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

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# Abstract

Climate change is predicted to impact insect herbivores and their host plants through increases in mean annual temperature and changes in annual precipitation. However, weather is also predicted to become more variable over time, so integrating the effects of climate on growth rates over years may not be appropriate, especially for organisms with multiple generations per year. Additionally, the effects of temperature and precipitation may differ between insect herbivores and their host plants and have the potential for delayed effects. We investigate the effects of daily changes in temperature and precipitation on the growth rate of tea (*Camellia sinensis* (L.) Kuntze) and a widespread, multivoltine tea pest, the tea green leafhopper (*Empoasca onukii* Matsuda) in a field study in Fujian Province, China in June and July 2017. Although *E. onukii* is often considered a pest, some tea farms, including the one in our study, appreciate and encourage *E. onukii* herbivory, which induces the production of volatiles by the tea plant and improves tea quality. Our results indicate that leafhopper density was highest under cool wet conditions, but that tea shoot growth was improved under warm, dry conditions. Precipitation had a stronger effect on both tea shoot growth and leafhopper density compared to temperature. Furthermore, the effects of weather on tea shoot growth were essentially immediate, while there was evidence of only lagged effects of temperature and both immediate and lagged effects of precipitation on leafhopper density. The delayed effects of weather may be an indication that earlier, less detectible life stages (i.e. eggs and early instar nymphs) may be more susceptible to desiccation. Although average yearly warming is expected to benefit insect pests, especially those that are multivoltine, our results show that within a growing season, cool wet conditions benefit the tea green leafhopper most.

# 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 (Porter *et al.*, 1991; Bale *et al.*, 2002; Berggren *et al.*, 2009), and to increase the latitudinal ranges and populations of some agricultural pests (Porter *et al.*, 1991; Bebber *et al.*, 2013; Macgregor *et al.*, 2019). 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). In tropical climates, where climate change is resulting in increasing frequency and severity of drought, insects may be at greater risk of desiccation over time (Bujan *et al.*, 2016). Espeset et al. (2016) found that the western population of monarch butterflies in North America benefitted from warm, wet springs. However, precipitation and increased humidity can also favor the spread of entomopathogenic fungi, which could reduce insect herbivore densities (Goettel & Glare, 2010).

Because the temperature optima of insects and plants are likely to differ, warming has the potential to have different impacts on plants and their insect herbivores culminating in predicted increases in rates of herbivory (Berggren *et al.*, 2009; DeLucia *et al.*, 2012). 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 organisms with long lifespans, it is difficult to study effects of climate change on their abundance. 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 cohort 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; Tobin *et al.*, 2008; Kerr *et al.*, 2019; Macgregor *et al.*, 2019). However, weather conditions within a year may affect the abundance of multivoltine insects independently from mean yearly trends in temperature and precipitation. For example, although the arrival date of the migratory crop pest, the potato leafhopper (*Empoasca fabae*) has been advancing with warming temperatures (-3 days per ºC), the arrival date had less of an impact on crop infestation than within-season temperatures (Baker *et al.*, 2015). For multivoltine organisms, focusing on changes in mean annual temperature and precipitation aggregates across multiple generations, and we lose information on responses to weather at more appropriate time scales.

Tea (*Camellia sinensis* (L.) Kuntze) is a long-lived perennial crop cultivated in sub-tropical regions predicted to be severely impacted by climate change (IPCC, 2014). Insect herbivores attack all parts of the tea plant and can be responsible for up to 55% yield loss (Hazarika *et al.*, 2009). The tea green leafhopper, *Empoasca onukii* Matsuda, is a widespread pest on tea (Jin *et al.*, 2012). Like other *Empoasca* species, *E. onukii* 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”. Although direct consumption of leaves by *E. onukii* is minimal, the effects of hopperburncan reduce tea yields by 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 (Cho *et al.*, 2007; Zeng *et al.*, 2019). One such tea produced from leafhopper attacked plants is known as Eastern Beauty oolong (东方美人, dongfang meiren) (Cho *et al.*, 2007; Scott & Orians, 2018). Eastern Beauty oolong originated in Taiwan but is now produced in 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 & Hauck, 2012). Therefore, there is the potential for within-season temperature and precipitation 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* (Jin *et al.*, 2012) so changes in shoot elongation must be considered together with *E. onukii* population in order to understand changes in functional density. As the climate becomes more variable, we anticipate changes in leafhopper abundance and tea plant growth, but it is unclear how temperature and precipitation will impact each species.

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 (potentially delayed) responses to recent temperature and precipitation.

If changes in temperature mainly affect plants and insects through changes in metabolic costs, we expect leafhopper density to have a higher temperature optimum compared to tea shoot growth. If tea plants were not water limited, we expect precipitation to have little effect on shoot growth. On the other hand, we expect precipitation to impact leafhopper densities through changes in relative humidity.

# 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. At our request, all harvests followed a plucking grade of 2 leaves and a bud, and the leaves were processed as Eastern Beauty oolong.

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 data was obtained for a weather station in nearby Sanming for June and July 2017 from the Chinese Agricultural Academy of Sciences.

## Distributed Lag Non-Linear Models

We assessed the effects of precipitation and temperature on leafhopper density and tea shoot growth rate (daily change in shoot height in cm). 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 non-linear 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) (Appendix 3). 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. Stem diameter and day post-harvest were used as co-variates as we expected shoot growth to be higher for larger stems and to change over time as shoots matured. 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. Here, days post-harvest is included as a co-variate to test for an effect of harvesting shoots on leafhopper population density. This GAM was fit using a Poisson family error distribution with a log link.

# Results

Mean precipitation (± standard deviation) was 6.9 ± 11.6 mm with 62% 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 leafhopper densities, the model with the lowest AIC included minimum daily temperature, followed by maximum daily temperature (dAIC = 17.8), mean daily temperature (dAIC = 19.4), and precipitation (dAIC = 22.9).

Lagged minimum temperature had a significant effect on leafhopper density (edf = 10.3, = 67.66, *P* < 0.001) with recent low temperatures strongly reducing leafhopper density (Figure 2A). However, for mean daily temperature, low temperatures 9 days ago had a moderate positive effect on leafhopper density (edf = 10.1, = 53.88, *P* < 0.001). At 9 days lag, predicted leafhopper density declines up to about 24 ºC, after which there is little effect of temperature (Figure 2B). There was little effect of temperature on leafhopper density with 1 day of lag. Lagged maximum temperature was also significant (edf = 9.9,= 51.93, *P* < 0.001) and showed similar patterns to mean daily temperature (supplemental).

High precipitation had a significant positive effect on leafhopper densities (edf = 9.4, = 47.36, *P* < 0.001). The strongest effect of precipitation was at 11 days lag where there was a monotonic increasing relationship between precipitation and leafhopper density (Figure 2C). More recent effects (1–5 days lag) of precipitation on leafhopper densities were minimal.

Number of days post-harvest was significant (*P* < 0.05) as a covariate only in the mean temperature and maximum temperature models and showed a linear decrease in leafhopper density with time after harvest (figure).

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Figure 2. Partial effects plot for the lagged effect of weather on leafhopper density from models including lagged daily minimum as a predictor (A), lagged daily mean temperature as a predictor (B), and daily precipitation as a predictor (C) . The highest leafhopper densities occurred when there were cool mean temperatures and high precipitation 9–12 days previous, but higher minimum temperatures recently, including the day of measurement.

For shoot growth, the minimum temperature model had the lowest AIC, followed by mean and maximum temperature, which were essentially equivalent (dAIC = 0.7 and 1.2, respectively). The precipitation model had a higher AIC than the temperature models (dAIC = 11.5).

Lagged minimum temperature (edf = 9.1, = 149.39, *P* < 0.001) and lagged mean temperature (edf = 11.8, , = 151.6, *P* < 0.001) had significant effects on growth in their respective models. Temperature effects were mostly immediate, with negligible effects of temperature lagged past 5 days (Figure 3A and 3B). At one day of lag, shoot growth increased with increasing minimum temperature up to about 21 ºC and mean temperature up to about 26 ºC and then leveled off. The relationship between temperature and shoot growth shows little effect of minimum temperatures above 21 ºC or mean temperatures above 26 ºC and beyond 5 days of lag (Figure 3A and 3B). Results for maximum temperature were similar to those of mean temperature (supplemental).

Precipitation also had a significant effect on plant growth (edf = 15.1, = 178.97, *P* < 0.001). At 1 day lag, the optimum precipitation for growth is 11.8 mm (growth rate = 0.28 cm/day) with a modest decrease in growth at the low end of observed precipitation (0.24 cm/day at 0 mm) and substantial decreases at the high end of observed precipitation (0.01 cm/day at 83.8 mm). The DLNM also indicates a lagged effect of precipitation on shoot growth with the highest growth rates occurring at high precipitation with 12 days of lag (Figure 3C).

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Figure 3. Partial effects plots for the effects of weather on shoot growth from the model including lagged daily minimum temperature (A), lagged daily mean temperature (B) or lagged precipitation as. Plots show predicted shoot growth from a two-dimensional cross-basis smooth and can be interpreted as the predicted effects of precipitation or temperature at lag times of 1–15 days, all else being equal.

Stem diameter had a significant effect on growth with wider shoots growing faster in all models (all *P* < 0.001) (Figure 4A). Number of days post-harvest was only a significant co-variate in the temperature models, and had a non-monotonic relationship with growth with the highest growth rate at about day 10 with declining growth after that (Figure 4B).

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Figure 4. Predicted effects of covariates from shoot growth 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 the model with precipitation as a predictor.

# Discussion

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 highest in wet and cool conditions. Responses of tea shoot growth to temperature and precipitation were essentially immediate, while temperature had only a delayed effect on leafhopper densities, and the effect of precipitation on leafhoppers was both immediate and delayed.

Leafhopper density increased in wet and cool conditions, which suggests that desiccation may be an important source of mortality for *E. onukii* in the field. This result is similar to that of Mao et al. (2014). They found that higher maximum daily temperatures corresponded to lower *E. onukii* densities in a field study in Shaanxi Province, although 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 9 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, colorless and therefore likely less detectible than later instars. 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) 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. If development times are similar for *E. onukii*, then a lag time of about 9 days could be explained by an effect of temperature on egg eclosion. 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 & 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. Future field studies that track abundances of *E. onukii* life stages separately might be able to infer the exact nature of these delayed effects.

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 (Kowalsick *et al.*, 2014; Kfoury *et al.*, 2018, 2019; Scott *et al.*, 2019). Weather may also directly impact the quality of tea leaves as a food source for leafhoppers, which could have a delayed effect on their densities. Because we did not census leafhopper predators or parasitoids or measure plant chemistry in this study, we cannot disentangle biotic and abiotic effects on population densities.

Interestingly, number of days post-harvest had no effect on leafhopper densities. We included this co-variate because the farm manager at Shanfu Tea Company 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).

In contrast to leafhoppers, tea shoot growth was favored by warmer temperatures and low precipitation, with precipitation having a stronger effect than temperature. 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. Temperature and precipitation had high concurvity (analogous to collinearity), and precipitation is likely a proxy for sunlight and photosynthetic activity in this experiment since high precipitation resulted in slower shoot growth. Faster growth under lower precipitation (higher light availability) is typical of woody understory plants that do not experience water limitation (Condit *et al.*, 2004). Responses to changes in temperature and precipitation by tea shoot growth were mostly immediate, as the relationship between growth and weather is strongest with only 1 day of lag.

It is 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 (Scott *et al.*, 2020), 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 where leafhopper density is not correlated with weather may help explore these interactions further.

Future impacts of global change on precipitation are less predictable and more geographically variable than warming. While increases in mean annual temperature may lengthen the growing season for multivoltine insects, this will not necessarily result in increases in population density if conditions within the growing season are not favorable. In this study, precipitation was a stronger driver of herbivore density and plant growth within the growing season compared to mean temperature. Furthermore, herbivores and plants responded in an opposite way to increases in precipitation, potentially compounding the effects of precipitation on herbivory (i.e. damage per young leaf). However, we suspect that the responses of plants and insect herbivores to changes in precipitation will vary widely over habitats and among species. For example, in more water-limited regions of China, increases in precipitation have been shown to increase rather than decrease tea plant growth (Ahmed *et al.*, 2014).

To cope with increasing variability in precipitation, tea farmers in Fujian province may benefit from switching from yield focused strategies during dry conditions to quality focused strategies during wetter conditions. For example, when leafhopper damage is too low, Shanfu Tea Company often plucks 3–4 leaves and a bud and processes tea as Iron Goddess of Mercy oolong, rather than plucking 2 leaves and a bud for Eastern Beauty oolong (Shanfu Tea Company, personal communication).

Because we asked that all harvests be processed as Eastern Beauty oolong, 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, 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* is not strongly correlated with *E. onukii* density when densities are below 0.5 leafhoppers per leaf. 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 (Scott *et al.*, 2020).

Because tea prices depend strongly on quality, tea farmer income may not be correlated to yield (Lou *et al.*, 2014). Tea quality 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, including allowing for some damage by *E. onukii* (Saijo, 1980; Cho *et al.*, 2007; Ahmed *et al.*, 2014). In fact, slow growth in itself 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 (Scott *et al.*, 2020).

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.

# Acknowledgments

We thank the Shanfu Tea Company who generously allowed us to use their farm as a study side and provided lodging, food, and tea for researchers on site. We especially thank the general manager Mr. Liu and the manager Mr. Zeng. Dr. Qihong Du introduced us to the Shanfu Tea Company and helped arrange travel and lodging in Shaxian. Gabriel Taylor assisted in data collection. Gabriel Taylor and M. Hanna Brush assisted in data entry. Collin E. Edwards advised us on implementing the distributed lag non-linear models. Funding was provided by NSF Grant ﻿BCS-1313775, the Tufts Institute for the Environment fellowship, and the National Key R&D Program of China (2017YFE0107500).

# Contribution of authors

# References

Ahmed, S., Stepp, J.R., Orians, C.M., Griffin, T., Matyas, C., Robbat, A., *et al.* (2014) Effects of Extreme Climate Events on Tea (*Camellia sinensis*) Functional Quality Validate Indigenous Farmer Knowledge and Sensory Preferences in Tropical China. *PLoS ONE*, **9**, e109126.

Backus, E.A., Serrano, M.S. & Ranger, C.M. (2005) Mechanisms of Hopperburn: An Overview of Insect Taxonomy, Behavior, and Physiology. *Annual Review of Entomology*, **50**, 125–151.

Baker, M.B., Venugopal, P.D. & Lamp, W.O. (2015) Climate Change and Phenology: *Empoasca fabae* (Hemiptera: Cicadellidae) Migration and Severity of Impact. *PLOS ONE*, **10**, e0124915.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.

Bebber, D.P., Ramotowski, M.A.T. & Gurr, S.J. (2013) Crop pests and pathogens move polewards in a warming world. *Nature Climate Change*, **3**, 985–988.

Beirne, B.P. (1970) EFFECTS OF PRECIPITATION ON CROP INSECTS. *The Canadian Entomologist*, **102**, 1360–1373.

Berggren, Å., Björkman, C., Bylund, H. & Ayres, M.P. (2009) The distribution and abundance of animal populations in a climate of uncertainty. *Oikos*, **118**, 1121–1126.

Bujan, J., Yanoviak, S.P. & Kaspari, M. (2016) Desiccation resistance in tropical insects: causes and mechanisms underlying variability in a Panama ant community. *Ecology and Evolution*, **6**, 6282–6291.

Cho, J.-Y., Mizutani, M., Shimizu, B., Kinoshita, T., Ogura, M., Tokoro, K., *et al.* (2007) Chemical Profiling and Gene Expression Profiling during the Manufacturing Process of Taiwan Oolong Tea “Oriental Beauty.” *Bioscience, Biotechnology and Biochemistry*, **71**, 1476–1486.

Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., *et al.* (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology*, **20**, 51–72.

Cook, J., Oreskes, N., Doran, P.T., Anderegg, W.R.L., Verheggen, B., Maibach, E.W., *et al.* (2016) Consensus on consensus: A synthesis of consensus estimates on human-caused global warming. *Environmental Research Letters*, **11**.

DeLucia, E.H., Nabity, P.D., Zavala, J.A. & Berenbaum, M.R. (2012) Climate change: Resetting plant-insect interactions. *Plant Physiology*, **160**, 1677–1685.

Deutsch, C.A., Tewksbury, J.J., Tigchelaar, M., Battisti, D.S., Merrill, S.C., Huey, R.B., *et al.* (2018) Increase in crop losses to insect pests in a warming climate. *Science*, **361**, 916–919.

Espeset, A.E., Harrison, J.G., Shapiro, A.M., Nice, C.C., Thorne, J.H., Waetjen, D.P., *et al.* (2016) Understanding a migratory species in a changing world: climatic effects and demographic declines in the western monarch revealed by four decades of intensive monitoring. *Oecologia*, **181**, 819–830.

Fu, J.-Y., Han, B.-Y. & Xiao, Q. (2014) Mitochondrial COI and 16sRNA Evidence for a Single Species Hypothesis of *E. vitis*, *J. formosana* and *E. onukii* in East Asia. *PLoS ONE*, **9**, e115259.

Gao, J., Zhao, D. & Chen, Z. (2004) Predatory function of *Evarcha albaria* upon *Empoasca vitis*. *Chinese Journal of Tropical Crops*.

Gasparrini, A. (2011) Distributed Lag Linear and Non-Linear Models in R : The Package dlnm. *Journal of Statistical Software*, **43**, 2–20.

Gasparrini, A., Scheipl, F., Armstrong, B. & Kenward, M.G. (2017) A penalized framework for distributed lag non-linear models. *Biometrics*, **73**, 938–948.

Goettel, M.S. & Glare, T. (2010) 11 Entomopathogenic Fungi and their Role in Regulation of Insect Populations. *Insect Control*.

Hazarika, L.K., Bhuyan, M. & Hazarika, B.N. (2009) Insect Pests of Tea and Their Management. *Annual Review of Entomology*, **54**, 267–284.

IPCC. (2007) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007*. Cambridge, United Kingdom.

IPCC. (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom.

Jin, S., Chen, Z.M., Backus, E.A., Sun, X.L. & Xiao, B. (2012) Characterization of EPG waveforms for the tea green leafhopper, *Empoasca vitis* Göthe (Hemiptera: Cicadellidae), on tea plants and their correlation with stylet activities. *Journal of Insect Physiology*, **58**, 1235–1244.

Kerr, N.Z., Wepprich, T., Grevstad, F.S., Dopman, E.B., Chew, F.S. & Crone, E.E. (2019) Developmental trap or demographic bonanza? Opposing consequences of earlier phenology in a changing climate for a multivoltine butterfly. *Global Change Biology*, 1–14.

Kfoury, N., Morimoto, J., Kern, A., Scott, E.R., Orians, C.M., Ahmed, S., *et al.* (2018) Striking changes in tea metabolites due to elevational effects. *Food Chemistry*, **264**, 334–341.

Kfoury, N., Scott, E.R., Orians, C.M., Ahmed, S., Cash, S.B., Griffin, T., *et al.* (2019) Plant-Climate Interaction Effects: Changes in the Relative Distribution and Concentration of the Volatile Tea Leaf Metabolome in 2014–2016. *Frontiers in Plant Science*, **10**, 1518.

Kowalsick, A., Kfoury, N., Robbat, A., Ahmed, S., Orians, C., Griffin, T., *et al.* (2014) Metabolite profiling of *Camellia sinensis* by automated sequential, multidimensional gas chromatography/mass spectrometry reveals strong monsoon effects on tea constituents. *Journal of Chromatography A*, **1370**, 230–239.

Lou, W., Sun, S., Wu, L. & Sun, K. (2014) Effects of climate change on the economic output of the Longjing-43 tea tree, 1972–2013. *International Journal of Biometeorology*, **59**, 593–603.

Macgregor, C.J., Thomas, C.D., Roy, D.B., Beaumont, M.A., Bell, J.R., Brereton, T., *et al.* (2019) Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. *Nature Communications*, **10**.

Mao, Y., Tan, R., Gong, Z. & Kuang, S. (2014) Relationships between population dynamics of *Empoasca vitis* and meteorological factors in tea plantation. *Hubei Agricultural Sciences*, **53**.

Meineke, E.K., Classen, A.T., Sanders, N.J. & Jonathan Davies, T. (2018) Herbarium specimens reveal increasing herbivory over the past century. *Journal of Ecology*, 1–13.

NOAA. (2020) *NOAA National Centers for Environmental Information, State of the Climate: Global Climate Report for Annual 2019*.

Porter, J.H., Parry, M.L. & Carter, T.R. (1991) The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology*, **57**, 221–240.

Reineke, A. & Hauck, M. (2012) Larval development of *Empoasca vitis* and *Edwardsiana rosae* (Homoptera: Cicadellidae) at different temperatures on grapevine leaves. *Journal of Applied Entomology*, **136**, 656–664.

Saijo, R. (1980) Effect of shade treatment on biosynthesis of catechins in tea plants. *Plant and Cell Physiology*, **21**, 989–998.

Scott, E.R., Li, X., Kfoury, N., Morimoto, J., Han, W.-Y., Ahmed, S., *et al.* (2019) Interactive effects of drought severity and simulated herbivory on tea (*Camellia sinensis*) volatile and non-volatile metabolites. *Environmental and Experimental Botany*, **157**, 283–292.

Scott, E.R., Li, X., Wei, J.-P., Kfoury, N., Morimoto, J., Guo, M.-M., *et al.* (2020) Changes in tea plant secondary metabolite profiles as a function of leafhopper density and damage. *Frontiers in Plant Science*, **11**, 636.

Scott, E.R. & Orians, C.M. (2018) Differential Changes in Tea Quality as Influenced by Insect Herbivory. In *Stress Physiology of Tea in the Face of Climate Change* (ed. by Han, W.-Y., Li, X. & Ahammed, G.J.). Springer Singapore, Singapore, pp. 217–240.

Shi, L.-Q., Zeng, Z.-H., Huang, H.-S., Zhou, Y.-M., Vasseur, L. & You, M.-S. (2015) Identification of *Empoasca onukii* (Hemiptera: Cicadellidae) and Monitoring of its Populations in the Tea Plantations of South China. *Journal of Economic Entomology*, **108**, 1025–1033.

Teller, B.J., Adler, P.B., Edwards, C.B., Hooker, G. & Ellner, S.P. (2016) Linking demography with drivers: Climate and competition. *Methods in Ecology and Evolution*, **7**, 171–183.

Tobin, P.C., Nagarkatti, S., Loeb, G. & Saunders, M.C. (2008) Historical and projected interactions between climate change and insect voltinism in a multivoltine species. *Global Change Biology*, **14**, 951–957.

Wood, S.N. (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society. Series B: Statistical Methodology*, **70**, 495–518.

Wood, S.N. (2017) *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC.

Xin, Z.-J., Li, X.-W., Bian, L. & Sun, X.-L. (2017) Tea green leafhopper, *Empoasca vitis*, chooses suitable host plants by detecting the emission level of (3Z)-hexenyl acetate. *Bulletin of Entomological Research*, **107**, 77–84.

Zeng, L., Watanabe, N. & Yang, Z. (2019) Understanding the biosyntheses and stress response mechanisms of aroma compounds in tea (*Camellia sinensis*) to safely and effectively improve tea aroma. *Critical Reviews in Food Science and Nutrition*, **59**, 2321–2334.