects. Arthropod predators or parasitoids are also sensitive to temperature and warmer temperatures may increase their population and/or improve their prey searching efficiency. Additionally, predators of leafhoppers rely on tea plant volatile organic compounds (VOCs) to find their prey (Gao et al., 2004) and tea VOC profiles may be altered by climate (Kfoury et al., 2018, 2019; Kowalsick et al., 2014; Scott et al., 2019). Because we did not census leafhopper predators or parasitoids in this study, we cannot disentangle biotic and abiotic effects on population densities.

It is also important to note that in this observational study, tea shoot growth may be partially confounded with leafhopper herbivory as one of the symptoms of hopperburn is stunted growth. However, leafhopper densities were quite low over this period compared to other studies that investigate the effects of leafhoppers on quality (Chapter 4), and we believe the variation in leafhopper densities we saw is unlikely to have large effects on tea shoot growth. Unfortunately, in this dataset we cannot completely disentangle the effects of precipitation, temperature, and leafhopper densities on tea shoot growth. More years of data or manipulative experiments may help explore these interactions further.

Interestingly, number of days post-harvest had no effect on leafhopper densities. We included this co-variate because the farm manager at Shanfu suggested that harvesting may help control leafhopper densities by removing food sources for leafhopper nymphs and potentially eggs which are laid under the epidermis of tea shoots (Xin et al., 2017). However, we found no evidence that harvesting affected leafhopper densities. In another study at Shanfu tea company, we harvested leafhopper eggs to rear a lab colony and eggs were often found below the second or third leaf of tea shoots and would not be removed by tea plucking (Scott, personal observation).

Because tea prices depend strongly on quality, tea farmer income may not be correlated to yield (Lou et al., 2014). Slow growth can actually be beneficial for quality and outweigh the reduction in yield in some systems. Long Jing tea, for example, is produced from one or two leaves and a bud and the slow shoot elongation typical of cool spring weather is important for quality (Lou et al., 2014). Shoot growth rate may also be important in Eastern Beauty oolong production in terms of the relative rates of new leaf production and leafhopper herbivory. If shoot growth outpaces herbivory, the apical leaves of tea shoots, which are the harvest unit for Eastern Beauty oolong, may never accumulate enough damage to produce a strong enough induced response to improve quality. On the other hand, slow shoot growth and high leafhopper densities may lead to accumulation of too much damage before shoots have developed enough for harvest. This could result in intense hopperburn symptoms that decrease yield such that it reduces farmer income despite an increase in quality due to induced defenses. Additionally, the changes in tea chemistry with leafhopper density are complex and non-linear and it is unclear how a range of leafhopper densities affects finished tea quality (Chapter 4). During the course of this study, harvest was delayed for one of the two fields due to insufficient accumulation of leafhopper damage (Shanfu Tea Company, personal communication). This was the longest inter-harvest period (32 days) during the study, and it corresponded to a relatively low mean leafhopper density (0.047 leafhoppers/leaf). Interestingly however, this particular harvest period experienced higher than average precipitation (mean = 9.23 mm, median = 2 mm, 72% of days with some rain) and slightly cooler than average temperatures (26.13 ºC). A previous study showed that feeding damage by *E. onukii* has a threshold type relationship with *E. onukii* population density with increases in damage only after a threshold leafhopper density. Therefore, while cool wet conditions support higher leafhopper densities, they may not necessarily result in increased leafhopper feeding and damage that farm managers are hoping for (Chapter 4).

Milder winters and longer growing seasons caused by increases in mean temperature are predicted to benefit population densities of multivoltine insect pests like the tea green leafhopper (Bale et al., 2002; Tobin et al., 2008). However, our results show that within the growing season, cool and wet conditions actually promoted higher leafhopper densities in the tea canopy and slower shoot elongation potentially leading to higher levels of leafhopper damage. This study demonstrates the importance of considering the effects of within-season climate variability in the field to understand future impacts of climate change on crop pests and other plant­–insect interactions.

As more extreme fluctuations in weather become more common in many tea growing regions, tea farmers will need strategies to adapt. Although it is predicted that pest insects like *E. onukii* will benefit from a warming climate, within-season climate variability may hinder the use of leafhopper herbivory as a strategy for improving tea crop quality. Reduced winter mortality and increased growing season may improve leafhopper densities, however our results show that cool, wet weather during the summer is most beneficial for this strategy because it results in higher leafhopper densities in the upper canopy and slower tea shoot growth.

As within season weather becomes less predictable, farmers will benefit from an improved understanding of how pest insects influence crop quality through induced defenses. By incorporating the potential benefits of herbivory to crop quality into decision making, farmers can adapt their practices to maximize income by switching from more yield focused tea production at low leafhopper densities to quality focused production at higher leafhopper densities, to pest-control strategies at even higher densities.

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