ORIGINAL CONTRIBUTION





Factoring distribution and prevalence of Fall armyworm in southwest China

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Abstract

Host plant growth changing with environmental conditions can impact the distribution of herbivores. The generalist herbivore fall armyworm (FAW), Spodoptera frugiperda (J. E. Smith) (Lepidoptera: Noctuidae), is an invasive pest rapidly spreading across the world and has recently invaded southern China. We studied effects of environmental factors on the distribution of the fall armyworm and its host (maize) plant growth in the tropical mountainous area of Huize County, province of Yunnan, southwest China. Moreover, the relationships among the FAW distribution, environmental factors (altitude, temperature and humidity) and plant growth (mean kernel weight, kernel number per ear and ear weight) were analysed. The results showed that FAW predominated at altitude 1,243.3 m, temperature 21.4°C and humidity 82.1%. The host plant grew best at 1,200-1,312 m, 21.0-21.7°C and 81.2%-82.0%. Environmental factors indirectly influenced the distribution of FAW via the host plant growth. Compared with environmental factors, the host plant growth had a simplistic positive linear relationship with the density of FAW. FAW is less impacted by abiotic factors rather it determined by host plant prevalence, and thus the locations where maize plants grow best are preferred by FAW and should be the focus of insecticide applications. Understanding the distribution of FAW under various environmental conditions provides a valuable reference for Chinese maize production and food security.

KEYWORDS

altitude, environmental factor, humidity, maize, plant growth, temperature

1 | INTRODUCTION

Environmental variables greatly impact the species distribution and community structure (Hodkinson, 2005). Since plant growth along environment conditions such as altitude, temperature and humidity changed largely in a small geographic area, host plant growth is an important biotic factor in the distribution of herbivores (Haslett, 1997; Hodkinson, 2005). Mountain ecosystems are notable for their high level of spatial heterogeneity (Körner, 2000), they have become an important tool for studying environmental factors shaping insect

distributions (Shoo et al., 2006). Mountain ecosystems affect the distribution of herbivores not only by impacting their adaptability to environmental conditions (Carracedo & Casares, 1986), but also by influencing the host plants (Kubota et al., 2007; Preszler & Boecklen, 1996; Yarnes & Boecklen, 2006). Many experiments focus on changes in plant growth among different environmental conditions (Dwyer and Tollenaar, 1989), greatly advancing our understanding of the improvement of maize productivity and accelerating the progress of choosing suitable areas from a pest management perspective.

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Former studies tend to focus on individual factors such as altitude, temperature and humidity, few studies simultaneously considered the effect of multiple factors to identify their importance on the insect distribution and the host plant growth (Bale, 1991; Eyre et al., 2005; Kubota et al., 2007). Therefore, it is necessary to consider the overall effect of various environmental factors to understand better the insect distribution.

Fall armyworm (FAW), Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae), is a pest noctuid moth native to the Americas. FAW has a wide host range containing 186 plant species from 42 families including many economically important crops such as rice, sugarcane and sorghum (Casmuz et al., 2010; Day et al., 2017). FAW is one of the most serious pests of maize, and the yield losses can reach up to 73% (Hruska et al., 1997; Murúa et al., 2006; Wyckhuys & O'Neil, 2006). In maize, FAW larvae feed on young leaf whorls, ears and tassels, and mature larvae can cut through the base of maize seedlings, killing the whole plant (Harrison et al., 2019). FAW lives yearround from tropical and sub-tropical regions of the Americas and undergoes seasonal migrations as far north as temperate North America (Jiang et al., 2018; Johnson, 1987; Westbrook et al., 2016).

In January 2016, a serious outbreak of FAW in West Africa starts to natural spread at a phenomenal rate. Within 2 years of arriving in West Africa, the moth is detected in 28 sub-Saharan African countries (Rwomushana et al., 2018; Stokstad, 2017). Then, the moth still spreads eastward, and successively reaches India, Myanmar and Thailand in 2018 (Guo et al., 2018; Firake and Behere, 2020). In January 2019, FAW was first found in Yunnan province, southwest China, and by September 2019 it has reached almost all southern Chinese provinces (Wu et al., 2019). China is the second largest maize producer in the world, and maize is grown in all the provinces (Li et al., 2020). Thus, it is necessary to study the distribution of FAW under various environmental conditions to provide a valuable reference for Chinese corn production and food security.

FAW can survive overwinter throughout Yunnan province and breed year-round in this area (Early et al., 2018). As a typical mountain ecosystem, Yunnan provides various mountain ecosystems ranging from 76.4-6,740 m. Studies on the distribution of FAW in response to environmental variables varying with altitude are meaningful from a community structure viewpoint, it can provide insights into the management of FAW. In this study, we addressed 3 main questions: (a) effects of environmental factors on the distribution of FAW; (b) effects of environmental factors on the host plant growth; (c) the relationship among the distribution of FAW, the environmental factors and the host plant growth. Compared to environmental factors, the host plant growth played an overriding role in the distribution of FAW. Indeed, environmental factors such as altitude, temperature and humidity influenced the insect distribution by affecting the host plant growth.

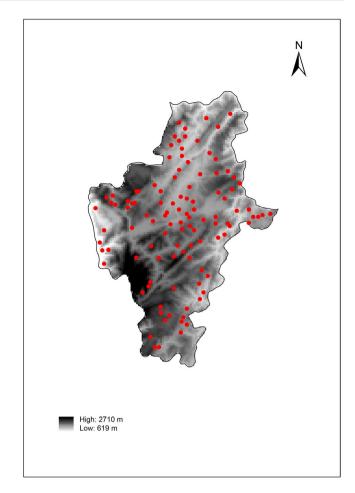


FIGURE 1 Distribution of survey points in Huize County, Yunnan province, China

2 | MATERIALS AND METHODS

2.1 | Study site

To assess the distribution of FAW across different environmental conditions, infested plants were surveyed from sites along various transects ranging from 619 to 2,710 m in the mountainous area of Huize County, Yunnan province, China, between latitudes 103°03′E-103°55′E and longitudes 25°48′N-27°04′N. The field surveys were conducted at 109 sites (Figure 1). Maize was planted in Jul 2019. Insect monitoring and data collection were performed weekly. All experiments were carried out in open maize fields.

2.2 | Effects of environmental conditions on FAW distribution

In each test site, to evaluate effects of the environmental conditions including altitude, temperature and humidity on the distribution of FAW, 50 maize plants in the areas without pesticide spray were randomly selected in each survey round. The survey was performed every 7 days from Aug to Sep 2019 (8 survey rounds), and

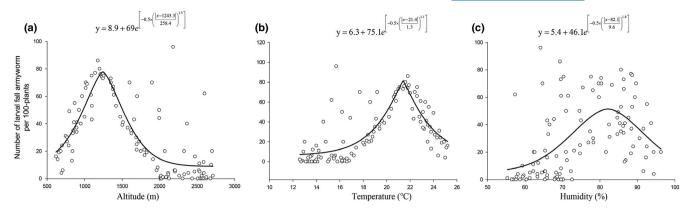


FIGURE 2 Effects of environmental factors on the distribution of fall armyworm (FAW). (a) altitude; (b) temperature; (c) humidity. Each data point represents the number of FAW larvae per 100-plants. Curves were fitted using the modified Gaussian equation

observation times ranged from 10 a.m. to 2 p.m. CCT each day. All leaf whorls, ears and tassels on the plant were visually examined. The number of FAW larvae within leaf whorls was recorded after dissecting the infested leaf whorls, species of the emerging individuals were identified via morphological identification. Moreover, the altitude, the temperature and the humidity of the site were recorded in each survey round to calculate the mean altitude, temperature and humidity values of the site.

2.3 | Effects of environmental conditions on plant growth

To estimate effects of environmental conditions on the plant growth, in each site 30 randomly selected plants were remained in the field until physiological maturity. Physiological maturity is characterized as 75% milk line. Each site consisted of 25–35 individuals grown in a single row, and every 10 consecutive plants within the row were selected. After physiological maturity, the 30 individuals were harvested from rows and were subsequently air-dried to examine kernel number per ear and mean kernel weight of 30 kernels from floret positions 10–15 from the bottom of the rachis. Kernel weight was tested after drying samples for at least 96 hr. The ear weight was calculated by mean kernel weight and kernel number per ear.

Ear weight (g) = [mean kernel weight (mg) \times kernel number per ear]/1000

2.4 | Statistical analysis

The logistic regression analysis indicated that our data fit Modified Gaussian (Equation 1) in effects of environmental conditions, so modified Gaussian equation was used to model the relationship between the insect distribution/plant growth (y) and environmental conditions (x):

$$y = y_0 + ae^{\left[-0.5\left(\frac{|x-x_0|}{b}\right)^c\right]}$$
 (1)

When $x = x_0$, y is maximum, $y_{max} = y_0 + a$.

All statistical analyses were performed with SPSS analysis software (20.0 for Windows; SPSS Inc.). Regression analyses were performed with SigmaPlot 12.0 software (Systat Software Inc.).

3 | RESULTS

3.1 | Effects of environmental conditions on FAW distribution

Mean densities of FAW larvae per 100-plants increased with increased environmental factors (altitude, temperature and humidity), and then, the densities did not increase until a certain threshold, reaching a peak. After this peak, the densities started to decrease (Figure 2). Thus, the data for effects of altitude ($R^2 = 0.6648$; $F_{4,104} = 51.5702$; p < .0001), temperature ($R^2 = 0.6605$; $F_{4,104} = 50.5874$; p < .0001) and humidity ($R^2 = 0.2856$; $F_{4,104} = 10.3965$; p < .0001) on the larval densities fitted the modified Gaussian model well. Compared with linear model, non-linear regression analysis was more suitable for estimating the relationships between environmental conditions and the distribution of FAW. When environmental factor $x = x_0$, that is $x_{\rm altitude} = 1,243.3$ m; $x_{\rm temperature} = 21.4$ °C; $x_{\rm humidity} = 82.1$ %, the numbers of FAW larvae per 100-plants were maximum. The thresholds were 77.9 (altitude), 81.4 (temperature) or 51.5 (humidity).

3.2 | Effects of environmental conditions on plant growth

Similar to the distribution of FAW, with increased environmental factors, the mean kernel weight, the kernel number per ear and the ear weight increased to a certain threshold, reaching a peak and then declined (Figure 3). The data for effects of environmental factors on plant growth fitted the modified Gaussian model well (Table 1). When the plant was located at 1,200, 1,312 and 1,270.4 m, the mean kernel weight, the kernel number per ear and the ear weight could reach up to 282.3 mg, 705.6 number and 198.6 g, respectively. When it

FIGURE 3 Effects of environmental factors on plant growth. Effects of altitude on (a) mean kernel weight, (b) kernel number per ear and (c) ear weight; Effects of temperature on (d) mean kernel weight, (e) kernel number per ear and (f) ear weight; Effects of humidity on (g) mean kernel weight, (h) kernel number per ear and (i) ear weight. Each data point represents the value of plant growth index. Curves were fitted using the modified Gaussian equation

put the temperature at 21.7°C (283.7 mg), 21°C (706 number) and 21.2°C (197.3 g), respectively, or when the maize was planted at 82% (249.8 mg), 81.20% (583.3 number), and 81.50% (146.8 g) humidity, respectively, the values of plant growth indices were maximum.

3.3 | Relationship between plant growth and insect distribution

The mean kernel weight, the kernel number per ear and the ear weight were positively correlated with the densities of FAW larvae per 100-plants. The densities with various mean kernel weights ($R^2=0.5876$, $F_{1,107}=152.4292$, p<.0001), kernel numbers per ear ($R^2=0.6449$, $F_{1,107}=194.3528$, p<.0001) and ear weights ($R^2=0.6581$, $F_{1,107}=205.9243$, p<.0001) fitted the linear equations well via linear regression analysis. Using the linear regression got a rule of one more larva per 100-plants for every 0.64 mg, 0.13 number or 0.41 g increased in the mean kernel weight, the kernel

number per ear or the ear weight. The overall mean kernel weight, the kernel number per ear and the ear weight in Huize area were 224.2 \pm 3.0 mg, 437.9 \pm 15.8 number and 102.8 \pm 5.0 g (Figure 4). As such, compared with environmental factors, the host plant growth has a simplistic positive linear relationship with the density of FAW. Environmental conditions are only indirect factors, the host plant growth is likely to directly influence the distribution of FAW.

4 | DISCUSSION

Mountain ecosystems are remarkable for their high level of spatial heterogeneity and thus act as an important tool for studying environmental factors shaping insect distributions (Körner, 2000; Shoo et al., 2006). They impact the distribution of herbivores by impacting both their adaptability to environmental conditions and the host plants (Kubota et al., 2007; Yarnes & Boecklen, 2006). We found that the distribution of FAW in mountain ecosystems in Huize County

TABLE 1 Parameter estimate of Modified Gaussian equation for effects of environmental factors on plant growth

х	у	R^2	F _{4,104}	р	Modified Gaussian equation	<i>x</i> ₀	y _{max}
Altitude	mean kernel weight	0.8774	186.1227	<.0001	$y = 193.3 + 89e^{\left[-0.5 \times \left(\frac{ x - 1200 }{300.3}\right)^{1.6}\right]}$	1,200 m	282.3 mg
	Kernel number per ear	0.9544	544.0863	<.0001	$y = 284.2 + 421.4e^{\left[-0.5 \times \left(\frac{ x-1312 }{384}\right)^3\right]}$	1,312 m	705.6
	Ear weight	0.9476	469.9193	<.0001	$y = 55.6 + 143e^{\left[-0.5 \times \left(\frac{ x - 1270.4 }{326.2}\right)^{2.3}\right]}$	1,270.4 m	198.6 g
Temperature	mean kernel weight	0.8855	200.9929	<.0001	$y = 193.2 + 90.5e^{\left[-0.5 \times \left(\frac{ x-21.7 }{1.7}\right)^{1.5}\right]}$	21.7°C	283.7 mg
	Kernel number per ear	0.9455	451.4197	<.0001	$y = 287.7 + 418.3e^{\left[-0.5 \times \left(\frac{ x-21 }{2.2}\right)^{2.9}\right]}$	21°C	706
	Ear weight	0.9422	423.7619	<.0001	$y = 56.4 + 140.9e^{\left[-0.5 \times \left(\frac{ x-21.2 }{1.9}\right)^{2.3}\right]}$	21.2°C	197.3 g
Humidity	mean kernel weight	0.5045	26.4721	<.0001	$y = 195.2 + 54.6e^{\left[-0.5 \times \left(\frac{ x-82 }{10.9}\right)^{4.2}\right]}$	82%	249.8 mg
	Kernel number per ear	0.4559	21.7879	<.0001	$y = 269.3 + 314e^{\left[-0.5 \times \left(\frac{ x-81.2 }{10.2}\right)^{2.7}\right]}$	81.20%	583.3
	Ear weight	0.45	21.2747	<.0001	$y = 54 + 92.8e^{\left[-0.5 \times \left(\frac{ x - 81.5 }{92.8}\right)^{32}\right]}$	81.50%	146.8 g

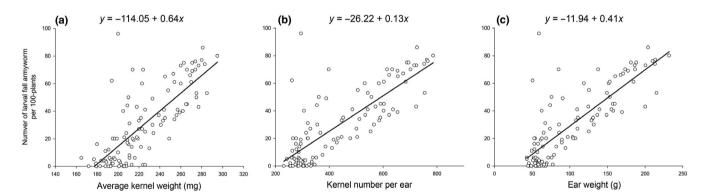


FIGURE 4 Relationship between the plant growth and the distribution of fall armyworm (FAW). (a) mean kernel weight, (b) kernel number per ear and (c) ear weight. Each data point represents the number of FAW larvae per 100-plants. Line was fitted by linear regression analysis

were associated with environmental factors including altitude, temperature and humidity. FAW larvae were found between 600 and 2,700 m and dominated at 1,243.3 m. As in the case of other herbivores (Hodkinson et al., 1999; Merrill et al., 2008), the distribution of FAW strongly linked with temperature, showing a sharp altitudinal gradient. FAW was not found and could not reproduce at altitudes where temperatures occasionally fell below 12.6°C, consistent with published results indicating that FAW is unable to develop at 12.69°C (Ali and Gaylor, 1990). Across the entire range of maize-growing areas in Huize (619-2,710 m), FAW populations occurred at lower altitudes, in agreement with the relatively lower levels of cold resistance exhibited by this species (Lu et al., 2019). Moreover, it could not develop at the highest temperature (>25.2°C) with the lowest altitudes of maize-growing areas. If the environment of maize-growing areas was too dry or too wet, FAW also could not grow well. Similar to optimum humidity of 80% under laboratory conditions (He et al., 2019), the field population got a maximum at 82.1% humidity. Because both larvae and adults of FAW are found in mountain ecosystems of Huize, the presence of FAW is not simply an

incursion by dispersing adults, but instead FAW appears to successfully breed across the entire range of maize-growing areas in Huize County.

We also found the plant growth was influenced by altitude-based environmental changes. Many literatures studied abiotic factor and maize productivity (Chen et al., 2013; Mi et al., 2010; Wang et al., 2020), but there was no clear linear trend in plant growth (mean kernel weight, kernel number per ear and ear weight) with increasing environmental factors (altitude, temperature and humidity). The plant growth that resulted in the highest yields of the maize differed at different environmental factors, it showed the highest yields at 1,200–1,312 m, 21.0–21.7°C and 81.2%–82.0%, respectively.

Our study suggests the distribution of FAW is influenced by environment-based changes in host plant composition. Some studies indicate the distributions of herbivores are partly impacted by escaping from their natural enemies (Randall, 1982; Hodkinson et al., 1999), but we found no evidence for this idea. Actually, the abundance and activity of FAW were expected to be relatively less dependent on environmental conditions, they were closely related

to plant growth. Because of temperature and humidity, the host plant composition was less diverse at too high or too low altitudes. In FAW systems, less diverse host plants may offer less favourable conditions for FAW activity, especially for this generalist herbivore switching between hosts (Montezano et al., 2018; Sparks, 1979). FAW diversity may also be influenced by pesticide applications. Above 1,700 m, maize is mainly grown in monoculture and farmers easily depend on pesticides for controlling maize pests and diseases (Yang et al., 2019). Farmers conventionally apply pesticides after planting at altitudes between 600 and 1,000 m, as these maize fields have easy access to the resident community (Harrison et al., 2019). In some moth populations, larval mortality caused by intraspecific competition may influence population dynamics (Parrella, 1987). High density of mature larvae in a plant can reduce access to food and then result in cannibalism (Raffa, 1987; Valicente et al., 2013). Although the intraspecific competition is observed in our laboratory trial, there is no evidence that intraspecific competition plays a role in the distribution of FAW. Since the feeding niche of each larva may not overlap much in the field, the densities of FAW in our survey are too low to cause a strong intraspecific competition affecting distributions. Thus, the distribution of FAW is not impacted by the intraspecific competition.

The results therefore suggest that, compared with environmental factors, the host plant growth plays an overriding role in the distribution of FAW. Actually, environmental factors such as altitude, temperature and humidity influence the insect distribution by affecting the host plant growth. Besides environmental factors, plant composition and pesticide application are also indirect factors impacting the insect distribution. Compared with these indirect factors, the host plant growth (mean kernel weight, kernel number per ear and ear weight) has a simplistic positive linear relationship with the density of FAW. Thus, environmental conditions are only indirect factors, and the host plant growth is likely to directly influence the distribution of FAW.

From a pest management perspective, identifying direct factors impacting the distribution of FAW contributes greatly to practical applications of the pesticides in controlling FAW. Maize plants grow best at 1,200-1,312 m, 21.0-21.7°C or 81.2%-82.0%, so these locations are preferred by FAW and should be the focus of insecticide applications. Understanding the distribution of FAW under various environmental conditions provides a valuable reference for Chinese maize production and food security. This study indicates that the altitudinal stratification of FAW is ubiquitous throughout various biogeographic areas and establishes potential baseline data which can be used to assess future impacts of climate change. In addition, the study adds to our knowledge of how a FAW group is distributed across environmental gradients altitudinally. An intrinsic quality of this type of extensive baseline research is the novel biogeographical data sets that are generated concerning FAW groups for which very little existing information has been available in China.

CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

RZ and MH conceived the research. JF and PW conducted experiments and statistical analyses. JF, PW QR and TT wrote the manuscript. RZ secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

Data supporting the information shown in the results are openly available in a public repository at: https://zenodo.org/record/41764 84#.X591Wm5ulOQ. Fan. (2021). Identifying factors determining the distribution of the invasive pest fall armyworm, Spodoptera frugiperda [Data set]. Zenodo. http://doi.org/10.5281/zenodo.4176484

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