



Differing non-linear, lagged effects of temperature and precipitation on an insect herbivore and its host plant

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Abstract. 1. Multivariate climate change is expected to impact insect densities and plant growth in complex, and potentially different, ways. Tea (*Camellia sinensis*) is a unique crop system where the increase in quality from chemical defences induced by *Empoasca onukii* (Homoptera: Cicadellidae) feeding can outweigh reductions in yield and make attack by this leafhopper desirable to tea farmers. Differential impacts of weather attributes on tea and herbivores could impact feasibility of this unique farming strategy in a rapidly changing climate.

2. We monitored leafhopper densities and tea shoot growth at a tea farm in Fujian Province, China for 2 months (June and July). We used distributed lag non-linear models to capture potentially delayed and non-linear effects of weather attributes on tea growth and leafhopper densities.

3. Weather attributes had contrasting effects on leafhopper density and tea shoot growth. Leafhopper densities were highest with low daily mean and maximum temperatures, while warm temperatures favoured tea growth. Effects of temperature on leafhoppers were delayed, while effects on tea growth were immediate. Precipitation reduced tea growth, and had a delayed positive effect on leafhopper density.

4. The delayed effects of weather attributes on leafhoppers indicate that earlier, less conspicuous life stages (i.e. eggs and early instar nymphs) may be susceptible to desiccation. Although increasing annual mean temperature is commonly predicted to benefit multivoltine insect pests, our results show that cool, wet conditions benefit *E. onukii* during summer months when they are most abundant. These results have implications for tea green leafhopper management strategies.

Key words. Climate change, distributed lag non-linear model, *Empoasca onukii*, insect pests, leafhopper, tea (*Camellia sinensis*).

Introduction

Climate change is causing increases in mean temperature as well as increased variability in temperature and precipitation globally (IPCC, 2014). In addition, the increase in mean annual temperature, the frequency of extreme events such as heat waves and precipitation anomalies have increased over the last century. Importantly, warming and changes in precipitation are expected to impact plant–herbivore interactions with consequences to both natural and managed systems (DeLucia *et al.*, 2012).

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The specific impacts of climate change on plant–herbivore interactions are predicted to vary by species and geography (Bale *et al.*, 2002).

The response of an insect herbivore to warming may depend on the part of its thermal niche it occupies (Boggs, 2016). Insect performance is a non-linear function of temperature with slowed metabolic rates at temperatures below an optimum and disruption of physiological processes at temperatures above that optimum (Roitberg & Mangel, 2016; González-Tokman *et al.*, 2020). Where insect herbivores are already near their temperature optimum, increases in temperature mean or variation is predicted to be detrimental to vital rates (Estay *et al.*, 2014). However, the temperature optimum of insects is thought to be relatively high and 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). Warming has already resulted in a documented increase in herbivory on herbarium specimens (Meineke *et al.*, 2019) and crops (Deutsch *et al.*, 2018) over time.

The predicted direct effects of changes in precipitation on insect populations are less clear, partly due to limited research relative to the number of studies on temperature (Bale *et al.*, 2002). In habitats that become drier, insects may be at greater risk of desiccation (Beirne, 1970; Bujan *et al.*, 2016; Espeset *et al.*, 2016). While wetter conditions reduce desiccation risk to insects, increased humidity can increase the spread of entomopathogenic fungi, which could reduce insect herbivore densities (Goettel *et al.*, 2010). However, intense rainfall events also have the potential to directly reduce survival and growth of small invertebrate herbivores (Chen *et al.*, 2019). Importantly, temperature and precipitation fluctuations often occur at short time scales—less than the developmental time of an insect—so incorporating these fluctuations can be important for modelling population growth outcomes (Baker *et al.*, 2015; Boggs, 2016).

Because the optimal weather conditions for insects and plants are likely to differ, climate change has the potential to have different impacts on plants and their insect herbivores. Insect populations are predicted to benefit more from high temperatures than their host plants, culminating in predicted increases in rates of herbivory (Berggren *et al.*, 2009; DeLucia *et al.*, 2012). Changes in precipitation can also impact plant-insect interactions. For example drought stress may increase the probability of insect herbivore outbreaks through plant metabolite mediated changes in herbivore preference and performance (Mattson & Haack, 1987; Scheirs & Bruyn, 2005; Weldegergis *et al.*, 2015).

Tea (*Camellia sinensis* (L.) Kuntze) is a long-lived perennial crop cultivated in sub-tropical regions predicted to be impacted strongly by climate change (Wang *et al.*, 2010; Boehm *et al.*, 2016). Tea is harvested continuously spring through autumn (Cranham, 1966), making it possible to study the effects of weather variables on both plant and insect herbivores over short time scales within the growing season. Because harvesting removes apical shoots, all growth within the harvest season is regrowth, making growth rates at different times of year comparable. Young tea shoots are not only the unit of harvest, but also the preferred feeding sites for many tea pests, so changes in tea shoot elongation must be considered together with herbivore populations.

The tea green leafhopper, *Empoasca onukii* Matsuda, is a widespread pest on tea that has multiple generations per year with the number of generations depending on climatic conditions (Fu *et al.*, 2014; Shi *et al.*, 2015). *Empoasca onukii* feeding causes reduction in tea yields of up to 50%–70% (Fu *et al.*, 2014; Yao *et al.*, 2020b). Despite reductions in yield, *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 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). Multivoltine insects, in particular, are expected to increase population densities in response to warming (Tobin *et al.*, 2008) and previous studies on other *Empoasca* species have shown that they are highly sensitive to changes in temperature within a growing season (Reineke & Hauck, 2012; Baker *et al.*, 2015). *Empoasca onukii*, in particular, can experience a decrease in population during the hottest months of the year in the warmer parts of their range (Wang *et al.*, 2013; Mao *et al.*, 2014).

We estimated *E. onukii* density and tea shoot growth in tea fields daily for 2 months and collected daily weather data. If leafhoppers are near the upper end of their thermal range in our study, then population densities should benefit from cooler than average conditions. We also predicted that *E. onukii* population density would be more sensitive to changes in temperature and precipitation compared to tea shoot growth. We expected effects of weather attributes on tea growth to be immediate, but predicted lagged effects on leafhoppers due to delayed physiological recovery from extreme temperatures (Roitberg & Mangel, 2016) or effects of temperature only manifesting in later demographic stages (e.g. heat exposure as nymphs affecting fecundity as adults).

Methods

Study site

The study was conducted at Shanfu Tea Company in Shaxian, Sanming Prefecture, Fujian Province, China ($26^{\circ}25'04.1''N$ $117^{\circ}44'56.8''E$, elevation ~ 200 m) from 3rd June to 22nd July 2017. Tea is grown between $49^{\circ}N$ and $33^{\circ}S$, optimally in regions with greater than 1000–1400 mm annual rainfall and mean annual temperatures above $14^{\circ}C$ (Shoubo, 1989). This area of Fujian province has a subtropical maritime monsoon climate with an annual average temperature of $16.9^{\circ}C$ and average annual rainfall of 1628 mm, making it a prime location for tea production (Kang *et al.*, 2017). Tea in Fujian Province, and at Shanfu Tea Company in particular, is harvested from April to September (Yao *et al.*, 2020a; Shanfu Tea Company, personal communication). However, production of Eastern Beauty oolong does not begin until June or July when leafhoppers become abundant in most years (Wang *et al.*, 2013; Shi *et al.*, 2015). Two adjacent fields (hereafter A and B) planted with the same tea cultivar (Tie Guan Yin) were used for this experiment. Tea plants in both fields were of similar age (ca. 30 years, according to the farm manager). Field A was on a slope facing north-east and Field B faced south and south-west. In each field, we labelled 10 randomly chosen plants.

A temperature sensor and datalogger (HOBO 8k Pendant® temperature data logger, Onset Computer Corporation, Bourne, Massachusetts) 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 used to calculate minimum, mean, and maximum daily temperatures. Precipitation data were obtained for a weather station in nearby Sanming for June and July 2017 from the

Chinese Agricultural Academy of Sciences. Temperature data from this weather station between 19th June and 2nd July were prepended to the data logger data to allow testing of delayed effects of weather conditions experienced by leafhoppers and tea plants before the start of the study (see Section 2.4). Mean daily temperature from the weather station and data logger were strongly correlated (Pearson's $r = 0.99$) and on average very similar ($\text{RMSE} = 0.48^\circ\text{C}$). Temperature data were missing for a total of 22 h across 2 days (24–25 May) due to instrument error. Because our modelling efforts (see Section 2.4) included lagged temperature effects, any observations within 15 days of these missing values would be excluded from the model data. Instead, we opted to impute the missing hourly data using the Amelia II programme (R package *amelia*) before aggregating to daily temperature minimum, mean, and maximum (Honaker *et al.*, 2011). Results with and without imputed data points were qualitatively similar (not shown).

Insect population growth

Empoasca onukii (Cicadellidae) is a common and widespread pest on tea (Jin *et al.*, 2012; Fu *et al.*, 2014). After hatching, leafhoppers pass through four nymphal instars before becoming winged adults about 3 mm long (Fu *et al.*, 2014). Development to adults can take between 8 and 14 days, depending on temperature, and the lifespan of adults in the field is unknown (Shi *et al.*, 2015). Adult females pierce young tea stems, petioles, and leaf mid-veins and oviposit under the epidermal tissue (Hou *et al.*, 2020; Yao *et al.*, 2020b). *Empoasca onukii* nymphs and adults feed on young leaves by rupturing cells, injecting a watery saliva, and ingesting fluids (Backus *et al.*, 2005; Jin *et al.*, 2012). *Empoasca onukii* feeding 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” (Backus *et al.*, 2005).

Each day at 6:00 hours, we counted leafhoppers on the undersides of the second leaf from the apical meristem of 30 or 50 haphazardly chosen shoots on these plants. *Empoasca onukii* is the only common leafhopper pest on tea (Mao *et al.*, 2014). All nymphal instars and adults of *E. onukii* were counted. We did not distinguish among life stages, since it is likely that adults are underrepresented by this sampling method, as they can escape more quickly in response to disturbance (Shi *et al.*, 2015). 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 24th June. Leafhopper counts were performed by three observers and observer ID was recorded along with the count data. Leafhopper counts were collected every day from 5th June to 24th July 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 28th June, 8th July, and 22nd July. Field B was harvested on 8th June, 13th July, and 24th July. Each combination of field and inter-harvest period (hereafter “harvest”) experienced a unique weather history and is treated as a blocking factor. Because our study began only 3 days before the first harvest of Field B, we excluded this first inter-harvest period from our analyses. At our request, all

harvests followed a plucking grade of two leaves and a bud, and the leaves were processed as Eastern Beauty oolong.

Plant shoot growth

Shoot growth was assessed using the plants marked for insect density counts. Seven actively growing shoots per plant were labelled 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 were harvested, young shoots were plucked from all plants in the field, including the plants we labelled. 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.

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 1 day ago, 2 days ago, etc.) as independent predictor variables would result in overfitting. Furthermore, the choice of how to discretise lag (days, weeks, etc.) is arbitrary, resulting in many possible models that could be tested. Rather than including weather variables at discrete time lags as covariates, we take a functional modelling approach. Functional models include a covariate that is a continuous function, such as a smooth function of weather over time, rather than using observations at different lag times as multiple covariates (McLean *et al.*, 2014; Teller *et al.*, 2016).

In addition to lagged effects, the effects of weather on leafhoppers and tea are expected to be non-linear because, for example organisms tend to have temperature optima with lower performance at higher and lower temperatures (Roitberg & Man gel, 2016). In order to accommodate potentially non-linear relationships with weather and through time, we used distributed lag non-linear models (DLNMs) (Gasparrini *et al.*, 2017). DLNMs model potentially delayed effects of predictor variables by fitting a bi-dimensional dose-lag-response association spline (called a “crossbasis” function) where the effect of a predictor can vary non-linearly through lag time and across predictor intensity. We constructed DLNM crossbasis functions using the *dlnm* package in R (Gasparrini, 2011) with a maximum lag effect of 15 days. This lag time was chosen to capture lagged effects during the development from first instar to adults, reported to be 14.1 days on average at a constant 25°C (Shi *et al.*, 2015). Penalised cubic regression splines were used for both dimensions with 10 knots for the response dimension and 14 knots for the lag dimension. The crossbasis functions were fit to data in the context of generalised additive models (GAMs) using the *mgcv* package in R with restricted maximum likelihood (Wood, 2017). In the process of fitting the model to data, the penalty on the

crossbasis smooth (and other smoothed terms) is optimised such that more linear shapes are favoured unless the data supports non-linearity. The model output reports effective degrees of freedom (edf), which represent the degree of non-linearity of fitted penalised splines. Preliminary analyses revealed high concavity between the temperature and precipitation cross-basis functions (Wood, 2008, 2017) (Fig. S1). To avoid unstable estimates resulting from this concavity, we fit separate models for precipitation, minimum daily temperature, mean daily temperature, and maximum daily temperature. We compared models using Akaike's Information Criterion (AIC) to determine, which weather variable model best fit the data (i.e. the model with the lowest AIC) (Burnham & Anderson, 2010; Wood *et al.*, 2016).

Effects of weather on leafhopper counts were modelled with the number of leafhoppers per plant as the response with an offset of number of leaves sampled per plant. The offset accounted for variation in sampling effort and to put the expected values in units of leafhoppers per leaf. Predictors included the crossbasis function for the weather variable over the past 15 days and a smooth function (cubic regression spline) of the number of days post-harvest. Days post-harvest is included as a covariate to test for an effect of harvesting shoots on leafhopper population density. In addition, the model included random effects of the harvest period blocking factor, the plant ID, and the observer who collected the observation. This GAM was fit using a Poisson family error distribution with a log link.

Linear shoot growth rate was calculated as the difference between height on the day measured and height on the previous day. Growth was modelled using the same predictors as in the leafhopper models with the addition of a smooth function of stem diameter as a covariate and the removal of random effect of observer since all shoot measurements were taken by the same person. We used a scaled t family error distribution because residuals followed a leptokurtic Gaussian distribution when a Gaussian family error distribution was used.

For each weather variable and response (leafhopper density or shoot growth) combination, we tested the significance of the crossbasis function with two likelihood ratio tests. First, we performed a likelihood ratio test comparing our full DLNM with a model that replaces the crossbasis function with the mean weather variable over the past 15 days as a simple fixed effect. A significant *P*-value shows that the crossbasis function (with potentially lagged and non-linear effects of weather) is a better predictor of leafhopper density or shoot growth than simply the mean weather conditions over the past 15 days. Second, we performed a likelihood ratio test of the full DLNM against a null model without a weather variable predictor (but still including covariates and random effects). A significant *P*-value for this test indicates a significant (non-linear, lagged) effect of the weather variable. For the *P*-values from these tests to be reliable, we constrained the smoothing penalties of covariates and random effects to keep estimated degrees of freedom similar for these terms across models (Wood, 2017).

Results

Mean daily precipitation (\pm SD) was 7.1 ± 11.7 mm with 62% of the days having some rain (Fig. 1a). The average minimum,

mean, and maximum daily temperatures over the experiment were 23.3, 26.9, and 33.8 °C, respectively (Fig. 1b).

Leafhopper population growth

Leafhopper density averaged 0.056 ± 0.046 leafhoppers per young leaf. Leafhopper densities were higher in field A on all but three dates (Fig. 1c). For leafhopper densities, the model with the lowest AIC was minimum daily temperature, followed by maximum daily temperature, mean daily temperature, and precipitation (Table 1).

The crossbasis functions of daily minimum, mean, and maximum temperatures over the previous 15 days were highly significant compared to both the mean over the past 15 days and a null model without a temperature predictor (Table 1). The DLNM for daily minimum temperature indicated that low minimum temperatures reduced leafhopper density (Fig. 2a). However, these results should be interpreted cautiously as only 4 days in the weather data had minimum temperatures below 18 °C, and only nine dates of leafhopper observations had these cool temperatures in their weather history. Therefore, certain combinations of low temperature and lag time were not observed in this experiment (represented by grey shading in Fig. 2). While the data do show some evidence for a delayed effect (by greater than 9 days) of minimum temperatures below 18 °C, we do not have the data to make any conclusions about more immediate effects of temperatures this low. The DLNM for mean daily temperature shows that leafhopper density declines as the temperature at around 9 days lag increases (Fig. 2b). This effect is non-linear with leafhopper density increasing as temperature rises up to about 22 °C, after which there is little effect of daily mean temperature (Fig. 2b). There was little effect of recent mean daily temperature on leafhopper density. The DLNM for maximum daily temperature showed similar patterns to mean daily temperature (Fig. 2c).

The crossbasis function for precipitation was also significant compared to both the mean precipitation over the previous 15 days and null model (Table 1). In the DLNM, high precipitation had a positive effect on leafhopper densities. The strongest effect of precipitation was at 12 days lag where there was a monotonic increasing relationship between precipitation and leafhopper density (Fig. 2d). More recent effects (1–5 days lag) of precipitation on leafhopper densities were minimal.

Number of days post-harvest had a linear negative effect on leafhopper density, although this effect was slight and was only significant ($P < 0.05$) in the mean temperature model (Fig. S2).

Plant shoot growth

Daily shoot growth rate during the study averaged 0.28 ± 0.38 cm day $^{-1}$ (mean \pm SD). For shoot growth, the minimum temperature model had the lowest AIC, followed by mean and maximum temperature, which were essentially equivalent (models within two AIC are considered equivalent), and then precipitation (Table 2).

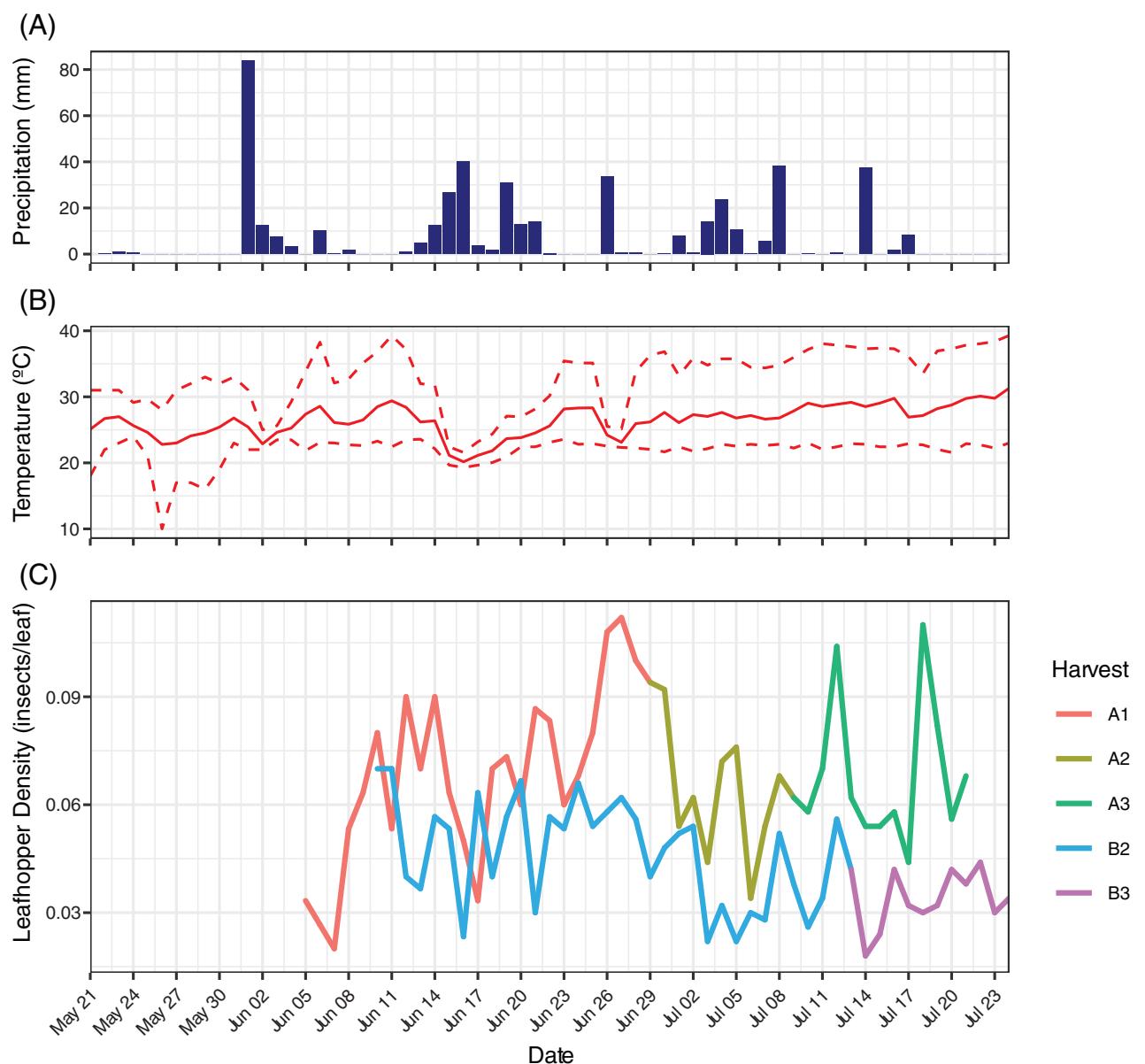


Fig. 1. Weather patterns and leafhopper densities over the course of this study (5th June through 26th July 2017). Precipitation data from weather station in Shaxian, Fujian Province, China (a). Mean (solid line), minimum, and maximum (dashed lines) temperatures from data logger on site (b). Mean number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

The crossbasis functions of daily minimum, mean, and maximum temperatures over the previous 15 days were highly significant compared to both the mean over the past 15 days and a null model without a temperature predictor (Table 2). The DLNMs for daily minimum, mean, and maximum temperature showed significant positive effects of increasing temperature on shoot growth in their respective models (Fig. 3a–c). Temperature effects were mostly immediate, with negligible effects of temperature lagged past 5 days (Fig. 3a–c). The relationship between temperature and shoot growth shows little effect of minimum temperatures above 21 °C, mean temperatures above

25 °C, or maximum temperatures above 30 °C, and little effect of temperature beyond 5 days of lag (Fig. 3a–c).

The DLNM for precipitation also showed a significant effect on plant growth (Table 2), but the shape of the crossbasis function is more complex (Fig. 3c). At 1 day lag, the optimum precipitation for growth is 12 mm (growth rate = 0.19 cm day⁻¹) with a modest decrease in growth at the low end of observed precipitation (0.16 cm day⁻¹ at 0 mm) and substantial decreases at the high end of observed precipitation (0.11 cm day⁻¹ at 44 mm). The DLNM also indicates a lagged effect of precipitation on shoot growth with the highest growth rates occurring at high

Table 1. Model statistics and results of likelihood ratio tests for distributed lag non-linear models (DLNM) with leafhopper density as a response variable.

	DLNM		LRT 1			LRT 2		
	R ²	ΔAIC	d.f.	χ ²	P	d.f.	χ ²	P
Minimum daily temp.	0.28	0	18.7	79.2	<0.001	19.7	80.8	<0.001
Mean daily temp.	0.29	6.8	21.7	56.8	<0.001	22.6	78.6	<0.001
Maximum daily temp.	0.28	9.1	19.5	47.4	<0.001	20.4	71.6	<0.001
Total daily precip.	0.29	7.5	24.7	57.8	<0.001	25.7	82.3	<0.001

Separate models using each weather variable as a predictor are shown with the adjusted R^2 and ΔAIC for the full model. The ΔAIC is the difference in AIC between a model and the model with the lowest AIC (i.e. the best fit to the data, $\Delta\text{AIC} = 0$). In addition, the results of two likelihood ratio tests comparing the full DLNM to a reduced model are shown. In the first test (LRT 1), the DLNM is compared to a model replacing the crossbasis function with the mean conditions over the past 15 days from an observation. In the second test (LRT 2), the DLNM is compared with a null model that includes covariates and random effects, but no weather variable. Degrees of freedom (d.f.) is the difference in model estimated degrees of freedom.

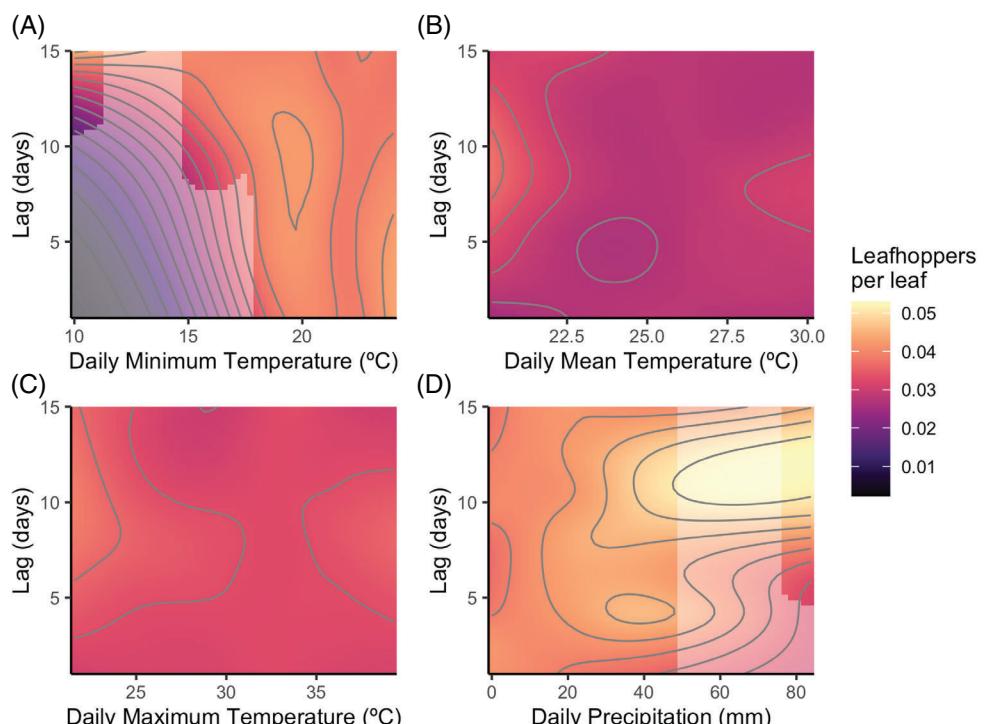


Fig. 2. Partial effects plot for the lagged effect of weather on leafhopper density from distributed lag non-linear models, including daily minimum temperature (a), daily mean temperature (b), or precipitation (c) as a predictor. Plots show predicted leafhopper densities from a two-dimensional cross-basis smooth and can be interpreted as the predicted effects of precipitation or temperature at lag times of 1–15 days, all else being equal. The highest leafhopper densities occurred when there were cool mean temperatures and high precipitation 9–12 days previous to an observation, but higher minimum temperatures on recent days. Greyed-out areas represent predicted values, which are too far from observed data to be reliable.

precipitation with 12 days of lag (Fig. 3c). Stem diameter had a significant effect on growth with wider shoots growing faster in all models (all $P < 0.001$) (Fig. 4a). Number of days post-harvest was only a significant covariate in the temperature models and had a non-monotonic relationship with growth rate decreasing after 10 days post-harvest (Fig. 4b).

Although the crossbasis functions were statistically significant for all shoot growth models, the adjusted R^2 values for these models were low (<0.1 ; Table 2), indicating there was still a large amount of unexplained variation in daily growth rate.

Discussion

Our distributed lag non-linear modelling approach revealed contrasting effects of weather on leafhopper density and tea shoot growth, both in the direction and delay of the response. Leafhopper density was highest in wetter and cooler conditions, and tea shoot growth was highest in warmer, drier periods relative to mean conditions during the study. This contrasting response of tea plants and leafhoppers could potentially compound the effects of weather on herbivory. For example because expanding

Table 2. Model statistics and results of likelihood ratio tests for distributed lag non-linear models (DLNM) with tea shoot growth as a response variable.

	DLNM		LRT 1			LRT 2		
	R ²	ΔAIC	d.f.	χ ²	P	d.f.	χ ²	P
Minimum daily temp.	0.095	0	19.4	162	<0.001	20.3	163	<0.001
Mean daily temp.	0.095	0.4	20.9	134	<0.001	21.7	164	<0.001
Maximum daily temp.	0.095	1.2	20.4	128	<0.001	21.1	162	<0.001
Total daily precip.	0.093	18.3	27.9	148	<0.001	28.9	158	<0.001

Separate models using each weather variable as a predictor are shown with the adjusted R^2 and ΔAIC for the full model. The ΔAIC is the difference in AIC between a model and the model with the lowest AIC (i.e. the best fit to the data, $\Delta\text{AIC} = 0$). In addition, the results of two likelihood ratio tests comparing the full DLNM to a reduced model are shown. In the first test (LRT 1), the DLNM is compared to a model replacing the crossbasis function with the mean conditions over the past 15 days from an observation. In the second test (LRT 2), the DLNM is compared with a null model that includes covariates and random effects, but no weather variable. Degrees of freedom (d.f.) is the difference in model estimated degrees of freedom.

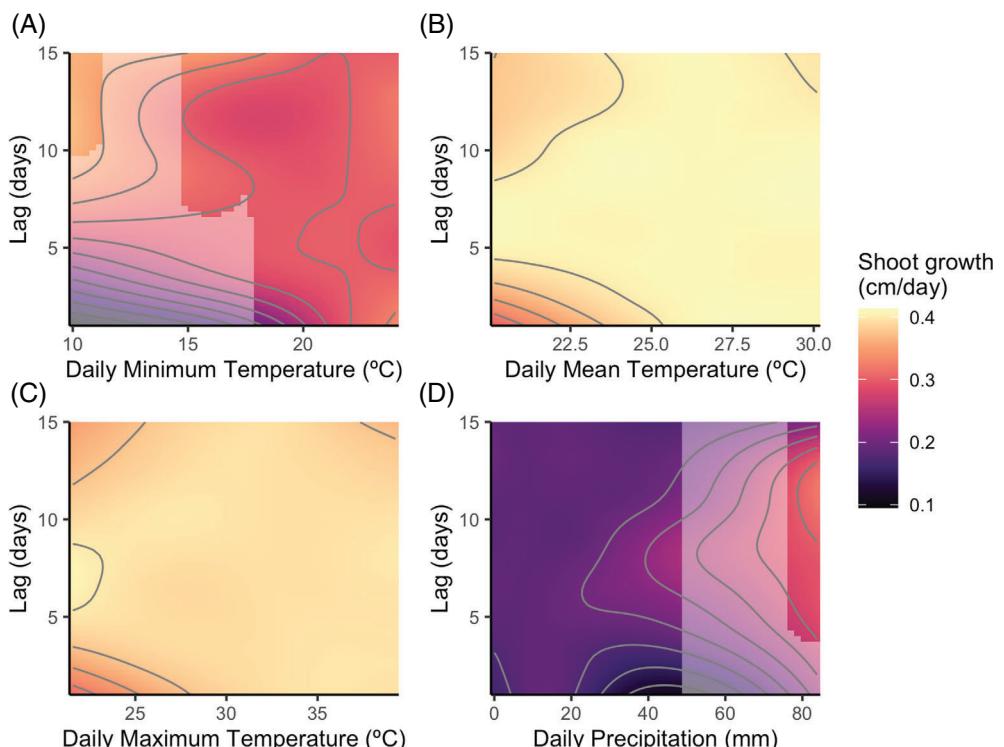


Fig. 3. Partial effects plots for the effects of weather on tea shoot growth from distributed lag non-linear models, including daily minimum temperature (a), daily mean temperature (b), or precipitation (c) as a predictor. Plots show predicted shoot growth from a two-dimensional cross-basis smooth and can be interpreted as the predicted effects of precipitation or temperature at lag times of 1–15 days, all else being equal. Greyed-out areas represent predicted values, which are too far from observed data to be reliable.

young leaves are often the most vulnerable to herbivory by insects (Boege & Marquis, 2005), the relative amount of leaf damage (i.e. percent leaf area removed) can increase with slower leaf maturation (Moles & Westoby, 2000). Responses of tea shoot growth to temperature and precipitation were essentially immediate, while mean and maximum temperature had only a delayed effect on leafhopper densities, and the effects of precipitation and minimum temperature on leafhoppers were both immediate and delayed.

Leafhopper density increased when precipitation was high and mean and maximum temperatures were low, which suggests that desiccation may be an important source of mortality for *E. onukii*

in the field. Mao *et al.* (2014) also found that lower maximum daily temperatures and higher minimum daily temperatures corresponded to higher *E. onukii* densities in a field study in Wuhan, Hubei Province, which has a similar summer climate to Fujian Province. However, this study did not account for non-linearity or delayed effects of weather variables.

The negative impact of increased temperature and precipitation on leafhoppers could be due to direct or indirect effects. The negative effects of warm and dry conditions on leafhopper densities were delayed, having the strongest effect 9–12 days prior to measurement suggesting the possibility of negative direct effects on earlier life stages, which are less conspicuous. For example

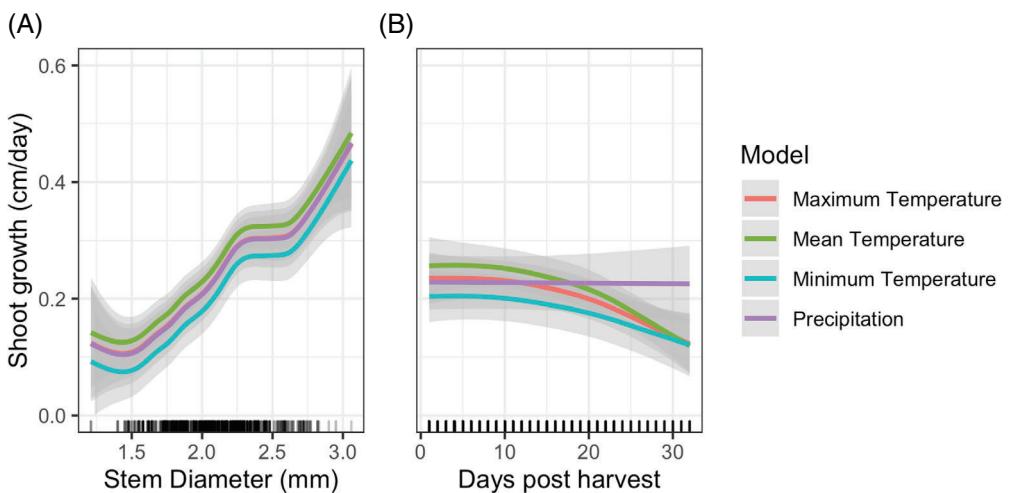


Fig. 4. Predicted effects of covariates from shoot growth distributed lag non-linear models. Plots show the effect of stem diameter (a) and number of days post-harvest (b) on shoot growth (cm day^{-1}). Predicted effects of covariates differed only slightly between the models. The effect of days post-harvest is not statistically significant for the model with precipitation as a predictor.

eggs are unaccounted for in this study and first instar nymphs may be underestimated because they are very small, colourless, and therefore, likely less detectable 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 detectable, the effects of that mortality on population densities would become noticeable. Although development rates of *E. onukii* under variable conditions has not been documented to our knowledge, Reineke and Hauck (2012) reported an average development time of 5.9 days from egg to second instar and 8.7 days from egg to third instar (at 15 °C night, 25 °C day) for a related species, *Empoasca vitis*. In addition, high temperatures had a stronger detrimental effect on eggs and early instars of *E. vitis* compared to later life stages. 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 or survival of early instar nymphs. It is also possible that adverse weather conditions affect the oviposition rates of adult female leafhoppers resulting in a delayed effect on nymph densities. Future field and lab studies that track *E. onukii* life stages separately might be able to infer the exact nature of these delayed effects.

Daily minimum temperature and precipitation also had immediate effects in addition to delayed effects, which may be more indicative of leafhopper behavioural responses. For example we searched for leafhoppers early in the morning because at cooler temperatures they are slower to hide deeper in the canopy and thus easier to find. Warmer minimum temperatures within the range we observed (the un-greyed area at the bottom of Fig. 2a) resulted in slightly lower leafhopper densities, but this could be due simply to lower detection probability as leafhoppers became more active. Similarly, recent high precipitation (the bottom of Fig. 2d) resulted in lower leafhopper densities, and this could be a result of leafhoppers seeking shelter deeper in the tea canopy.

Alternatively, the negative impact of high temperatures on leafhoppers 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. In addition, 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 weather (Kowalsick *et al.*, 2014; Kfouri *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.

In contrast to leafhoppers, tea shoot growth was favoured by warmer temperatures and low precipitation. While we did not measure photosynthetic activity or water stress, these results suggest that tea plants in this experiment were not water limited, which is expected as this region receives ample rainfall for tea cultivation. Temperature and precipitation were correlated in this study, and precipitation may more accurately represent a proxy for sunlight and photosynthetic activity since high recent 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). In fact, there is a delayed positive effect of precipitation indicated by our model, which could possibly reflect a positive effect of high soil moisture (i.e. rain in the past). The relatively low R^2 values for the shoot growth models compared to leafhopper models may indicate that tea is less sensitive to fluctuations in temperature and precipitation on a short time scale. Alternatively, there may be other factors that explain variation in growth rate among shoots that we have not included in our models. For example although only shoots that were actively growing after a harvest were sampled, we cannot be certain that all shoots were at a similar developmental stage.

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 a previous study that investigated the effects of leafhoppers on tea metabolites (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.

Our results have implications for tea production in this region. Cooler, wetter summer weather may favour production of so-called “bug-bitten” tea, which relies on leafhopper herbivory for increased quality (Cho *et al.*, 2007; Scott *et al.*, 2020). Warmer and drier summer weather, on the other hand, might be an indicator of upcoming low leafhopper densities and may favour more traditional tea production. However, the changes in tea chemistry that result from leafhopper herbivory are complex and it is still unclear precisely how leafhopper density affects finished tea quality (Scott *et al.*, 2020). More studies that track the effects of climate change on herbivores and tea quality from farm to cup are needed before comprehensive management guidelines for bug-bitten tea can be fully developed.

In southern China where this study was conducted, tea growing regions are predicted to experience a 2–5 °C increase in mean temperatures over the next century, as well as fewer rainy days (Wang *et al.*, 2010; Boehm *et al.*, 2016). Our models predict this warming to be detrimental to leafhoppers and beneficial to tea shoot growth. This would make Eastern Beauty oolong production less feasible in this region. However, we suspect that the responses of tea plants and leafhoppers to climate change will vary widely over tea growing regions. 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).

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 June and July, 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 intra-annual variability in weather under realistic field conditions in order to understand future impacts of climate change on crop pests and other plant–insect interactions.

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Author contributions

ERS, CMO, XL, and W-YH conceived and designed the study. W-YH and XL selected and secured the use of the field site. ERS and J-PW collected data in the field. XL and W-YH procured precipitation data. ERS analysed the data and led the writing of the manuscript with contributions from CMO. All authors contributed significantly to the drafts and gave their final approval for publication.

Data availability statement

All data and analysis code are archived with Zenodo at <https://doi.org/10.5281/zenodo.3964647>.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1: Relationship between daily total precipitation and daily mean temperature for the duration of this experiment and 15 days prior to the first observation. Fit line is a penalised cubic spline $\pm 95\%$ confidence interval. We fit a GAM for shoot growth using both cross-basis smooths for precipitation and temperature as predictors along with co-variates of days post-harvest and stem diameter with random effects of harvest and plant ID. We then checked for concavity with the *concurvity()* function in the *mgcv* package. Concurvity is calculated with three different indices. For the temperature cross-basis, the “worst” index was one, the “observed” index was 0.81, and the “estimate” index was 0.82. For precipitation, the “worst” index was one, the “observed” index was 0.96, and the “estimate” index was 0.98. Inspecting pairwise concavity showed that precipitation had high concavity with temperature (worst = 1.0, observed = 0.92, estimate = 0.96).

Figure S2. Marginal effect of days post-harvest on leafhopper density on young shoots. The effect is only significant for the model with daily mean temperature as a response ($P = 0.021$).

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