Article

# Influence of weather factors on seasonal population dynamics of *Coelaenomenodera elaeidis* (Coleoptera: Chrysomelidae) and its natural enemies in NIFOR, Nigeria

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# Abstract

The leaf miner (Coelaenomenodera elaeidis Mlk) is the major pest of the oil palm. The seasonality of C. elaeidis, its natural enemies and their relationship with temperature, rainfall and relative humidity was observed between January 2009 and December 2010 at the main station of the Nigerian Institute for Oil Palm Research, Nigeria. Past leaf miner population estimates were obtained from NIFOR entomology division from 1976 - 1980. This study analyses temporal patterns in leaf miner abundance, and elucidates general patterns and factors influencing leaf miner abundance. Multiple linear regressions were used to analyze the relationship between abundance of leaf miner, its parasitoids and predators and the following climatic variables: maximum and minimum temperature (°C), rainfall (mm) and relative humidity (%). For the analyses, climate variables from the month of collection (control variable) or from the month before the collection (delayed variable) were used. The abundance of leaf miner and predatory ants peaked in the dry season, while parasitoids were most abundant in the rainy season. Significant correlations ( $P \le 0.05$ ) were found between leaf miner, its natural enemies and both control and delayed weather variables. For all years, maximum temperature was the most dominant variable for all the leaf miner stages. Significant correlations were found between leaf miner, its natural enemies and both control and delayed weather variables. This indicates that the weather variables at both the month of collection and with a delayed month in relation to collection is critical for pest-weather evaluation. This is important for leaf miner control. Temperature, rainfall and relative humidity had an effect on the population of C. elaeidis, and this effect was manifested primarily in seasonal fluctuations in oil palm agroecosystems. Dry season months with resultant higher temperatures recorded higher population of C. elaeidis.

Keywords seasonality; Coelaenomenodera elaeidis; oil palm, weather variables; pest management.

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# **1** Introduction

Seasonal variation in abundance of tropical insects is a common phenomenon (Wolda, 1988; Pinheiro et al., 2002). Insect abundance can change over time for a variety of reasons, including macroclimatic and microclimatic changes, and variation in the availability of food resources (Wolda, 1988). The effect of climate change in Nigeria is already contributing to extreme weather events: amount of rainfall, proliferation of pests, crop diseases and high temperature effects (NEST, 2004). Insects are able to function faster and more efficiently at higher temperatures. They can feed, develop, reproduce, and disperse when the climate is warm, though they may live for a shorter time (Drake, 1994). From an ecological point of view, particular variables such as the annual minimum temperature (Alward et al., 1999, Godefroid and Tanghe, 2000; Walther, 2000) or temperature in specific months (Beebee 1995, Sparks and Yates 1997, Brown et al. 1999) may be more important than the annual mean. Many biological processes undergo sudden shifts at particular threshold values (Allen and Breshears, 1998, Hoegh-Guldberg, 2001; Easterling et al., 2000a, b). Existing studies suggest that direct effects of temperature are likely to be larger and more important than any other factor (Bale et al., 1997). In oil palms, the central role of natural balance in the control of leaf-eating insects continues to be recognized and investigated, with emphasis on selective control measures applied only in response to census counts. In a review of integrated pest management (IPM) developments, Ho and Teh (1997) describe improving knowledge of technical aspects of the response system, and the relationship of known natural enemies to their flower food plants. Information on weather influence on leaf miner, its parasitoid and predator abundance patterns have not been obtained.

This study analyses temporal patterns in leaf miner abundance and its natural enemies, and elucidates general patterns and factors influencing leaf miner abundance in NIFOR between January 2009 and December 2010.

### 2 Materials and Methods

### 2.1 Study site

The study site is located at the main station of the Nigerian Institute for Oil Palm Research (NIFOR). It lies on the coordinates of latitude  $6^0$  30' N and longitude  $5^0$  40' E. It is located in the forest zone of South-West Nigeria. The natural vegetation has been replaced by oil palm and coconut cultivation during the past 50 years. The study site was planted in 2000, whose crown canopy had not formed a continuous layer and sunlight could still penetrate to the ground. There are two seasons; wet and dry seasons. November to March is dry season while April to October is rainy season. Average mean temperature is  $26.6^{\circ}$ C.

# 2.2 Sampling technique

The study involved simple random sampling surveys for leaf miner on a plot 9 years old. Data was collected monthly from January 2009 – December 2010. It involved observing and counting of leaf miner and its natural enemies. No pesticides were applied during the study period, purposely to simulate a natural ambience in the sample plot. A sampling intensity of 21 palms was used, selecting 1 palm per line. The larval, pupal and adult stages of the *Coelaenomenodera elaeidis* were counted. The independent variables were temperature, rainfall and relative humidity. The dependent variable was *C. elaeidis* counts and its natural enemies. At each point, *C. elaeidis* were counted on fronds inclining at 45° (number 17 and 25 on the phyllotactic spiral). In shorter palms, fronds were pulled down by a stick, but in taller ones a ladder was used. A different palm was used at successive counts.

The plot was planted in 2000 and comprised of 443 palms (2.95 hectares). Harvesting of plot 54 began in 2005. Leaf miner counts on the palm leaflets within the field plot. NIFOR palms are planted in a triangular pattern, so census lines ran in three directions. Access points were marked with reference to field boundaries

and harvesting paths. The most common predatory ants, *Micromischoides sp.*, were identified and counted. Census on the basis of damage was done monthly by walking the full length of a planted line, assessing damage on each palm and cutting 5 severely damaged leaflets from a palm frond with a harvesting knife. The leaflets were opened up in the laboratory and immature stages of *C. elaiedis* were counted.

Parasitoids of *C. elaeidis* were identified and counted using the direct count method. Sampling was conducted monthly between 7 - 11am. Methods for insect sampling included use of insect sweep net, direct handpicking and leaflet sampling.

# 2.3 Past data collection

Leaf miner past population estimates were obtained from NIFOR entomology division from 1976 - 1980.

### 2.4 Statistical analysis

Multiple linear regressions were used to analyze the relationship between abundance of leaf miner, its parasitoids and predators and the following climatic variables: maximum and minimum temperature (°C), rainfall (mm) and relative humidity (%). Climate variables from the month of collection (control variable) or from the month before the collection (delayed variable) were used. Monthly means were used.

# **3 Results**

Table 1 shows relationship between mean weather factors and leaf miner insect stages, predators and parasitoids for 2009 - 2010. In 2009, adult leaf miner had a significant relationship for both control (0.008) with maximum temperature and relative humidity being the dominant variables and delayed (0.007) with rainfall being the dominant variable. Parasitoids had a significant relationship for control (0.001) with maximum temperature, rainfall and relative humidity all dominant variables. There was a significant relationship for grouped leaf miner stages in the control (0.039) and delayed (0.029) in 2009 with rainfall being the dominant variable.

In 2010, adult leaf miner had a significant relationship for control (0.048) with relative humidity being the dominant variable. Parasitoids had a significant relationship for delayed (0.047) with minimum temperature being the dominant variable. Predators had a significant relationship for delayed (0.001) with minimum temperature being the dominant variable. Table 2 shows rainy season relationship between mean weather factors and leaf miner insect stages, predators and parasitoids for 2009 - 2010. In 2009, Predators had a significant relationship for control (0.029) with relative humidity being the dominant variable. In 2010, there was no recorded dominant variable during this period. Table 3 shows dry season relationship between mean weather factors and leaf miner insect stages (larvae, pupae and adult), predators and parasitoids for 2009 -2010. For both years, maximum temperature was the most dominant variable for all the leaf miner stages, predators and parasitoids. Table 4 shows relationship between mean weather factors and leaf miner insect stages for 1976 - 1980. In 1976, larvae had a significant relationship for delayed (0.041) with maximum temperature being the dominant variable. In 1980, larvae had a significant relationship for control (0.044) with minimum temperature being the dominant variable. In 1976, pupae had a significant relationship for control (0.028) with maximum and minimum temperature being the dominant variables and delayed (0.019) with maximum temperature being the dominant variable. In 1980, pupae had a significant relationship for delayed (0.015) with rainfall, maximum and minimum temperature being the dominant variables. Table 5 shows rainy season relationship between mean weather factors and leaf miner insect stages for 1976 - 1980. In 1979, larvae had a significant relationship for control (0.046) with relative humidity, maximum and minimum temperature being the dominant variables. Also in 1979, pupae had a significant relationship for control (0.024) with rainfall, relative humidity and maximum temperature being dominant variables during this period. In 1980, pupae had a significant relationship for control (0.042) with maximum temperature being dominant variable.

Insect Stage	$\mathbf{R}^2$	R	P-value	Climatic variable	
Larvae					
2009	0.352	0.593	0.490	Control	
	0.277	0.526	0.633	Delayed	
2010	0.427	0.654	0.355	Control	
	0.375	0.613	0.446	Delayed	
Pupae					
2009	0.448	0.670	0.320	Control	
	0.266	0.516	0.653	Delayed	
2010	0.250	0.500	0.685	Control	
	0.508	0.713	0.232	Delayed	
Adult					
2009	0.827	0.909	0.008**	Max.T <sup>0</sup> C,RH	
-007	0.837	0.915	0.007**	Delayed(RF)	
2010	0.707	0.841	0.048	Control (RH)	
2010	0.510	0.714	0.230	Delayed	
Parasitoid	0.510	0.714	0.250	Denayeu	
2009	0.909	0.954	0.001**	Max.T <sup>0</sup> C,RF,RH	
2007	0.607	0.779	0.119	Delayed	
2010	0.291	0.540	0.605	Control	
2010	0.201	0.814	0.047**	Min.T <sup>0</sup> C	
	0.708	0.014	0.047	Will. I C	
Predator					
2009	0.604	0.777	0.122	Control	
2007	0.388	0.623	0.423	Delayed	
2010	0.596	0.025	0.130	Control	
2010	0.350	0.904	0.001**	Min.T <sup>0</sup> C	
Grouped leaf	0.017	0.704	0.001	Will.1 C	
Miner					
2009	0.725	0.851	0.039**	RF	
<b>400</b> /	0.725	0.747	0.029**	RF	
		0.747	0.271	Control	
2010					
2010	0.519 0.599	0.721	0.127	Delayed	

**Table 1** Relationship between mean weather factors and leaf miner stages (larvae, pupae, adult), predators and parasitoids for 2009 – 2010.

\*\*Significance P  $\leq$  0.05

Control - Climatic variable from month of collection

Delayed - Climatic variable with a delayed month in relation to collection

 $R^2-Coefficient$  of determination

R – Correlation coefficient

Insect Stage	$\mathbf{R}^2$	R	P-value	Climatic variable
Larvae				
2009	0.655	0.809	0.571	Control
	0.099	0.314	0.990	Delayed
2010	0.097	0.311	0.991	Control
	0.957	0.978	0.084	Delayed
Pupae				
2009	0.625	0.791	0.609	Control
	0.772	0.878	0.404	Delayed
2010	0.927	0.963	0.141	Control
	0.732	0.855	0.465	Delayed
Adult				
2009	0.911	0.954	0.170	Control
	0.930	0.964	0.135	Delayed
2010	0.735	0.857	0.460	Control
	0.900	0.949	0.190	Delayed
Parasitoid				
2009	0.519	0.720	0.731	Control
	0.852	0.923	0.273	Delayed
2010	0.890	0.943	0.208	Control
	0.633	0.796	0.599	Delayed
Predator				
2009	0.986	0.993	0.029**	RH
	0.525	0.962	0.144	Delayed
2010	0.292	0.540	0.915	Control
	0.745	0.863	0.445	Delayed
Grouped leaf				
Miner				
2009	0.615	0.785	0.621	Control
	0.563	0.751	0.682	Delayed
2010	0.386	0.622	0.851	Control
	0.575	0.758	0.670	Delayed

 Table 2 Rainy season relationship between mean weather factors and leaf miner stages (larvae, pupae, adult), predators and parasitoids for 2009 – 2010.

\*\*Significance P  $\leq$  0.05

**Table 3** Dry season relationship between mean weather factors and leaf miner stages (larvae, pupae, adult), predatorsand parasitoids for 2009 - 2010.

Insect Stage	$\mathbf{R}^2$	R	P-value	Climatic variable
Larvae	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. $T^0C$
Pupae	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. T <sup>0</sup> C
Adult	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. $T^0C$
Parsitoid	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. T <sup>0</sup> C
Predator	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. $T^0C$
Grouped leaf	1.0	1.0	0.000**	Max. T <sup>0</sup> C
miner	1.0	1.0	0.000**	Max. T <sup>0</sup> C

\*\*Significance P  $\leq$  0.05

Insect Stage	$\mathbf{R}^2$	R	P-value	Climatic variable
Larvae				
1976	0.699	0.836	0.052	Max. $T^0C$
	0.719	0.848	0.041**	Max. $T^0C$
1977	0.477	0.692	0.273	Control
	0.621	0.788	0.107	Delayed
1978	0.433	0.658	0.345	Control
1970	0.494	0.703	0.252	Delayed
1979	0.523	0.723	0.213	Control
1)//)	0.340	0.583	0.512	Delayed
1980	0.714	0.845	0.044**	Min. T <sup>0</sup> C
1900	0.465	0.682	0.294	Delayed
D	0.465	0.082	0.294	Delayed
Pupae	0 7 5 1	0.077	0.020.00	
1976	0.751	0.867	0.028**	Max. & Min. $T^0C$
	0.779	0.883	0.019**	Max. T <sup>0</sup> C
1977	0.371	0.609	0.454	Control
	0.343	0.585	0.507	Delayed
1978	0.305	0.552	0.579	Control
	0.344	0.586	0.504	Delayed
1979	0.223	0.473	0.736	Control
	0.714	0.845	0.044**	RF, Max. $T^0C$
1980	0.214	0.463	0.752	Control
	0.793	0.890	0.015**	RF, Max. & Min. T <sup>0</sup> C
Adult				
1976	0.330	0.575	0.530	Control
	0.188	0.434	0.800	Delayed
1977	0.223	0.472	0.737	Control
1,777	0.041	0.204	0.987	Delayed
1978	0.257	0.507	0.672	Control
1)//0	0.112	0.335	0.919	Delayed
1979	0.316	0.562	0.557	Control
1979	0.242	0.302	0.337	Delayed
1000	0.242	0.492	0.693	Control
1980				
~	0.322	0.567	0.547	Delayed
Grouped lea	ıf			
miner				
1976	0.378	0.615	0.441	Control
	0.062	0.248	0.973	Delayed
1977	0.335	0.579	0.520	Control
	0.306	0.553	0.577	Delayed
1978	0.280	0.530	0.626	Control
	0.072	0.269	0.964	Delayed
1979	0.300	0.548	0.588	Control
	0.165	0.406	0.839	Delayed
1980	0.130	0.361	0.894	Control
2,00	0.535	0.731	0.197	Delayed
	0.555	0.751	0.177	Deluyeu

 Table 4 Relationship between mean Weather factors and leaf miner stages (larvae, pupae, adult) for 1976 - 1980

Insect Stage	$\mathbf{R}^2$	R	<b>P-value</b>	Climatic variable
Larvae				
1976	0.978	0.989	0.043**	RF
	0.764	0.874	0.416	Delayed
1977	0.710	0.842	0.496	Control
	0.711	0.843	0.495	Delayed
1978	0.683	0.826	0.534	Control
	0.589	0.768	0.653	Delayed
1979	0.938	0.968	0.121	Control
	0.969	0.985	0.046**	RH, Max.&Min. T <sup>0</sup> C
1980	0.600	0.775	0.640	Control
	0.809	0.900	0.345	Delayed
Pupae				
1976	0.857	0.926	0.265	Control
	0.928	0.758	0.140	Delayed
1977	0.769	0.877	0.409	Control
	0.574	0.758	0.670	Delayed
1978	0.857	0.926	0.265	Control
	0.751	0.866	0.437	Delayed
1979	0.643	0.802	0.587	Control
	0.988	0.994	0.024**	RF,RH, Max.T <sup>0</sup> C
1980	0.630	0.794	0.603	Control
	0.979	0.989	0.042**	Max.T <sup>0</sup> C
Adult				
1976	0.799	0.894	0.361	Control
	0.602	0.776	0.638	Delayed
1977	0.598	0.773	0.643	Control
	0.709	0.842	0.497	Delayed
1978	0.806	0.898	0.351	Control
	0.562	0.866	0.684	Delayed
1979	0.610	0.781	0.628	Control
	0.827	0.910	0.315	Delayed
1980	0.717	0.847	0.486	Control
	0.314	0.560	0.902	Delayed
Grouped leaf				
miner				
1976	0.834	0.943	0.305	Control
	0.344	586	0.882	Delayed
1977	0.292	0.540	0.915	Control
	0.582	0.763	0.661	Delayed
1978	0.866	0.931	0.250	Control
	0.526	0.725	0.724	Delayed
1979	0.652	0.808	0.574	Control
	0.739	0.859	0.455	Delayed
1980	0.647	0.804	0.582	Control
	0.769	0.877	0.408	Delayed
				ž

**Table 6** Dry season relationship between mean Weather factors and Leaf miner stages (larvae, pupae, adult) for1976 – 1980.

Insect Stage	$\mathbf{R}^2$	R	P-value	Climatic variable
Larvae	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. T <sup>0</sup> C
Pupae	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. T <sup>0</sup> C
Adult	1.0	1.0	0.000**	Max. T <sup>0</sup> C
	1.0	1.0	0.000**	Max. T <sup>0</sup> C
Grouped leaf	1.0	1.0	0.000**	Max. T <sup>0</sup> C
miner	1.0	1.0	0.000**	Max. T <sup>0</sup> C

\*\*Significance  $P \le 0.05$ 

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### **4** Discussion

An understanding of the interactions between insect pests, temperature, rainfall and relative humidity would help in developing improved pest control strategies. There was a higher relationship between leaf miner and weather factors during the 2009 – 2010 periods (Table 1) in comparison with the 1976 -1980 periods (Table 4). This could be attributed to higher mean temperatures prevailing at the 2009 – 2010 periods. This also implies that progressively higher temperatures, lower rainfall and relative humidity values could be implicated in the increase in leaf miner abundance. If these patterns continue, prediction of leaf miner response to climate variability will have to account for the magnitude and timing. Weather controls the development rate, survival, fitness, and level of activity of individual insects: the phenology, distribution, size, and continuity of insect populations; migration and their establishment; and initiation of insect outbreaks (Pedgley, 1990). Among the weather elements, temperature, humidity, and wind play the major roles in insect life (Mavi and Tupper, 2005). The leaf miner adult is the only stage that lives outside the mines and its external environment, and it's the stage that is in direct contact with weather factors.

The rainy season generally had lower leaf miner and parasitoid abundance for both 2009 and 2010. The higher parasitoid population could probably explain low leaf miner population. Rainfall could also lead to disruption in breeding and mortality of the leaf miner and *Micromischoides sp*.

The dry season generally had higher leaf miner and predator abundance and lower parasitoid populations for both 2009 and 2010. Higher mean temperatures prevail at this time and is the most important factor affecting leaf miner abundance (Table 3). Similar findings were made from records between 1976 and 1980 (Table 5). Although many studies have concluded that insect pests will become more abundant as temperatures increase (Watt et al., 1990; Cammell and Knight, 1992; Harringhton et al., 1995), there are many uncertainties involved, particularly in predicting the result of interacting effects of rising  $CO_2$  (and other greenhouse gases) and temperature. Significant correlations were found between leaf miner, its natural enemies and both control and delayed weather variables. This indicates that the weather variables at both the month of collection and with a delayed month in relation to collection is critical for pest-weather evaluation.

### **5** Conclusion

It can be concluded that temperature, rainfall and relative humidity had an effect on the population of *C*. *elaeidis*, and this effect is manifested primarily in seasonal fluctuations in oil palm agroecosystems. Weather influenced the seasonal population dynamics of *C*. *elaeidis*, facilitating early season build-up on the oil palm host crop. Dry season months with resultant higher temperatures recorded higher population of *C*. *elaeidis*.

This study provides a better understanding of how insect pest population dynamics and seasonal weather variation mechanism can fine-tune pest management strategies and response to pest attacks. This study has focused on ecological principles that are cheap and sustainable, relying on need/timing for control of insect pests of the oil palm. The importance of indigenous knowledge of the physical and biological environments of insect pests is emphasized and the need for collection of minimum data sets over several seasons in order to quantify key factors necessary for designing pest management programs.

# References

Allen CD, Breshears DD. 1998. Drought induced shift of a forest woodland Ecotone: Rapid landscape response to climate variation. Proceedings of the National Academy of Sciences of USA, 95: 14839-14842

Alward RD, Ketling JK, Milchunas DG. 1999. Grassland vegetation changes and noctunal global warming. Science, 283: 229-231

- Bale JS, Hodkinson ID, Block W, et al. 1997. Life strategies of Arctic terrestrial arthropods. In: The Ecology of Arctic Environments (Woodin SJ, Marguiss M, eds). 137-165, Blackwell Science, Oxford, UK
- Beebee TJC. 1995. Amphibian breeding and climate. Nature, 374: 219-220
- Brown JL, Li SH, Bhagabati N. 1999. Long-term trend toward earlier breeding in An American bird: A response to global warming? Proceedings of the National Academy of Sciences of USA, 96: 5565-5569
- Cammell ME, Knight JD. 1992. Effects of climatic change on the population dynamics of crop pests. Advances in Ecological Research, 22: 117-162
- Drake VA. 1994. The influence of weather and climate on agriculturally important insects: An Australia perspective. Australian Journal of Agricultural Research, 45: 487-509.
- Easterling DR, Evans JL, Groisman PY, et al. 2000a. Observed variability and trends in extreme climate events: a brief review. Bulletin of the American Meteorological Society, 81(3): 417-425
- Easterling DR, Meehl GA, Parmesan C, et al. 2000b. Climate extremes: Observations, modeling and impacts. Science, 289: 2068-2074
- Ho CT, Teh CL. 1997. Integrated pest management in plantation crops in Malaysia. Challenges and realities.
   In: Proceedings of the 1997 International Planters Conference Plantation management for the 21<sup>st</sup> Century (Vol. 1). Part I ix, Pp 1-192). 125-149, The Malaysian Plant Protection Society, Kuala Lumpur, Malaysia
- Hoegh-Guldberg O. 2001. Sizing the Impact: Coral reef ecosystems as early casualties of Climate change. In:
   Fingerprints of Climate Change Adapted Behavior and Shifting Species Ranges (Walther GR, C.A. Burga CA, Edwards PJ, eds). 205-230, Kluwer Academic Publ., USA
- Mavi HS, Tupper GJ. 2005. Agrometeorology: Principles and Applications of Climate Studies in Agriculture. The Haworth Press, Inc., New York, USA
- Nigerian Environmental Study/Action Team (NEST). 2004. Executive Summary of Five Sector Surveys on Nigeria's Vulnerability and Adaptation to Climate Change. Nigeria
- Pedgley DE. 1990. Concentration of flying insects by the wind. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 328: 113-135
- Pinheiro MHO, Monteiro R, Cesar O. 2002. Levantamento fitossociológico da floresta estacional semidecidual do Jardim Botânico Municipal de Bauru, São Paulo. Naturalia, 27: 145-164
- Sparks TH, Yates TJ. 1997. The effect of spring temperature on the appearance dates of British butterflies 1883-1993. Ecography, 20: 368-374
- Watt AD, Ward LK, Eversham BC. 1990. Invertebrates. In: The Greenhouse Effects and Terrestrial Ecosystems of the UK (Cannell MGR., Hopper MD, eds). 32-37, Institute of Terrestrial Ecology research publication 4. HMSO, London, UK
- Wolda H. 1988. Insect seasonality: Why? Annual Review of Ecology and Systematics, 19: 1-18

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