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ORIGINAL PAPER

Timing matters: remotely sensed vegetation greenness can predict insect vector migration and therefore outbreaks of curly top disease

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Abstract

Due to climate change, outbreaks of insect-vectored plant viruses have become increasingly unpredictable. In-depth insights into region-level spatio-temporal dynamics of insect vector migration can be used to forecast plant virus outbreaks in agricultural landscapes; yet, it is often poorly understood. To explore this, we examined the incidence of *beet curly top virus* (BCTV) in 2,196 tomato fields from 2013 to 2022. In America, the beet leafhopper (*Circulifer tenellus*) is the exclusive vector of BCTV. We examined factors associated with BCTV incidence and spring migration of the beet leafhopper from non-agricultural overwintering areas. We conducted an experimental study to demonstrate beet leafhopper dispersal in response to greenness of plants, and spring migration time was estimated using a model based on vegetation greenness. We found a negative correlation between vegetation greenness and spring migration probability from the overwintering areas. Furthermore, BCTV incidence was significantly associated with spring migration time rather than environmental conditions *per se*. Specifically, severe BCTV outbreaks in California in 2013 and 2021 were accurately predicted by the model based on early beet leafhopper spring migration. Our results provide experimental and field-based support that early spring migration of the insect vector is the primary factor contributing to BCTV outbreaks. Additionally, the predictive model for spring migration time was implemented into a web-based mapping system, serving as a decision support tool for management purposes. This article describes an experimental and analytical framework of considerable relevance to region-wide forecasting and modeling of insect-vectored diseases of concern to crops, livestock, and humans.

Keywords Enhanced vegetation index · Flight behavior · Migration mapping · Satellite imagery

Introduction

Outbreak patterns of crop diseases and pests are becoming increasingly unpredictable in both space and time due to global environmental changes (e.g., climate change, biodiversity loss, and urbanization) (Knops et al. 1999; Johnson et al. 2010; Roossinck and García-Arenal 2015; Harvey et al. 2020). Effective spatio-temporal forecasting of outbreaks and epidemiology of crop diseases and pests is needed to meet the demand of 60% increase in food production to feed 10 billion people by 2050 (Fedoroff 2015; Ristaino et al. 2021). Globally, crop diseases and pests cause significant yield losses in major food crops, including: wheat (21.5%), rice (30.0%), maize (22.5%), potato (17.2%), and soybean (21.4%) (Savary et al. 2019). Plant-pathogenic viruses account for about 50% of plant disease epidemics worldwide (Anderson et al. 2004; Jones and Naidu 2019). Most plant-pathogenic viruses are dependent on insect vectors for their ability to infect crops (Whitfield et al. 2015), and management of diseases caused by insect-transmitted viruses focuses primarily on management of the insect vectors (Perring et al. 1999).

Predictive modeling approaches have been widely used to assess risks of plant-pathogenic viruses and to develop effective management strategies (Jones et al. 2010; Juroszek

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and von Tiedemann 2015). Spatio-temporal modeling of the epidemiology of plant-pathogenic virus outbreaks is typically driven by ambient temperatures, as these are assumed to drive insect vector population dynamics and their dispersal propensity (Canto et al. 2009; Zeilinger et al. 2017; Donnelly and Gilligan 2022; Vasquez et al. 2022). However, prediction of transmission time of plant-pathogenic virus by insect vectors is crucial for optimizing the timing of pest management interventions. Furthermore, understanding insect vector migration may provide valuable insight into dynamics of spatio-temporal patterns as insect vectors migrate over long distances and between agricultural and non-agricultural landscapes (Jeger et al. 2018).

Here, we describe a study of beet leafhopper, *Circulifer tenellus* (Baker) (Hemiptera: Cicadellidae), the only known vector of *beet curly top virus* (BCTV) (Geminiviridae) in the New World (Stahl and Carsner 1923). BCTV is an economically important plant-pathogenic virus in the western US infecting several crops, including tomato, *Solanum lycopersicum* L. (Solanaceae), sugar beet, *Beta vulgaris* L. (Amaranthaceae), pepper, *Capsium annum* L. (Solanaceae), common bean, *Phaselous vulgaris* L. (Fabaceae), and potato, *S. tuberosum* L. (Solanaceae) (Bennett 1971). In 2013 in the San Joaquin Valley of California, a BCTV outbreak caused ~$100 million loss in tomato production (Chen and Gilbertson 2016). Another major BCTV outbreak occurred in the Sacramento Valley in 2021 (Figure S1). In California, overwintering viruliferous (carrying BCTV) beet leafhoppers migrate from coastal mountain ranges (referred to here as "coastal foothills"), to crop fields in the spring (Lawson et al. 1951; Douglass and Cook 1954). Spring migrations of beet leafhoppers have been hypothesized as being elicited by host plant senescence in coastal foothills (Lawson et al. 1951; Cook 1967), but this hypothesis has never been tested experimentally. We describe the first model-based forecasting of beet leafhopper spring migrations from coastal foothills into crop fields in the Sacramento and the San Joaquin Valleys (Figure S2). The over-arching hypothesis is that onset of spring migration by beet leafhoppers from coastal foothills is triggered by a combination of low greenness of natural vegetation (loss of food source) and ambient temperatures above a specific threshold. To address this hypothesis, individual plants from two species [sugar beet and redstem filaree, *Erodium cicutarium* (L.) L'Hér. (Geraniaceae)] were experimentally infested with beet leafhoppers. The relationship between plant greenness and beet leafhopper flight propensity was determined experimentally to evaluate the greenness index as a potential predictor for spring migration. Temporal dynamics of spring migration of beet leafhoppers were monitored at three field sites during two seasons. Ambient temperatures and vegetation greenness (derived from freely available satellite imagery) were used as explanatory variables of spring migration timing. The spring migration model was implemented into a web-based mapping system at landscape scale as a forecasting tool of spatio-temporal dynamics of beet leafhopper migration. We investigated potential causative trends in spring migration timing and other environmental conditions for incidence of BCTV symptoms in tomato fields for the past 22 years. The model accurately predicted major BCTV outbreaks in 2013 and 2021 as years with unusually early spring migration timing from coastal foothills.

Materials and methods

Plant greenness effects on flight propensity of beet leafhoppers

We measured departure rates from each host as an indicator of flight propensity of beet leafhoppers. Two host plants were selected: redstem filaree and sugar beet as an inferior and superior host plant, respectively. Redstem filaree seeds were collected from plants growing in coastal foothills in Kings County, California (36.038°N, –120.115°W), and sugar beet seeds were obtained from commercial seed suppliers. Plants were watered daily and fertilized with 0.5% soluble N-P-K fertilizer (6:1:4) in 200 ml of water in a greenhouse (25 ± 5 °C and 80 ± 10% RH). Four weeks after emergence, we generated variations in plant greenness of redstem filaree (n = 60) and sugar beet (n = 59) by not watering the plants for various durations (0, 3, 6, and 9 days) at 35 °C and 50% RH in a Conviron E7 growth chamber (Conviron, Winnipeg, Canada). Inside a mesh dorm cage (61 × 61 × 61 cm, Megaview Science, Taichung, Taiwan), four yellow sticky cards (15.2 × 20.3 cm) were placed around a plant and then ten adult beet leafhoppers were released. After 24 h, we counted beet leafhoppers on yellow sticky cards as an estimate of flight propensity. Subsequently, plant greenness was measured using a hyperspectral camera (PIKA L; www.resonon.com) as described in Nguyen and Nansen (2020) (Fig. 1a). Enhanced vegetation index (EVI) was calculated for aerial parts of the plant using the bands positioned at 850–880 nm (near-infrared), 640–670 nm (red), and 450–510 nm (blue). The equation and parameters for EVI calculation were the same as the moderate resolution imaging spectroradiometer (MODIS) EVI algorithm (Didan et al. 2015). We performed regression analysis to examine relationships between plant greenness and flight propensity for each plant species using a generalized linear model (GLM). Analysis of covariance (ANCOVA) was used to determine host plant species-specific effects on the relationship between EVI decrease and flight propensity. All statistical analyses were performed in R version 4.1.2 (R Core Team 2021) with $\alpha = 0.05$.

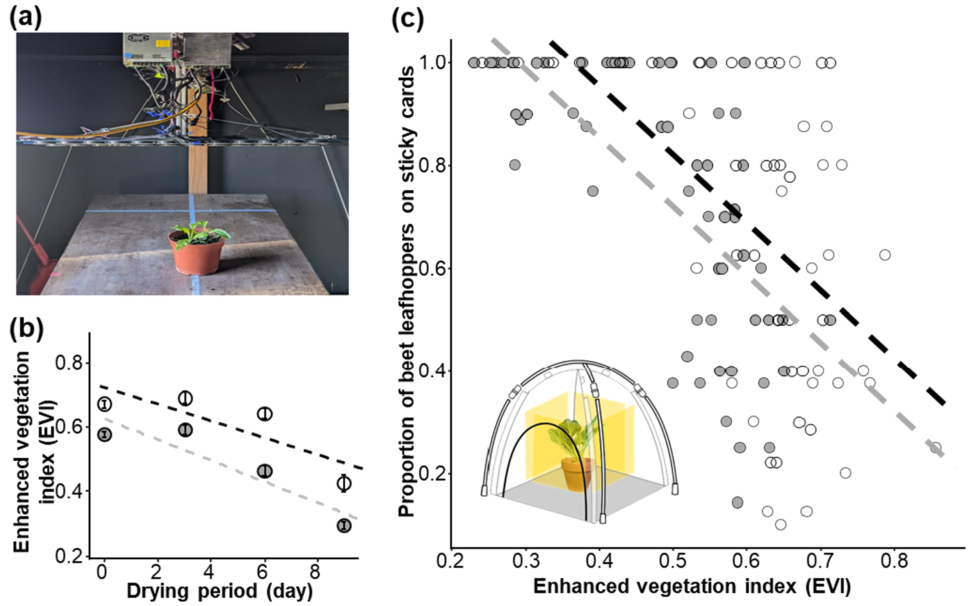


Fig. 1 Plant greenness dependent beet leafhopper flight propensity. **a** Hyperspectral imaging system for measuring plant greenness. **b** Enhanced vegetation index (EVI) (mean ± SEM) changes in redstem filaree (gray dots) ($n = 60$) and sugar beet (open dots) ($n = 59$) plants according to drying period. **c** Relationships between EVI value and flight propensity of beet leafhoppers on redstem filaree and sugar beet. Linear regressions for redstem filaree (gray dashed line) and sugar beet (black dashed line)

Beet leafhopper spring migration modeling

Seasonal dynamics of beet leafhopper flights, and timing of spring migration in particular, was monitored from January 2019 to June 2020 at the base of coastal foothills in Fresno (36.629°N, –120.641°W), Kings (36.038°N, –120.115°W), and Kern (35.124°N, –119.509°W) counties in California. At each site, ten yellow sticky cards (15.2 × 20.3 cm) were deployed 1 m above the ground. Yellow sticky cards were replaced biweekly (every two weeks), and beet leafhoppers on the cards were counted using a binocular stereomicroscope (Olympus SZ51; Olympus, Tokyo, Japan). To compare spring migration timing among study sites and years, numbers of migrating beet leafhoppers were transformed into cumulative proportions. EVI values of the study sites were extracted from 16-day composites MODIS EVI (MOD13Q1 from Terra) at a spatial resolution of 250 m (Didan 2015). The relationship between cumulative proportion of migrating beet leafhoppers and EVI value was modeled using a Weibull function:

$$f(t) = 1 - \exp\left[-\left(\frac{\mathrm{EVI}_t}{a}\right)^b\right]$$

where $f(t)$ and EVI_t are the cumulative proportion of migrating beet leafhoppers and the EVI values at Julian day t, respectively. The parameters, a and b, determine the scale and shape of the Weibull function, respectively. All parameters were estimated with a least-squares method and iterative process of Gauss–Newton using R version 4.1.2 (R Core Team 2021).

Surveys for BCTV symptoms in tomato fields

The incidence of BCTV symptoms was surveyed 2,196 commercial tomato fields in California from 2013 to 2022 (Table S1). In some years and regions, surveys were not carried out due to the COVID-19 pandemic or low levels of threat. The surveys were conducted each year from April to October, with staggered planting schedules establishing the timeline. An entire tomato field was broken down into blocks, and a survey was conducted in randomly selected 6–8 blocks per field. A large portion of a block was walked in a zig-zag pattern, inspecting 100 plants at random during each walk-through. Plants were examined for BCTV symptoms such as leaf curling, stunted growth, early fruit onset, purple leaves and veins, and yellow or light green discoloration. The incidence of BCTV symptoms was assigned to each block of the field based on the number of damaged plants out of the inspected plants. The overall incidence for the field was calculated as the average of logit transformed incidences across the inspected blocks. For each region, a one-way ANOVA and pairwise comparisons (Tukey's HSD test) were conducted to test whether the incidence of BCTV symptoms differed significantly by year.

Annual trends in winter environmental conditions and spring migration timing

We evaluated mean winter environmental conditions over the areas in coastal foothills categorized as shrubland, grass/pasture, and fallow/idle lands by the National Agricultural Statistics Service (NASS) (Boryan et al. 2011). The level III ecoregion classification from the US Environmental

Protection Agency (USEPA) was used to geographically select coastal foothills in California (https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states). Mean winter environmental conditions were calculated from January to March between 2001 and 2022. Over the selected regions, mean values of daily temperature, monthly total precipitation, and 16-day EVI were obtained from MODIS product MOD11A1 (Terra daily 1 km) (Wan et al. 2021), (Daly et al. 2008) and MOD13Q1 (Terra 16-day 250 m) (Didan 2015), respectively. In addition, spring migration probability over coastal foothills was calculated using the spring migration model based on the EVI value of each pixel with 15.56 °C as the minimum threshold temperature for flight activity (Lawson et al. 1951). At each pixel, we considered spring migration to occur when the migration probability reached 0.5. The annual trends in spring migration timing for the Sacramento Valley and the San Joaquin Valley were described using a logistic function:

$$f(x) = \frac{1}{1 + e^{-k(x-x_0)}}$$

where $f(x)$ is the proportion of spring migration-occurred area at x Julian day, and k and x_0 are estimated parameters representing the steepness and the midpoint of the curve, respectively. The midpoints of individual logistic curves (x_0) were considered median spring migration times and compared to estimate variations in annual spring migration timing. We performed regression analysis to examine the relationship between the winter environmental conditions (i.e., temperature, precipitation, and EVI) and the median spring migration times (i.e., x_0) with surveyed incidence of BCTV symptoms in tomato fields using a GLM.

Results

Flight propensity of beet leafhopper

For this highly controlled experiment (controlled drought regimes, experimental infestations of individual plants with beet leafhoppers, and optical sensing under controlled/artificial lighting) to be relevant to the study hypothesis, hyperspectral optical sensing data needed to be converted into a measurement of vegetation greenness that would be available via satellite imagery. There is ample evidence supporting the notion that leaf reflectance features can be used to detect plant responses to biotic and abiotic stressors (Jackson 1986; Nansen and Elliott 2016). From preliminary assessments of normalized difference vegetation index (NDVI) and EVI, the latter index was found to provide the most consistent response to imposed drought regimes and was therefore selected. Both redstem filaree (inferior host) and sugar beet (superior host) plants showed decreased EVI values as a function of experimentally simulated drought (Fig. 1b) (all P values < 0.001). Flight propensity of beet leafhoppers on each plant species was negatively correlated with EVI values (all P values < 0.001) (Fig. 1c). Negative slopes of linear regressions of plant greenness as a predictor of beet leafhopper flight propensity were not significantly different between the two plant species ($P = 0.105$), suggesting that decreasing plant greenness of host plants, regardless of host plant species, may be considered a reliable indicator of flight initiation and possibly flight propensity more generally by beet leafhoppers.

Model for estimating spring migration probability

Time series of beet leafhopper trap counts were acquired at three study sites (Fresno, Kern, and Kings counties) from 2019 to 2020. Fluctuations in these time series were used to detect what was considered spring migration peaks. In 2019, one simultaneous peak of migration was observed at all study sites, but in 2020, broad and indistinct peaks were observed (Fig. 2a and b). In 2019, EVI values of natural vegetation in coastal foothills derived from satellite imagery showed similar temporal trends among the three study sites (Fig. 2c). In 2020, temporal series of EVI values at the Kern site were comparatively lower during winter and spring compared to the other sites (Fig. 2d). In 2019 and 2020 and at all three study sites, spring migrations of beet leafhoppers initiated when EVI values declined to 0.2–0.3. Cumulative proportion of migrating beet leafhoppers increased with decreasing EVI values (Fig. 2e). The relationship between EVI values and cumulative proportion of migrating beet leafhoppers was modeled using a Weibull function. Estimated Weibull parameters for a and b were 0.1667 (SE = 0.0035) and −5.5953 (SE = 0.8926), respectively ($F[46,1] = 234.1$, $P < 0.001$). Finally, the spring migration model was implemented into a web-based mapping system (https://hyslee.users.earthengine.app/view/beet-leafhopper-migration-in-ca) as a decision support tool for BCTV management (Figure S3).

BCTV symptoms field survey

BCTV incidence in tomato fields in California was surveyed from 2013 to 2022 (Fig. 3 and Table S1). In the Sacramento Valley, highest incidence was observed in 2021 ($F_{4,570} = 25.5$, $P < 0.001$), with a few outbreaks observed in both 2016 and 2022. In the San Joaquin Valley, the most severe BCTV outbreak was in 2013 ($F_{7,1613} = 121.7$, $P < 0.001$), and localized outbreaks were observed during most of the years examined in this study. BCTV is considered an important plant-pathogenic virus predominantly

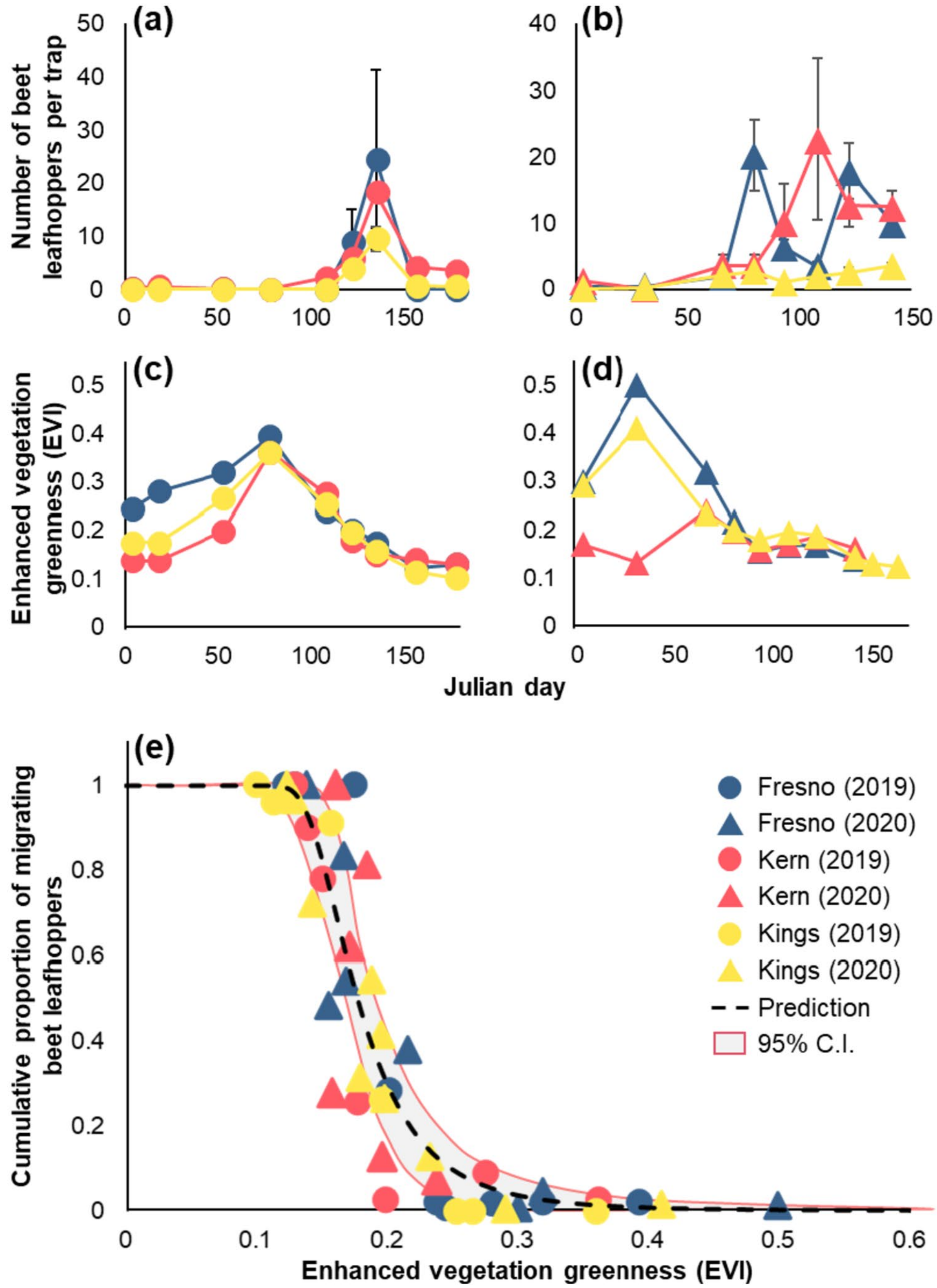


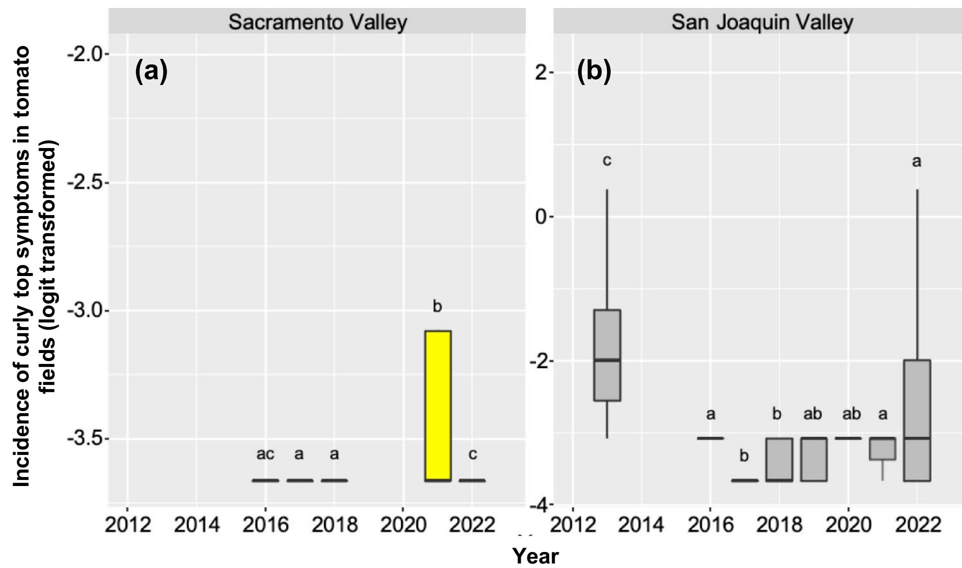
Fig. 2 Field monitoring of beet leafhopper migration. Field observation (mean ± SD) of migrating beet leafhoppers in coastal foothills in California in 2019 (**a**) and 2020 (**b**). Remotely sensed enhanced vegetation index (EVI) at the study sites in 2019 (**c**) and 2020 (**d**). **e** The relationship between EVI values and cumulative proportion of migrating beet leafhoppers. The observation data were fitted to a Weibull function (adjusted $R^2 = 0.76$) (dashed line)

affecting tomatoes in the San Joaquin Valley, and average incidence was higher there than in the Sacramento Valley.

Winter environmental conditions

Annual trends in winter environmental conditions (i.e., temperature, precipitation, and EVI) in coastal foothills in both the Sacramento Valley and the San Joaquin Valley were examined from 2001 to 2022. Although mean winter temperatures in BCTV outbreak years (2021 for the Sacramento Valley and 2013 for the San Joaquin Valley) were higher than the 22-year average, they were not the warmest years recorded in either the Sacramento Valley or the San Joaquin Valley (Fig. 4a, b). Similarly, mean winter precipitation and EVI values were lower than the 22-year average, but were not the lowest recorded in either the Sacramento Valley or the San Joaquin Valley (Fig. 4c–f). Mean values of winter environmental conditions in BCTV outbreak years were within ± 2 SD of the 22-year averages.

Fig. 3 Incidence of beet curly top virus symptoms in tomato fields. Surveyed incidence of beet curly top virus symptoms (i.e., leaf curling, stunted growth, early fruit onset, purple leaves, and veins, and yellow or light green discoloration) (mean ± SEM) in tomato fields in the Sacramento Valley (**a**) and the San Joaquin Valley (**b**). In total, 2,196 tomato fields were surveyed in 2013, 2016–2022. Different letters represent significant differences at $P < 0.05$ (one-way ANOVA with Tukey's post hoc test)



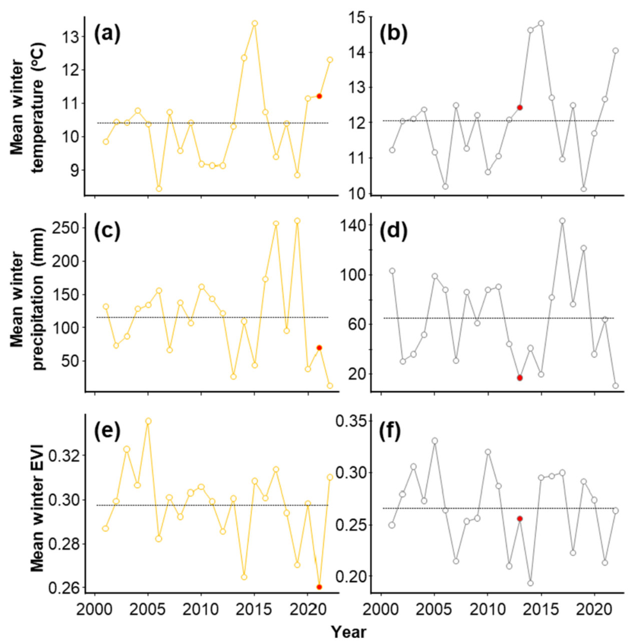


Fig. 4 Winter environmental conditions from 2001 to 2022. Trends in mean winter temperature (**a**, **b**), precipitation (**c**, **d**), and enhanced vegetation index (EVI) (**e**, **f**) in coastal foothills in the Sacramento Valley (yellow lines) and the San Joaquin Valley (gray lines). Broken lines are the average values over the entire period. Red dots are the data points for the beet curly top virus outbreak years (i.e., 2021 for the Sacramento Valley and 2013 for the San Joaquin Valley)

Trends in spring migration

Temporal trends in spring migration timing were examined regionally by estimating increases in coastal foothill areas where migration occurred and median times at which spring migration occurred in 50% of coastal foothills in the Sacramento Valley and the San Joaquin Valley from 2001 to 2022. Temporal trends were well described by a logistic function (Figure S4 and Table S2 for the Sacramento Valley and Figure S5 and Table S3 for the San Joaquin Valley). Spring migration started earlier in the San Joaquin Valley than in the Sacramento Valley in most years (Fig. 5a, b). In particular, spring migration began earlier in years in which BCTV outbreaks developed in both the Sacramento Valley and the San Joaquin Valley. In the Sacramento Valley, onset of spring migration was in May, but in 2021, a year with major BCTV outbreak, spring migration started in April (Figure S6). In addition, spring migration started in March in 2013 about a month earlier than most other years (Figure S7). This was also evident in the median spring migration time, which occurred more than 25 days earlier in 2013 than the 22-year average in the BCTV outbreak years (Fig. 5c).

Vector migration timing associated with incidence of BCTV symptoms

Regional median times of spring migration and winter environmental conditions were correlated with incidence of BCTV symptoms surveyed in tomato fields in the Central Valley. Incidence of BCTV symptoms was negatively correlated with the regional median spring migration times for the Sacramento Valley and the San Joaquin Valley (slope: −0.013 for the Sacramento Valley, −0.037 for the San Joaquin valley; both P values < 0.01) (Fig. 6), but most winter environmental conditions were not directly correlated with BCTV incidence (Figures S8 and S9). Therefore, we conclude that timing of spring migration is more critical than high beet leafhopper population density in coastal foothills as a predictor of BCTV outbreak risk.

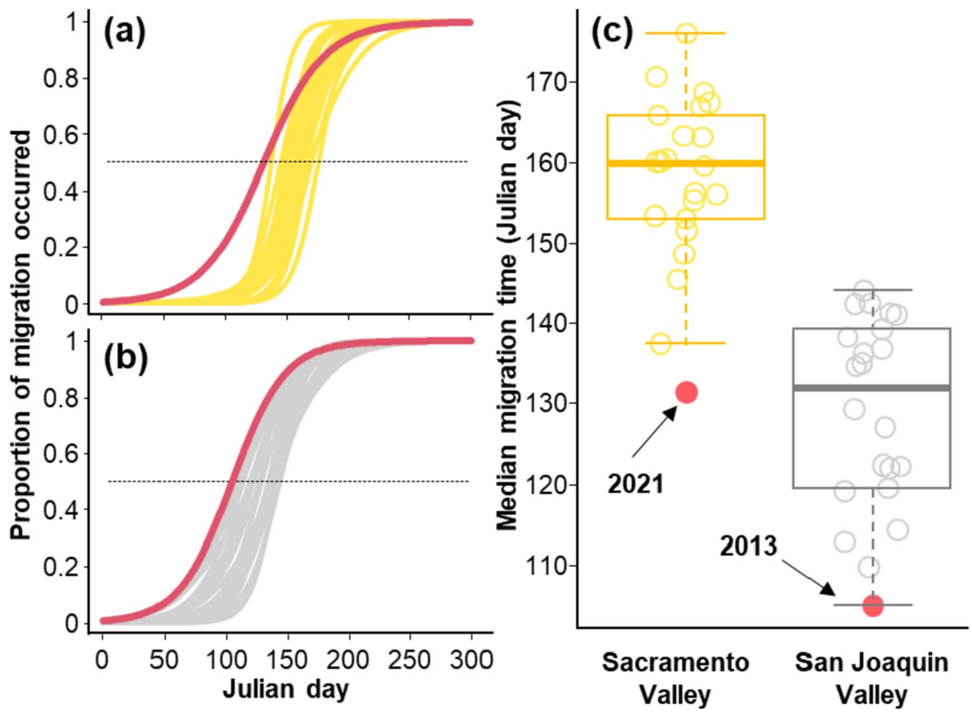


Fig. 5 Beet leafhopper spring migration time. Annual trends in beet leafhopper migration time in the Sacramento Valley (**a**) and the San Joaquin Valley (**b**). Red lines represent logistic regression lines of the outbreak years (i.e., 2021 for the Sacramento Valley and 2013 for the San Joaquin Valley). **c** Annual median migration times in both the regions from 2001 to 2022. Each point represents each year, jittered for visibility. Red dots are the median migration time for the beet curly top virus outbreak years

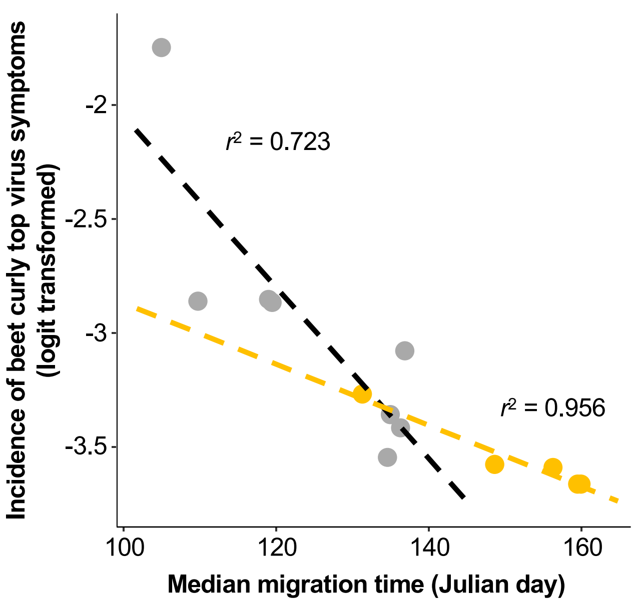


Fig. 6 Association of migration timing and incidence of beet curly top virus (BCTV) symptoms. The relationship between the median spring migration time of beet leafhoppers and mean incidence of BCTV symptoms each year in the Sacramento Valley (yellow dots) and the San Joaquin Valley (gray dots). The Sacramento Valley data are from 2016 to 2022, excluding 2019 and 2020. The San Joaquin Valley data are from 2013 to 2022, excluding 2014 and 2015. The broken lines denote the linear regression lines determined by the least-squares method ($P < 0.01$ for both)

Discussion

In this study, we experimentally manipulated drought regimes of individual plants and acquired optical sensing data to directly associate drought stress with plant leaf reflectance features. Plant reflectance profiles were used to generate standardized indices of greenness (i.e., EVI), so that individual plant data could be extrapolated and used to develop a region-wide GIS model based on satellite imagery. Plants were placed inside cages and experimentally infested with beet leafhoppers. Yellow sticky cards inside cages were used to trap dispersing beet leafhoppers, and we found a significantly negative correlation between EVI and flight propensity in two plant species. Furthermore, regression slopes for two different plants were not significantly different. Using freely available satellite imagery from two tomato growing seasons, spring migration timing was closely linked with a decrease in EVI-based greenness of natural vegetation in coastal foothills. Based on spring migration model predictions, we found a significant negative correlation between timing of spring migration and regional incidence of BCTV symptoms in the Central Valley of California. Examining temporal trends in spring migrations across ten growing seasons, major BCTV outbreaks were observed in years with early beet leafhopper spring migration.

The spring migration timing of beet leafhoppers varies annually and has become increasingly unpredictable due to climate change. However, predicting this timing is essential due to its significant impact on BCTV outbreaks. Migrating insects are either obligatory migrants (i.e., occurring independently of habitat or environmental factors) or facultative migrants (i.e., migration determined by habitat or environmental conditions) (Jyothi et al. 2021). Accordingly, experimental and in-depth analyses of environmental triggers of migration are essential. Historical data on various abiotic factors and vegetation conditions (e.g., greenness and plant phenology) at habitats can be estimated through long-term accumulated satellite data (Zeng et al. 2020). Therefore, by utilizing environmental conditions estimated through remote sensing data, we can enhance our ability to predict the migration of various insect vectors with facultative migration and develop more sustainable and effective management strategies.

Abiotic conditions (i.e., temperature, precipitation) have been described as important factors influencing beet leafhopper population dynamics (Lehnhoff and Creamer 2020). Notably, beet leafhoppers in California overwinter in unmanaged coastal foothills, where winter environmental factors play a crucial role in their population growth (Lee et al. 2022b). While it has been suspected that high density of insect vectors leads to plant-pathogenic virus outbreaks (Zeilinger et al. 2017; Lehnhoff and Creamer 2020; Gilbertson et al. 2021), we did not observe any significant correlation between incidence of BCTV symptoms and environmental conditions during winter months. Thus, we hypothesized that individual abiotic factors and associated beet leafhopper density did not appear to directly explain the risk of BCTV outbreaks.

Younger tomato plants are more susceptible to viral infections (Duffus and Skoyen 1977), and this phenomenon has been described as age-related resistance (Kus et al. 2002; Bruns et al. 2022). Early spring migration would expose young tomato plants to BCTV infection, resulting in more severe BCTV outbreaks (Wang et al. 1999; Wintermantel and Kaffka 2006). Additionally, as most tomato plants in California are mechanically transplanted (Hartz et al. 2008), initial stress on seedlings makes them more vulnerable to BCTV infection. Across all seasons examined, onset of spring migrations was about one month later in the Sacramento Valley compared to the San Joaquin Valley (Fig. 5). Tomato transplanting typically begins in March in the San Joaquin Valley and April in the Sacramento Valley, so regional synchrony between beet leafhopper spring migration and transplanting could be critical for BCTV outbreaks (see Figures S6 and S7).

Spatio-temporal dynamics of BCTV outbreaks can also be influenced by tri-trophic interactions (plant-pathogenic virus, insect vector, and host plant). Host preference of beet leafhoppers may impact spatial spread of BCTV (Lee et al. 2022a), especially considering the diverse range of crop plants cultivated in the Central Valley. Although tomato plants are not preferred host plants by beet leafhoppers (Thomas 1977), BCTV has a potential to manipulate the relative attractiveness of tomato plants for this insect vector (Lee et al. 2022a). Furthermore, there are 11 identified strains of BCTV (Creamer 2020), and their symptom severity is specific to both BCTV strain and host plant species (Stenger et al. 1990). Future research is needed to investigate the possible influence of other factors contributing to the interactions leading to BCTV outbreaks, including the prevalence of specific BCTV strains and co-infection with multiple strains.

Drought leads to various morphological and physiological changes in plants, including plant greenness (Xu et al. 2011), reduced leaf size (Toscano et al. 2014), decreased chlorophyll contents (LI et al. 2006), and increased production of secondary metabolites (Fàbregas and Fernie 2019). The response to drought stress is also influenced by species-specific drought tolerance (Engelbrecht and Kursar 2003; Matías et al. 2012). However, we found no significant difference between redstem filaree and sugar beet in stimulating flight behavior of beet leafhoppers depending on changes in plant greenness although the average greenness differed among plant species. As a result, we determined that EVI was suitable for measuring relative quality of plants and developing a predictive model. EVI is commonly employed to mitigate the influence of soil-induced noise and periodically measured globally by various satellites (e.g., Landsat, Sentinel, and PRISMA), allowing us to consistently monitor changes over time (Villamuelas et al. 2016). In addition, several other vegetation indices (VIs) have been developed for diverse purposes, including estimating plant phenology (Motohka et al. 2010) and determining the abundance and richness of specific insect species (Eklundh et al. 2009; Edward D. Deveson 2013; Huang et al. 2021). Moreover, as vegetation indices are archived in diverse digital repositories encompassing multiple temporal and geospatial scales, various web implementations leveraging these data are feasible. VIs hold potential for various applications, such as predicting regional hotspots of BCTV and beet leafhoppers by estimating the density and species composition of plants, which directly impact their population growth.

High temperatures and spring drought are significant factors that contribute to the early-season vegetation depletion in coastal foothills. Predictions indicate that global warming and the El Niño/Southern Oscillation (ENSO) will likely lead to an increase in the frequency of extreme climatic events (Cai et al. 2015). California, in particular, has been grappling with a rise in frequency and intensity of severe weather events (Williams et al. 2020). This, coupled with noticeable temperature increases and severe spring drought in recent years, has resulted in earlier spring migration of beet leafhoppers (see Figures S4 and S5). In addition, California is expected to experience increasing ambient temperatures and declining precipitation in autumn (Jones et al. 2022). Following the end of crop growing seasons in the fall, suitable habitats for overwintering can be limited and scattered in coastal foothills, which influences the density and distribution of overwintering leafhopper populations. However, abiotic factors have complex interactions with vegetation conditions (Jones et al. 1989). Therefore, directly quantifying the vegetation condition through VIs would be essential in association with extreme climatic events. Given the expected persistence of interannual extreme events, there is a considerable need for decision support tools to forecast spatio-temporal risks of outbreaks by major crop diseases (Jeger et al. 2018).

BCTV resistant varieties are not available in tomato. Current management strategies for plant-pathogenic viruses rely almost exclusively on prophylactic insecticide applications, some cultural practices, and sanitation (Gilbertson et al. 2021). The California Department of Food and Agriculture (CDFA) operates the Curly Top Virus Control Program (CTVCP), which conducts sweep net surveys for beet leafhoppers and sprays insecticides in coastal foothills when beet leafhopper densities exceed certain thresholds. However, BCTV outbreaks have occurred in spite of CTVCP efforts in some years, and the effectiveness of the program in reducing BCTV incidence remains unclear. This mapping system can serve as a decision support tool to optimize existing beet leafhopper management strategies and mitigate the incidence of BCTV. The integration with the cloud platform allowed the output to remain up to date with the latest satellite observations. This capability empowers stakeholders to assess the probability of beet leafhopper migration in specific areas of interest. Because remote sensing data can cover large geographic areas, this platform has the potential to be used in developing decision support tools for managing other insect pests and diseases in both forest and agricultural systems, as well (Calderón et al. 2013; Pettorelli et al. 2014; Dash et al. 2017).

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