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

Eric R. Scott, Ji-Peng Wei, Xin Li, Colin M. Orians

# 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).

Many studies of climate effects on insect herbivore populations focus on trends across multiple years. However, within-season climate variability can have important effects on insect abundance. For example, favorable conditions early in the season may have a greater effect on populations of multivoltine insects than favorable conditions late in the season due to compounding effects over time. For example, in bumblebees (which can be considered effectively multivoltine), a pulse of resources early in the season results in larger colony sizes and greater reproductive output compared to a similar pulse later in the season (Malfi et al., 2019). Within-season climate variability can also influence insect populations independently of yearly increases in mean temperature. For example, infestation severity on crops by the migratory, multivoltine, polyphagous crop pest, *Empoasca fabae* is more dependent on within-season temperatures than on advancing phenology due to warming (Baker et al., 2015).

Because insects are poikilotherms, changes in temperature are likely to affect insects most directly (Bale et al., 2002). 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. Multivoltine insects in particular may benefit from warming, as faster development and longer growing seasons allow for more generations and greater potential population growth (Bale et al., 2002; Kerr et al., 2019; Macgregor et al., 2019; Tobin et al., 2008).

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. Hot, 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). However, precipitation and increased humidity can also favor the spread of entomopathogenic fungi, which could reduce insect herbivore densities (Goettel and Glare, 2010).

The temperature optima of plants and their insect herbivores differ (Berggren et al., 2009). Insects are predicted to benefit more from high temperatures than plants due to plants experiencing photorespiration at high temperatures. Temperature can also alter effective herbivore density, that is, the relative growth rate of plants and insect herbivore populations. For example, if host plant growth is too slow due to cold temperatures, or if leaf maturation is too fast due to high temperatures, the relative herbivore density (insects per young leaf) may increase, and there may not be enough young leaf tissue to support herbivores (Bale et al., 2002).

[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 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 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). *E. 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 these as potentially lagged responses to 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 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). 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 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. *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, but switched to counting 50 leaves 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. 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 (hereafter “harvest”) experienced a unique weather history and is treated like 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 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. Shoot diameter was measured once per harvest to use as a covariate. Because our study began only three days before the harvest of Field B, we excluded this first inter-harvest period from analyses of shoot growth.

A temperature sensor and datalogger (HOBO 64k 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. 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 We report results of both models, 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.

Penalized cubic regression splines were used for all fixed effects. Penalization allows splines to approach linear functions when there isn’t support for a more complicated relationship. Effective degrees of freedom (edf) represent the complexity 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.

# Results

For plant growth, the temperature model had a lower AIC than precipitation (dAIC = 8.8). 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. 1C). 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. Diameter had a significant, nearly linear effect on growth with wider shoots growing faster (edf = 2.6, p < 0.001)(Fig. 1B). Number of days 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)(Fig. 1A).

A close up of a map

Description automatically generated

Figure 1. Partial effects plots for the model of shoot growth including lagged temperature as a predictor. Given all else is constant, plots show the effect of number days post-harvest (A), stem diameter (B), and lagged temperature (C) on shoot growth (cm/day). C is the result of a two-dimensional cross-basis smooth and can be interpreted as the predicted effects of temperature at lag times of 0–15 days, all else being equal. For example, 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 27.5ºC.

Precipitation also had a significant negative effect on plant growth with little evidence of delayed effects (Fig 2C). 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. In the precipitation model, the diameter and day post-harvest co-variates had a similar relationship with shoot growth as the temperature model (Fig 2, A and B), although only stem diameter was statistically significant (diameter: edf = 2.6, p < 0.001; days post-harvest: edf = 2.5, p = 0.436).

A close up of a map

Description automatically generated

Figure 2. Partial effects plots for the model of shoot growth including lagged precipitation as a predictor. Given all else is constant, the effects of number of days post-harvest (A), stem diameter (B), and lagged precipitation (C) on shoot growth (cm/day). C is the result of a two-dimensional cross-basis smooth and can be interpreted as the predicted effects of precipitation at lag times of 0–15 days, all else being equal. For example, precipitation has a nearly linear relationship with shoot growth at 0–4 days of lag with higher precipitation resulting in slower shoot growth.

Lagged temperature had a significant effect on leafhopper density (edf = 7.0, p < 0.001), although this model had a higher AIC than the precipitation model (dAIC = 15.2). High temperatures had detrimental effects on leafhopper densities and there was evidence for delayed effects of temperature as well (Fig. 3). 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, although the effect of lag is much weaker at high temperatures (Fig. 3). Number of days post-harvest had no significant effect on leafhopper density (edf = 0, p = 0.769).

A screenshot of a cell phone

Description automatically generated

Figure 3. Partial effects plot for the lagged effect of temperature on leafhopper density (model 3). The highest leafhopper densities occurred when there were cool temperatures 8–10 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.

The precipitation model for leafhopper density had a lower AIC than temperature (dAIC = 0). 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. Number of days post-harvest had no significant effect on leafhopper density (edf = 0, p = 0.769).

A screenshot of a cell phone

Description automatically generated

Figure 4. Partial effects plot for the lagged effect of precipitation on leafhopper density (model 4). Very low precipitation (near 0 mm) up to 15 days in the past results in a lower leafhopper density than recent high-precipitation days. The effect of precipitation is strongest (i.e. the steepness of the surface going left to right) at about 3–4 days of lag.

# 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 reduced under warm dry conditions. Responses of tea shoot growth to temperature and precipitation were essentially immediate, while weather conditions had a delayed effect on leafhopper densities.

Warmer temperatures and low precipitation resulted in the fastest tea shoot growth. These two variables had high concurvity, 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, benefitted from 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. 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. A laboratory study on *Empoasca vitis* on grape leaves 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, this study showed a strong decrease in egg hatching at temperatures above 18 ºC at night and 28 ºC in the day. 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. 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 improve their population numbers of 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 (frontiers manuscript), 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 (frontiers manuscript). 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 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 *E. onukii* densities are not linearly correlated to leaf damage, so while cool wet conditions support higher leafhopper densities, they may not necessarily result in increased leafhopper feeding and damage that farm managers are looking for (frontiers manuscript).

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.

A possible plot 1 or supplementary plot:

A close up of text on a white background

Description automatically generated

Temperature is min (lower dashed), mean (solid), and max (upper dashed).

# Works Cited

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. doi:10.1371/journal.pone.0109126.

Backus, E. A., Serrano, M. S., and Ranger, C. M. (2005). Mechanisms of Hopperburn: An Overview of Insect Taxonomy, Behavior, and Physiology. *Annu. Rev. Entomol.* 50, 125–151. doi:10.1146/annurev.ento.49.061802.123310.

Baker, M. B., Venugopal, P. D., and Lamp, W. O. (2015). Climate Change and Phenology: Empoasca fabae (Hemiptera: Cicadellidae) Migration and Severity of Impact. *PLoS One* 10, e0124915. doi:10.1371/journal.pone.0124915.

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. *Glob. Chang. Biol.* 8, 1–16. doi:10.1046/j.1365-2486.2002.00451.x.

Bebber, D. P., Ramotowski, M. A. T., and Gurr, S. J. (2013). Crop pests and pathogens move polewards in a warming world. *Nat. Clim. Chang.* 3, 985–988. doi:10.1038/nclimate1990.

Beirne, B. P. (1970). EFFECTS OF PRECIPITATION ON CROP INSECTS. *Can. Entomol.* 102, 1360–1373. doi:10.4039/Ent1021360-11.

Berggren, Å., Björkman, C., Bylund, H., and Ayres, M. P. (2009). The distribution and abundance of animal populations in a climate of uncertainty. *Oikos* 118, 1121–1126. doi:10.1111/j.1600-0706.2009.17558.x.

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.” *Biosci. Biotechnol. Biochem.* 71, 1476–1486. doi:10.1271/bbb.60708.

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. *Environ. Res. Lett.* 11. doi:10.1088/1748-9326/11/4/048002.

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 (80-. ).* 361, 916–919. doi:10.1126/science.aat3466.

Fu, J.-Y., Han, B.-Y., and 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. doi:10.1371/journal.pone.0115259.

Gao, J., Zhao, D., and Chen, Z. (2004). Predatory function of *Evarcha albaria* upon *Empoasca vitis*. *Chinese J. Trop. Crop.*

Gasparrini, A. (2011). Distributed Lag Linear and Non-Linear Models in R : The Package dlnm. *J. Stat. Softw.* 43, 2–20. doi:10.18637/jss.v043.i08.

Gasparrini, A., Scheipl, F., Armstrong, B., and Kenward, M. G. (2017). A penalized framework for distributed lag non-linear models. *Biometrics* 73, 938–948. doi:10.1111/biom.12645.

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

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

Jin, S., Chen, Z. M., Backus, E. A., Sun, X. L., and 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. *J. Insect Physiol.* 58, 1235–1244. doi:10.1016/j.jinsphys.2012.06.008.

Kerr, N. Z., Wepprich, T., Grevstad, F. S., Dopman, E. B., Chew, F. S., and Crone, E. E. (2019). Developmental trap or demographic bonanza? Opposing consequences of earlier phenology in a changing climate for a multivoltine butterfly. *Glob. Chang. Biol.*, 1–14. doi:10.1111/gcb.14959.

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 Chem.* 264, 334–341. doi:10.1016/j.foodchem.2018.05.040.

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. *Front. Plant Sci.* 10, 1518. doi:10.3389/fpls.2019.01518.

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. *J. Chromatogr. A* 1370, 230–239. doi:10.1016/j.chroma.2014.10.058.

Lou, W., Sun, S., Wu, L., and Sun, K. (2014). Effects of climate change on the economic output of the Longjing-43 tea tree, 1972–2013. *Int. J. Biometeorol.* 59, 593–603. doi:10.1007/s00484-014-0873-x.

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. *Nat. Commun.* 10. doi:10.1038/s41467-019-12479-w.

Malfi, R. L., Crone, E., and Williams, N. (2019). Demographic benefits of early season resources for bumble bee (B. vosnesenskii) colonies. *Oecologia* 191, 377–388. doi:10.1007/s00442-019-04472-3.

Mao, Y., Tan, R., Gong, Z., and Kuang, S. (2014). Relationships between population dynamics of *Empoasca vitis* and meteorological factors in tea plantation. *Hubei Agric. Sci.* 53. doi:10.14088/j.cnki.issn0439-8114.2014.24.032.

Meineke, E. K., Classen, A. T., Sanders, N. J., and Jonathan Davies, T. (2018). Herbarium specimens reveal increasing herbivory over the past century. *J. Ecol.*, 1–13. doi:10.1111/1365-2745.13057.

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

Porter, J. H., Parry, M. L., and Carter, T. R. (1991). The potential effects of climatic change on agricultural insect pests. *Agric. For. Meteorol.* 57, 221–240. doi:10.1016/0168-1923(91)90088-8.

Reineke, A., and Hauck, M. (2012). Larval development of Empoasca vitis and Edwardsiana rosae (Homoptera: Cicadellidae) at different temperatures on grapevine leaves. *J. Appl. Entomol.* 136, 656–664. Available at: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1439-0418.2011.01699.x.

Saijo, R. (1980). Effect of shade treatment on biosynthesis of catechins in tea plants. *Plant Cell Physiol.* 21, 989–998. doi:10.1093/oxfordjournals.pcp.a076087.

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. *Environ. Exp. Bot.* 157, 283–292. doi:10.1016/j.envexpbot.2018.10.025.

Shi, L.-Q., Zeng, Z.-H., Huang, H.-S., Zhou, Y.-M., Vasseur, L., and You, M.-S. (2015). Identification of Empoasca onukii (Hemiptera: Cicadellidae) and Monitoring of its Populations in the Tea Plantations of South China. *J. Econ. Entomol.* 108, 1025–1033. doi:10.1093/jee/tov054.

Teller, B. J., Adler, P. B., Edwards, C. B., Hooker, G., and Ellner, S. P. (2016). Linking demography with drivers: Climate and competition. *Methods Ecol. Evol.* 7, 171–183. doi:10.1111/2041-210X.12486.

Tobin, P. C., Nagarkatti, S., Loeb, G., and Saunders, M. C. (2008). Historical and projected interactions between climate change and insect voltinism in a multivoltine species. *Glob. Chang. Biol.* 14, 951–957. doi:10.1111/j.1365-2486.2008.01561.x.

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

Xin, Z.-J., Li, X.-W., Bian, L., and Sun, X.-L. (2017). Tea green leafhopper, Empoasca vitis, chooses suitable host plants by detecting the emission level of (3Z)-hexenyl acetate. *Bull. Entomol. Res.* 107, 77–84. doi:10.1017/S000748531600064X.

Zeng, L., Watanabe, N., and Yang, Z. (2019). Understanding the biosyntheses and stress response mechanisms of aroma compounds in tea (Camellia sinensis ) to safely and effectively improve tea aroma. *Crit. Rev. Food Sci. Nutr.* 59, 2321–2334. doi:10.1080/10408398.2018.1506907.