

This electronic thesis or dissertation has been downloaded from the King's Research Portal at <https://kclpure.kcl.ac.uk/portal/>



Investigating the Impact of Landscape Fire Smoke on Migratory Insect Flight

Liu, Yanan

Awarding institution:
King's College London

The copyright of this thesis rests with the author and no quotation from it or information derived from it may be published without proper acknowledgement.

END USER LICENCE AGREEMENT



Unless another licence is stated on the immediately following page this work is licensed

under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International

licence. <https://creativecommons.org/licenses/by-nc-nd/4.0/>

You are free to copy, distribute and transmit the work

Under the following conditions:

- Attribution: You must attribute the work in the manner specified by the author (but not in any way that suggests that they endorse you or your use of the work).
- Non Commercial: You may not use this work for commercial purposes.
- No Derivative Works - You may not alter, transform, or build upon this work.

Any of these conditions can be waived if you receive permission from the author. Your fair dealings and other rights are in no way affected by the above.

Take down policy

If you believe that this document breaches copyright please contact librarypure@kcl.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.

King's College London
Department of Geography

**Investigating the Impact of Landscape Fire
Smoke on Migratory Insect Flight**

Yanan Liu

Student ID: 1892183

Supervised by:

Prof. Martin Wooster

Prof. Rorbet Francis

Submitted in part fulfilment of the requirements for the degree of
Doctor of Philosophy of King's College London
Department of Geography
Faculty of Social Science & Public Policy
King's College London
2023

Abstract

Smoke emissions from landscape fires contain trace gases and aerosols - some of which not only pose hazards to human health but also have potential ecological impacts. Since insects play an important role in ecosystems, this research focuses on the potential that smoke has to impact insect migration which may be related to insect dispersal and distribution and which has not been much studied thus far. The overall aim is to use laboratory experiments to quantify the potential effects of landscape fire smoke pollution on migratory insect flight, and to explore which smoke components may be contributing to any effect. Comparative laboratory experiments were conducted to explore these impacts, based around *Vanessa cardui* L. (Painted lady butterfly) as the research target as they are famous for their annual migration between Africa and Europe. A tethered flight mill (TFM) approach was used to quantitatively study the flight behaviour of the adult butterflies, including total flight distance (m), average speed ($\text{m}\cdot\text{s}^{-1}$), maximum speed ($\text{m}\cdot\text{s}^{-1}$), and flight durations (minutes). Adult butterflies were exposed to different smoke conditions and their flight behaviour compared to butterflies being flown in clean-air conditions (as a control group). To ensure the experiments produced smoke with realistic properties, the emissions characteristics of agricultural residue burning and incense burning (as used in the experiments) were measured.

Vanessa cardui L. was found to have a complex response to different smoke conditions - as assessed by fine particulate matter ($\text{PM}_{2.5}$) concentration. There is a negative linear relationship between flight speed and $\text{PM}_{2.5}$ concentration when *Vanessa*

cardui L. are exposed to very high PM_{2.5} concentrations (up to 4000 µg·m⁻³) for relatively short amounts of time (less than thirty minutes), and other behavioural parameters associated with flight also show a significant decrease. However, the butterflies increased their flight speed by around 50% as when exposed to a lower, stable smoke PM_{2.5} concentration of 127 µg·m⁻³ for six hours. The research finds that the emissions from incense burning are similar to that from landscape fire agricultural residue burning, with similar emission factors of CO₂, CO, CH₄, and PM_{2.5}, and suggests that it is the particulates rather than the trace gas component of the smoke that is the main driver for the flight behaviour impact. We conclude that exposure to smoke from landscape burning significantly affects the flight behaviour of adult *Vanessa cardui* L, although the exact impacts depend on the smoke concentration and the duration of exposure. There appears to be reasonable evidence that smoke released from landscape fires may thus affect insect migration, especially when periods of widespread and intense agricultural or other burning closely match migration times.

Acknowledgements

I would like to extend my heartfelt gratitude and appreciation to all those who have supported me during my PhD study. Their unwavering encouragement, guidance, and assistance have been invaluable in shaping my research journey and contributing to the successful completion of this thesis.

First and foremost, I would like to express my sincere appreciation to my supervisor, Martin Wooster. His profound expertise, guidance, and passion for his work have been instrumental in shaping the direction and quality of my research. I am truly grateful for his mentorship and dedication to my academic development.

I would also like to acknowledge the contributions to my second supervisor, Robert Francis, for his invaluable advice and support, not only in academic paper writing but also in career development. Additionally, I am grateful to my external supervisor, Ka Sing Lim, for providing the research project idea that laid the foundation for this study.

I extend my sincere thanks to my colleague, Mark Grosvenor, for his invaluable discussions, assistance with the experimental setup, and mentorship throughout my PhD journey. I would also like to express my gratitude to Bruce Main, James Johnson, and Farrer Owsley-Brown for their contributions to my experimental process. Furthermore, I would like to thank Ceri Watkins and Rebecca Nesbit from Rothamsted Research for their support during my butterfly experiment.

I am deeply grateful to my family, Qingchao Liu, Haixia Li, Ruzhong Yan, and Qing Liu, for their unwavering love, support, and belief in me. Their encouragement has been a constant source of motivation during my PhD journey.

Lastly, I would like to express my heartfelt gratitude to my husband and friend, Su Yan, for his unwavering support, encouragement, and understanding. His presence

and belief in me have been the driving force behind my perseverance and completion of this PhD study.

I am immensely grateful to all those mentioned above, as well as others who may have been inadvertently omitted but have played a significant role in my research journey. Their support, guidance, and belief in me have been invaluable, and I am truly thankful for their contributions.

Covid-19 Impact Statement

To complete my PhD, I mainly designed and conducted three experiments. The first and second experiments were completed as planned. However, my third experiment was to investigate the emissions from Chinese agricultural residue burning, which was planned to be conducted not only in the laboratory in the UK but also on agricultural lands in China. Because of the Covid-19 restrictions, I was not able to fly back to China personally after a long postponement in the end. Instead, I shipped the smoke measurement device back to China and guided my father and uncles to complete rough measurements in the field. Moreover, the Chinese agricultural residues required for my laboratory experiment were finally shipped to the UK after a long wait and at a high cost. For these reasons, my third experiment was not completed with the ideal quality, though satisfactory results were still obtained.

Meanwhile, apart from the negative psychological impacts due to the long-time quarantine, I was actually infected with the Covid-19 virus twice between February to November 2022, which took me a long time to get recovered back to my research. After a delay of four months compared to my original plan, I completed my PhD research with my full efforts, eventually and fortunately.

Declaration of Originality

I, Yanan Liu, herewith declare that the content of PhD thesis titled 'Investigating the impact of landscape fire smoke on migratory Insect flight' is the product of my own work under the guidance of my PhD supervisors, Prof. Martin Wooster and Prof. Robert Francis. This thesis is no more than 100,000 words in length including quotes and exclusive of tables, figures, appendices, references and footnotes. All material that is not my own work has been properly acknowledged. The content of this thesis has not been and will not be submitted for another degree at any other university or institution.

Yanan Liu

Contents

Abstract	1
List of Abbreviations	13
List of Tables	16
List of Figures	23
1 Introduction	24
1.1 Overview of the Thesis	26
1.2 Publications	29
1.2.1 Published	29
1.2.2 To be Submitted	30
2 Background, Aim and Objectives	31
2.1 Systematic Mapping and Review of Landscape Fire Smoke (LFS) Exposure Impacts on Insects	31
2.2 Insect Migration	46
2.3 Migratory Insect Roles in Ecosystem	46
2.3.1 Pollinators	47
2.3.2 Seed disperser	47
2.3.3 Decomposers	48
2.3.4 Bioindicator	48
2.3.5 Herbivores	48

2.3.6	Predators/Preys	49
2.4	Environmental factors impacting insect migration	49
2.4.1	Effects of wind on insect migration	49
2.4.2	Effects of temperature on insect migration	50
2.4.3	Effects of climate change on insect migration	50
2.5	Techniques to Study Insect Migration	51
2.5.1	Entomological radar observation (ERO)	51
2.5.2	Weather surveillance radar (WSR)	52
2.5.3	Stable-hydrogen isotope (SHI)	53
2.5.4	Tethered flight mill (TFM)	53
2.6	Thesis Aim	55
2.7	Specific Objectives	55
2.7.1	Determination of suitable migratory insect species as research target	55
2.7.2	Quantitative method to study the impact of LFS on migratory insects	56
2.7.3	New field and laboratory methods to measure landscape fire emissions	57
2.7.4	Study whether LFS impact migratory insects	58
2.7.5	Explore what LFS components may impact migratory insects	58
3	Measurement of gaseous and particulate emissions from agricultural residue burning	59
3.1	Introduction	59
3.2	Background	60
3.2.1	Agricultural Residue Burning	60
3.2.2	Emissions from Agricultural Residue Burning	61
3.3	Methodology	62
3.3.1	Experimental Overview	62
3.3.2	Laboratory Experiment	63
3.3.3	Field Sampling Approach	68

3.3.4	Quantitative Analysis Methodology	69
3.4	Results and Discussion	72
3.4.1	Laboratory Results	72
3.4.2	Emission Factor Estimation from Field Data	79
3.5	Incense Stick Burning	83
3.6	Summary	86
4	Impact of dense smoke conditions on butterfly flight performance	89
4.1	Introduction	89
4.2	Strong impacts of smoke polluted air demonstrated on the flight be- haviour of the painted lady butterfly (<i>Vanessa cardui</i> L.)	90
4.3	<i>Vanessa cardui</i> (<i>Painted lady butterfly</i>)	105
4.4	Tethered Flight Mill Techniques	107
4.4.1	Butterfly preparation for TFMs	107
4.4.2	TFM accuracy test on flight performance	109
4.5	Smoke Consistency Measurements	111
4.6	Summary	114
5	Impacts of light smoke conditions on butterfly flight performance over long flight periods	115
5.1	Introduction	115
5.2	Background	116
5.3	Methodology	117
5.3.1	Experiment setup	117
5.3.2	Determination of butterfly flight duration on TFM	119
5.3.3	Experiment design	120
5.3.4	Post-exposure examination using scanning electron microscopy (SEM)	123
5.3.5	Statistical analysis	124
5.4	Results	125
5.4.1	Incense coils successfully created three smoke conditions . . .	125
5.4.2	Flight speed change in smoke condition	126

5.4.3	Flight performance comparison between gas and smoke conditions	133
5.4.4	Scanning electron microscopy of butterfly body	136
5.5	Discussion	138
5.5.1	Incense coils burning generated different PM _{2.5} concentrations that simulated real landscape fire smoke exposure	138
5.5.2	Smoke conditions impact butterfly flight performance	139
5.5.3	Particles may be the main cause of the accelerated flight of butterfly	141
5.5.4	Particles distributed on the antennae may be the main cause of changes in butterfly flight performance	141
5.5.5	Particles may impact butterfly flight performance from other aspects	143
5.6	Summary	144
6	Conclusion and Future Work	145
6.1	Summary of Thesis Achievements	145
6.2	Future Work	148
6.2.1	Effects of the light smoke environment on the flight behaviour of the butterfly	148
6.2.2	Effects of the smoke components on the flight behaviour of the butterfly	149
6.2.3	Effects of the smoke emissions on the flight direction of migratory insects	149
6.2.4	Effects of the smoke emissions on the actual insect migration .	150
6.2.5	Effects of the landscape fire smoke on the other insects	150
6.2.6	Effects of the landscape fire on migratory insects	151
	References	152

List of Abbreviations

ANOVA	Analysis of Variance
BC	Black carbon
CAMS	Copernicus Atmosphere Monitoring Service
CC	Control condition
EF	Emission factor
ER	Emission ratio
ERO	Entomological radar observation
FRP	Fire power radiation
FL	Flaming phase
FS	Flight simulator
Gaslab	Gaslab Multi Gas Sampling Data Logger
GFAS	Global Fire Assimilation System
HD	High density
HS	High smoke
IQR	Interquartile Range
LFS	Landscape fire smoke
LGR	Los Gatos Research Ultraportable Greenhouse Gas Analyser
LD	Low density
LS	Low smoke
MCE	Modified combustion efficiency
MD	Medium density
MODIS	Moderate Resolution Imaging Spectroradiometer

MS	Medium smoke
OC	Organic carbon
OLS	Ordinary least squares
PAH	Polycyclic aromatic hydrocarbon
PM	Particulate matter
RFM	Rotational flight mill
SEM	Scanning electron microscopy
SD	Standard deviation
SHI	Stable-hydrogen isotope
SIR	Scanning insect radar
SM	Smouldering phase
SPSS	Statistical Package for the Social Sciences
TFM	Tethered flight mill
VLR	Vertical looking radar
WSR	Weather surveillance radar

List of Tables

3.1	Fires measured in the laboratory with different biomass, fire types, packing volume, mass, moisture contents, and durations. Each fire was repeated 3 times.	64
3.2	Weighted average modified combustion efficiency (MCE) for integrated phases and weighted average emission factor (EF) of trace gases and PM _{2.5} with standard deviations in different combustion phases, including integrated, pure flaming (FL), and pure smouldering (SM) phases, calculated from burning 100 g of different types of straw in completely dry conditions as bonfires.	75
3.3	PM _{2.5} concentration statistics of the two different smoke treatments created in the combustion chamber. Ignition of the straw occurred at time T ₁ . Total time-integrated PM _{2.5} concentration and mean PM _{2.5} concentration are given, both for the period from T ₁ up to 10 minutes after straw ignition (T ₁ + 10 minutes) and also up to 20 minutes after ignition (T ₁ + 20 minutes).	83
3.4	Weighted average MCE and weighted average EFs of trace gases and PM _{2.5} (g·kg ⁻¹) from burning different numbers of incense sticks. . . .	87

4.1	Descriptive statistics of flight behaviour variables (total flight distance, average speed, maximum speed, and flight duration) from six moth species (Family: Noctuidae) within one hour on tethered flight mill (TFM) collected from our pilot experiment, and flight behaviour variables (total flight distance and maximum speed) collected from H. B. Jones et al. (2016). Maximum speeds recorded from both experiments are in bold for comparison.	112
5.1	Summary of experiment design, indicating the number of butterflies used in Experiments A and B, where CC represents control condition, LS represents low smoke, MS represents medium smoke and HS represents high smoke.	121
5.2	The mean value of flight behaviour variables, including total flight distance, average flight speed, maximum speed, and flight duration, in the control conditions in six hours with standard deviation (SD). The data was collected from Experiment A.	128
5.3	The mean value of flight behaviour variables, including total flight distance, average flight speed, maximum speed, and flight duration, in the control conditions and three smoke conditions (LS, MS, and HS) in six hours with standard deviation (SD). Data was collected from Experiment A.	130
5.4	The mean value of flight behaviour variables, including total flight distance, average flight speed, maximum speed, and flight duration, in the gas conditions and HS conditions in six hours with standard deviation (SD). Data was collected from experiment B.	138

List of Figures

1.1	Global distribution of (a) Fire Radiative Power (FRP) areal density ($\text{W}\cdot\text{m}^{-2}$) coming from Global Fire Assimilation System (GFAS) derived using Moderate Resolution Imaging Spectroradiometer (MODIS) FRP data from the MODIS active fire product; (b) annual averaged $\text{PM}_{2.5}$ surface level concentrations caused by landscape fire-emitted $\text{PM}_{2.5}$ from the Copernicus Atmosphere Monitoring Service (CAMS) calculated over the period 2016–2019 (Figure is copied from Roberts and Wooster (2021) with copyright permission).	27
1.2	The distribution of migratory butterflies in the world, including five families. Colours on the map indicate the percentage of all described butterflies for each zoogeographic region that are considered migrants (Figure is copied from Chowdhury, Zalucki, et al. (2021) with copyright permission).	28
3.1	Schematic graph of the experiment setup: (a) combustion chamber, containing (1) burning tray (2) smoke extraction hood, (3) scale, (4) vent, and (5) extraction flue; (b) laboratory platforms with a series of associated instruments, including (6) Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyser, (7) TSI Dusttrak II Aerosol monitor 8530, (8) Gaslab Multi Gas Sampling Data Logger, (9) Extraction fan.	65

3.2	Photographs of (a) bonfire and (b) spreading fire during burning 100 g of rice straw in the ambient conditions on burning tray.	66
3.3	Ordinary least squares (OLS) linear regression showing the relationship between the smoke data collected from burning 100 g of soybean and millet straw in the ambient condition with LGR and Gaslab (a) mixing ratio of CO ₂ and (b) mixing ratio of CO.	73
3.4	Weighted average MCE for integrated phases and weighted average EFs of trace gases and PM _{2.5} (g·kg ⁻¹) with standard deviations in different combustion phases, including integrated, flaming (FL), and smouldering (SM) phases, calculated from burning 100 g of rice straw in ambient condition (with 10% moisture content) with different combustion types for three replicates.	77
3.5	Weighted average MCE for integrated phases and weighted average EFs of trace gases and PM _{2.5} (g·kg ⁻¹) with standard deviations in different combustion phases, including integrated, flaming (FL), and smouldering (SM) phases, calculated from burning 100 g of rice straw with different moisture contents. A least-squares linear trend line based on the results from integrated combustion is shown in each subplot, along with the coefficient of variation (R^2) and correlation coefficient (R).	78
3.6	Weighted average MCE for integrated phases and weighted average EFs of trace gases and PM _{2.5} (g·kg ⁻¹) with standard deviations in different combustion phases, including integrated, flaming (FL), and smouldering (SM) phases, calculated from burning rice straw with different packing densities, including low, medium and high density (LD, MD and HD). A least-squares linear trend line based on the results from integrated combustion is shown in each subplot, along with the coefficient of variation (R^2) and correlation coefficient (R).	80

3.7	Measured mixing ratios of CO and CO ₂ from rice straw burning in the actual agricultural land (blue dots) and from the burning 100 g of rice in the ambient condition as bonfires in the laboratory (red dots). ERs between CO and CO ₂ for pure flaming and smouldering phases of the two combustions are presented by blue and red lines, respectively.	81
3.8	Scatterplots of weighted average EFs of trace gases (g·kg ⁻¹) and MCE of all rice straw burning in the laboratory. Dashed line in each subplot represents the OLS best-fitting to the data, whose equation is shown along with the coefficient of variation (R^2) and correlation coefficient (R).	82
3.9	Mean atmospheric PM _{2.5} concentration timeseries calculated from the three replicates performed for each of the two different experimental smoke treatments made by 30 g and 60 g wheat straw in ambient conditions. Data are shown from the time of straw ignition (T ₁) to T ₁ +20 minutes. See Table 3.3 for the total time-integrated and mean PM _{2.5} concentrations for each treatment recorded over the same time periods.	84
3.10	Measurement of burning one incense stick on the burning tray.	85
3.11	Measured mixing ratios of CO and CO ₂ from incense stick burning are plotted in orange spots. The slope of the least squares linear best fit to these data (blue dashed line) along with 95% confidence interval (blue shaded area) is used to derive the ER_{CO/CO_2} .	86
4.1	Preparation of processed <i>Vanessa cardui</i> L. in the preparation stage before putting <i>Vanessa cardui</i> L. on the tethered flight mill technique (a) cutting a 3 cm length of steel wire; (b) making a pin by bending the end into a loop; (c) secured butterfly with net; (d) removing the surface of thorax (e) pin glued to the surface of thorax; (f) fed with honey water.	108
4.2	A light trap for capturing nocturnal moths. The white sheet is used to reflect the light and increase the overall light intensity.	110

4.3	TSL SidePak Aerosol Monitors were put in different heights and positions in the combustion chamber to record $PM_{2.5}$ concentrations, which were created by burning straw in the burn tray (SidePak 1 in the middle of the empty space; SidePak 2 is the bottom left, SidePak 3 is on the top right, SidePak 4 is on the bottom right and SidePak 5 is on the top left). Three small fans were put next to the burn tray to make the distribution of particles uniform in the whole chamber. .	113
4.4	Time-series $PM_{2.5}$ concentrations recorded by the five SidePak Aerosol Monitors shown in Figure 4.3 when burning (a) 15 g straw, (b) 30 g straw, (c) 60 g straw. The instrument becomes saturated at $PM_{2.5}$ concentrations above $27 \text{ mg}\cdot\text{m}^{-3}$ after applying calibration factor of 0.27.	114
5.1	A diagram of the experimental setup. Individuals were put in (a) smoke enclosure or (b) control enclosure. Smoke was released from burning incense coils in a smoke box (1) and transported to the smoke enclosure by tube (2). Three axial fans (3) were placed in right, left, and underneath the enclosure to promote air circulation, exhaust fan (4) and extract duct was to remove excess smoke. The TFM equipment (6) was used to record the butterfly flight performance. A particulate sensor (7) and PurpleAir PA-II SD air quality sensor (8) were to record $PM_{2.5}$ concentration. A temperature-humidity sensor (9) and light intensity sensor (10) recorded the environmental factors.	117
5.2	Flight speed of eight sample butterflies flown under clean-air conditions for 24 hours. Most have ceased flying by 8 hours.	120

-
- 5.3 Atmospheric conditions in the smoke enclosure and control enclosure, measured across all experiments for (a) air temperature, (b) relative humidity, and (c) light intensity. Box plots illustrate the upper quartile (75th percentile), the median (50th percentile) and the lower quartile (25th percentile), with upper whiskers reaching $Q_3 + 1.5 \times \text{interquartile range (IQR)}$ and lower whiskers $Q_1 - 1.5 \times \text{IQR}$. The red square is the mean. 122
- 5.4 Boxplots showing gaseous emissions from high smoke conditions in smoke enclosure and gas conditions in control enclosure, measured across all experiment B for (a) CO_2 concentration (b) CO concentration and (c) CH_4 concentration. Box plots illustrate the upper quartile (75th percentile), the median (50th percentile) and the lower quartile (25th percentile), with upper whiskers reaching $Q_3 + 1.5 \times \text{interquartile range (IQR)}$ and lower whiskers $Q_1 - 1.5 \times \text{IQR}$. The red square is the mean and outliers beyond these limits are plotted as black circle. 124
- 5.5 Timeseries of mean atmospheric $\text{PM}_{2.5}$ concentration of different smoke conditions calculated from the four replicates in five different conditions, including control, LS, MS, HS, and gas conditions. Data are shown from the time of incense stick ignition (T_1) to $T_1 + 6$ hours. $\text{PM}_{2.5}$ concentration data was collected from the particulate sensors and oscillates within a certain range for each condition. 125
- 5.6 Boxplots showing the flight speed of butterflies from control conditions separated into 36 10-minute timesteps, collected from Experiment A. (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying completely. The higher and lower bars of the plots are the maximum and minimum values respectively, while the rectangle illustrated the first quartile, the median, and the third quartile (bottom to top). The blue square is the mean and black circle is outliers. 127

5.7 Bar charts showing percentage of flying for 36 10-minutes timesteps in control conditions calculated from Experiment A. 128

5.8 Boxplots showing the flight speed of butterflies from different smoke conditions (red) and control conditions (blue) separated into 36 10-minute, collected from Experiment A. (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying completely. The higher and lower bars of the plots are the maximum and minimum values respectively, while the rectangle illustrated the first quartile, the median, and the third quartile (bottom to top). The red square is the mean and black circle is outliers. 129

5.9 Bar charts showing percentage of flying for 36 10-minutes timestep in different smoke conditions (LS, MS, and HS) and control conditions calculated from Experiment A. 130

5.10 Scatterplots of mean flight speed changes over time extracted from data without the zero value flight speeds as was the case with Figure 5.8b in different smoke conditions (LS, MS, and HS) and control conditions. The blue line represents the least squares linear best-fit for control, LS, and MS conditions and nonlinear best-fit for HS conditions, along with the 95% confidence intervals on the slop (light blue area). The equations for which is shown along with the coefficient of variation (R^2). The dashed line showed the flight speed variance thresholds, which divided the flight speed variance into two parts-increasing trend and decreasing trend. 132

5.11 Stem plots show the difference of mean flight speed between (a) LS conditions (Red line), (b) MS conditions (Yellow line) and (c) HS conditions (Green line) and control conditions calculated from all data with the zero value flight speeds removed as was the case with Figure 5.8b. The flight value without zero value in control conditions are regarded as baseline. 133

5.12 Boxplots showing the flight speed of butterflies from different smoke conditions (red) and gas conditions (green) separated into 36 10-minute, collected from experiment B. (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying completely. The higher and lower bars of the plots are the maximum and minimum values respectively, while the rectangle illustrated the first quartile, the median, and the third quartile (bottom to top). The red square is the mean and black circle is outliers. 134

5.13 Bar charts showing percentage of flying for 36 10-minutes timestep in HS conditions and gas conditions calculated from experiment B with four replicates. 135

5.14 Scatterplots of mean flight speed changes over time extracted from data without the zero value flight speeds as was the case with Figure 5.12b in HS conditions and gas conditions. The blue line represents the least squares linear best-fit for gas conditions and non-linear best fit for HS conditions, along with the 95% confidence intervals on the slop (light blue area). The equations for which is shown along with the coefficient of variation (R^2). The dashed line showed the flight speed variance thresholds, which divided the flight speed variance into two parts-increasing trend and decreasing trend. 136

5.15 Scanning electron microscopy images of (a) antenna (b) abdomen in butterfly with $\times 1500$ magnification to show the presence of PM_{10} / $PM_{2.5}$ / PM_{10} from (i) control condition; (ii) LS condition; (iii) MS condition; and (iv) HS condition. The red square shows the area where the particles potentially appeared. 137

Chapter 1

Introduction

This thesis describes work conducted to improve the understanding of the impact of smoke pollution from landscape fires on migratory insects, in particular focusing on flight performance. Landscape fires, containing both wildfires and prescribed fires, are occurring increasingly due to climate change and anthropogenic activities (Dupuy et al., 2020; Moritz et al., 2012). Smoke pollution released from landscape fires is comprised of various chemicals, including trace gases (such as CO₂, CO, NO_x, and SO₂) and atmospheric aerosols (Cascio, 2018; Johnston et al., 2012; X. Li et al., 2007). The impacts of smoke pollution on human health have been extensively studied (Cascio, 2018), for example, respiratory problems (Henderson et al., 2011; Henderson and Johnston, 2012), cardiovascular diseases (Henderson et al., 2011), and mortality (Johnston et al., 2012; O'Dell et al., 2021). However, there has been less attention given to the impacts of smoke pollution on ecosystems and other species.

Insects occupy a key position natural environment and play different roles in ecosystems, such as predators (T. R. New et al., 1992), parasites (Schmid-Hempel, 1998), and pollinators (McGregor, 1976). Moreover, they work as bioindicators of their habitat or ecosystem health because they are quite sensitive to environmental pollu-

tion and provide useful information on environmental alterations (Ghannem et al., 2018; Parikh et al., 2021). The butterfly in particular is considered a bioindicator in studies as, in addition to their high sensitivities to environmental changes, they are relatively easy to classify and track (Hirowatari et al., 2007; Parmesan, 2019). Moreover, the richness and abundance of butterfly species have been shown to be directly related to forest fires, possibly through the destruction of their habitat by fires (Cleary and Grill, 2004; Topp et al., 2022). For instance, in Indonesian fires during 1997-1998, butterfly species richness declined remarkably from over 200 species pre-fire to less than 40 species post-fire so that the community composition altered obviously, however, The presence of most butterfly species is determined by plant composition, the number of *Jamides celeno* (The common cerulean) increased by over 50% from pre-fire to post-fire due to their host plant was abundant (Cleary and Grill, 2004). In addition to the direct effects, landscape fires may have some indirect effects on insects, for example, the derivatives of landscape fire-smoke emissions may also have potential effects on insects. The research in Tan et al. (2018) indicated fire smoke impacts the development of butterflies. However, there are fewer studies on other perspectives, for instance, insect migration. Many migratory insects in the southern hemisphere migrate during December and February (Farrow, 1984; Maelzer et al., 1996; Qi et al., 2021; Smithers, 1983), such as *Spodoptera frugiperda* (Fall armyworm) (Qi et al., 2021), *Helicoverpa punctigera* (the native budworm) (Maelzer et al., 1996). However, insects, such as *Agrotis ipsilon* (Dark sword-grass) (Zeng et al., 2020), *Mythimna separata* (Oriental armyworm) (X. Jiang et al., 2011), in the northern hemisphere mainly have three migration periods, including spring period (early March-May), summer period (June- July), and autumn period (September-October) (R.-L. Chen et al., 1989; H. Feng et al., 2004; H.-Q. Feng et al., 2003; Hallworth et al., 2018; X. Jiang et al., 2011; Zeng et al., 2020). The migration periods between May and June, September and October coincide with the time of some seasonal biomass burning (Tang et al., 2013; Xia et al., 2013). Thus, fire smoke may affect their flight performance during migration, change the breeding sites of insects, and alter the local ecological landscape. In addition to coinciding in time, they may also coincide in location, with implications. The global distribution of fire

activity determined from Fire Radiative Power (FRP) data and the modelled mean annual average surface level PM_{2.5} concentration resulting from smoke emitted from landscape fire have been shown in Figure 1.1 (from Roberts and Wooster (2021)). Figure 1.2 shows the global distribution of migratory butterflies (except Antarctica), which indicates that butterflies are globally migratory although the species and number vary among regions (Chowdhury, Fuller, et al., 2021). From these two figures, there seems overlap between where fires occur and migratory butterflies are located. However, no study has addressed the potential impact of smoke pollution from landscape fires on the flight performance of migratory insects.

In this thesis, *Vanessa cardui* L. (Painted lady butterfly) has been chosen as the research target because of its wide distribution, strong flight ability, and regular migration (Abbott, 1951; Chowdhury, Fuller, et al., 2021; Ecuador, 1992; Stefanescu et al., 2017; Stefanescu et al., 2013). For example, *Vanessa cardui* migrates between Africa and Europe every year, sometimes in large numbers (Stefanescu et al., 2007; Stefanescu et al., 2013). The flight performance of *Vanessa cardui* is quantitatively measured in different smoke conditions and clean-air conditions to explore whether smoke pollution impacts their flight performance. In addition, the emissions from landscape fires are studied to understand the specific substances contained in the smoke and their relative abundance. This study aims to evaluate the effects of smoke pollution from landscape fires on the flight performance of butterflies, helping understand how insects might respond to air pollution during migration.

1.1 Overview of the Thesis

The contents of this thesis comprise five further chapters.

Chapter 2: Background, Aim and Objectives. This chapter provides an overview of the literature on smoke emissions from landscape fires, the roles of insects in ecosystems, and the impacts of landscape fires smoke on insects. In this chapter, a published paper is presented (Y. Liu et al., 2022), which focuses on the

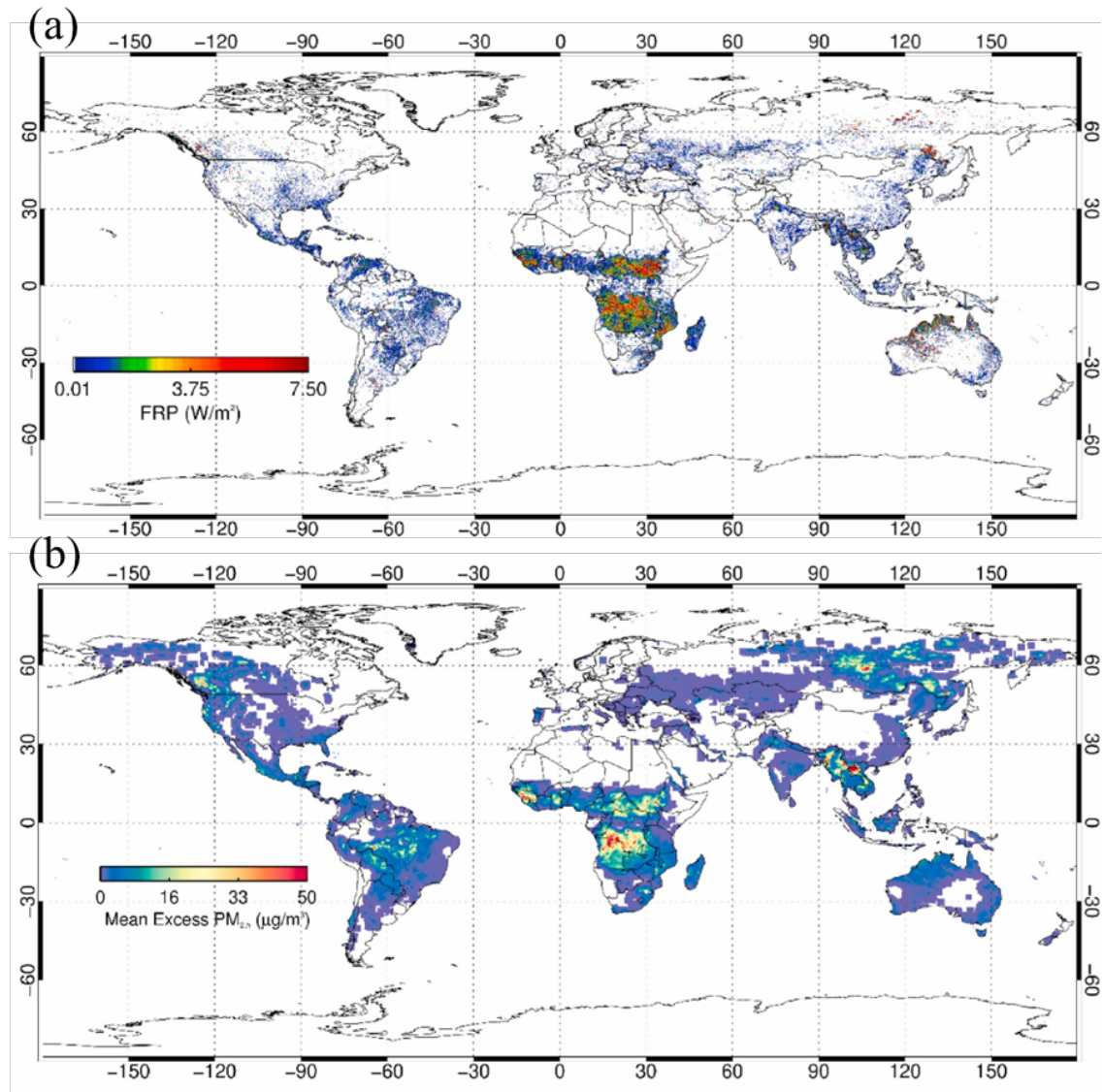


Figure 1.1: Global distribution of (a) Fire Radiative Power (FRP) areal density ($\text{W}\cdot\text{m}^{-2}$) coming from Global Fire Assimilation System (GFAS) derived using Moderate Resolution Imaging Spectroradiometer (MODIS) FRP data from the MODIS active fire product; (b) annual averaged $\text{PM}_{2.5}$ surface level concentrations caused by landscape fire-emitted $\text{PM}_{2.5}$ from the Copernicus Atmosphere Monitoring Service (CAMS) calculated over the period 2016–2019 (Figure is copied from Roberts and Wooster (2021) with copyright permission).

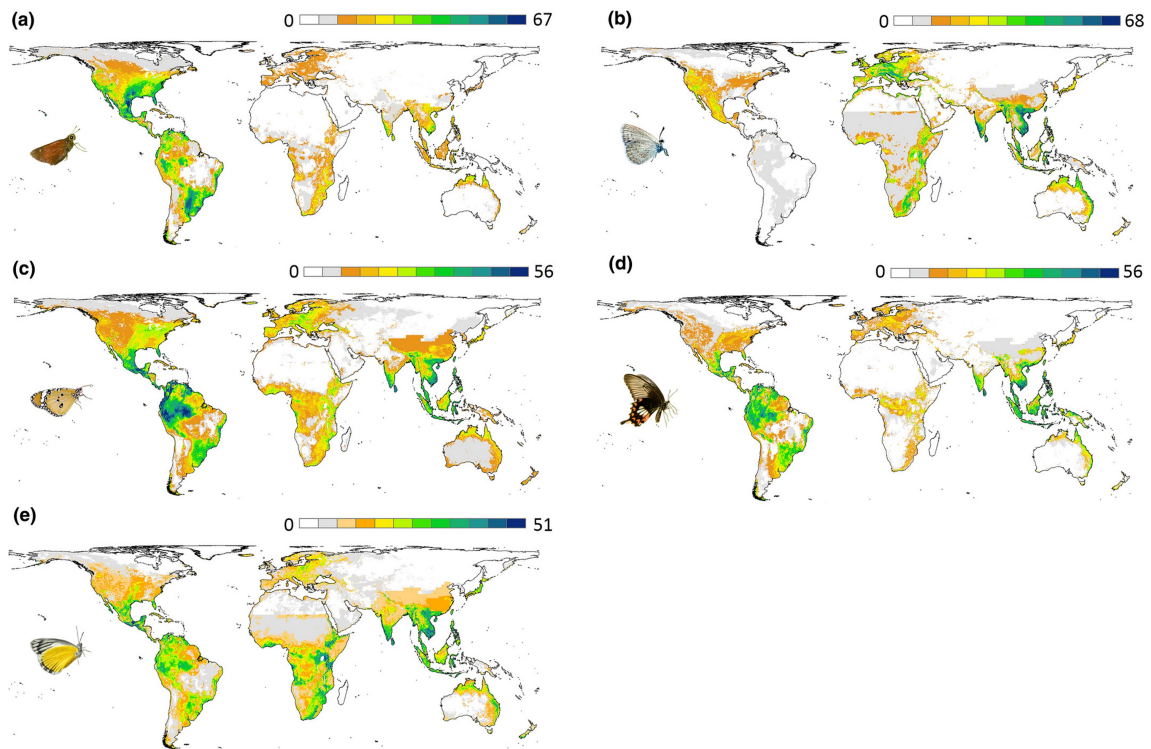


Figure 1.2: The distribution of migratory butterflies in the world, including five families. Colours on the map indicate the percentage of all described butterflies for each zoogeographic region that are considered migrants (Figure is copied from Chowdhury, Zalucki, et al. (2021) with copyright permission).

review of the impact of smoke pollution from landscape fires on insects. Also, this chapter concludes with a series of specific research objectives addressed in the later chapters.

Chapter 3: Measurement of gaseous and particulate emissions from agricultural residue burning. This chapter mainly contains measurements of emission factors of trace gases and aerosol from agricultural fires in China, mainly comparing the emissions from different agricultural residues (rice straws, wheat straws, millet straws, soybean straws, and corn straws). These samples are burned in different ways to understand the variability in emissions based on different packing densities and moisture contents. Furthermore, incense sticks are shown to have similar smoke emissions as biomass burning, so that they are used to create stable smoke environments for further experiments.

Chapter 4: Impact of dense smoke conditions on butterfly flight performance. This chapter aims to study whether emissions from fires have an impact on butterflies. Part of the content in this chapter presents a published paper (Y. Liu et al., 2021), which focuses on investigating the impact of dense smoke pollution on the flight performance of butterflies.

Chapter 5: Impacts of light smoke conditions on butterfly flight performance over long flight periods. This chapter is to explore the potential impacts of landscape fire smoke on insect migration and to explore what substances in the smoke emissions impact butterfly flight performance.

Chapter 6: Conclusion and future work.

1.2 Publications

The material presented in this thesis has led to the following papers published or to be submitted.

1.2.1 Published

- **Liu, Y.**, Francis, R. A., Wooster, M. J., Grosvenor, M. J., Yan, S., & Roberts, G. (2022). Systematic Mapping and Review of Landscape Fire Smoke (LFS) Exposure Impacts on Insects. *Environmental Entomology*, 51(5), 871-884.
- **Liu, Y.**, Wooster, M. J., Grosvenor, M. J., Lim, K. S., & Francis, R. A. (2021). Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.). *Ecological Entomology*, 46(2), 195-208.

1.2.2 To be Submitted

- Estimating emissions from agricultural burning based on laboratory measurements. Journal paper.
- Impacts of light smoke conditions on the flight performance of painted lady butterfly (*Vanessa cardui* L.) over long periods. Journal paper.

Chapter 2

Background, Aim and Objectives

This Chapter reviews the literature related to this PhD and identifies a set of aims and objectives for the work. Section 2.1 includes a literature review looking at studies on the impacts of smoke pollution from landscape fires already published as a systematic review paper. Since migratory insects are the research targets in this thesis, Section 2.2) introduces insect migration, and Section 2.3) describes the roles of migratory insects in ecosystems which emphasizes their importance. The environmental factors that might impact insect migrations are introduced in section 2.4. The focus then turns to different techniques used to study the impact of environmental changes on insect migration (Section 2.5). After reviewing the related literature, aims and objectives of this thesis are summarised in Sections 2.6 and 2.7.

2.1 Systematic Mapping and Review of Landscape Fire Smoke (LFS) Exposure Impacts on Insects

Environmental Entomology, 51(5), 2022, 871–884

<https://doi.org/10.1093/ee/nvac069>

Advance Access Publication Date: 21 September 2022

Review



Review

Systematic Mapping and Review of Landscape Fire Smoke (LFS) Exposure Impacts on Insects

Yanan Liu,^{1,2,6,✉} Robert A. Francis,¹ Martin J. Wooster,^{1,2,3} Mark J. Grosvenor,^{1,2,3} Su Yan,^{4,✉} and Gareth Roberts⁵

¹Department of Geography, King's College London, Bush House, 40 Aldwych, London, WC2B 4BG, UK ²Leverhulme Centre for Wildfires, Environment and Society, King's College London, London WC2R 2LS, UK ³NERC National Centre for Earth Observation, King's College London, London WC2R 2LS, UK ⁴Department of Electrical and Electronic Engineering, Imperial College London, London SW7 2BX, UK ⁵Geography and Environmental Science, University of Southampton, Southampton, UK and ⁶Corresponding author, e-mail: yanan.liu@kcl.ac.uk

Subject Editor: Darrell Ross

Received 13 April 2022; Editorial decision 16 August 2022.

Abstract

Landscape fire activity is changing in many regions because of climate change. Smoke emissions from landscape fires contain many harmful air pollutants, and beyond the potential hazard posed to human health, these also have ecological impacts. Insects play essential roles in most ecosystems worldwide, and some work suggests they may also be sensitive to smoke exposure. There is therefore a need for a comprehensive review of smoke impacts on insects. We systematically reviewed the scientific literature from 1930 to 2022 to synthesize the current state of knowledge of the impacts of smoke exposure from landscape fires on the development, behavior, and mortality of insects. We found: (1) 42 relevant studies that met our criteria, with 29% focused on the United States of America and 19% on Canada; (2) of these, 40 insect species were discussed, all of which were sensitive to smoke pollution; (3) most of the existing research focuses on how insect behavior responds to landscape fire smoke (LFS); (4) species react differently to smoke exposure, with for example some species being attracted to the smoke (e.g., some beetles) while others are repelled (e.g., some bees). This review consolidates the current state of knowledge on how smoke impacts insects and highlights areas that may need further investigation. This is particularly relevant since smoke impacts on insect communities will likely worsen in some areas due to increasing levels of biomass burning resulting from the joint pressures of climate change, land use change, and more intense land management involving fire.

Key words: landscape fire, smoke, insect, behavior, development

Landscape fires, including wildfires and fires purposely lit for clearing or managing land, are widespread globally, occurring in almost all vegetated biomes worldwide (Fried et al. 2004, 2008; Johnston et al. 2012; Roberts and Wooster 2021). Whilst many biomes may benefit from landscape fires ecologically, not all are well suited to the presence of fire (Keane et al. 2008). In some regions, anthropogenic fires have become too widespread, or are so disparate from the natural regimes that the ecological benefits of fires have diminished (Syphard et al. 2007, 2009). Beyond terrestrial impacts such as the removal of vegetation and the combustion of organic soil, landscape fire has

a significant effect on the atmosphere through the smoke released (Keshkar and Ashbaugh 2007, Gadde et al. 2009, Shi et al. 2014).

This smoke is composed of a mix of gases and airborne particulates, some of which pose risks to normal biological functioning (Erb et al. 2018, Vokina et al. 2019, Sanderfoot et al. 2021). The smoke emissions can affect the air quality locally or even far from the fires (Einfeld et al. 1991, Ward et al. 1992, Streets et al. 2003, Chen et al. 2017, Cascio 2018, Wang et al. 2020, Roberts and Wooster 2021). Whilst most research has focused on the effect of this air pollution on human health (Reid et al. 2016, Roberts and

© The Author(s) 2022. Published by Oxford University Press on behalf of Entomological Society of America.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

871

Wooster 2021, Sanderfoot et al. 2021), other animals, including insects, may also be affected. Landscape fires emit thousands of kilograms of carbon into the atmosphere every year – predominantly carbon dioxide (CO₂), carbon monoxide (CO), and methane (CH₄) (Jenkins et al. 1992, Andreae and Merlet 2001, Gupta et al. 2004, Gadde et al. 2009, Van der Werf et al. 2010, Zhang et al. 2015, Li et al. 2019, Ravindra et al. 2019). Additionally, nitrogenous gases such as ammonia (NH₃), nitric oxide (NO), nitrogen dioxide (NO₂), and nitrous oxide (N₂O) are also released from fires (Gupta et al. 2004, Oppenheimer et al. 2004, Li et al. 2019, Ravindra et al. 2019). Another group of gaseous emissions emitted in smaller quantities are sulfur-containing gases such as sulfur dioxide (SO₂) (Gadde et al. 2009; Akagi et al. 2011; Li et al. 2017, 2019), along with smaller quantities of toxic and/or carcinogenic compounds such as hydrogen cyanide (HCN), hydrogen chloride (HCl), benzene (C₆H₆), and polycyclic aromatic hydrocarbons (PAH). Certain constituents of the smoke can react to generate other toxic pollutants downwind, such as tropospheric ozone (O₃) (Jaffe and Wigder 2012, Marlier et al. 2013). These gases may pose a hazard to insects in sufficient concentrations. For example, short term exposure to CO₂ can act as an anesthetic for *Drosophila melanogaster* (Diptera: Drosophilidae), which leads to a significant decrease in their electroretinogram responses to light stimulation (Stark 1972, Wong et al. 1972, Nicolas and Sillans 1989). CO affects the respiration of insects and causes them to become less active and consume less food (Baker and Wright 1977). NO₂ has been shown to interfere with the olfactory responses of *Asobara tabida* (Hymenoptera: Braconidae) (Gate et al. 1995). *Drosophila melanogaster*, when exposed to SO₂ concentrations of around 0.4 ppm in the environment, displayed significantly decreased pupal survival and adult endurance to the polluted environment (Ginevan and Lane 1978).

Particulate matter (PM) is another risk-related concern from LFS (landscape fire smoke), especially those particles of less than 10 microns in diameter (PM₁₀) and less than 2.5 microns in diameter (PM_{2.5}) (Simoneit 2002, Dhammapala et al. 2007, Broyles 2013). The PM is mainly found in black and organic aerosols, and the PM size distribution is typically skewed strongly toward smaller size particles (Reid et al. 2005, Rissler et al. 2006, Zhang et al. 2011, Roberts and Wooster 2021). The finer PM_{2.5} is regarded as the most significant, health-impacting, and widely transported particulate component of smoke (Johnston et al. 2012, Chen et al. 2017). Fig. 1 shows the fire radiative power density and averaged PM_{2.5} surface level concentration caused by landscape fire in 2017, which Roberts and Wooster (2021) calculated exposed over 65 million people to hazardous PM_{2.5} conditions worldwide. These particulate concentrations are likely to also have direct impacts on insects. For instance, increased concentrations of airborne PM_{2.5} have been linked with shortened lifespans of *Drosophila melanogaster*; in a treatment with an average PM_{2.5} concentration of 80 µg m⁻³, 50% of males and females died after 20 and 21 d respectively, while 50% of flies in filtered air (with an average PM_{2.5} concentration of 4 µg m⁻³) died after 48 and 40 d, respectively (Wang et al. 2017).

Previous review articles primarily focused on the effects of LFS on human health (Reid et al. 2016), while the impacts on ecosystems have been less extensively summarized. A comprehensive and systematic synthesis of present research on the effects of LFS on insects is needed to predict the changes in ecosystem services and manage the impact of LFS effectively. This review examines the evidence for the impacts of smoke exposure on insects. Here we focus on LFS and some indoor biomass burning, since the composition of smoke from indoor sources, such as indoor fuelwood burning and incense sticks, is relatively similar to the smoke components from landscape fires (Jetter et al. 2002, Lin et al. 2008, See and Balasubramanian 2011). For instance, in some laboratory work to observe insect response to

smoke, smoke emitted from incense coils is used to simulate the haze from forest fires (Tan et al. 2018, Liu et al. 2021). Anthropogenic burning sources such as industrial coal fire, domestic fossil fuel combustion, and traffic engine combustion, were not considered because these commonly occur in anthropogenic settings according to the classification from De Gouw et al. (2004). We used a systematic mapping approach to review the effects of LFS (and other smoke sources that have similar compositions) on insects and we summarized how insects responded to the LFS. Our classification and summary will consolidate the current state of knowledge in this area to facilitate future research on the effects of air pollution on ecosystems and further understand the impacts of climate change on insects.

Methodology

Systematic Mapping Methods

Unlike traditional inductive methods for collating information, systematic mapping is a method of organizing, describing, and categorizing available evidence on a specific subject by using an objective and transparent manner to format a usable database and understand knowledge deficiencies (Haddaway et al. 2016, James et al. 2016). We searched papers on PubMed, Web of Science, and Google Scholar using keywords ('smok*' and 'landscape burning' and 'insec*'; also with suitable alternatives) to identify those associated with LFS exposure and relevant insect impacts.

Following standard systematic mapping methods, including identification, searching, and screening (James et al. 2016, Berger-Tal et al. 2018), we found 293 articles in PubMed, 296 articles in Web of Science, and 7,070 articles in Google Scholar up to, and including, January 2022. All records obtained were considered, from the earliest articles incorporated in the databases (1930–2022). From these, we removed articles if they described mosquito coil smoke impacts on various types of mosquitoes or focused on tobacco smoke impacts. Mosquito coils are made from base materials such as teak wood and coconut shell powder (Pauluhn 2006). However, they are usually used indoors and overnight to repel mosquitoes by gradually releasing insecticide (Pauluhn 2006, Hogarth et al. 2016). Tobacco is made by drying leaves from tobacco plants, and its smoke contains not only CO₂, CO, hydrocarbons but also nicotine and aromatic amines (Rodgman and Perfetti 2013). Since the nicotine from tobacco is toxic to many insects, it has been commonly used as a commercial pesticide (Gorrod and Jacob III 1999). We, therefore, did not include those studies because the insecticide chemicals and nicotine released from these sources do not naturally occur in smoke from landscape or domestic wood fires.

After reading abstracts, we scrutinized all records and selected studies that focused on the impacts of real-world LFS and simulated LFS on insects, excluding articles that only studied LFS and were not related to insects, or if they assessed the insect response to stressors not associated with LFS. After accounting for duplicates, we identified 42 unique articles. From the remaining environmental entomology studies (N = 42), we extracted the following information from each paper: (1) insect species covered; (2) type and source of smoke pollution; (3) aspects of insect ecology impacted by the pollutant – categorized into development, behavior, and mortality; and (4) geographical location of study.

Results

Species of Insect Occurring in Relevant LFS

Literature

A total of 42 studies met the criteria for this review, with 40 species of insect studied for their response to smoke polluted conditions.

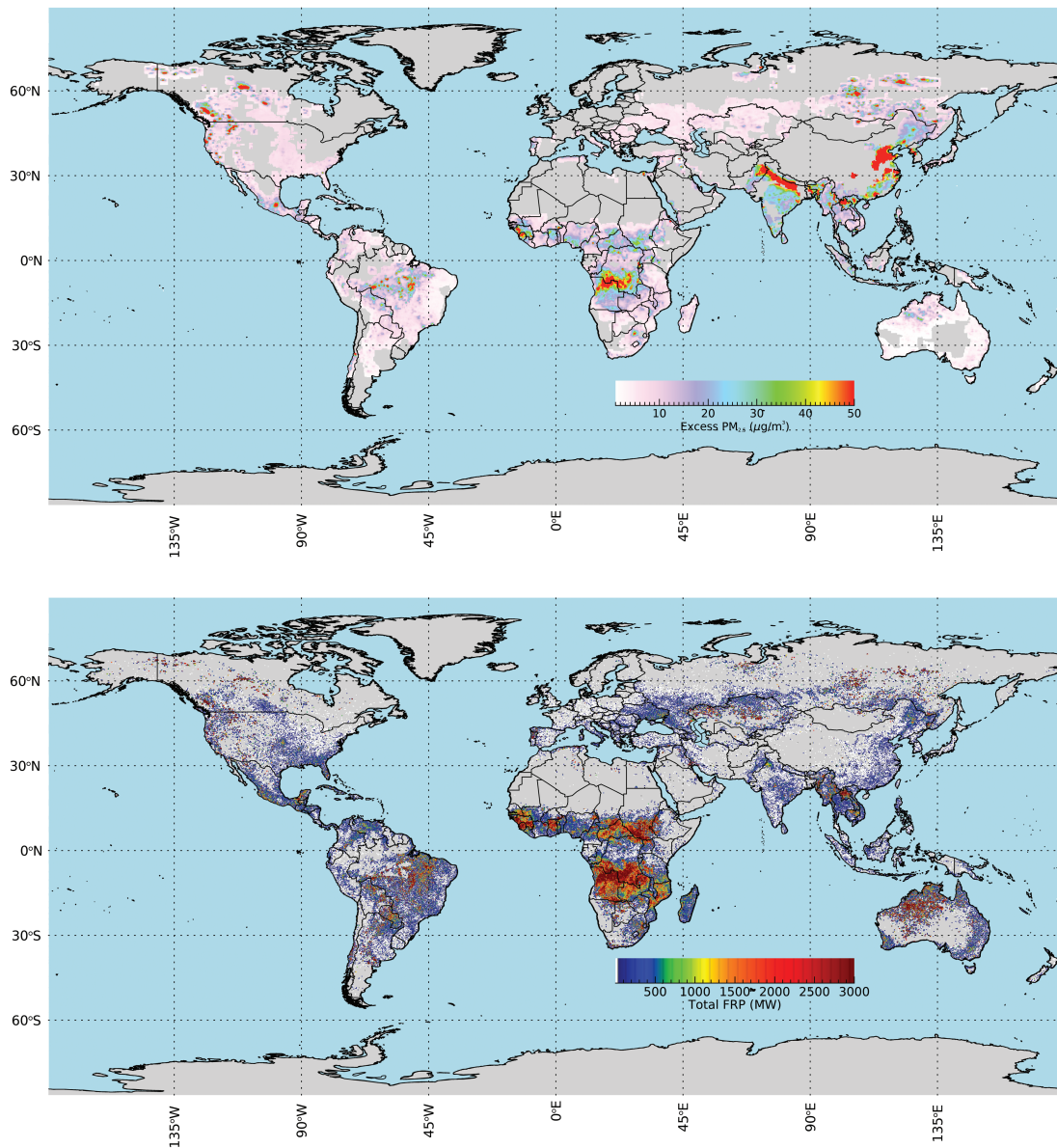


Fig. 1. Globally mapped outputs calculated in 2017, with (a) GFAS Fire radiative power (FRP) areal density and (b) the averaged $PM_{2.5}$ surface level concentrations caused by landscape fire-emitted $PM_{2.5}$ (For more information, refer to [Roberts and Wooster 2021](#) for a description of how these data are constructed, and to view longer-term mean plots derived from multiple years).

These 40 species were included in twenty-three families and seven orders, including Coleoptera (18 studies), Diptera (12 studies), Hymenoptera (8 studies), Lepidoptera (5 studies), Hemiptera (1 study), Phasmatodea (1 study) and Orthoptera (1 study).

Many species only occurred once in the studies mapped, but some were the foci of several papers. For instance, of the eighteen Coleoptera studies, three focused on *Melanophila acuminata* (Coleoptera: Buprestidae) and other species had two studies individually, including *Monochamus galloprovincialis* (Coleoptera: Cerambycidae), *Rhyzopertha dominica* (Coleoptera: Bostrichidae), *Sericoda bembidioides* (Coleoptera: Carabidae) and *Sitophilus oryzae*

(Coleoptera: Curculionidae). Six of twelve Diptera studies referred to *Anopheles gambiae* (Diptera: Culicidae). Five out of eight studies on Hymenoptera focused on *Apis mellifera* (Hymenoptera: Apidae).

Smoke Types and Sources

Landscape fires contain various fire types, including forest fires, savanna fires, peat fires, and agricultural fires ([Finney 1999, 2004; Keane and Finney 2003; Giglio et al. 2018](#)). A range of smoke sources covered in the literature, is drawn from landscape fires and indoor burning. This study reclassified the reported

smoke sources into the two broad indoor and outdoor smoke source categories, with ten specific categories (Fig. 2). Twenty-two studies described the actual landscape fires, of which seventeen articles studied smoke generated from wildfires, and others consisted of wood fire and prescribed fires. Fourteen out of the seventeen wildfire studies focused on forest fires; others included bushfires and savanna fires.

Twenty studies utilized indoor biomass burning to simulate smoke conditions from landscape fires, using fuel such as burlap, cow dung cake, wood, and weeds. Indoor sources in this context include those studies that covered the actual domestic fuel burning activities and biomass sources used in the experimental work to allow more direct measurement of pollutants and particulates. This included where incense coils/sticks were used in the laboratory work, which mainly consist of wood, organic adhesive, and potassium nitrate (Yadav et al. 2020), and therefore, the smoke released by incense has similar components to the smoke from biomass burning (Jetter et al. 2002, Lee and Wang 2004, Lin et al. 2008, Shi et al. 2014). Another two biomass fuels commonly burned indoors are burlap—a woven fabric usually made from the skin of the jute plant and widely used by beekeepers, and hop pellets – which are dried from *Humulus lupulus* (Reilly 1906, Van Cleemput et al. 2009, Gage et al. 2018).

Overall, forty-two papers described eighteen different biomass sources, with one-third of the articles focusing on forest fires (Fig. 2). The dominant emissions in those studies were generically described as ‘smoke’ or ‘volatiles’. Although most papers did not measure the specific gases or particulates produced, they suggested that the smoke emissions from forest fires, vegetation fires, and wood fires contain similar components (Larson and Koenig 1994, Goldammer et al. 2008, Simpson et al. 2011).

Impacts of Smoke Pollution on Insects

The impacts of smoke pollution on insects recorded in the published literature were divided into three broad aspects: (1) larval development (3 studies); (2) behavior (33 studies); and (3) mortality (6 studies) (Fig. 3). From the literature, four species of insects were demonstrably impacted by smoke across more than one aspect (e.g., Lepidoptera (Family: Noctuidae) had smoke-related impacts on larval development, behavior, and mortality). Three insect orders had evidence of results from only one part: e.g., Hemiptera, Orthoptera, and Hymenoptera were affected in their behavior. The overall findings are summarized below.

Impacts on Insect Larval Development

Smoke pollution from burning activities can affect insect growth and lifespan, with one relevant study reporting positive, and two reporting negative influences. Firstly, the larval development of some insect species can be affected. Forest fire smoke was associated with over 90% of eggs of three stick insect species (*Ctenomorphodes tessulatus* [Phasmatodea: Phasmatidae], *Podacanthus wilkinsoni* [Phasmatodea: Phasmatidae], and *Didymuria violescens* [Phasmatodea: Phasmatidae]) failing to hatch (Campbell 1961). Tan et al. (2018) demonstrated that *Bicyclus anynana* (Lepidoptera: Nymphalidae) larvae exposed to burning incense coil simulating forest fire smoke of average PM_{2.5} concentration at 120 µg m⁻³ exhibited significantly decreased survival, prolonged larval development time, and reduced pupal weight compared with those exposed to an average PM_{2.5} concentration of 50 µg m⁻³ (control treatment). An increase in development time and a decrease in pupal weight were also observed when larvae were fed on corn plants exposed to the same concentration of smoke, demonstrating an indirect impact of exposure to smoke. Nevertheless, not all smoke-related impacts are harmful, and some insects respond positively to LFS. The volatiles from burned vegetation stimulated the biosynthesis of virgin female juvenile hormones of *Actebia fennica* (Lepidoptera: Noctuidae), which would accelerate sexual maturation and reduce the period of mating and oviposition. The average number of chorionic eggs in smoke-exposed females was twice that of the control group (Everaerts et al. 2000).

Impacts on Insect Behavior

In addition to directly affecting the growth of insects, smoke also impacts insect behavior. Insects may be attracted to, or repelled by, potential substratum-rich recently burned habitats due to the smoke and heat (Evans 1972; Saint-Germain et al. 2008, Tribe et al. 2017). Fire-favoring beetles, such as *Buprestidae* (Coleoptera) and *Cerambycidae* (Coleoptera), were attracted to fire activity by smoke and reproduced quickly in the freshly-burned forest (Linsley 1943, Gardiner 1957, Ross 1960, Evans 1972, Leatherman and Aguayo 2002, Koivula et al. 2006, Saint-Germain et al. 2008, Paczkowski et al. 2013, Álvarez et al. 2015, Milberg et al. 2015, Elia et al. 2016, Ali et al. 2017). The smoke plumes can attract these insects (Saint-Germain et al. 2008) to habitats where landscape fires are still occurring or have just ended (Richmond and Lejeune 1945, McCullough et al. 1998, Leatherman and Aguayo 2002, Koivula and Spence 2006, Koivula et al. 2006). Guaiacol derivatives released from burning *Pinus sylvestris* (Scots pine) can stimulate the

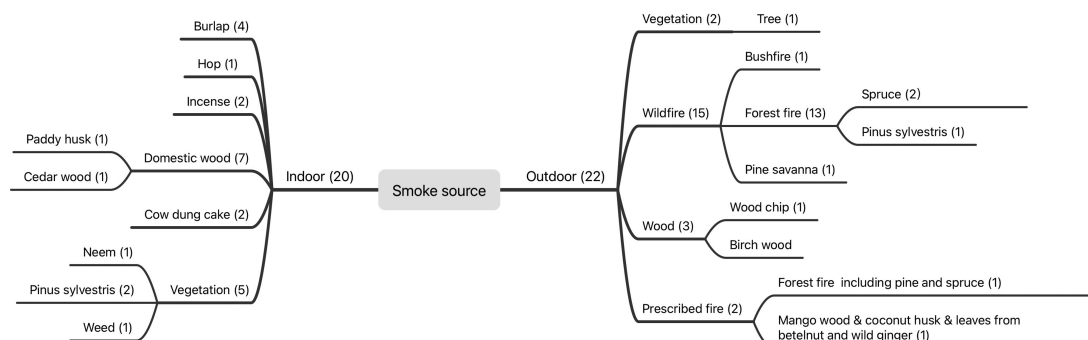
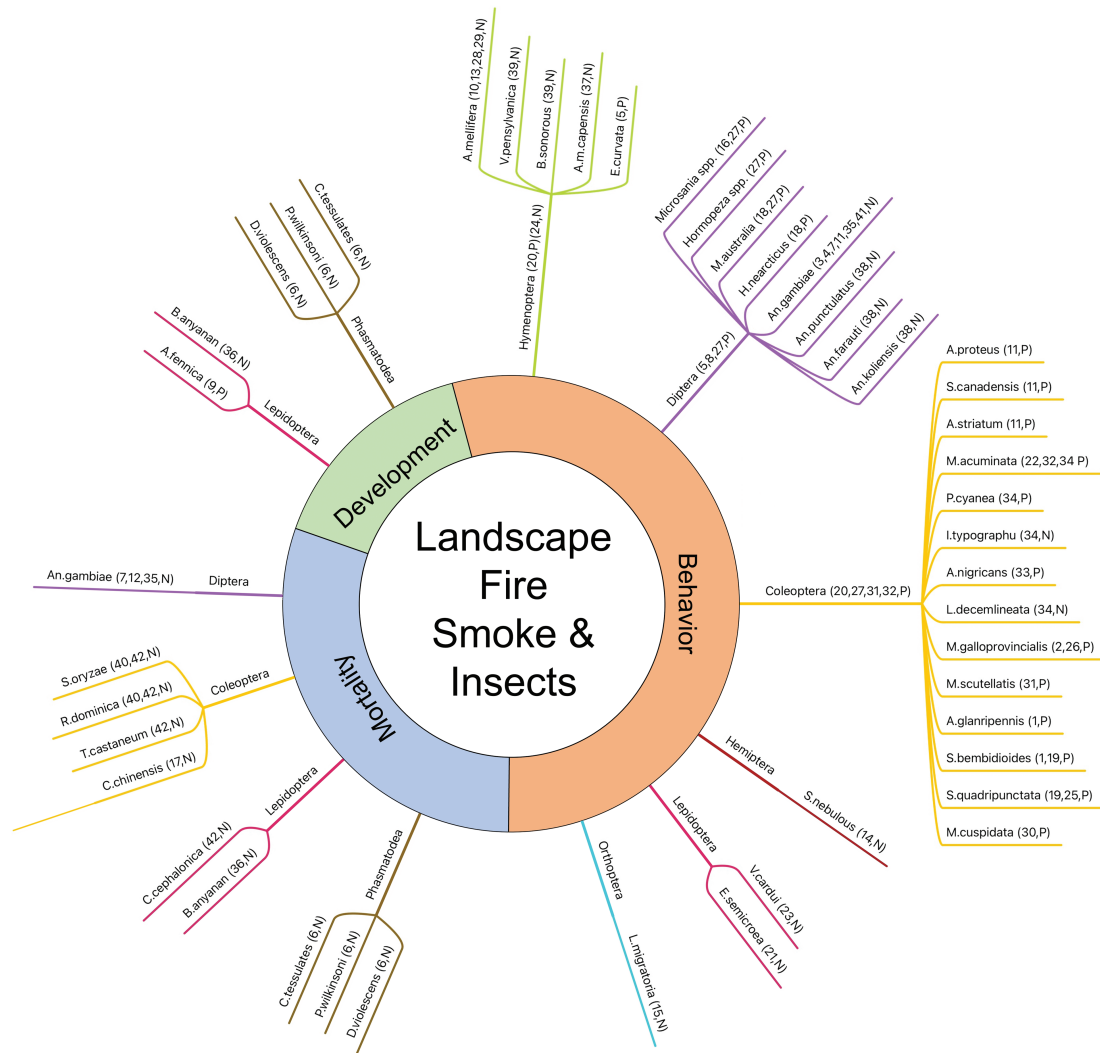


Fig. 2. Hierarchy plot showing smoke source classifications collected from 42 papers reviewed, including two general categories (indoor and outdoor) and ten more specific sources, with the number of studies in brackets. Some studies included more than one burning source.



Reference

- | | | | |
|-----------------------------|-----------------------------------|----------------------------------|---------------------------------|
| (1) Ali et al. (2017) | (12) Gibbins (1933) | (23) Liu et al. (2020) | (33) Schmitz et al. (2008) |
| (2) Álvarez et al. (2015) | (13) Harrison et al. (2019) | (24) Love and Cane (2016) | (34) Schütz et al. (1999) |
| (3) Biran et al. (2007) | (14) Hegedüs et al. (2017) | (25) Matti et al. (2006) | (35) Symes (1930) |
| (4) Bockarie et al. (1994) | (15) Johnson et al. (2005) | (26) McCullough et al. (1998) | (36) Tan et al. (2018) |
| (5) Bruces (1950) | (16) Kessel (1947) | (27) Milberg et al. (2015) | (37) Tribe et al. (2017) |
| (6) Campbell (1961) | (17) Kishor and Tiwari (2021) | (28) Newton (1968) | (38) Vernede et al. (1994) |
| (7) De Meillon (1930) | (18) Klocke et al. (2011) | (29) Newton (1969) | (39) Visscher and Vetter (1995) |
| (8) Evans (1971) | (19) Koivula et al. (2006) | (30) Paczkowski et al. (2013) | (40) Wijayaratne et al. (2009) |
| (9) Everaerts et al. (2000) | (20) Leatherman and Aguayo (2002) | (31) Richmond and LeJeune (1945) | (41) Wilson (1936) |
| (10) Gage et al. (2018) | (21) Lee et al. (2016) | (32) Saint-Germain et al. (2008) | (42) Yadav and Tiwari (2018) |
| (11) Gardiner (1957) | (22) Linsley (1943) | | |

Fig. 3. Insect species were studied concerning smoke from landscape fire activities within the published literature. The smoke-related impacts from landscape fire activities on insects have been divided into three aspects, including development, behavior, and mortality. The order and species of insects studied are listed. P refers to Positive impacts and N refers to Negative impacts.

antennae of Jewel beetles (Coleoptera: Buprestidae) (Schütz et al. 1999, Paczkowski et al. 2013). For instance, *Melanophila acuminata* (Coleoptera: Buprestidae) are highly sensitive to guaiacol (Schütz et al. 1999), but *Phaenops cyanea* (Coleoptera: Buprestidae) and *Ips typographus* (Coleoptera: Curculionidae) are less so, although they

show escape behavior regarding LFS (Schütz et al. 1999, Schmitz et al. 2000, Álvarez et al. 2015, Ali et al. 2017). More specifically, there are several types of sensilla on the antenna, among which the basal sensilla respond to odor stimulation (Ali et al. 2017). A group of nine cells in *Monochamus galloprovincialis* (Coleoptera: Cerambycidae)

was sensitive to smoke plumes which helped them to detect smoke from several kilometers away (Álvarez et al. 2015).

Smoke as a product of fire has also been observed to attract fire-favoring flies, such as *Hormopeza* spp. (Diptera: Empididae) and *Microsania* spp. (Diptera: Platypezidae) (Kessel 1947, Brues 1950, Evans 1972, Leatherman and Aguayo 2002, Milberg et al. 2015). It was reported that dozens of *Microsania* flies (Diptera: Platypezidae) aggregated and swarmed within the smoke plume due to forest fires (Klocke et al. 2011a, Milberg et al. 2015). In addition to smoke from fires, impacts can also be seen from 'cold smoke' sources, for example, an aerosol-bomb-dispensed smoke concentrate used by beekeepers, can also attract *Microsania* spp. (Kessel 1960). Moreover, the burnt sites after a fire can also attract *Hypocerides nearcticus* (Diptera: Phoridae) aggregating and swarming outside the smoke plumes (Klocke et al. 2011a).

Smoke generated from wildfires has also been shown to affect Hymenoptera, including indirectly through habitat change, or directly through injury or death (Love and Cane 2019). Brues (1950) observed that *Eumenes curvata* (Hymenoptera: Vespidae) were attracted to smoke generated from burning weeds, lingering in smoke as they moved back and forth from their nests. However, more studies have observed that smoke could restrain honey bees for an extended period. For instance, *Apis mellifera capensis* (Hymenoptera: Apidae) as a subspecies of *Apis mellifera* (Hymenoptera: Apidae) have been observed to stay far away from their nests because they are sensitive to fire smoke and have continuous absconding behavior (Tribe et al. 2017). This may be because smoke blocks their chemical communication that is needed to coordinate swarming, in particular through weakening of the electroantennography response of their antennae to alarm pheromones (Visscher et al. 1995).

Honey bees whose sensory perceptions were blocked by smoke exposure performed apparent and temporary suppression of aggression compared to those allowed to recognize typical social cues (Harrison et al. 2019). Smoke can affect whether droplets of venom are released with the stinger, although it may have no impact on the likelihood of the sting extending. Smoke from burlap and hops has also been shown to reduce droplet formation and possibly lead to fewer alarm pheromones being released (Gage et al. 2018). When *Apis mellifera* were exposed to smoke, the bees in the colony became engorged (Newton 1968). Smoke also reduces the number of guards and foragers due to the alarm pheromone isopentyl acetate (Newton 1969). Extending the impact to other species, the number of attacks by *Bombus sonoroides* (Say) (Hymenoptera: Apidae) and *Vespa pensylvanica* (Saussure) (Hymenoptera: Vespidae) reduced by over two- and ten-fold respectively when smoke was close to their colonies (Visscher and Vetter 1995).

Lepidoptera are also affected by smoke; *Exyra semicrocea* (Lepidoptera: Noctuidae) initiate flight in response to smoke from a periodic fire in pine savannas (Lee et al. 2016). The flight performance of *Vanessa cardui* (Lepidoptera: Nymphalidae) was significantly affected by smoke-contaminated air showing that dense smoke conditions negatively impact the flight performance of the butterfly (Liu et al. 2021).

When smoke from large forest fires darkened the sky, some insects such as grasshoppers and seed bugs decreased their flight distances or delayed their flights/migrations until the weather cleared (Johnson et al. 2005, Hegedüs et al. 2007).

Moreover, smoke from burning domestic fuels has been found to show repellent effects on *Anopheles gambiae* (Diptera: Culicidae) in some developing countries (De Meillon 1930, Symes 1930, Gibbins 1933, Wilson 1936, Bockarie et al. 1994, Biran et al. 2007). It has also been discussed that smoke can have a series of effects on

mosquitoes, including deterrence, expellence, reduced abilities to find hosts and bite, knockdown, and death (Vernède et al. 1994).

Impacts on Insect Mortality

Smoke can impact insect dynamics at individual and population levels by affecting their growth and behavior and even directly determining their mortality. Over 80% of *Bicyclus anynana* larvae and pupae could not survive in the presence of smoke from incense coil burning (Tan et al. 2018). Smoke from wildfires can also cause bee mortality (Love and Cane 2019). Smoke created from burning cow dung and neem leaves accounted for the high mortality of some Coleoptera species, including *Rhyzopertha dominica* (Coleoptera: Bostrichidae), *Sitophilus oryzae* (Coleoptera: Curculionidae), *Tribolium castaneum* (Coleoptera: Tenebrionidae), and *Callosobruchus chinensis* (Coleoptera: Chrysomelidae) (Yadav and Tiwari 2018, Kishor and Tiwari 2021). In addition, smoke, at a concentration where CO exceeded 5000 ppm, generated by the combustion of dried harvested paddy, may lead to more than 50% deaths of *Rhyzopertha dominica* and *Sitophilus oryzae* when those insects were in a sealed environment for up to 72 hr (Wijayarathne et al. 2009). Furthermore, there was nearly 70% mortality when adult *Corcyra cephalonica* (Lepidoptera: Pyralidae) were exposed to smoke generated from biomass burning for 72 hr (Yadav and Tiwari 2018). However, several early observational studies from Africa showed that the decrease in *Anopheles funestus* (Diptera: Culicidae) does not appear to be caused by the smoke from domestic fires (De Meillon 1930, Symes 1930, Gibbins 1933).

Positive or Negative Impacts From LFS on Insects

LFS has both positive and negative impacts on insects. The positive impacts are reflected in LFS attracting insects, especially fire-loving insects, mainly from four insect orders, including Coleoptera, Diptera, Hemiptera, and Lepidoptera (Fig. 3). Some fire-loving insects typically rely on forest fires to reproduce, especially, pyrophilous beetles. They quickly approach persistent fires using antenna sensors to detect the smoke and locate hot spots using infrared radiation sensors, generally located on the thorax or abdomen. Both sensors help pyrophilous beetles to find burning areas. Once they arrive, they can occupy these burnt areas immediately after the fire (for example, Leatherman and Aguayo 2002, Milberg et al. 2015). These pyrophilous insects find suitable habitats by detecting smoke plumes and breeding in these areas, increasing their population.

LFS restricts insect development and repels insects, that are regarded as negative impacts. LFS can inhibit butterfly growth and cause their mortality (for example, Tan et al. 2018). The smoke keeps bees away by disturbing their sense of smell. LFS can suppress the alarm pheromones secreted by bees, and if LFS is sensed by bees, they can be driven to leave their current habitat (for example, Tribe et al. 2017). Sometimes, LFS induces anomalous sky polarization, in which LFS causes reddish skylight, and the degree of linear polarization between skylight and the sun is less than 90°, which can disorient insects (Hegedüs et al. 2007). Moreover, LFS can repel the insects by acting as a camouflage for the signals emitted by the host plant, and insects are sensitive to chemicals in the smoke (Vernède et al. 1994).

Geographical Distribution of Studies

Of the 42 studies reviewed here, 41 studies were conducted in 6 continents, including North America (20 studies), Asia (6 studies), Europe (5 studies), Africa (6 studies), and Australia (4 studies). The remaining 1 study only referred to 'developing countries' rather than

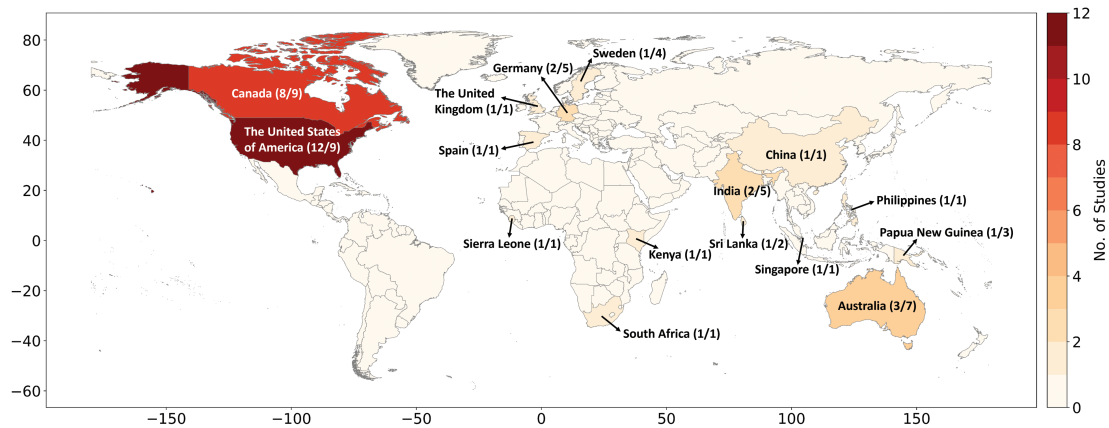


Fig. 4. The global distribution of 38 out of 42 smoke-insect studies as determined from a systematic mapping exercise, covering 16 countries, with the number of studies and insect species per country in brackets.

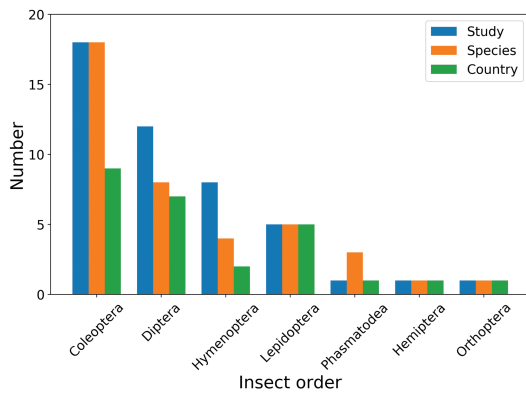


Fig. 5. Total number of species, the number of studies, and the number of countries included in the seven insect orders.

specific locations. Thirty-eight articles were associated with 16 countries (Fig. 4). Most of the research took place in the United States of America (12 studies), Canada (8 studies), Australia (3 studies), Germany (2 studies), and India (2 studies), with only 1 study in each country of the remaining 12 countries, including Kenya, Sierra Leone, South Africa, China, Singapore, Sri Lanka, Philippines, Papua New Guinea, Spain, Sweden, and the United Kingdom.

The findings are transferable to other locations for some studies involving lab work. For example, lab work conducted in the United Kingdom by Liu et al. (2021), investigating the impact of smoke on butterflies in a combustion chamber, could be applied to various geographical contexts. While these are the countries where impacts are well known, they are not necessarily the countries experiencing the most severe effects from smoke. This is because the relevant research articles on smoke-insect interactions are relatively limited. We did not consider the effect of mosquito coil smoke on insects for the reasons given earlier, however, there are many studies on the repellent effect of household mosquito coils on mosquitoes in Southern Asia (Liu et al. 2003, 2013; Hamid et al. 2017; Amelia-Yap et al. 2018).

The number of specific species studied worldwide is summarized in Fig. 4. The species in those papers investigating the effects of

smoke on insects are mainly from the United States of America (9 species), Canada (9 species), Australia (7 species), Germany (5 species) and India (5 species). Three Diptera species and one Coleoptera species were studied in Sweden (Milberg et al. 2015). Three Diptera species were mentioned in Papua New Guinea (Vernède et al. 1994), and two Coleoptera species were studied in Sri Lanka. The remaining eight countries all cover only one insect species.

The number of specific species, the number of studies, and the number of distributed countries related to the nine known insect species mentioned previously are summarized in Fig. 5. Research on Coleoptera (18 species) was the most prevalent, with 18 studies in 9 countries, including the United States of America, Canada, Germany, Australia, China, India, Spain, Sweden, Sri Lanka. Hymenoptera studies were distributed in the United States of America and South Africa. Diptera studies had a wide research range, including Australia, Philippines, Sweden, and the United States of America, Papua New Guinea, Kenya, and some south and east African areas. Lepidoptera studies were distributed in the United States of America, Canada, India, Singapore the United Kingdom. The Hemiptera study and Orthoptera study were in Canada. Phasmatodea were only studied in Australia. The number of studies did not precisely match the number of insect species investigated in each country because some studies covered more than one insect species, and several papers covered the same species.

Discussion

Evidence suggests that LFS exposure impacts insect population dynamics through development, behavior, and mortality, although the literature is limited. Approximately 80% of studies discussed how insect behavior responds to LFS, mainly reflected in mating and flight (Hegedüs et al. 2007, Bazzett 2008, Schmitz et al. 2008). These behaviors comprise an extensive range of activities and can eventually affect many aspects including population viability, species persistence, and so on, as described in Lester et al. (2007) and Berg et al. (2010). Understanding the behavior of insects could improve both pest management and conservation programs (Cunningham et al. 1999, Witzgall et al. 2010), and therefore is particularly relevant to human health (e.g., mosquitoes; Greenberg 2019, Steven et al. 2020) and economics (e.g., honeybees; Smith et al. 2013).

Main Insect Species Studied

In the LFS related articles, we found that three insect groups were most discussed and studied. The most commonly occurring insects in the literature were beetles (Order: Coleoptera), which can be abundant in wildfire areas. Various fire-loving beetles can inhabit burning or burned trees by detecting smoke and heat (Schmitz et al. 2008, Klocke et al. 2011b, Álvarez et al. 2015). For instance, woodboring beetles (e.g., *Buprestidae* and *Cerambycidae*) that regard dead trees as habitat, have a high reproduction rate leading to impacts in their population dynamics (Saint-Germain et al. 2008). Moreover, the population of adult buprestids is found to be higher when burn severity is higher (Ray et al. 2019). Outbreaks of beetles are common in the areas of the U.S. and Canada where wildfires occur frequently due to the increasingly severe drought (McCullough et al. 1998, Gillett et al. 2004, Gavin et al. 2007, Marlon et al. 2012, Ray et al. 2019).

The second group of insects is related to economic activities, such as honeybees (Order: Hymenoptera), which are highly valued worldwide for not only producing honey and wax but also pollinating many crops (Sabbahi et al. 2005, vanEngelsdorp and Meixner 2010, Smart et al. 2016). Smoke can reduce the aggression of bees and is therefore used as the most basic and effective method to obtain honey (Crane 1983). Moreover, bees are sensitive to smoke, so bee behavior may be used to predict the impact of LFS on their colony, particularly in forested areas (Moretti et al. 2009, Galbraith et al. 2019).

The third group of studies focused on those insects having a direct relationship to human health, such as flies and mosquitoes (Order: Diptera), through their spread of diseases and their being of general public health concern (Harrison 1979, Beier 1998, Lacroix et al. 2005, Peter et al. 2005, Vijay Kumar and Ramaiah 2008, Greenberg 2019, Steven et al. 2020). For example, *Drosophila melanogaster* has been commonly used as a research model for human diseases because it is a widely studied and efficiently handled genetic model organism (Kale and Baum 1982, Hamatake et al. 2009, Yamaguchi and Yoshida 2018, Santalla et al. 2021). *Anopheles gambiae* has been studied for decades because it spreads malaria. Smoke from burning plants or wood is often used to repel mosquitoes (Vernède et al. 1994), and therefore, information on their efficacy is vital in a public health context.

Main Smoke Sources Studied

LFS comes from various natural sources, but most attention is given to wildfires, particularly forest fires, while others include wood fires and prescribed fires. Fires and insects work interactively as the disturbance agents to the ecosystems of many forests, which have effects on the composition of the species in the forests (McCullough et al. 1998, Swengel 2001). Prescribed fires are primarily used as a land management tool to control the natural fires and reduce the frequency or severity of wildfires (Ryan et al. 2013). Swengel (2001) summarized how insects responded to fires, including wildfire and prescribed fires. Several pieces of evidence showed that local ecosystems would be maintained and improved by managed fires because they are controlled and can have positive impacts on biodiversity while wildfire is normally uncontrolled, irregular, and damaging (Ferrenerg et al. 2006, Fernandes et al. 2013). Hence, some insects associated with herbaceous vegetation responded favorably. For instance, the exacerbated landscape fires induced by the El Niño Southern Oscillation (ENSO) event of 1997-1998 in East Kalimantan, via its ability to depress rainfall, caused approximately 90% of forest cover over a 400 km² area in the Balikpapan-Samarinda

region to burn (Harrison 2000, Cleary and Grill 2004). Although many insect species significantly declined following this event, the proportion of *Jamides celeno* (Lepidoptera: Lycaenidae) increased from less than 5% in the pre-ENSO butterfly assemblage to over 50% in the post-ENSO assemblage, becoming the dominant butterfly species in the local area (Cleary and Grill 2004). However, whether wildfire or prescribed fires, the smoke emissions are similar, and the concentration of the emitted substances depends on the proximity to the source of the fire (Navarro et al. 2018). In the related articles studying the impacts of LFS on insects, it is hard to collect accurate information on wildfire density, length, and area because researchers have predominantly focused on how insects respond to smoke from forest fires rather than studying the fires themselves. Some observations were over a short period (e.g., five days, Richmond and Lejeune 1945; Johnson et al. 2005), while some were studied over a far more extended period (e.g., 30 yr, Saint-Germain et al. 2008). One driver of this lack of study may be that fire-loving insects are difficult to sample, except after a bushfire (Milberg et al. 2015). Most of the articles qualitatively described the observed smoke conditions or weather changes caused by the smoke, and a few articles quantified the concentration of the gases and PM_{2.5} to specify the severity of the smoke conditions (Wijayaratne et al. 2009, Tan et al. 2018, Liu et al. 2021).

Main Locations Studied

The distribution of insect studies broadly follows trends in global wildfire distribution, particularly for field-based studies. Lu et al. (2021) studied global fire distribution using remote sensing data (VIIRS 750m) and showed that high-frequency fires are distributed in North America, Australia, and Africa. The historical focus on these geographical regions is understandable. However, it is still somewhat surprising that there is so little focus on the ecological impacts of smoke on insects, particularly given (1) their critical functional roles in ecosystems globally (Humphrey et al. 1999), (2) the global diversity of insects (Gaston 1991), (3) the increasing and dramatic ecological impacts that may result from changing wildfire regimes in some regions (McKenzie et al. 2014), and (4) the extensive entomological literature that covers many thousands of species. Indeed, the relationships between insects and smoke need further investigation. Most published research has focused on impacts on insect behavior and larval development and to a lesser extent mortality. There is a gap for more research, particularly into smoke impacts on population ecology and how this may influence community composition and diversity.

Other Fire Factors Impacting Insects

In addition to LFS, other fire factors may also influence the insect community. Koltz et al. (2018) summarized the direct and indirect impacts of fire factors on insects, such as fire intensity, frequency, and severity. These fire factors may impact insect dispersal ability, life stages, diet, and habitat utilization. Fire at high frequency but low severity may attract fire-loving insects and increase insect diversity, while fire at high frequency and high severity may negatively impact insect recovery (New 2014). Fire at high frequency but low intensity can significantly reduce some insect numbers, such as beetles and bugs (York 1999). Swengel (2001) illustrated that insect species abundance significantly reduced after a fire, which can be an effective conservation management tool for open habitats. The magnitude of the reduction in insect populations was related to flame exposure. However, insect species diversity can be increased due to frequent prescribed fires by controlling the local plants and

maintaining habitats (Ferrenberg et al. 2006, Ulyshen et al. 2021). For instance, the species richness of saproxylic beetles increased after a prescribed fire compared to a set of unburned sites (Ulyshen et al. 2020). As Kral et al. (2017) show, the response of different species of insects to fire is variable, not simply an increase or decline, and is driven by multiple factors.

Climate Change Impacts on LFS

Changes in fire frequency, intensity, and severity lead to potential impacts on the ecology of a region (Dale et al. 2001). Climate change increases the temperature globally and changes precipitation patterns, which aggravates frequency, severity, and extent of landscape fire activities (Moritz et al. 2012, Pachauri et al. 2014, Reid et al. 2016). Dupuy et al. (2020) indicated that the probability of wildfires in Europe increases by 2% this century due to climate change, while the burned area is likely to increase by 45%. This increase in wildfires could result in severe atmospheric pollution both locally, and globally (Reid and Maestas 2019). For instance, Indonesian forest fires have been shown to impact air pollution in the neighboring country of Singapore (Sheldon and Sankaran 2017). The increase in the burned area could lead to a doubling of the current carbonaceous aerosol emissions from wildfires by 2050 (Spracklen et al. 2009). These fire smoke impacts may be seen in the structure and function of insect communities (Koltz et al. 2018).

Recommendations for Future Research

Most behavioral work has examined how smoke (and burning more generally) may attract or repel insects, with some biochemical work on response mechanisms. As insects have different functional roles within ecosystems, such as plant pollinators (Ollerton 2017) and seed dispersers (Farwig and Berens 2012), one potential research area is the impact of LFS on insect ecosystem services. Sagili and Chakrabarti (2021) suggested that smoke pollution from wildfires decreased the pollination services of honey bees, providing rare evidence showing that LFS impacts insect ecological function. We suggest that the impact of various types, concentrations, and compositions of smoke emission on ecosystem service aspects of insect ecology should be priorities for future research.

Another potential direction is studying the flight behavior of insects under smoke conditions, especially as many impacted functions of insects relate to their flight behavior. Apart from some recent work on butterflies (Liu et al. 2021), there is little work on how smoke may impact the flight behavior of insects, including flight initiation, speed, duration and flight direction-finding ability. It is necessary to explore their flight performance under different LFS conditions. Conditions in the atmospheric environment can substantially impact insect migration, one of which is that insect migration usually occurs on clear days (Drake and Farrow 1988). LFS can cause extreme weather phenomena that are detrimental to insect migration. If insects do not migrate, they are likely to be trapped in the fire-prone region, ultimately threatening survival (Hegedüs et al. 2007).

In addition, it would be important to investigate how smoke emissions may impact insect reproductive behavior (Ridley 1988, Musolin 2007). As Tan et al. (2018) have shown, not only can smoke pollution negatively impact butterfly development, but also reproductive capacity and behavior. Some fire-loving insects complete their reproduction in burning trees during forest fires (Schmitz et al. 2008). Usually, plant succession after landscape fires creates habitats for various insects, which causes insect outbreaks (Sanderfoot et al. 2021). For instance, the abundant resprouting of host plants after a fire provides a habitat for butterflies, allowing their populations to

increase (Cleary and Grill 2004). When LFS impacts insect population distribution and habitat, it may impact insect metapopulations at a broad spatio-temporal scale, where effects are seen among interacting insect populations (Singer and Wee 2005), including population genetics (Nyabuga et al. 2012). The environmental change also impacts the structure of insect assemblages, although the correlation between environmental variables and assemblage structure is relatively weak (Heino and Mykrä 2008). Knowledge of these areas is essential not just for understanding the ecology of insects but also for the ecosystem services that are associated with them because insects are crucial components of biodiversity in most terrestrial ecosystems – as predators, parasites, herbivores, saprophages, and pollinators (Schowalter 2016, Brockhoff and Liebhold 2017). More evidence is needed to determine what specific components in LFS impact insects to better predict insect performance under various degrees of atmospheric pollution.

Furthermore, the responses of insects to different sources of smoke pollution can be studied and summarized. For example, when *Drosophila melanogaster* are exposed to cigarette smoke for over six hours, there is an increasing possibility of gene mutagenesis (Uchiyama et al. 2016). Some butterfly species can display mortality when exposed to high-level air pollution induced by coal power plants, like *Thecla betulae* (Lepidoptera: Lycaenidae) (Corke 1999). Although the chemical components in cigarette smoke, power plant emissions, and LFS are different, similar impacts may (or may not) result. More specifically, the concentrations of gas and particulates in the smoke need to be measured in the future study. There were some pieces of evidence showing that specific gas component impacts insects. For instance, *Drosophila melanogaster* exposed to SO₂ concentrations at 400 mg m⁻³ significantly decreased pupal survival and adult endurance in the polluted environment (Ginevan and Lane 1978). Also, this was observed for the larvae of *Junonia coenia* (Lepidoptera: Nymphalidae), when reared under high CO₂ conditions (700 mg m⁻³) grew significantly slower and took longer to pupate compared to those larvae in ambient CO₂ conditions (300 mg m⁻³) (Fajer et al. 1991). Although some studies measured PM_{2.5} concentration to show how severe the smoke conditions, such as Tan et al. (2018) and Liu et al. (2021), many LFS-insects studies did not describe the specific components in the smoke.

To achieve what has been mentioned above, both field work and laboratory experiments are required to enable controlled conditions and allow target organisms to react more naturally to smoke in their environment. Specific measurements of smoke characteristics can be challenging, but as far as possible, this should be conducted in future work to increase comparability and transferability of results. It was not always possible to ascertain key smoke characteristics from some of the studies reviewed here, for example, smoke concentrations or components. Many papers considered only general smoke from wildfires, meaning that while the impacts may be clear, in the absence of details on concentrations and components, the key drivers of the impact may not become apparent. An essential aspect of future research will be the more significant investigation of smoke components from different sources, including different types of wildfires, controlled agricultural burning, and domestic sources (Sun et al. 2014, Tan et al. 2018).

Conclusions

We reviewed the effects of LFS on insects and summarized the information identified. LFS can be used as a cue to attract insects who ultimately find suitable habitats, such as fire-loving beetles (Saint-Germain et al. 2008). However, it can also trap or repel insects, such

as honey bees (Tribe et al. 2017). Besides the impact on insect behavior, LFS can also inhibit insect development and cause mortality, for example, in butterflies (Tan et al. 2018) and moths (Yadav and Tiwari 2018). Most studies relating to LFS effects on insects have concentrated on developed countries, though landscape fire activity is highest in developing countries and regions. More information is needed in these areas to develop a comprehensive understanding of ecological feedback in response to LFS, such as in regions of Southern Africa, South Asia, and South America. So far, only seven orders have been studied concerning the effects of LFS. Therefore, a wider range of insects need to be taken into consideration to understand the broader effects of LFS and enable these impacts to be considered when attempting to understand the future impacts of landscape fires under changing climate and human activity.

Acknowledgments

We would like to acknowledge two anonymous reviewers for their constructive comments that significantly help us to improve the early versions of the paper. We would like to also thank Brandon Mak and Mingzhu Cai for their suggestions and support on the methodology. The work is supported by NERC National Capability funding to the National Centre for Earth Observation (NERC grant no. NE/R016518/1). The authors declare that they have no conflict of interest.

References Cited

- Akagi, S. K., R. J. Yokelson, C. Wiedinmyer, M. J. Alvarado, J. S. Reid, T. Karl, J. D. Crouse, and P. O. Wennberg. 2011. Emission factors for open and domestic biomass burning for use in atmospheric models. *Atmos. Chem. Phys.* 11: 4039–4072.
- Ali, S., S. Ali, L. Lina, W. Zhou, M. I. Waris, A. M. Ali, and M. Wang. 2017. Chemical ecology of Asian long horned beetle (*Anoplophora glabripennis*) – a review. *Pak. J. Zool.* 49: 1093–1105.
- Álvarez, G., B. Ammagarahlali, D. R. Hall, J. A. Pajares, and C. Gemenio. 2015. Smoke, pheromone and kairomone olfactory receptor neurons in males and females of the pine sawyer *Monoctonus galloprovincialis* (Olivier) (Coleoptera: Cerambycidae). *J. Insect Physiol.* 82: 46–55.
- Amelia-Yap, Z. H., C. D. Chen, M. Sofian-Azirun, K. W. Lau, I. W. Suana, H. E. Syahputra, A. Razak, and V. L. Low. 2018. Efficacy of mosquito coils: cross-resistance to pyrethroids in *Aedes aegypti* (Diptera: Culicidae) from Indonesia. *J. Econ. Entomol.* 111: 2854–2860.
- Andreae, M. O., and P. Merlet. 2001. Emission of trace gases and aerosols from biomass burning. *Glob. Biogeochem. Cy.* 15: 955–966.
- Baker, G. M., and E. Wright. 1977. Effects of carbon monoxide on insects. *Bull. Environ. Contam. Toxicol.* 17: 98–104.
- Bazzett, T. J. 2008. *An introduction to behavior genetics*, Oxford University Press.
- Beier, J. C. 1998. Malaria parasite development in mosquitos. *Annu. Rev. Entomol.* 43: 519–543.
- Berg, M. P., E. T. Kiers, G. Driessen, M. Van Der Heijden, B. W. Kooi, F. Kuenen, M. Liefing, H. A. Verhoef, and J. Ellers. 2010. Adapt or disperse: understanding species persistence in a changing world. *Glob. Chang. Biol.* 16: 587–598.
- Berger-Tal, O., A. L. Greggor, B. Macura, C. A. Adams, A. Blumenthal, A. Bouskila, U. Candolin, C. Doran, E. Fernández-Juricic, K. M. Gotanda, et al. 2018. Systematic reviews and maps as tools for applying behavioral ecology to management and policy. *Behav. Ecol.* 30: 1–8.
- Biran, A., L. Smith, J. Lines, J. Ensink, and M. Cameron. 2007. Smoke and malaria: are interventions to reduce exposure to indoor air pollution likely to increase exposure to mosquitoes? *Trans. R. Soc. Trop. Med. Hyg.* 101: 1065–1071.
- Bockarie, M. J., M. W. Service, G. Barnish, W. Momoh, and F. Salia. 1994. The effect of woodsmoke on the feeding and resting behaviour of *Anopheles gambiae* s.s. *Acta Trop.* 57: 337–340.
- Brockerhoff, E., and A. Liebhold. 2017. Ecology of forest insect invasions. *Biol. Invasions* 19: 3141–3159.
- Broyles, G. A. 2013. *Wildland firefighter smoke exposure study*. Master of Natural Resources, Utah State University.
- Brues, C. T. 1950. Vespidae wasps (*Eumenes curvata*) attracted to smoke. *Psyche* 57: 114–115.
- Campbell, K. G. 1961. The effects of forest fires on three species of stick insects (Phasmatidae: Phasmatodea) occurring in plagues in forest areas of south-eastern Australia. *Proc. Linn. Soc. N. S. W.* 86: 112–121.
- Cascio, W. E. 2018. Wildland fire smoke and human health. *Sci. Total Environ.* 624: 586–595.
- Chen, J., C. Li, Z. Ristovski, A. Milic, Y. Gu, M. S. Islam, S. Wang, J. Hao, H. Zhang, and C. He. 2017. A review of biomass burning: emissions and impacts on air quality, health and climate in China. *Sci. Total Environ.* 579: 1000–1034.
- Cleary, D. F. R., and A. Grill. 2004. Butterfly response to severe ENSO-induced forest fires in Borneo. *Ecol. Entomol.* 29: 666–676.
- Corke, D. 1999. Are honeydew/sap-feeding butterflies (Lepidoptera: Rhopalocera) affected by particulate air-pollution? *J. Insect Conserv.* 3: 5–14.
- Crane, E. 1983. *The archaeology of beekeeping*, Duckworth, United Kingdom.
- Cunningham, J. P., M. P. Zalucki, and S. A. West. 1999. Learning in *Helicoverpa armigera* (Lepidoptera: Noctuidae): a new look at the behaviour and control of a polyphagous pest. *Bull. Entomol. Res.* 89: 201–207.
- Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, and C. J. Peterson. 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *Bioscience* 51: 723–734.
- De Gouw, J., O. Cooper, C. Warneke, P. Hudson, F. Fehsenfeld, J. Holloway, G. Hübler, D. Nicks, Jr, J. Nowak, and D. Parrish. 2004. Chemical composition of air masses transported from Asia to the US west coast during ITCT 2K2: fossil fuel combustion versus biomass-burning signatures. *J. Geophys. Res.* Atmos. 109: D23–S20.
- De Meillon, B. 1930. *Anopheles funestus* (Giles) in smoke-filled native huts. *J. Med. Assoc. S. Afr.* 4: 693.
- Dharmapala, R., C. Claiborn, J. Jimenez, J. Corkill, B. Gullett, C. Simpson, and M. Paulsen. 2007. Emission factors of PAHs, methoxyphenols, levoglucosan, elemental carbon and organic carbon from simulated wheat and Kentucky bluegrass stubble burns. *Atmos. Environ.* 41: 2660–2669.
- Drake, V., and R. Farrow. 1988. The influence of atmospheric structure and motions on insect migration. *Annu. Rev. Entomol.* 33: 183–210.
- Dupuy, J. -I., H. Fargeot, N. Martin-StPaul, F. Pimont, J. Ruffault, M. Guijarro, C. Hernandez, J. Madrigal, and P. Fernandes. 2020. Climate change impact on future wildfire danger and activity in southern Europe: a review. *Ann. For. Sci.* 77: 1–24.
- Einfeld, W., D. E. Ward, and C. Hardy. 1991. Effects of fire behavior on prescribed fire smoke characteristics: A case study [Chapter 50], pp. 412–419. In J. S. Levine (ed.), *Global biomass burning: Atmospheric, climatic, and biospheric implications*. MIT Press, Cambridge, MA.
- Elia, M., R. Lafortezza, E. Tarasco, and G. Sanesi. 2016. Response of beetle communities five years after wildfire in Mediterranean forest ecosystems. *Redia* 99: 107–116.
- vanEngelsdorp, D., and M. D. Meixner. 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J. Invertebr. Pathol.* 103: S80–S95.
- Erb, W., E. Barrow, A. Hofner, S. Utami-Atmoko, and E. Vogel. 2018. Wildfire smoke impacts activity and energetics of wild Bornean orangutans. *Sci. Rep.* 8: 1–8.
- Evans, W. G. 1972. The attraction of insects to forest fires. *Tall Timbers Conf. Ecol. Anim. Control Habitat Manage.* 3: 115–127.
- Everaerts, C., M. Cusson, and J. N. McNeil. 2000. The influence of smoke volatiles on sexual maturation and juvenile hormone biosynthesis in the black army cutworm, *Actebia femica* (Lepidoptera: Noctuidae). *Insect Biochem. Mol. Biol.* 30: 855–862.
- Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1991. The Effects of Enriched CO₂ Atmospheres on the Buckeye Butterfly, *Junonia Coenia*. *Ecol.* 72: 751–754.

- Farwig, N., and D. G. Berens. 2012. Imagine a world without seed dispersers: a review of threats, consequences and future directions. *Basic Appl. Ecol.* 13: 109–115.
- Fernandes, P. M., G. M. Davies, D. Ascoli, C. Fernández, F. Moreira, E. Rigolot, C. R. Stoof, J. A. Vega, and D. Molina. 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. *Front. Ecol. Environ.* 11: e4–e14.
- Ferrenberg, S. M., D. W. Schwilk, E. E. Knapp, E. Groth, and J. E. Keeley. 2006. Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. *Fire Ecol.* 2: 79–102.
- Finney, M. A. 1999. Mechanistic modeling of landscape fire patterns, pp. 186–209. In D. J. Mladenoff, and W. L. Baker (eds.), *Spatial modeling of forest landscapes: approaches and applications*. Cambridge University Press, Cambridge.
- Finney, M. A. 2004. Landscape fire simulation and fuel treatment optimization, pp. 117–131. In J. L. Hayes, A. A. Ager and R. J. Barbour (eds.), *Methods for integrated modeling of landscape change: interior northwest landscape analysis system*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Fried, J. S., M. S. Torn, and E. Mills. 2004. The impact of climate change on wildfire severity: a regional forecast for northern California. *Clim. Change.* 64: 169–191.
- Fried, J. S., J. K. Gillies, W. J. Riley, T. J. Moody, C. Simon de Blas, K. Hayhoe, M. Moritz, S. Stephens, and M. Torn. 2008. Predicting the effect of climate change on wildfire behavior and initial attack success. *Clim. Change.* 87: 251–264.
- Gadde, B., S. Bonnet, C. Menke, and S. Garivait. 2009. Air pollutant emissions from rice straw open field burning in India, Thailand and the Philippines. *Environ. Pollut.* 157: 1554–1558.
- Gage, S. L., F. Ahumada, A. Rivera, H. Graham, and G. DeGrandi-Hoffman. 2018. Smoke conditions affect the release of the venom droplet accompanying sting extension in honey bees (Hymenoptera: Apidae). *J. Insect Sci.* 18: 1–7.
- Galbraith, S. M., J. H. Cane, A. R. Moldenke, and J. W. Rivers. 2019. Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere.* 10: 1–19.
- Gardiner, L. 1957. Collecting wood-boring beetle adults by turpentine and smoke. *Can. For. Serv. Bi-Monthly Progr. Rep.* 13: 2.
- Gaston, K. J. 1991. The magnitude of global insect species richness. *Conserv. Biol.* 5: 283–296.
- Gate, I. M., S. McNeill, and M. R. Ashmore. 1995. Effects of air pollution on the searching behaviour of an insect parasitoid. *Water Air Soil Pollut.* 85: 1425–1430.
- Gavin, D. G., D. J. Hallett, F. S. Hu, K. P. Lertzman, S. J. Prichard, K. J. Brown, J. A. Lynch, P. Bartlein, and D. L. Peterson. 2007. Forest fire and climate change in western North America: insights from sediment charcoal records. *Front. Ecol. Environ.* 5: 499–506.
- Gibbins, E. G. 1933. The domestic Anopheles mosquitoes of Uganda. *Ann. Trop. Med. Parasitol.* 27: 15–25.
- Giglio, L., L. Boschetti, D. P. Roy, M. L. Humber, and C. O. Justice. 2018. The collection 6 MODIS burned area mapping algorithm and product. *Remote Sens. Environ.* 217: 72–85.
- Gillett, N. P., A. J. Weaver, F. W. Zwiars, and M. D. Flannigan. 2004. Detecting the effect of climate change on Canadian forest fires. *Geophys. Res. Lett.* 31: 1–4.
- Ginevan, M. E., and D. D. Lane. 1978. Effects of sulfur dioxide in air on the fruit fly, *Drosophila melanogaster*. *Environ. Sci. Technol.* 12: 828–831.
- Goldammer, J. G., M. Statheropoulos, and M. O. Andreae. 2008. Impacts of vegetation fire emissions on the environment, human health, and security: a global perspective, pp. 3–36. In A. Bytnerowicz, M. J. Arbaugh, A. R. Riebau, and C. Andersen (eds.), *Developments in Environmental Science*, vol. 8. Elsevier, Amsterdam, The Netherlands.
- Gorrod, J. W., and P. Jacob III. 1999. *Analytical determination of nicotine and related compounds and their metabolites*. Elsevier Science, Amsterdam, The Netherlands.
- Greenberg, B. 2019. *Flies and disease: II. biology and disease transmission*. Princeton University Press.
- Gupta, P. K., S. Sahai, N. Singh, C. K. Dixit, D. P. Singh, C. Sharma, M. K. Tiwari, R. K. Gupta, and S. C. Garg. 2004. Residue burning in rice-wheat cropping system: causes and implications. *Curr. Sci.* 87: 1713–1717.
- Haddaway, N. R., C. Bernes, B. G. Jonsson, and K. Hedlund. 2016. The benefits of systematic mapping to evidence-based environmental management. *Ambio.* 45: 613–620.
- Hamatake, Y., A. Morita, Y. Yuma, K. Okamoto, S. Arimoto, T. Suzuki, H. Kasai, K. Kawai, and T. Negishi. 2009. Hypersensitivity of a urate-null strain of *Drosophila melanogaster* to the toxic effects of environmental cigarette smoke. *Genes Environ.* 31: 43–46.
- Hamid, P. H., J. Prastowo, A. Widyasari, A. Taubert, and C. Hermosilla. 2017. Knockdown resistance (kdr) of the voltage-gated sodium channel gene of *Aedes aegypti* population in Denpasar, Bali, Indonesia. *Parasites Vectors* 10: 1–9.
- Harrison, G. 1979. *Mosquitoes, malaria and man: a history of the hostilities since 1880*. Dutton.
- Harrison, R. D. 2000. Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. *Proc. R. Soc. Lond. B. Biol. Sci.* 267: 911–915.
- Harrison, J. W., J. H. Palmer, and C. C. Rittschof. 2019. Altering social cue perception impacts honey bee aggression with minimal impacts on aggression-related brain gene expression. *Sci. Rep.* 9: 1–8.
- Hegedüs, R., S. Åkesson, and G. Horváth. 2007. Anomalous celestial polarization caused by forest fire smoke: why do some insects become visually disoriented under smoky skies? *Appl. Opt.* 46: 2717–2726.
- Heino, J., and H. Mykrä. 2008. Control of stream insect assemblages: roles of spatial configuration and local environmental factors. *Ecol. Entomol.* 33: 614–622.
- Hogarh, J. N., P. Antwi-Agyei, and K. Obiri-Danso. 2016. Application of mosquito repellent coils and associated self-reported health issues in Ghana. *Malar. J.* 15: 1–7.
- Humphrey, J. W., C. Hawes, A. J. Peace, R. Ferris-Kaan, and M. R. Jukes. 1999. Relationships between insect diversity and habitat characteristics in plantation forests. *For. Ecol. Manage.* 113: 11–21.
- Jaffe, D. A., and N. L. Wigder. 2012. Ozone production from wildfires: a critical review. *Atmos. Environ.* 51: 1–10.
- James, K. L., N. P. Randall, and N. R. Haddaway. 2016. A methodology for systematic mapping in environmental sciences. *Environ. Evid.* 5: 1–13.
- Jenkins, B. M., S. Q. Turn, and R. B. Williams. 1992. Atmospheric emissions from agricultural burning in California: determination of burn fractions, distribution factors, and crop-specific contributions. *Agric. Ecosyst. Environ.* 38: 313–330.
- Jetter, J. J., Z. Guo, J. A. McBrien, and M. R. Flynn. 2002. Characterization of emissions from burning incense. *Sci. Total Environ.* 295: 51–67.
- Johnson, D., D. Naylor, and G. Scudder. 2005. Published. Red sky in day, bugs go astray. In *Meeting of the Canadian Association of Geographers, Western Division, 12 March 2005*, Lethbridge, Alberta, Canada.
- Johnston, F. H., S. B. Henderson, Y. Chen, J. T. Randerson, M. Marlier, R. S. DeFries, P. Kinney, D. M. Bowman, and M. Brauer. 2012. Estimated global mortality attributable to smoke from landscape fires. *Environ. Health Perspect.* 120: 695–701.
- Kale, P. G., and J. W. Baum. 1982. Mutagenicity of cigarette smoke in *Drosophila melanogaster*. *Mutat. Res. Lett.* 105: 149–155.
- Keane, R. E., and M. A. Finney. 2003. The simulation of landscape fire, climate, and ecosystem dynamics, pp. 32–68, In *Fire and climatic change in temperate ecosystems of the Western Americas*, vol. 160. Springer, New York, USA.
- Keane, R. E., J. K. Agee, P. Fule, J. E. Keeley, C. Key, S. G. Kitchen, R. Miller, and L. A. Schulte. 2008. Ecological effects of large fires on US landscapes: benefit or catastrophe? *Int. J. Wildland Fire.* 17: 696–712.
- Keshtkar, H., and L. L. Ashbaugh. 2007. Size distribution of polycyclic aromatic hydrocarbon particulate emission factors from agricultural burning. *Atmos. Environ.* 41: 2729–2739.
- Kessel, E. L. 1947. American smoke flies (Microsania: Clythiidae). *Wasman Collect.* 7: 23–30.
- Kessel, E. 1960. Microsania attracted to cold smoke (Diptera: Platypzeidae). *Wasmann J. Biol.* 18: 312–313.

2.1. Systematic Mapping and Review of Landscape Fire Smoke (LFS) Exposure Impacts on Insects

882

Environmental Entomology, 2022, Vol. 51, No. 5

- Kishor, K., and B. M. R. Tiwari. 2021. Effect of cow dung smoke on pulse beetle, *Callosobruchus chinensis* (Linn.) and quality parameters of stored pulses at Pantnagar, Uttarakhand. *J. Entomol. Zool. Stud.* 9: 1288–1294.
- Klocke, D., A. Schmitz, and H. Schmitz. 2011a. Fire-adaptation in *Hypocerides nearcticus* Borgmeier and *Anabarhynchus hyalipennis hyalipennis* Marquart and new notes about the Australian smoke fly *Microsania australis* Collart (Diptera: Phoridae, Therevidae and Platypezidae). *Open Entomol. J.* 5: 10–14.
- Klocke, D., A. Schmitz, H. Soltner, H. Bousack, and H. Schmitz. 2011b. Infrared receptors in pyrophilous ('fire loving') insects as model for new un-cooled infrared sensors. *Beilstein J. Nanotech.* 2: 186–197.
- Koivula, M., and J. R. Spence. 2006. Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). *For. Ecol. Manag.* 236: 102–112.
- Koivula, M., T. Cobb, A. Déchêne, J. Jacobs, and J. Spence. 2006. Responses of two Sericoda Kirby, 1837 (Coleoptera: Carabidae) species to forest harvesting, wildfire, and burn severity. *Entomol. Fenn.* 17: 315–324.
- Koltz, A. M., L. A. Burkle, Y. Pressler, J. E. Dell, M. C. Vidal, L. A. Richards, and S. M. Murphy. 2018. Global change and the importance of fire for the ecology and evolution of insects. *Curr. Opin. Insect Sci.* 29: 110–116.
- Kral, K. C., R. F. Limb, J. P. Harmon, and T. J. Hovick. 2017. Arthropods and fire: previous research shaping future conservation. *Rangel. Ecol. Manag.* 70: 589–598.
- Lacroix, R., W. R. Mukabana, L. C. Gouagna, and J. C. Koella. 2005. Malaria infection increases attractiveness of humans to mosquitoes. *PLoS Biol.* 3: 1590–1593.
- Larson, T. V., and J. Q. Koenig. 1994. Wood smoke: emissions and noncancer respiratory effects. *Annu. Rev. Public Health.* 15: 133–156.
- Leatherman, D., and I. Aguayo. 2002. Insects and diseases associated with forest fires. *Colorado State University Cooperative Extension.*
- Lee, S. C., and B. Wang. 2004. Characteristics of emissions of air pollutants from burning of incense in a large environmental chamber. *Atmos. Environ.* 38: 941–951.
- Lee, J., J. Brumley, M. Ryckley, C. Smith, J. Lemaster, C. Ricci, A. J. Meier, and B. McPhail. 2016. Pitcher plant moths (Exyra) fly from pitchers in response to smoke. *J. Lepid. Soc.* 70: 268–270.
- Lester, S. E., B. I. Ruttenberg, S. D. Gaines, and B. P. Kinlan. 2007. The relationship between dispersal ability and geographic range size. *Ecol. Lett.* 10: 745–758.
- Li, M., Q. Zhang, J. I. Kurokawa, J. H. Woo, K. He, Z. Lu, T. Ohara, Y. Song, D. G. Streets, G. R. Carmichael, Y. Cheng, C. Hong, H. Huo, X. Jiang, S. Kang, F. Liu, H. Su, and B. Zheng. 2017. MIX: a mosaic Asian anthropogenic emission inventory under the international collaboration framework of the MICS-Asia and HTAP. *Atmos. Chem. Phys.* 17: 935–963.
- Li, R., W. Chen, A. Xiu, H. Zhao, X. Zhang, S. Zhang, and D. Q. Tong. 2019. A comprehensive inventory of agricultural atmospheric particulate matters (PM₁₀ and PM_{2.5}) and gaseous pollutants (VOC, SO₂, NH₃, CO, NO_x and HC) emissions in China. *Ecol. Indic.* 107: 1–14.
- Lin, T.-C., G. Krishnaswamy, and D. S. Chi. 2008. Incense smoke: clinical, structural and molecular effects on airway disease. *Clin. Mol. Allergy.* 6: 1–9.
- Linsley, G. E. 1943. Attraction of melanophila beetles by fire and smoke. *J. Econ. Entomol.* 36: 341–342.
- Liu, W., J. Zhang, J. H. Hashim, J. Jalaludin, Z. Hashim, and B. D. Goldstein. 2003. Mosquito coil emissions and health implications. *Environ. Health Perspect.* 111: 1454–1460.
- Liu, H., Y. Lu, Q. Liu, X. Huo, B. Peng, D. Ren, D. Wu, J. Wang, X. Wang, Z. Tang, et al. 2013. Comparison of pyrethroid resistance in adults and larvae of *Culex pipiens pallens* (Diptera: Culicidae) from four field populations in China. *J. Econ. Entomol.* 106: 360–365.
- Liu, Y., M. J. Wooster, M. J. Grosvenor, K. S. Lim, and R. A. Francis. 2021. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.). *Ecol. Entomol.* 46: 195–208.
- Love, B. G., and J. H. Cane. 2019. Mortality and flowering of great basin perennial forbs after experimental burning: implications for wild bees. *Rangel. Ecol. Manag.* 72: 310–317.
- Lu, X., X. Zhang, F. Li, M. A. Cochrane, and P. Ciren. 2021. Detection of fire smoke plumes based on aerosol scattering using VIIRS data over global fire-prone regions. *Remote Sens.* 13: 1–22.
- Marlier, M. E., R. S. DeFries, A. Voulgarakis, P. L. Kinney, J. T. Randerson, D. T. Shindell, Y. Chen, and G. Faluvegi. 2013. El Niño and health risks from landscape fire emissions in southeast Asia. *Nat. Clim. Change.* 3: 131–136.
- Marlon, J. R., P. J. Bartlein, D. G. Gavin, C. J. Long, R. S. Anderson, C. E. Briles, K. J. Brown, D. Colombaroli, D. J. Hallett, M. J. Power, et al. 2012. Long-term perspective on wildfires in the western USA. *Proc. Natl. Acad. Sci.* 109: E535–E543.
- McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annu. Rev. Entomol.* 43: 107–127.
- McKenzie, D., U. Shankar, R. E. Keane, E. N. Stavros, W. E. Heilman, D. G. Fox, and A. C. Riebau. 2014. Smoke consequences of new wildfire regimes driven by climate change. *Earths Future* 2: 35–59.
- Milberg, P., K. -O. Bergman, H. Norman, R. B. Pettersson, L. Westerberg, L. -O. Wikars, and N. Jansson. 2015. A burning desire for smoke? Sampling insects favoured by forest fire in the absence of fire. *J. Insect Conserv.* 19: 55–65.
- Moretti, M., F. De Bello, S. P. M. Roberts, and S. G. Potts. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *J. Anim. Ecol.* 78: 98–108.
- Moritz, M. A., M. -A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. *Ecosphere.* 3: 1–22.
- Musolin, D. L. 2007. Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Glob. Chang. Biol.* 13: 1565–1585.
- Navarro, K. M., D. Schweizer, J. R. Balmes, and R. Cisneros. 2018. A review of community smoke exposure from wildfire compared to prescribed fire in the United States. *Atmosphere.* 9: 1–11.
- New, T. R. 2014. *Insects, fire and conservation.* Springer.
- Newton, D. C. 1968. Behavioural response of honeybees to colony disturbance by smoke. I. Engorging behaviour. *J. Apic. Res.* 7: 3–9.
- Newton, D. C. 1969. Behavioural response of honeybees to colony disturbance by smoke. II. Guards and foragers. *J. Apic. Res.* 8: 79–82.
- Nicolas, G., and D. Sillans. 1989. Immediate and latent effects of carbon dioxide on insects. *Annu. Rev. Entomol.* 34: 97–116.
- Nyabuga, F. N., H. D. Loxdale, D. G. Heckel, and W. W. Weisser. 2012. Coevolutionary fine-tuning: evidence for genetic tracking between a specialist wasp parasitoid and its aphid host in a dual metapopulation interaction. *Bull. Entomol. Res.* 102: 149–155.
- Ollerton, J. 2017. Pollinator diversity: distribution, ecological function, and conservation. *Annu. Rev. Ecol. Syst.* 48: 353–376.
- Oppenheimer, C., V. I. Tsanev, A. G. Allen, A. J. S. McGonigle, A. A. Cardoso, A. Wiatr, W. Paterlini, and C. de Mello Dias. 2004. NO_x emissions from agricultural burning in São Paulo, Brazil. *Environ. Sci. Technol.* 38: 4557–4561.
- Pachauri, R. K., M. R. Allen, V. R. Barros, J. Broome, W. Cramer, R. Christ, J. A. Church, L. Clarke, Q. Dahe, P. Dasgupta, et al. 2014. *Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change.* IPCC, Geneva, Switzerland.
- Paczkowski, S., M. Paczkowska, S. Dippel, N. Schulze, S. Schütz, T. Sauerwald, A. Weiß, M. Bauer, J. Gottschald, and C. -D. Kohl. 2013. The olfaction of a fire beetle leads to new concepts for early fire warning systems. *Sens. Actuators B Chem.* 183: 273–282.
- Pauluhn, J. 2006. Mosquito coil smoke inhalation toxicity. Part I: Validation of test approach and acute inhalation toxicity. *J. Appl. Toxicol.* 26: 269–278.
- Peter, R. J., P. V. Bossche, B. L. Penzhorn, and B. Sharp. 2005. Tick, fly, and mosquito control—Lessons from the past, solutions for the future. *Vet. Parasitol.* 132: 205–215.
- Ravindra, K., T. Singh, and S. Mor. 2019. Emissions of air pollutants from primary crop residue burning in India and their mitigation strategies for cleaner emissions. *J. Clean Prod.* 208: 261–273.
- Ray, C., D. R. Cluck, R. L. Wilkerson, R. B. Siegel, A. M. White, G. L. Tarbill, S. C. Sawyer, and C. A. Howell. 2019. Patterns of woodboring beetle activity following fires and bark beetle outbreaks in montane forests of California, USA. *Fire Ecol.* 15: 1–20.
- Reid, C. E., and M. M. Maestas. 2019. Wildfire smoke exposure under climate change: impact on respiratory health of affected communities. *Curr. Opin. Pulm. Med.* 25: 1–15.

Downloaded from https://academic.oup.com/ee/article/51/5/871/6710218 by guest on 07 January 2023

- Reid, J., R. Koppmann, T. Eck, and D. Eleuterio. 2005. A review of biomass burning emissions part II: intensive physical properties of biomass burning particles. *Atmos. Chem. Phys.* 5: 799–825.
- Reid, C. E., M. Brauer, F. H. Johnston, M. Jerrett, J. R. Balmes, and C. T. Elliott. 2016. Critical review of health impacts of wildfire smoke exposure. *Environ. Health Perspect.* 124: 1334–1343.
- Reilly, T. F. 1906. The therapeutics of lupulin. *JAMA*. XLVI: 1021–1022.
- Richmond, H. A., and R. R. Lejeune. 1945. The deterioration of fire-killed white spruce by wood-boring insects in northern Saskatchewan. *For. Chron.* 21: 168–192.
- Ridley, M. 1988. Mating frequency and fecundity in insects. *Biol. Rev.* 63: 509–549.
- Rissler, J., A. Vestin, E. Swietlicki, G. Fisch, J. Zhou, P. Artaxo, and M. O. Andreae. 2006. Size distribution and hygroscopic properties of aerosol particles from dry-season biomass burning in Amazonia. *Atmos. Chem. Phys.* 6: 471–491.
- Roberts, G., and M. Wooster. 2021. Global impact of landscape fire emissions on surface level PM_{2.5} concentrations, air quality exposure and population mortality. *Atmos. Environ.* 252: 1–17.
- Rodgman, A., and T. Perfetti. 2013. *The chemical components of tobacco and tobacco smoke*. CRC Press.
- Ross, D. A. 1960. Damage by long-horned wood borers in fire-killed white spruce, central British Columbia. *For. Chron.* 36: 355–361.
- Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Front. Ecol. Environ.* 11: e15–e24.
- Sabbahi, R., D. DeOliveira, and J. Marceau. 2005. Influence of honey bee (Hymenoptera: Apidae) density on the production of canola (Crucifera: Brassicaceae). *J. Econ. Entomol.* 98: 367–372.
- Sagili, R. R., and P. Chakrabarti. 2021. Investigating effects of fire and smoke on honey bees exposed to wildfires, p. 22. In, *80th Annual Pacific Northwest Insect Management Conference, 4–5 January 2021, Virtual*. Pacific Northwest Insect Management Conference.
- Saint-Germain, M., P. Drapeau, and C. M. Buddle. 2008. Persistence of pyrophilous insects in fire-driven boreal forests: population dynamics in burned and unburned habitats. *Divers. Distrib.* 14: 713–720.
- Sanderfoot, O. V., S. B. Bassing, J. L. Brusa, R. L. Emmet, S. J. Gillman, K. Swift, and B. Gardner. 2021. A review of the effects of wildfire smoke on the health and behavior of wildlife. *Environ. Res. Lett.* 16: 1–24.
- Santalla, M., L. Pagola, I. Gómez, D. Balcazar, C. A. Valverde, and P. Ferrero. 2021. Smoking flies: testing the effect of tobacco cigarettes on heart function of *Drosophila melanogaster*. *Biol. Open* 10: 1–12.
- Schmitz, H., A. Schmitz, and H. Bleckmann. 2000. A new type of infrared organ in the Australian 'fire-beetle' *Merimna atrata* (Coleoptera: Buprestidae). *Naturwissenschaften*. 87: 542–545.
- Schmitz, H., A. Schmitz, E. Kreiss, M. Gebhardt, and W. Gronenberg. 2008. Navigation to forest fires by smoke and infrared reception: the specialized sensory systems of Fire-Loving beetles. *Navigation*. 55: 137–145.
- Schwalter, T. D. 2016. *Insect ecology: an ecosystem approach*, Academic press.
- Schütz, S., B. Weissbecker, H. E. Hummel, K. -H. Apel, H. Schmitz, and H. Bleckmann. 1999. Insect antenna as a smoke detector. *Nature*. 398: 298–299.
- See, S. W., and R. Balasubramanian. 2011. Characterization of fine particle emissions from incense burning. *Build. Environ.* 46: 1074–1080.
- Sheldon, T. L., and C. Sankaran. 2017. The impact of Indonesian forest fires on Singaporean pollution and health. *Am. Econ. Rev.* 107: 526–529.
- Shi, T., Y. Liu, L. Zhang, L. Hao, and Z. Gao. 2014. Burning in agricultural landscapes: an emerging natural and human issue in China. *Landsc. Ecol.* 29: 1785–1798.
- Simoneit, B. R. T. 2002. Biomass burning — a review of organic tracers for smoke from incomplete combustion. *Appl. Geochem.* 17: 129–162.
- Simpson, I. J., S. K. Akagi, B. Barletta, N. J. Blake, Y. Choi, G. S. Diskin, A. Fried, H. E. Fuelberg, S. Meinardi, F. S. Rowland, et al. 2011. Boreal forest fire emissions in fresh Canadian smoke plumes: C₁-C₁₀ volatile organic compounds (VOCs), CO₂, CO, NO₂, NO, HCN and CH₃CN. *Atmos. Chem. Phys.* 11: 6445–6463.
- Singer, M. C., and B. Wee. 2005. Spatial pattern in checkerspot butterfly—host plant association at local, metapopulation and regional scales. *Ann. Zool. Fenn.* 42: 347–361.
- Smart, M., J. Pettis, N. Rice, Z. Browning, and M. Spivak. 2016. Linking measures of colony and individual honey bee health to survival among apiaries exposed to varying agricultural land use. *PLoS One*. 11: 1–28.
- Smith, K. M., E. H. Loh, M. K. Rostal, C. M. Zambrana-Torrel, L. Mendiola, and P. Daszak. 2013. Pathogens, Pests, and Economics: Drivers of Honey Bee Colony Declines and Losses. *EcoHealth* 10: 434–445.
- Spracklen, D. V., L. J. Mickley, J. A. Logan, R. C. Hudman, R. Yevich, M. D. Flannigan, and A. L. Westerling. 2009. Impacts of climate change from 2000 to 2050 on wildfire activity and carbonaceous aerosol concentrations in the western United States. *J. Geophys. Res. Atmos.* 114: 1–17.
- Stark, W. 1972. The effect of ether and carbon dioxide on the components of the ERG of *Drosophila*. *Drosoph. Inf. Serv.* 48: 82.
- Steven, M. C., G. W. Sibadogil, S. S. S. A. Rahim, R. Avoi, F. Robinson, A. S. Musleh, M. S. Jeffree, and M. R. Hassan. 2020. Host and environmental factors that influence *Plasmodium knowlesi* malaria infection in humans: a systematic review. *Borneo Epidemiol. J.* 1: 104–115.
- Streets, D. G., K. F. Yarber, J. -H. Woo, and G. R. Carmichael. 2003. Biomass burning in Asia: Annual and seasonal estimates and atmospheric emissions. *Glob. Biogeochem. Cy.* 17: 1–20.
- Sun, Y., Q. Jiang, Z. Wang, P. Fu, J. Li, T. Yang, and Y. Yin. 2014. Investigation of the sources and evolution processes of severe haze pollution in Beijing in January 2013. *J. Geophys. Res. Atmos.* 119: 4380–4398.
- Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodivers. Conserv.* 10: 1141–1169.
- Symes, C. B. 1930. Anophelines in Kenya. *Ke. East Afr. Med. J.* 7: 2–11.
- Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, S. I. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. *Ecol. Appl.* 17: 1388–1402.
- Syphard, A. D., V. C. Radeloff, T. J. Hawbaker, and S. I. Stewart. 2009. Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conserv. Biol.* 23: 758–769.
- Tan, Y. Q., E. Dion, and A. Monteiro. 2018. Haze smoke impacts survival and development of butterflies. *Sci. Rep.* 8: 1–10.
- Tribe, G., J. Tautz, K. Sternberg, and J. Cullinan. 2017. Firewalls in bee nests—survival value of propolis walls of wild Cape honeybee (*Apis mellifera capensis*). *Sci. Nat.* 104: 1–4.
- Uchiyama, T., R. Koike, Y. Yuma, K. Okamoto, S. Arimoto-Kobayashi, T. Suzuki, and T. Negishi. 2016. Somatic-cell mutation induced by short exposures to cigarette smoke in urate-null, oxidative stress-sensitive *drosophila*. *Mutagenesis*. 31: 9–15.
- Ulyshen, M. D., A. Lucky, and T. T. Work. 2020. Effects of prescribed fire and social insects on saproxylic beetles in a subtropical forest. *Sci. Rep.* 10: 1–9.
- Ulyshen, M. D., A. C. Wilson, G. C. Ohlson, S. M. Pokswinski, and J. K. Hiers. 2021. Frequent prescribed fires favour ground-nesting bees in southeastern US forests. *Insect Conserv. Divers.* 14: 527–534.
- Van Cleemput, M., K. Cattoor, K. De Bosscher, G. Haegeman, D. De Keuleleire, and A. Heyerick. 2009. Hop (*Humulus lupulus*)-derived bitter acids as multipotent bioactive compounds. *J. Nat. Prod.* 72: 1220–1230.
- Van der Werf, G. R., J. T. Randerson, L. Giglio, G. Collatz, M. Mu, P. S. Kasibhatla, D. C. Morton, R. DeFries, Y. V. Jin, and T. T. van Leeuwen. 2010. Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009). *Atmos. Chem. Phys.* 10: 11707–11735.
- Vernède, R., M. M. van Meer, and M. P. Alpers. 1994. Smoke as a form of personal protection against mosquitoes, a field study in Papua New Guinea. *Southeast Asian J. Trop. Med. Public Health.* 25: 771–775.
- Vijay Kumar, K. N., and K. D. Ramaiah. 2008. Usage of personal-protection measures against mosquitoes and the low prevalences of *Wuchereria bancrofti* microfilaraemia in the Indian city of Chennai. *Ann. Trop. Med. Parasitol.* 102: 391–397.
- Visscher, K. P., and R. S. Vetter. 1995. Smoke and target color effects on defensive behavior in yellowjacket wasps and bumble bees (Hymenoptera: Vespidae, Apidae) with a description of an electronic attack monitor. *J. Econ. Entomol.* 88: 579–583.
- Visscher, K. P., R. S. Vetter, and G. E. Robinson. 1995. Alarm pheromone perception in honey bees is decreased by smoke (Hymenoptera: Apidae). *J. Insect Behav.* 8: 11–18.

- Vokina, V., M. Novikov, A. Alekseenko, L. Sosedova, E. Kapustina, E. Bogomolova, and T. Elfimova. 2019. Experimental evaluation of effect of wildfire smoke exposure on reproductive function of small mammals and their offspring. *Bull. Irkutsk State Univ. Ser. Biol. Ecol.* 29: 88–98.
- Wang, X., M. Chen, M. Zhong, Z. Hu, L. Qiu, S. Rajagopalan, N. G. Fossett, L. -C. Chen, and Z. Ying. 2017. Exposure to concentrated ambient PM_{2.5} shortens lifespan and induces inflammation-associated signaling and oxidative stress in *Drosophila*. *Toxicol. Sci.* 156: 199–207.
- Wang, Q., L. Wang, X. Li, J. Xin, Z. Liu, Y. Sun, J. Liu, Y. Zhang, W. Du, X. Jin, et al. 2020. Emission characteristics of size distribution, chemical composition and light absorption of particles from field-scale crop residue burning in Northeast China. *Sci. Total Environ.* 710: 1–13.
- Ward, D. E., R. A. Susott, J. B. Kauffman, R. E. Babbitt, D. L. Cummings, B. Dias, B. N. Holben, Y. J. Kaufman, R. A. Rasmussen, and A. W. Setzer. 1992. Smoke and fire characteristics for cerrado and deforestation burns in Brazil: BASE-B experiment. *J. Geophys. Res. Atmos.* 97: 14601–14619.
- Wijayaratne, L., M. Fernando, and K. Palipane. 2009. Control of insect pests under ware-house conditions using smoke generated from partial combustion of rice (paddy) husk. *J. Natl. Sci. Found.* 37: 125–134.
- Wilson, D. B. 1936. *Report of the malaria unit, Tanga, 1933-34; together with a report on a study of malaria in India*. Government Printer, Dar es Salaam.
- Witzgall, P., P. Kirsch, and A. Cork. 2010. Sex Pheromones and Their Impact on Pest Management. *J. Chem. Ecol.* 36: 80–100.
- Wong, P. T., W. D. Kaplan, W. E. Trout, and B. Hanstein. 1972. Carbon dioxide induced changes in the electroretinogram of *Drosophila* unaccompanied by altered phototactic behaviour. *J. Insect Physiol.* 18: 1493–1500.
- Yadav, U., and R. Tiwari. 2018. Effect of smoke on insect mortality and quality parameters of stored wheat at Pantnagar, Uttarakhand. *J. Entomol. Zool. Stud.* 6: 1661–1666.
- Yadav, V. K., N. Choudhary, S. Heena Khan, A. Khayal, R. K. Ravi, P. Kumar, S. Modi, and G. Gnanamoorthy. 2020. Incense and incense sticks: types, components, origin and their religious beliefs and importance among different religions. *J. Bio Innov.* 9: 1420–1439.
- Yamaguchi, M., and H. Yoshida. 2018. *Drosophila* as a model organism, pp. 1–10. In M. Yamaguchi (ed.), *Drosophila models for human diseases*. Springer, Singapore.
- York, A. 1999. Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. *J. Insect Conserv.* 3: 191–199.
- Zhang, H., D. Hu, J. Chen, X. Ye, S. X. Wang, J. M. Hao, L. Wang, R. Zhang, and Z. An. 2011. Particle size distribution and polycyclic aromatic hydrocarbons emissions from agricultural crop residue burning. *Environ. Sci. Technol.* 45: 5477–5482.
- Zhang, T., M. J. Wooster, D. C. Green, and B. Main. 2015. New field-based agricultural biomass burning trace gas, PM_{2.5}, and black carbon emission ratios and factors measured in situ at crop residue fires in Eastern China. *Atmos. Environ.* 121: 22–34.

2.2 Insect Migration

The definition of ‘migration’ from the Cambridge English Dictionary is ‘*the process of animals travelling to a different place, usually when the season changes*’. C. Williams (1957) mentioned that the term ‘migration’ pertains to the deliberate movements of animals, wherein they have a direction, covering a certain distance that leads to a temporary or permanent shift in their habitat. Migration is a widespread phenomenon observed across all major insect orders and occupies a significant role in the evolutionary development of various life-history strategies (Denno et al., 2001). The distances covered by insects during migration exhibit significant variation, ranging from localized movements within a specific area to traversing thousands of kilometers between continents and even hemispheres (J. W. Chapman et al., 2015; Chowdhury, Fuller, et al., 2021; Denno et al., 1985; Dingle, 2014). Also, insect migration typically occurs during specific seasons or periods of the year, sometimes coinciding with favorable conditions, such as resource availability and climate patterns (Carlson et al., 1992; Dingle and Drake, 2007; Stefanescu et al., 2017). Besides, insect migration might involve movements over multiple breeding generations, such as monarch butterflies, painted lady butterflies, fall armyworm (Flockhart et al., 2013; Stefanescu et al., 2017; J. Westbrook et al., 2019). In summary, most migratory insect species engaged in large-scale, seasonal timing, multi-generational, and long-distance journeys. (J. W. Chapman et al., 2015; Chowdhury, Fuller, et al., 2021; Denno et al., 1985; Dingle, 2014), including butterflies, dragonflies, moths, aphids, and flies (Clem et al., 2022; H.-Q. Feng et al., 2007; Hobson et al., 2021; Lundmark, 2010; J. R. Riley et al., 1995).

2.3 Migratory Insect Roles in Ecosystem

Insects are the most abundant and diverse animals on the planet, with an estimated 5-15 million species (over 60% of all animal species) (Dirzo and Raven, 2003; Jankielsohn, 2018; May, 1988; Sabrosky, 1953). The migratory insect is a type of insect species that exhibits regular and predictable movements across large distances during specific times or seasons, including butterflies, moths, dragonflies, beetles, bees,

and certain species of flies (J. W. Chapman et al., 2015; Satterfield et al., 2020; C. Williams, 1957). As migratory insect species can be found in various functional groups of insects, including pollinators, herbivores, predators (in a general sense), decomposers, and pests (Chowdhury, Fuller, et al., 2021; Dingle, 2006; D. Reynolds et al., 2006; Walther et al., 2002), they are inextricably linked to the whole ecosystem functions, and have both direct and indirect impacts on ecosystems. Therefore, we review some key roles of migratory insects in ecosystems in greater depth in Sections 2.3.1 to 2.3.6.

2.3.1 Pollinators

Over 1500 crops worldwide rely on insects to complete pollinations and reproduction (Klein et al., 2007). Depending on the crop species, insect pollination has been shown to increase average crop yield by varying percentages, ranging from 18% to over 70% (Bartomeus et al., 2014). There exists a pollination mutualistic relationship between insects and plants, such as fig and fig wasps (Cook and Rasplus, 2003), glochidion trees and epicephala moths (Kawakita and Kato, 2006), yuccas and yucca moths (James et al., 1994). Among pollinating insect species, bees are regarded as the most economically valuable pollinator for most crops, especially *Aplis mellifera* (Honeybees), because of their wide range of applications, convenience, and low cost (Khalifa et al., 2021; Pardo and Borges, 2020; Watanabe, 1994). Insects are beneficial to plant diversity and indirectly affect landscape structure (Jankielsohn, 2018).

2.3.2 Seed disperser

Insects, such as beetles (de Vega et al., 2011), grasshoppers (Duthie et al., 2006), and hornets (G. Chen et al., 2017) also provide seed dispersal service, with over 90% plant species is dispersed by insects in tropical regions (Howe and Smallwood, 1982). They transport seeds from one place to another, helping plants colonize new areas, maintain genetic diversity, and expand their range. This process contributes to plant community dynamics and ecosystem resilience (Díaz et al., 2013; Kremen

et al., 2007).

2.3.3 Decomposers

Certain insects also work as decomposers in breaking down and decomposing organic matter (Galante and Marcos-Garcia, 2008). For example, grasshoppers are major components of the food web, and sometimes their presence is critical to rapidly breaking down the nutrition of plant litter, speeding up the nutrient cycling, to ensure a quick return of nutrients to the primary producers and finally increase plant production (Belovsky and Slade, 2000).

2.3.4 Bioindicator

Some migratory insects exhibit an enhanced sensitivity to environmental fluctuations, making them valuable bioindicators for assessing the condition of habitats or ecosystems, such as beetles (Ghannem et al., 2018), butterflies (Pan et al., 2015), and dragonflies (Shafie et al., 2017). This is due to their close interaction with various toxic elements found in soil, water, and air. Their population dynamics, migration patterns, and responses to climate and habitat alterations provide valuable insights into the impacts of human activities on ecosystems (Ghannem et al., 2018).

2.3.5 Herbivores

Insects also occupy an important place in the food web. Approximately 50% of all living insects are herbivores (Wiens et al., 2015), which are the primary consumers in the food web, such as grasshoppers (Belovsky and Slade, 2000), moths (Harvey et al., 2010), and butterflies (Hawkins and Porter, 2003). Insect herbivores can act as regulators of forest primary production, keeping water and nutrient application at sustainable levels (Schowalter, 2012). However, large insect herbivores may have negative impacts on plant consumption, which is harmful to chemical element cycling and net primary production (Throop and Lerdau, 2004).

2.3.6 Predators/Preys

Some insects are secondary consumers (carnivorous predators) that can control the population growths of herbivores below threshold, especially pests. In the insect orders, Odonata (dragonflies) and Neuroptera (lacewings and antlions), all insect species are predators, normally eating crop pests (Zada et al., 2016). For example, *Othetrum sabina* (Slender skimmer) *Crocothemis servilia* (Scarlet skimmer), and *Crocothemis erythraea* (Broad scarlet) have consumed large number of rice pests (Yousuf et al., 1998). However, insects are also the main diets to many birds (Rytönen et al., 2019), fish (Barroso et al., 2014), and mammals (Sánchez-Muros et al., 2014).

2.4 Environmental factors impacting insect migration

2.4.1 Effects of wind on insect migration

Although migration is an active behaviour of insects to enable them to search for more quality resources (Dingle, 2014), the migration distance and habitat locations are also driven by metrological phenomena and climate change (Dingle and Drake, 2007; Lemoine, 2015; Sparks et al., 2007). Wind is probably the primary environmental factor influencing insect migration (Becciu et al., 2019), as insects can take advantage of wind conditions to maximize flight distance and optimize migration route (J. W. Chapman et al., 2010; J. W. Chapman et al., 2015; Hu et al., 2016). For instance, the average flight speed of *Autographa gamma* (Sliver Y) is only around $5 \text{ m}\cdot\text{s}^{-1}$. However, they can select the fastest airstreams to maximise their migration speed and distance to achieve movements of up to $24 \text{ m}\cdot\text{s}^{-1}$ (J. W. Chapman et al., 2008). Similarly, studies have shown that *Anax junius* (Common green darner dragonfly) could fly at speeds up to $21 \text{ m}\cdot\text{s}^{-1}$ daytime with the favor of wind (Knight et al., 2019) when tracking their autumn migration between Canada and the United States. In addition to speeding up migration, wind can also shift the direction of insect migration (J. W. Chapman et al., 2015) as typically migrators

maintain a common heading that coincides with the wind direction (downwind). For example, *Autographa gamma* (Sliver Y) showed the same migration orientation as the downwind direction during autumn migration in the UK (J. W. Chapman et al., 2008).

2.4.2 Effects of temperature on insect migration

In addition to the wind, the optimal flight performance of insects occurs within the temperature range to which they are adapted (Minter et al., 2018; D. R. Reynolds et al., 2017). When the average temperature is above or below the limit that best supports their life cycle, the flight behavior of insects will probably be inhibited (X. Jiang et al., 2011; Z. Liu et al., 2011). At temperatures within insect habitual ranges, normally there is a positive relationship such that flight speed increases with increasing air temperature (Minter et al., 2018). For example, *Anax junius* (green darners) were observed to move faster with increasing temperatures within the range 18°C to 23°C. At higher than 23°C, *Anax junius* flew slower with higher temperatures (Knight et al., 2019). Similarly, the most flight activity of *Mythimna separata* (Northern armyworm) occurs at temperatures from 11°C to 32°C, but the optimum occurs at 17°C to 22°C (X. Jiang et al., 2011). Air temperature may influence insect migration through its implications on take-off time, transfer speed, direction, distance, and altitude (R.-L. Chen et al., 1989; B. Jiang et al., 2003).

2.4.3 Effects of climate change on insect migration

Since insects have an optimal air temperature range for flights, Climate change may have potential impacts on insect migration. Sparks et al. (2007) indicated that the frequency of insect migration to northern altitudes is rising due to climate change. Climate change is characterized by rising air temperature, increased levels of carbon dioxide, and changing precipitation patterns, impacting extend to both individual species and entire ecosystems. Migratory insects, in particular, are highly susceptible to the effects of climate change due to their reliance on multiple habitats and sites for breeding, feeding, and relaxing during their migration. Climate change has the

potential to disrupt insect migrations by altering habitat quality, changing resource availability, increase habitat disturbance (Moore, 2011). For instance, the number of *Danaus plexippus* (Monarch butterfly) migrating to Mexico has been greatly reduced by the loss of breeding habitat, as climate change lead a reduction in the extent of areas with suitable microclimate conditions, as well as a potential limitation in the number of host plant (*Asclepias* spp.) for *Danaus plexippus* (Howard and Davis, 2009).

2.5 Techniques to Study Insect Migration

In order to detect and monitor the migration of insects, a few techniques have been created, some of which are briefly detailed below.

2.5.1 Entomological radar observation (ERO)

ERO can be effectively used to detect and monitor insect migration (Drake and Reynolds, 2012; Dwivedi et al., 2020), as it works in different weather conditions, mainly based on transmitting radio frequency electromagnetic waves to the insects and receiving the target backscattered echoes (Long et al., 2020). Since 1960s, the insect system radar was firstly built to detect migration of locust, moth, and butterfly (Schaefer, 1969), and a number of insect radar with special applications were subsequently developed, especially scanning insect radar (SIR), vertical looking radar (VLR) (J. W. Chapman et al., 2003; J. Chapman et al., 2002; Long et al., 2020; Smith et al., 1993), and weather radar (Leskinen et al., 2011; Rennie, 2014).

2.5.1.1 Scanning insect radar (SIR)

SIR is modified from marine radar with a wavelength of 320 mm since the 1960s, which is used to detect insect species with medium to large body size at 0.5-4 cm² in the range of 1-2 km (Schaefer, 1969). Later, SIR with a shorter wavelength at 8.8 mm was applied to detect small insects starting in the 1980s (D. Reynolds, Riley, et al., 1997). For example, *Nilaparvata lugens* (planthopper) was observed by SIR that fly between 400 m and 1000 m above ground during September in Nanjing City,

southeast China (J. Riley et al., 1991). However, it is hard to identify insect species and monitor long-period migration (Long et al., 2020).

2.5.1.2 Vertical-looking radar (VLR)

VLR has improved in insect species identification and long-term migration detection, as it can provide more detailed information in insect characteristics by emitting a plane-polarised vertically directed beam and receiving signals between 150 m and 1200 m above the radar. VIR can be set to detect the insect targets from 15 altitude bands for 24 hours per day when insects fly through the beam. Insects that pass through the radar beam reflect back a signal, and once signal is received, they are automatically analysed by an iterative procedure depends on components of their Fourier transformation, which provides information in size, shape, positions of insect target (J. W. Chapman et al., 2003; J. Chapman et al., 2002; Smith et al., 1993), and furthermore provides information in insect density and migration (Long et al., 2020). For example, the flight intensity, flight altitude, and movement direction of *Vanessa cardui* was provided by VLR located at Hampshire, UK to analyse butterfly migration pattern (Stefanescu et al., 2013). VLRs are well-calibrated, and self-running, and the analysis of their observations benefits from a priori information about the organism being observed (Lukach et al., 2022).

Entomological radars play an important role in insect migration. However, they are few in number and have limited spatial coverage (Lukach et al., 2022), and they still need improvements in detection of lower-altitude movement and vertical resolution (J. W. Chapman et al., 2003).

2.5.2 Weather surveillance radar (WSR)

WSR is used extensively to provide aero-ecological observations at large scale. Although it is mainly applied to meteorological observations, such as rain, storm, and hail (Stepanian et al., 2016), it can also detect movements of birds (O’Neal et al., 2015; Van Doren et al., 2016), bats (Frick et al., 2012; McCracken et al., 2008), and insects (J. Westbrook et al., 2014; J. K. Westbrook, 2008) in a large spatial and

temporal domains with resolution of less than 1 km and 5 minutes (Stepanian et al., 2016; J. Westbrook and Eyster, 2017). WSR has a similar principle as SIR (X-band) which monitors transmitted radar energy reflected back to the radar by insects. For instance, WRS was applied to demonstrate the abundance and displacement of *Helicoverpa zea* (Corn earworms) over a large area in North America (J. Westbrook et al., 2014). However, WRS has a problem in discriminating between different types of bio-reflectors in the atmosphere (Gauthreaux Jr et al., 2008).

2.5.3 Stable-hydrogen isotope (SHI)

SHI detects insect migration mainly by estimating the birth origin of insects collected in different locations, thereby predicting the population size of insect species and then understating insect migration strategy (Hobson et al., 2021; Miller et al., 2011). For example, SHI was applied to the wings of *Danaus plexippus* collected from different sites along the eastern United States coasts to determine their place of origin and found that 90% *Danaus plexippus* originated from the Great Lakes regions by analyzing SHI composition (Miller et al., 2011). However, it hardly provides information on specific behavior changes during migration.

2.5.4 Tethered flight mill (TFM)

In addition to the previously mentioned technologies used to track insect flight behavior in natural settings, tethered flight mills (TFMs) serve as an affordable, flexible, and laboratory-based flight system that provides a practical method for quantifying the flight behavior of migratory insects (Attisano et al., 2015; H. B. Jones et al., 2016; Minter et al., 2018; Naranjo, 2019). TFMs offer a viable approach to studying and analyzing the various aspects of insect flight within experimental conditions (Minter et al., 2018). There are two main tethered flight techniques, one is the rotational flight mill and another one is the flight simulator.

2.5.4.1 Rotational flight mill (RFM)

RFM is commonly used to evaluate the relative flight performance of migratory insects, encompassing flight distance, speed, and duration (H. B. Jones et al., 2016; Minter et al., 2018; J. Riley et al., 1997). The RFM has been applied to study insect flight performance since the 1950s (Hocking et al., 1953; Krogh and Weis-Fogh, 1952), and the current operation principle of RFM involves attaching the insect to one side arm of the mill by adhering it to the back of the thorax, while a counterweight is affixed to the opposite side of the mill to maintain balance. This arrangement enables the insects to fly continuously in a cyclical manner. The central arm axle remains vertically stabilized through opposing magnetic forces exerted by two magnets, facilitating minimal friction rotation when the insect applies sufficient force to initiate arm movement (Fahrner et al., 2014; Martí-Campoy et al., 2016; Minter et al., 2018). Flight performance data is detected using a light sensor, with more comprehensive information available in Chapter 4. However, the flight performance observed on the tethered flight mill (TFM) for migratory insects is not natural as the experimental setup lacks environmental cues that could potentially stimulate (such as wind) or suppress flight (Hoddle et al., 2015; Minter et al., 2018; R. A. Taylor et al., 2010).

2.5.4.2 Flight simulator (FS)

FS is a tracking system specifically designed to monitor the horizontal orientation of migratory insects during their flight (Merlin et al., 2009; Minter et al., 2018; Mouritsen and Frost, 2002; Nesbit et al., 2009). The FS setup consisted of white plastic barrels, within which the insects are suspended on a delicate tungsten rod. The rod is connected to an optical encoder, enabling accurate the precise recording of the heading of the insects as they fly. Using the FS, the flight path of individual insects can be recorded, allowing for easy analysis of their preferred orientation (Dreyer et al., 2021; Minter et al., 2018; Nesbit et al., 2009). This information provides valuable insights into the flight behavior and orientation of migratory insects. However, tethered flying insects are deprived of certain visual stimuli that free-flying insects experience (Dreyer et al., 2021).

2.6 Thesis Aim

In this chapter, the impact of air pollution from landscape fire smoke (LFS) on insects and how insect migrations are influenced by climatic factors have been reviewed. The review of the literature identified neither studies describing the impact of LFS on insect migration nor any studies exploring the specific components of smoke and how these might impact insect movements. As shown in the review, insect migration can have large implications on ecological landscapes - as the insects settle down in a new habitat where they may provide essential ecosystem services such as crop pollination (Holland et al., 2006; Wotton et al., 2019). It is important therefore to understand the impact of LFS on migratory insects, to further understand the impact on ecosystems and landscape change. There is also significant uncertainty in how global landscape fire activity may develop in the future in response to changing climate and anthropogenic activities (K. L. Riley et al., 2019), which may further alter the impact that landscape fires have on these phenomena.

The aims of this thesis are therefore to understand (i) whether LFS impacts the movement of migratory insects; (ii) how it does so if they are affected; and (iii) which of the various components of LFS might be responsible. The specific objectives designed to achieve these aims are presented in Section 2.7.

2.7 Specific Objectives

2.7.1 Determination of suitable migratory insect species as research target

In the last two decades, research has estimated that there are between 5 to 30 million insect species on Earth (Espírito-Santo and Fernandes, 2007). Among this remarkable diversity, a significant number of insect species engage in extensive long-scale seasonal migrations, with notable examples found within the orders of Lepidoptera, Orthoptera, and Hemiptera (J. W. Chapman et al., 2015; Guo et al., 2020). The main objective of this study is to select a suitable insect species that possesses sev-

eral key characteristics. Ideally, the chosen species should have a global distribution, large population size, strong flight abilities, and high sensitivity to environmental factors. Furthermore, it is desirable for the selected species to inhabit areas prone to significant landscape fires, as this will enhance the likelihood of observing the effects of fire and smoke on their migration patterns. Butterflies, in particular, fulfill these criteria, as they are highly responsive to environmental disturbances and simple to identify and monitor (Mills et al., 2017; T. New, 1997; Parikh et al., 2021; Tan et al., 2018). Moreover, certain butterfly species, such as *Danaus plexippus* (monarch butterfly), *Vanessa atalanta* (red admiral butterfly), and *Vanessa cardui* (painted lady butterfly), are known for their impressive migration performances (Cuadrado, 2017; Reppert and de Roode, 2018; Stefanescu, 2001; Talavera and Vila, 2017). However, when comparing these species, *Vanessa cardui* possesses distinct advantages for investigating the impact of LFS on migratory insects.

In contrast to the round-trip migration of *Danaus plexippus* involving up to five generations between Canada and Mexico, *Vanessa cardui* exhibits a more expansive distribution encompassing various regions globally (Ecuador, 1992). Additionally, *Vanessa cardui* demonstrates greater dietary flexibility, as it can utilize a diverse range of plant species (Talavera and Vila, 2017). There is no doubt that *Vanessa cardui* is widely recognized and highly regarded as one of the most prominent and well-studied migratory butterflies globally, particularly in the context of the United Kingdom, where it is one of the most abundant immigrant butterflies regularly observed (Asher et al., 2001; Stefanescu, 2011). Overall, *Vanessa cardui* as a representative insect species has been selected for this study. More details have been described in Chapter 4.

2.7.2 Quantitative method to study the impact of LFS on migratory insects

The second objective is to apply suitable tools and methods to quantitatively study the impact of LFS on migratory insects. While several methods discussed in Section

2.5 have yielded valuable insights into tracking and characterizing insect migration patterns, their efficacy in accurately elucidating the effects of environmental changes on migration specifics, particularly individual movement patterns, is hindered by limited information on fixed displacement points and the diminutive size of the insects. This rather requires a detailed exploration of individual insect behavior in a controlled environment, as the behavior of migratory insects will directly influence the outcome of their migration. To fulfill this requirement, the application of tethered flight mills (TFM) emerges as an appropriate approach to quantitatively assess the impact of LFS on migratory insects. TFM, being a laboratory-based technique, enables the precise measurement of the influence of environmental factors on flight behavior in controlled settings which described in Section 2.5.4. The TFM setup details can be found in Chapter 4.

2.7.3 New field and laboratory methods to measure landscape fire emissions

Following Section 2.7.2, we also need to assess the different components of landscape fire smoke. The so-called emission factors (EFs) of landscape fires have been commonly derived from laboratory work (França et al., 2012; Koss et al., 2018; H. Zhang et al., 2008), but may not be fully representative of the smoke from real landscape fires as fire behavior may differ from real landscape-scale fires (Delmas et al., 1995; M. Wooster et al., 2011). It is harder to generate field-derived EFs because many instruments for precise measurement of smoke constituents cannot be used in the field, and also the smoke from many landscape fires is driven vertically upwards making it difficult to sample without aircraft or UAVs (Vernooij et al., 2022). Here the task will be to measure the EFs of agricultural residue materials that are very commonly burned in countries such as China and India from combined laboratory-field-work. Certain measurements of smoke in the field will be made, along with measurements of burning the same material in a combustion chamber using more sophisticated instruments. Through comparisons of the measurements from laboratory work and fieldwork, the EFs of a range of substances emitted from actual landscape burning

but only measured in the laboratory are hoped to be determined.

2.7.4 Study whether LFS impact migratory insects

Depending on the laboratory-based flight system selected in the prior objective, insect individuals will be put in ambient (“clean air”) conditions and also in conditions representative of smoke-polluted air for various time periods in order to comprehensively determine whether LFS impacts migratory insect behaviors in ways that might affect their migration. The study will assess statistically how sets of individual insects respond to different LFS conditions. A key task will be to create stable real-world landscape fire smoke environments (Finney, 2004; Giglio et al., 2018).

2.7.5 Explore what LFS components may impact migratory insects

Finally, a further task will be to build on the work done under Section 2.7.4 to identify which component of landscape fire smoke is the one more likely to affect the insect behavior - for example, which of trace gases or aerosols. This will enable us to learn more about the effects of specific components of the gaseous and aerosol environments on butterflies based on their responses to gases and particulate matter.

Chapter 3

Measurement of gaseous and particulate emissions from agricultural residue burning

3.1 Introduction

In this chapter, we identified the smoke components and estimated the smoke emissions released by landscape burning, specifically by agricultural residue burning, based on emission factors (EFs) measured through a combination of laboratory and field experiments. Besides, we also investigated whether incense sticks can produce smoke of a similar composition to agricultural residue burning, such that the former can be more confidently used as a smoke source within the planned laboratory experiments in the later chapters.

In Section 3.3, we first describe the detail of experiments designed to characterise smoke from actual agricultural residue burning. Different agricultural residues, including rice, wheat, millet, soybean and corn straw, are burnt in the lab under different conditions, such as moisture contents, packing densities and combustion

types - and the results compared to measurements conducted in the field (Section 3.4). Assessments of both trace gases and aerosols are conducted, and Section 3.5 investigates the similarity between these emissions and those from incense sticks, so as to determine whether the latter can be a stand-in for the former in our TFM experiments.

3.2 Background

3.2.1 Agricultural Residue Burning

Fire is a critical landscape process in the Earth system that has shaped many landscapes for thousands of years (Finney et al., 1999; Keane and Finney, 2003). Landscape fires are widespread and relatively frequent in the world. Depending on different land types, they are divided into forest fires, shrubland fires, savanna fires, grassland fires and cropland fires (Finney, 2004; Giglio et al., 2018). The estimated burned area was over 40 million km² from 1997 to 2008, which is equivalent of approximately 40% of the total terrestrial vegetation area on Earth in these eleven years (Giglio et al., 2010; Giglio et al., 2018; M. J. Wooster et al., 2013). The average annual global burned area between 1997 to 2008 was quite similar at between 3 and 5 million km² (Chuvieco et al., 2018; Giglio et al., 2010). In fact, many landscape fires are small fires (less than 0.5 km²) (Fornacca et al., 2017), which are hard to be captured through satellite remote sensing products and so these figures maybe somewhat underestimated (Randerson et al., 2012).

Agricultural residue fires normally occur in small patches, with an average area of 0.16 km² (McCarty et al., 2009). It is a seasonal activity conducted by farmers actively igniting fires to clear crop residues after harvest, including straw, stubble, weeds, and hulls (Gadde et al., 2009; Shi et al., 2014). Agricultural burning in general has two peak periods at the global scale, one is between May and June for instance in China (Tao et al., 2013; T. Zhang et al., 2018), and the other one is concentrated in September for example in Brazil (Reinhardt et al., 2001). Compared to other methods to process agricultural residues, such as landfill and mechanized

disposal, agricultural burning is the easiest, fastest, and cheapest way to process agricultural residues (D. Jiang et al., 2012; Shi et al., 2014). Such burning is widely applied in the developing countries, despite the fact that there are many policies prohibiting it (Bhuvaneshwari et al., 2019; H. Zhang et al., 2008; T. Zhang et al., 2015). It is estimated that close to 30% of crop residues are burned in agricultural lands in China and India (Venkataraman et al., 2006; Yan et al., 2006) - so the impact on the atmosphere and air quality from the emitted smoke can be quite extreme (Du et al., 2011; W. Li et al., 2010). In addition to Asia, crop residues are produced cumulatively in many countries in Africa and Latin America. Africa produces 10% of the total agricultural residues in the developing world, including in countries such as Egypt, Madagascar and South Africa (Yevich and Logan, 2003).

3.2.2 Emissions from Agricultural Residue Burning

Smoke released from burning biomass contains a variety of trace gases, including CO₂, CO and CH₄, as well as particulates such as black carbon (BC) and organic carbon (OC) (H. Zhang et al., 2017; H. Zhang et al., 2008; L. Zhang et al., 2016; T. Zhang et al., 2015). These emissions have a significant impact on worldwide atmospheric chemistry and radiative forcing since they not only degrade local air quality but also can spread thousands of kilometres downwind from the source (J. Chen et al., 2017; Z. Cheng et al., 2014; Satyendra et al., 2013). In addition, particulate emission from agricultural burning has been regarded as one of the major contributors to haze formation during the harvest seasons, which can both impact human health and visibility (Gadde et al., 2009; Keshtkar and Ashbaugh, 2007; Shi et al., 2014). An important parameter called the emission factor (EF) is widely used to quantitatively demonstrate how much amount of chemical species will be released from per kilogramme of a fuel burnt. It is derived from emission ratios $ER_{x/y}$ which is defined as the relatively excess amounts of two smoke species $[x]$ and $[y]$ (M. Wooster et al., 2011). A lot of laboratory work, such as H. Zhang et al. (2008) and França et al. (2012), and *in situ* measurements, such as T. Zhang et al. (2015), has been conducted to measure the EFs of trace gases and particles from agricultural burning. However, laboratory studies may lack some realism since fires created in

the laboratory are smaller and perhaps burn differently to real agricultural burning (M. Wooster et al., 2011). *In situ* measurements though are more difficult to make in the field, for example because the smoke moves about with the wind and may also travel vertically upwards, and certain of the equipment is hard to operate outside of the laboratory (X. Li et al., 2007; Sahai et al., 2007). For this reason, this thesis combines laboratory work and fieldwork to assess the EFs of agricultural residue burning. It quantitatively analyses the effects of moisture content and packing density of straw on these EFs, and since fires have different combustion phases (M. Wooster et al., 2011), it calculates EFs for each entire fire but also for its pure flaming and smouldering phases. The EFs of trace gases and aerosol generated from burning incense sticks are also assessed to determine how similar these are actual agricultural residue burning.

3.3 Methodology

3.3.1 Experimental Overview

This experiment measures smoke from burning the following residues - rice, wheat, millet, soybean and corn straw. The experiment consisted of two parts. One part was carried out in the laboratory to precisely estimate the emission factors (EFs) of the trace gases and aerosols by continuously measuring the mixing ratios of various trace gases (CO_2 , CO and CH_4) and concentrations of aerosols ($\text{PM}_{2.5}$) under controlled conditions. Since the literature (Andreae and Merlet, 2001; He et al., 2011; Van der Werf et al., 2010) suggests that the EFs of certain smoke components are affected by the properties of the biomass, different moisture contents, packing densities, and types of combustion (bonfire and spreading fire) were considered, and data for the pure flaming and pure smouldering phases were analysed as well as the ‘total fire’. The second part of the work was conducted on the agricultural land measuring the emission ratio of CO and CO_2 to understand how close this was to that of the laboratory fires. The mixing ratios of CO and CO_2 were collected with a Gaslab Multi Gas Sampling Data Logger (Gaslab), a sensor also used in the laboratory experiments.

3.3.2 Laboratory Experiment

3.3.2.1 Experiment Setup

The laboratory experiment was conducted with a Combustion and Measurement System at Rothamsted Research Institution, UK, as shown in Figure 3.1. It consisted of a combustion chamber and a laboratory platform. A square burning tray (diameter 100 cm) was placed in the combustion chamber (Figure 3.1a) and a set of analytical instruments for trace gases and particles were equipped in the laboratory platform (Figure 3.1b). Agricultural straws were put on the burning tray and weighted during the combustion process by a scale that was placed at the bottom of the burning tray. Fresh air was introduced into the combustion chamber through a small vent on the bottom left. There was an extraction hood on the top of the burning tray which extracted the emissions from the burning activities to an extraction flue (diameter 15 cm) connected with a stainless-steel tube. Two instruments were connected to the stainless-steel tube, including Gaslab Multi Gas Sampling Data Logger (Gaslab) to measure the mixing ratios of CO₂ and CO, and a TSI Dusttrak II Aerosol Monitor 8530 for PM_{2.5} concentrations measurement. Besides, another stainless-steel tube was put above the fire emissions, which was connected to a Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyser for measuring the mixing ratios of CO₂, CO and CH₄.

3.3.2.2 Experimental Design

The overall design of the laboratory experiment is summarised in Table 3.1. Five agricultural residues, including rice, wheat, millet, soybean straw and corn straw, were chosen as representatives of agricultural crop residues because they are the most abundant crops in the world (Leff et al., 2004). These straws were collected after harvest from a rural region in Shaanxi province, China.

Our first objective is to quantify the EFs of trace gases and particles from different agricultural residues. In order to avoid the effects of other factors, all five types of agricultural straw are burnt as bonfires with a mass of 100 g in a completely

Table 3.1: Fires measured in the laboratory with different biomass, fire types, packing volume, mass, moisture contents, and durations. Each fire was repeated 3 times.

Fire No.	Biomass	Fire type	Volume (cm ³) (L × W × H)	Mass (g)	Moisture contents (%)	Duration (minutes)
1	Rice straw	Bonfire	12250 (35 × 35 × 10)	100	0	6
						7
						8
2	Rice straw	Bonfire	12250 (35 × 35 × 10)	100	10	11
						11
						8
3	Rice straw	Spreading fire	12500 (50 × 50 × 5)	100	10	8
						5
						7
4	Rice straw	Spreading fire	12500 (50 × 50 × 5)	150	10	10
						11
						9
5	Rice straw	Spreading fire	12500 (50 × 50 × 5)	200	10	11
						9
						9
6	Wheat straw	Bonfire	5000 (25 × 25 × 8)	100	0	17
						15
						11
7	Wheat straw	Bonfire	5000 (25 × 25 × 8)	100	5	22
						27
						10
8	Wheat straw	Bonfire	5000 (25 × 25 × 8)	100	10	16
						19
						22
9	Wheat straw	Bonfire	5000 (25 × 25 × 8)	100	15	23
						15
						16
10	Wheat straw	Bonfire	5000 (25 × 25 × 8)	100	20	19
						21
						25
11	Millet straw	Bonfire	12250 (35 × 35 × 10)	100	0	5
						6
						6
12	Soybean straw	Bonfire	4800 (30 × 20 × 8)	100	0	14
						11
						10
13	Corn straw	Bonfire	6400 (40 × 20 × 8)	100	0	13
						13
						13

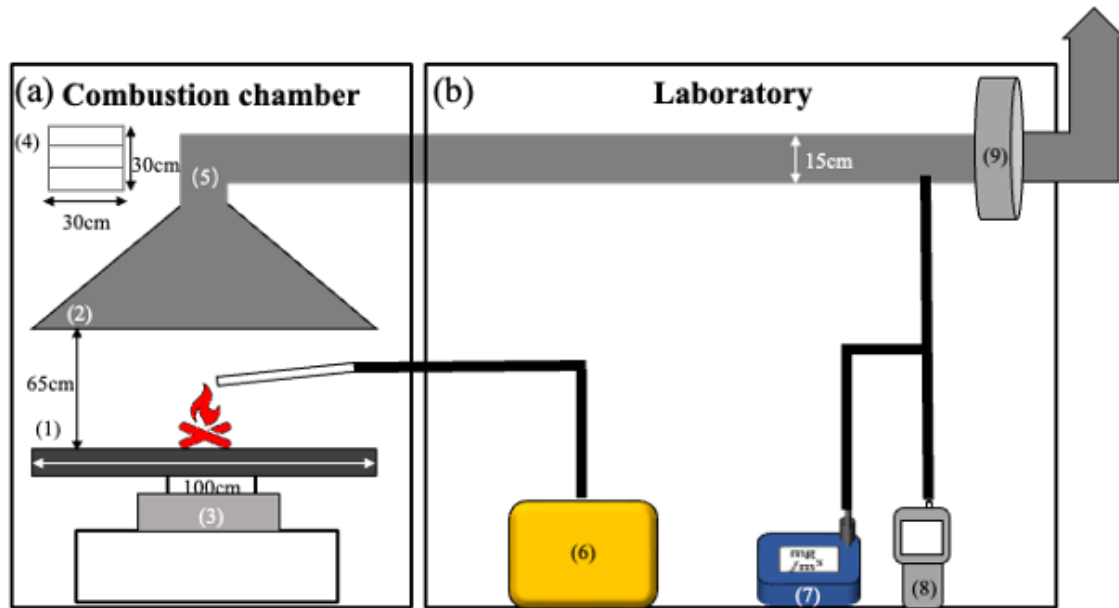


Figure 3.1: Schematic graph of the experiment setup: (a) combustion chamber, containing (1) burning tray (2) smoke extraction hood, (3) scale, (4) vent, and (5) extraction flue; (b) laboratory platforms with a series of associated instruments, including (6) Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyser, (7) TSI Dusttrak II Aerosol monitor 8530, (8) Gaslab Multi Gas Sampling Data Logger, (9) Extraction fan.

dry condition. The straw was placed in an oven at a constant temperature of 60°C overnight to evaporate the original moisture. The straw was weighed before and after placement in the oven until the weight remained constant, at which point the straw was considered to be in a completely dry condition and the moisture content inside was regarded as 0%.

Moreover, to understand the effects of different combustion types on EFs of trace gases and particles, 100 g rice straw in ambient conditions was burned as bonfires and spreading fires. The main difference between bonfire and spreading fire is that biomass is piled up differently. To create a bonfire, biomass is piled up as a rectangle, while spreading fire is created by spreading the biomass out on the ground, which leads to a different area of biomass surface in contact with air (T. Zhang et al., 2015). For example, a bonfire was created by burning rice straw burn as bonfire fire with 12250 cm^3 with a length of 35 cm, width of 35 cm and height of 10 cm (Figure 3.2a) and a spreading fire with a length of 50 cm, width of 50 cm and height of 5

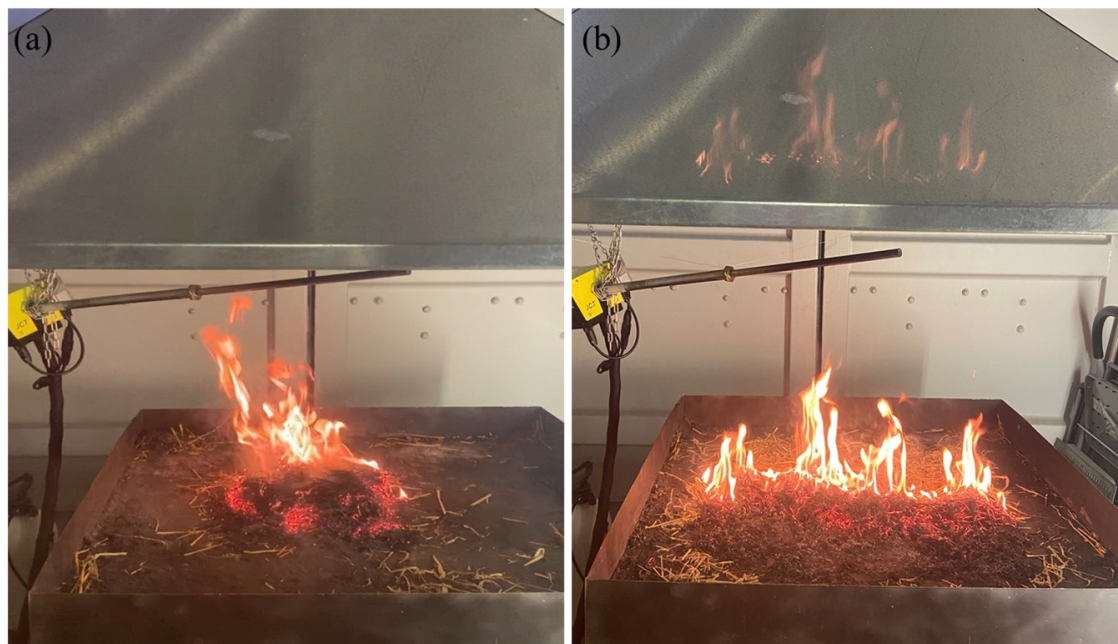


Figure 3.2: Photographs of (a) bonfire and (b) spreading fire during burning 100 g of rice straw in the ambient conditions on burning tray.

cm (Figure 3.2b).

Then we investigated the influence of moisture content on agricultural residues burning. A sample of 100 g wheat straw was burned as a bonfire with different moisture contents, including 0%, 5%, 10%, 15%, and 20%. To obtain wheat straw with different moisture contents, the completely dried straw was sprayed with different weights of water and placed in sealed plastic bags to allow the water to permeate the straw. For example, to obtain 100 g of straw with 5% moisture content, 95 g of straw in completely dry condition was added with 5 g of water. In addition, measurements on the straw collected from ambient conditions showed that it contained roughly 10% moisture content, similar to the straw used in X. Li et al. (2007).

Furthermore, we studied the impact of packing density on EFs of trace gases and particles. Rice straw in ambient condition were burned as spreading fires. To change the packing density, the packing volume of the rice straw at each time was fixed to 12500 cm^3 with length of 50 cm, width of 50 cm, and height of 5 cm but its mass was changed from 100 g, 150 g, to 200 g. In this way, the resulting packing densities

are $0.008 \text{ g}\cdot\text{cm}^{-3}$ as low density (LD), $0.012 \text{ g}\cdot\text{cm}^{-3}$ as medium density (MD), and $0.016 \text{ g}\cdot\text{cm}^{-3}$ as high density (HD), respectively.

3.3.2.3 Experimental Procedure

Prior to conducting the experiments, the monitoring instruments of TSI Dusttrak II Aerosol monitor 8530, Gaslab, and LGR were properly connected and activated to commence recording ambient air conditions for approximately 20 minutes. These instruments provided real-time information on various atmospheric parameters, including $\text{PM}_{2.5}$ concentration, and mixing ratio of CO_2 , allowing for a comprehensive assessment of the ambient air conditions and their stability. Additionally, they facilitated the verification of the mixing ratio of CO and CH_4 remains at zero. Once a reliable average value of ambient air conditions was obtained, the burning experiment can start.

To ensure accurate measurement of crop straw, a counter scale was strategically positioned beneath the burning tray. This counter scale enabled precise weighing of the straw, such as 100g. The straw was left on the burning tray for an additional 5 minutes to allow for stabilization of the ambient conditions before ignition. Once the straw was ignited, the door of the combustion chamber was quickly closed. Throughout the burning process, the observers had a clear view of the experiment's progress through the glass window installed in the door, which effectively separated the combustion chamber from the laboratory environment.

Throughout the experiment, an extraction fan always operated consistently at a specific flow speed to extract the smoke from the combustion chamber until the straw was completely burnt. The smoke emitted during the combustion process was then directed into a stainless-steel tube and extraction flue, which were seamlessly connected to various measurement instruments. These instruments, including the TSI Dusttrak II Aerosol Monitor 8530, Gaslab, and LGR, diligently recorded the entirety of the burning process, with a sampling rate set at one data sample per second, except for the Gaslab instrument, which operated at a frequency of one data

sample every two seconds. The burning process was considered complete when the mixing ratio of CO₂ and PM_{2.5} concentration returns to ambient levels. Additionally, the mixing ratio of CO and CH₄ remained at zero. Furthermore, the stability of the readings on the scales positioned beneath the burning tray was a reliable indicator of the tray's cleanliness and readiness for subsequent combustion experiments. All these aspects meet the standard, signifying the restoration of baseline conditions.

To maintain experimental integrity, thorough cleaning of the burning tray was diligently conducted before each combustion. This meticulous cleaning procedure, coupled with the presence of the counter scale beneath the tray, ensured the removal of any residue from previous combustions. A reading of zero on the counter scale signified the successful removal of all remnants, affirming the tray's cleanliness and suitability for the subsequent burning experiments. These meticulous monitoring and recording processes contributed to the reliable and accurate execution of the burning experiments.

3.3.3 Field Sampling Approach

The measurements in the agricultural land was taken place in Luochuan county (35.26N, 109.13E), Northwest China, in June 2022, coinciding with the burning period in northern China (Huang et al., 2012; Q. Wang et al., 2020). During the measurements, rice straws were burned in their most common way as bonfires. Gaslab was applied in the *in situ* to record the mixing ratios of CO and CO₂ emitted from agricultural fires. During fire spreading, smoke is mainly dispersed with wind direction, but roughly upwards. Therefore, a 1.5 m transparent plastic tube was connected to the inlet of data logger, which was fixed to a long wooden stick so that the tube could be more easily controlled and capture the vertical rising smoke, something found especially important for the bonfires.

3.3.4 Quantitative Analysis Methodology

In this section, a few parameters are introduced to quantitatively analyse the acquired data from both the laboratory and field experiments. These parameters include emission ratio (ER), emission factor (EF) and modified combustion efficiency (MCE).

3.3.4.1 Emission ratio (ER)

Emission ratio (ER) is usually defined as the slope of the best-fit line of the linear regression between the excess abundance of the trace gas compound $[x]$ to the excess abundance of reference compound $[y]$, represented by $ER_{x/y}$ (Yokelson et al., 1996). CO_2 is the dominant component in the released smoke during the flaming phase of a fire while CO is dominant during the smouldering phase (Andreae and Merlet, 2001), therefore, CO_2 is normally used as the reference compound during flaming and CO is used for smouldering. ER of species $[x]$ relative to CO_2 (ER_{x/CO_2}) is given by dividing the excess mixing ratio of $[x]$ above the ambient levels by the excess mixing ratio of CO_2 (M. Wooster et al., 2011; H. Zhang et al., 2008). The $ER_{\text{CO}/\text{CO}_2}$ is a common way to characterize the state of combustion in a plume (Fernandez-Gomez et al., 2011; Lobert et al., 1991), as CO_2 and CO emissions are mostly associated with flaming and smouldering phases of a fire (L.-W. Chen et al., 2010). The ERs calculated in the pure flaming and pure smouldering phases are represented by $\widehat{ER}_{x/\text{ref}}$ and $\widetilde{ER}_{x/\text{ref}}$, respectively. More importantly, ERs are widely used to derive the EFs of trace gases and particles (Piazzalunga et al., 2011; Reisen et al., 2018; M. Wooster et al., 2011). In addition, we compared $ER_{\text{CO}/\text{CO}_2}$ from burning same biomass in both laboratory and fieldwork to estimate the emission factors (EFs) of other trace gases and aerosol for the actual field burning.

3.3.4.2 Emission factor (EF)

Emission factor (EF) is normally defined as the mass of trace gases of species $[x]$ released from biomass of unit mass burnt, in a unit of $\text{g}\cdot\text{kg}^{-1}$, given by Equation

(3.1) (Andreae, 2019; Stockwell et al., 2014).

$$EF_x = 1000 \times \frac{\text{mass}_x}{\text{mass}_{\text{biomass}}}. \quad (3.1)$$

However, this equation can only be applied if the total mass of species $[x]$ and the total mass of straw burnt can be measured (Andreae and Merlet, 2001). A simplified way to calculate EF of species $[x]$ is from the ER using carbon mass balance method (Yokelson et al., 1999), which is derived under the assumption that the carbon content of the straw is released as measurable carbon-containing species during the combustion, expressed as:

$$EF_x = F_{\text{carbon}} \times 1000 \times \frac{MM_x}{12} \times \frac{C_x}{C_T}, \quad (3.2)$$

where F_{carbon} is the mass fraction of carbon content in the burned straw which was assigned by a value of 0.5, according to Akagi et al. (2011). MM_x is the molecular mass of species $[x]$ and MM_{carbon} is the atomic mass of carbon, which is 12. $\frac{C_x}{C_T}$ refers to the ratio of the number of moles of species $[x]$ (C_x) divided by the total number of moles of carbon emitted (C_T), which is equivalent to:

$$\frac{C_x}{C_T} = \frac{ER_{x/\text{ref}}}{\sum_{y=1}^Y NC_y \times ER_{y/\text{ref}}}. \quad (3.3)$$

according to (Guérette et al., 2018). NC_y is the number of carbon atoms in species $[y]$ and Y is the total number of carbon-containing species measured in the smoke, which mainly refer to CO_2 , CO and CH_4 as they comprise over 95% of the carbon compounds from biomass burning (Akagi et al., 2011; Yokelson et al., 1999). As a result, the calculation of EF becomes:

$$EF_x = F_{\text{carbon}} \times 1000 \times \frac{MM_x}{12} \times \frac{ER_{x/\text{ref}}}{\sum_{y=1}^Y NC_y \times ER_{y/\text{ref}}}. \quad (3.4)$$

The whole process of combustion was recorded and the different phases of combustion were distinguished to obtain an accurate estimate of the emission factors from the different phases, including integrated phases (which represented the entire burn

(e.g, T. Zhang et al. (2015)), pure flaming phases, and pure smouldering phases.

Similarly to ERs, we can also calculate the EF of species $[x]$ in the pure flaming and smouldering phases by Equations (3.5) and (3.6), denoted with \widehat{EF}_x and \widetilde{EF}_x , respectively.

$$\widehat{EF}_x = F_{\text{carbon}} \times 1000 \times \frac{MM_x}{12} \times \frac{\widehat{ER}_{x/\text{ref}}}{\sum_{y=1}^Y NC_y \times \widehat{ER}_{y/\text{ref}}}, \quad (3.5)$$

$$\widetilde{EF}_x = F_{\text{carbon}} \times 1000 \times \frac{MM_x}{12} \times \frac{\widetilde{ER}_{x/\text{ref}}}{\sum_{y=1}^Y NC_y \times \widetilde{ER}_{y/\text{ref}}}. \quad (3.6)$$

M. J. Wooster et al. (2018) derived the EFs of $\text{PM}_{2.5}$ based on the emission factor of CO and CO_2 , as shown in Equations (3.7) and (3.8):

$$EF_{\text{PM}_{2.5}/\text{CO}} = a \times ER_{\text{PM}_{2.5}/\text{CO}} \times EF_{\text{CO}}, \quad (3.7)$$

$$EF_{\text{PM}_{2.5}/\text{CO}_2} = b \times ER_{\text{PM}_{2.5}/\text{CO}_2} \times EF_{\text{CO}_2}, \quad (3.8)$$

where a and b are unit conversion factors which convert ppm to $\text{mg}\cdot\text{m}^{-3}$.

After obtaining the EF of species $[x]$ for all the sampling points, an averaged EF can be calculated by:

$$\overline{EF}_x = \frac{\sum_{n=1}^N EF_x[n]}{N}, \quad (3.9)$$

where N is the total number of data samples collected. However, due to the fact that the smoke components emitted from different combustion phases vary greatly, we propose a weighted averaged EF to reduce the biases, inspired by M. Wooster et al., 2011, given by:

$$\overline{\overline{EF}}_x = \frac{\sum_{n=1}^N EF_x[n] \times C_T[n]}{\sum_{n=1}^N C_T[n]}, \quad (3.10)$$

3.3.4.3 Modified Combustion Efficiency (MCE)

Modified combustion efficiency (MCE) is described as the ratio of released carbon in the form of carbon dioxide to the total carbon released from the fire (Ward et al.,

1992). It tells how efficient a combustion is and is calculated by:

$$MCE[n] = \frac{1}{1 + \frac{\Delta CO[n]}{\Delta CO_2[n]}}. \quad (3.11)$$

Similarly, a weighted averaged MCE can be calculated to reduce the biases, expressed as:

$$\overline{MCE} = \frac{\sum_{n=1}^N MCE[n] \times C_T[n]}{\sum_{n=1}^N C_T[n]}, \quad (3.12)$$

As MCE is based on the ratio between CO and CO₂, it can be used to characterize the flaming and smouldering phases of a fire. A flaming combustion is generally associated with MCE values greater than 0.9 to 1.0 while smouldering combustion has MCE values below 0.9 (Akagi et al., 2011; Reisen et al., 2018).

3.4 Results and Discussion

3.4.1 Laboratory Results

3.4.1.1 Trace Gases and Aerosol Concentration Measurements

Since two different measurement devices, LGR and Gaslab, were used to record the CO₂ and CO mixing ratios, we applied ordinary least squares (OLS) linear regression to find the relationship between the data recorded by them. Figure 3.3a shows the OLS linear best fit line based on mixing ratios of CO₂ collected from LGR and Gaslab, while Figure 3.3b shows the OLS linear best fit line based on mixing ratios of CO. The data shown in the figure was collected from burning 100 g soybean and millet straw in an ambient condition. It can be seen from Figure 3.3 that a slope of 0.95 best fitted the mixing ratios of CO₂ collected by the LGR and the Gaslab, and 1.40 was for CO. Applying these coefficients allows for the conversion of one data type to simulate the other.

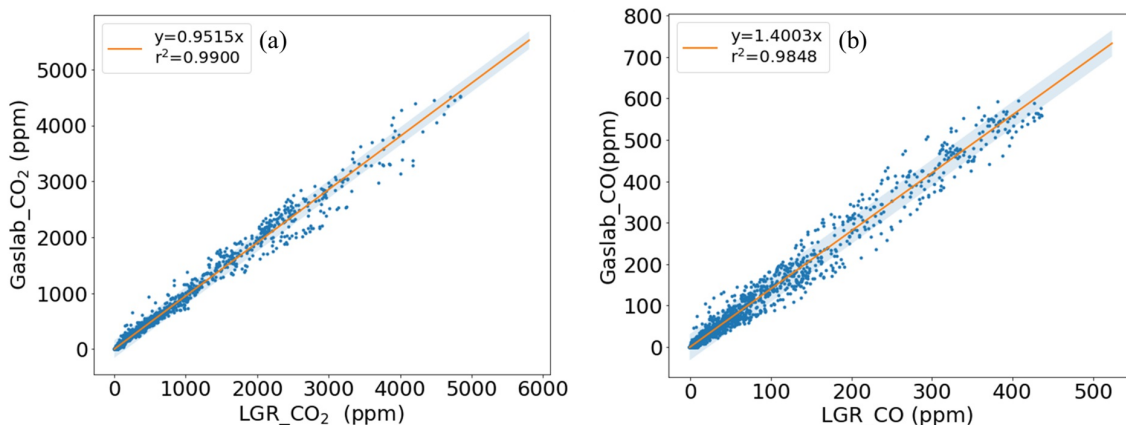


Figure 3.3: Ordinary least squares (OLS) linear regression showing the relationship between the smoke data collected from burning 100 g of soybean and millet straw in the ambient condition with LGR and Gaslab (a) mixing ratio of CO₂ and (b) mixing ratio of CO.

3.4.1.2 Modified Combustion Efficiency (MCE) and Emission Factor (EF)

3.4.1.2.1 Different types of biomass The MCEs and EFs of trace gases and PM_{2.5} emitted from different biomass in different combustion phases have been summarized in Table 3.2. The weighted average MCEs for different biomass burning were quite similar as they were all in completely dry conditions. Although the EFs of CO₂ in our study are not exactly same as those of published studies (X. Li et al., 2007; H. Zhang et al., 2008; T. Zhang et al., 2015), they are reasonable. For example, EFs of CO₂ for rice straw and wheat straw bonfires in completely dry conditions are 1636 g·kg⁻¹ and 1646 g·kg⁻¹, respectively. This is lower than the 1761 g·kg⁻¹ and 1739 g·kg⁻¹ reported in T. Zhang et al. (2015), but higher than the 791.3 g·kg⁻¹ and 1558 g·kg⁻¹ in H. Zhang et al. (2008) and 1194 g·kg⁻¹ and 1162 g·kg⁻¹ in Cao et al. (2008). The results from Table 3.2 obviously showed that EFs of CO₂ followed the order of millet straw > corn straw > soybean straw > wheat straw > rice straw with weighted averages calculated from three replicates. However, EFs of CO followed an opposite order of millet straw < corn straw < wheat straw < soybean straw < rice straw. These EFs of CO were higher than those reported straw burnings, such as 66.69 g·kg⁻¹ for wheat straw, 31.39 g·kg⁻¹ for rice straw, and 38.78 g·kg⁻¹ for corn straw reported in Cao et al. (2008) as well as 60 g·kg⁻¹ for wheat straw and 53 g·kg⁻¹

for corn straw reported in X. Li et al. (2007). Moreover, the EFs of CH₄ followed the order of wheat straw > rice straw > corn straw > millet straw > soybean straw. These EFs of CH₄ were in a reasonable range compared it to the published literature (X. Li et al., 2007; H. Zhang et al., 2008).

The EFs of PM_{2.5} with CO₂ as reference followed the order of wheat straw > rice straw > millet straw > corn straw > soybean straw. The EFs of PM_{2.5} with CO as reference had the same order with similar values. These values are comparable to the EFs reported in the literature (Sanchis et al., 2014; Y. Zhang et al., 2013), except that the EFs for wheat straw are much higher than the 6.1 g·kg⁻¹ reported in T. Zhang et al. (2015) and 7.6 g·kg⁻¹ reported in X. Li et al. (2007). As the EFs of PM_{2.5} from wheat straw is the highest compared with those from other straw types, it also proved that higher PM_{2.5} emissions were related to lower combustion efficiency (Dong et al., 2020).

In addition, EFs of CO₂ in the flaming combustion phases appear higher than those in the smouldering phases while EFs of CO and CH₄ are higher in smouldering phases, which is very much expected (e.g. Reisen et al. (2018)). This is due to more complete combustion of fuel carbon in the flaming phase, hence the increase in CO₂ and less CO, whereas in the smouldering phase, slightly less CO₂ and much more CO (M. Wooster et al., 2011). EFs of PM_{2.5} using either CO₂ or CO as reference in flaming phases are higher than those in smouldering phases, which represented more PM_{2.5} generated by the burning during smouldering phases.

3.4.1.2.2 Different combustion types The weighted average MCE and the EFs of CO₂, CO, CH₄, and PM_{2.5} from different combustion types have been plotted in Figure 3.4. The results show that the weighted average MCE calculated from spreading fires (0.92) is higher than that from bonfires (0.88). It also shows that burning the same mass of rice straw as spreading fires has higher EFs of CO₂ at $1681 \pm 18.53 \text{ g}\cdot\text{kg}^{-1}$, but lower EFs of CO, CH₄, PM_{2.5}/CO₂ and PM_{2.5}/CO at $91.54 \pm 11.18 \text{ g}\cdot\text{kg}^{-1}$, $3.34 \pm 0.37 \text{ g}\cdot\text{kg}^{-1}$, $9.73 \pm 2.28 \text{ g}\cdot\text{kg}^{-1}$, and $9.69 \pm 2.27 \text{ g}\cdot\text{kg}^{-1}$

Table 3.2: Weighted average modified combustion efficiency (MCE) for integrated phases and weighted average emission factor (EF) of trace gases and PM_{2.5} with standard deviations in different combustion phases, including integrated, pure flaming (FL), and pure smouldering (SM) phases, calculated from burning 100 g of different types of straw in completely dry conditions as bonfires.

Parameter	Smoke component	Combustion phase	Straw type				
			Rice	Wheat	Millet	Soybean	Corn
MCE		Integrated	0.92	0.90	0.94	0.94	0.93
EF	CO ₂	Integrated	1636 ± 33.26	1646 ± 18.99	1683 ± 69.14	1661 ± 34.26	1667 ± 28.13
		Pure FL	1789 ± 9.68	1794 ± 22.90	1803 ± 10.12	1776 ± 28.95	1776 ± 28.95
		Pure SM	1496 ± 13.37	1573 ± 35.59	1526 ± 8.71	1508 ± 22.93	1591 ± 18.76
CO	CO	Integrated	116 ± 17.27	104 ± 10.51	89.86 ± 40.85	105 ± 21.70	94.85 ± 17.97
		Pure FL	26.28 ± 5.51	22.46 ± 14.23	18.00 ± 5.89	18.41 ± 1.02	32.25 ± 16.20
		Pure SM	196 ± 4.99	147.15 ± 23.36	185 ± 3.53	205 ± 28.35	144 ± 15.12
CH ₄	CH ₄	Integrated	5.67 ± 2.25	8.89 ± 1.18	3.42 ± 1.95	3.00 ± 0.06	4.69 ± 1.16
		Pure FL	1.24 ± 0.38	1.48 ± 0.28	0.77 ± 0.32	0.58 ± 0.02	2.42 ± 1.30
		Pure SM	10.91 ± 2.07	10.87 ± 1.65	6.33 ± 2.21	4.82 ± 0.76	6.35 ± 2.93
PM _{2.5} /CO ₂	PM _{2.5} /CO ₂	Integrated	27.47 ± 7.66	37.94 ± 8.19	9.59 ± 1.12	3.07 ± 0.44	9.18 ± 1.75
		Pure FL	11.41 ± 8.53	19.70 ± 1.68	3.03 ± 0.19	2.13 ± 0.69	5.76 ± 2.03
		Pure SM	30.29 ± 7.42	60.86 ± 3.80	10.28 ± 1.12	3.68 ± 0.50	10.11 ± 1.19
PM _{2.5} /CO	PM _{2.5} /CO	Integrated	27.29 ± 7.75	37.80 ± 8.16	9.53 ± 1.11	3.08 ± 0.45	9.15 ± 1.74
		Pure FL	11.36 ± 8.50	19.62 ± 1.68	3.02 ± 0.19	2.12 ± 0.69	5.74 ± 2.02
		Pure SM	30.18 ± 7.39	60.63 ± 3.79	10.25 ± 1.14	3.66 ± 0.50	10.07 ± 1.19

respectively. The potential reason is that more biomass was burnt in the flaming combustion phases as a spreading fire (M. Wooster et al., 2011; T. Zhang et al., 2015). For the same mass of rice straw, burning as spreading fire leads to a larger area of fuel in contact with the air, so that the straw burnt more completely with higher MCE. When the rice straw was burnt in a bonfire, the combustion on the surface is flaming - but the combustion of the straw underneath is more smouldering.

3.4.1.2.3 Different moisture contents To investigate the impact of moisture contents of biomass on EFs, the weighted average MCEs and the weighted average EFs of CO₂, CO, CH₄, and PM_{2.5} with standard deviation, calculated from burning 100 g of wheat straw as bonfires with 0%, 5%, 10%, 15% and 20% moisture contents, have been plotted in Figure 3.5. It clearly shows that MCE decreased from 0.91 to 0.87 as moisture content increased, supporting the finding that the moisture content of biomass affects combustion efficiency (Possell and Bell, 2012; Tihay-Felicelli et al., 2017). This is mainly due to the amount of smouldering combustion increasing, leading to a lower MCE as moisture content increased (Possell and Bell, 2012).

The EFs of CO₂ generally showed a decreasing trend from $1646 \pm 18.99 \text{ g}\cdot\text{kg}^{-1}$ to $1568 \pm 11.21 \text{ g}\cdot\text{kg}^{-1}$ as the moisture content increased from 0% to 20%. A least-squares linear trend line was applied to the EFs of CO₂, showing a negative relationship between EFs of CO₂ and moisture contents, with the correlation coefficient $R = -0.937$. However, the EFs of CO and CH₄ generally showed upward trends, from $104 \pm 10.51 \text{ g}\cdot\text{kg}^{-1}$ to $150 \pm 5.90 \text{ g}\cdot\text{kg}^{-1}$ and $8.89 \pm 1.18 \text{ g}\cdot\text{kg}^{-1}$ to $11.25 \pm 0.74 \text{ g}\cdot\text{kg}^{-1}$ respectively with increasing moisture contents. The linear fittings showed clear positive relationships between EFs of CO and moisture content, as well as the EFs of CH₄ and moisture content, with correlation coefficients $R = 0.936$ and $R = 0.915$ respectively. Moreover, the EFs of PM_{2.5}/CO₂ increased significantly from $37.91 \pm 8.13 \text{ g}\cdot\text{kg}^{-1}$ to $177 \pm 15.88 \text{ g}\cdot\text{kg}^{-1}$ and the EFs of PM_{2.5}/CO increased from $37.76 \pm 8.10 \text{ g}\cdot\text{kg}^{-1}$ to $177 \pm 15.82 \text{ g}\cdot\text{kg}^{-1}$ as moisture content of wheat straw increased from 0% to 20%. These results align with those in the literature (Fachinger et al., 2017; Magnone et al., 2016; Price-Allison et al., 2019; Price-Allison et al.,

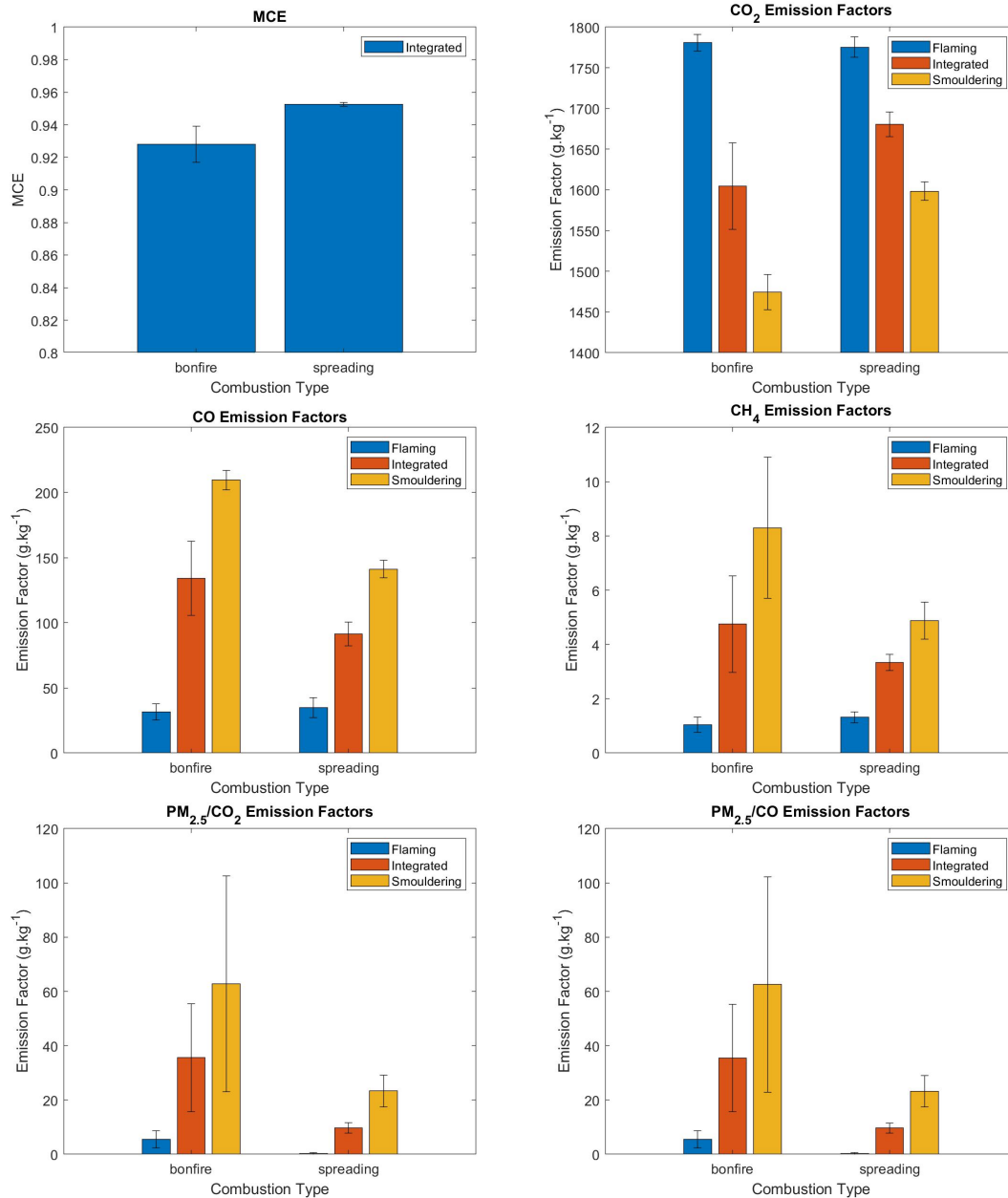


Figure 3.4: Weighted average MCE for integrated phases and weighted average EFs of trace gases and PM_{2.5} (g·kg⁻¹) with standard deviations in different combustion phases, including integrated, flaming (FL), and smouldering (SM) phases, calculated from burning 100 g of rice straw in ambient condition (with 10% moisture content) with different combustion types for three replicates.

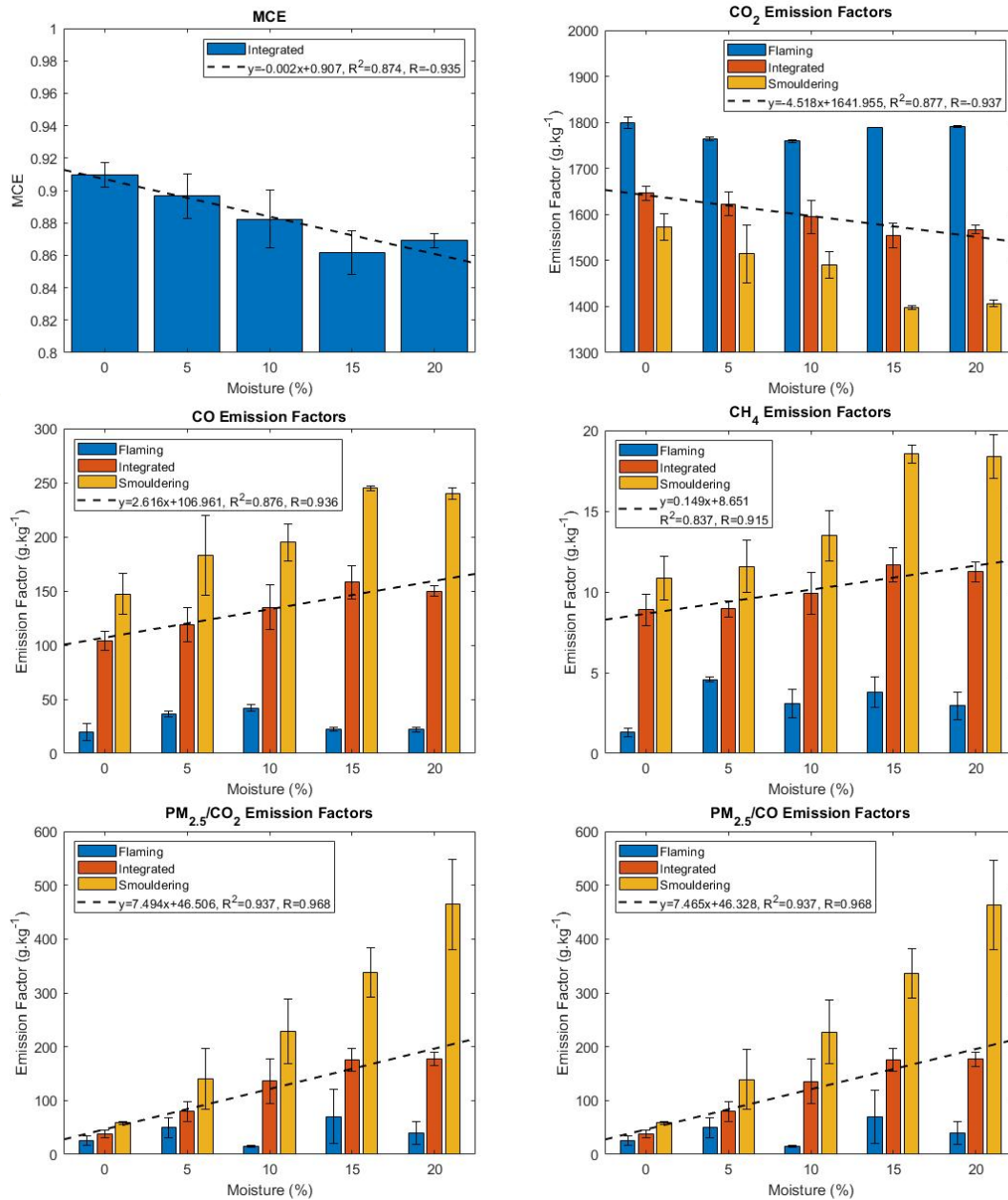


Figure 3.5: Weighted average MCE for integrated phases and weighted average EFs of trace gases and PM_{2.5} (g·kg⁻¹) with standard deviations in different combustion phases, including integrated, flaming (FL), and smouldering (SM) phases, calculated from burning 100 g of rice straw with different moisture contents. A least-squares linear trend line based on the results from integrated combustion is shown in each subplot, along with the coefficient of variation (R^2) and correlation coefficient (R).

2021; Sanchis et al., 2014) that higher moisture contents generally result in higher PM emission factors from biomass burning. The linear fitting showed a significantly positive relationship between EFs PM_{2.5} and moisture content. Moreover, the EFs of PM_{2.5} were higher in smouldering phases than those in flaming phases, which are same as the finding in Reisen et al. (2018) from forest fires. These results above showed that the EFs of trace gases are greatly impacted by the moisture content of the biomass, consistent with published studies (Price-Allison et al., 2021; Rau, 1989).

3.4.1.2.4 Different packing densities Finally, 100 g, 150 g, and 200 g of rice straws were burned as spreading fires with the same packing volume, resulting in three packing densities of 0.008 g·cm⁻³ as low density (LD), 0.012 g·cm⁻³ as medium density (MD), and 0.016 g·cm⁻³ as high density (HD). The resulting MCEs and the EFs of trace gases and PM_{2.5} with different packing densities have been plotted in Figure 3.6. It demonstrated that MCE has a negative relationship with fuel packing density, with a correlation coefficient $R = -1.00$. Moreover, the EFs of CO₂ for integrated burning decreased with increasing packing densities. They were mainly impacted by the smouldering phases as the EFs of CO₂ were decreased in the smouldering phases while there is no obvious change in the flaming phases. Furthermore, least-squares linear trend lines indicated that the EFs of CO, CH₄, and PM_{2.5} increased as packing density increased. The increases in the EFs of CO, CH₄, and PM_{2.5} were caused by the increase in the amount of smouldering combustion as packing densities increased.

3.4.2 Emission Factor Estimation from Field Data

Since the Gaslab was used in both the laboratory and the *in situ* experiments to record the mixing ratios of CO₂ and CO, these data can be used to compare the laboratory burning and the field fires. The ER_{CO/CO_2} derived from actual field measurements of burning rice straw was compared to those derived from the measurements in the laboratory. The ER_{CO/CO_2} of the field measurements is very close that of the burning 100 g of rice in ambient conditions as bonfires in the laboratory

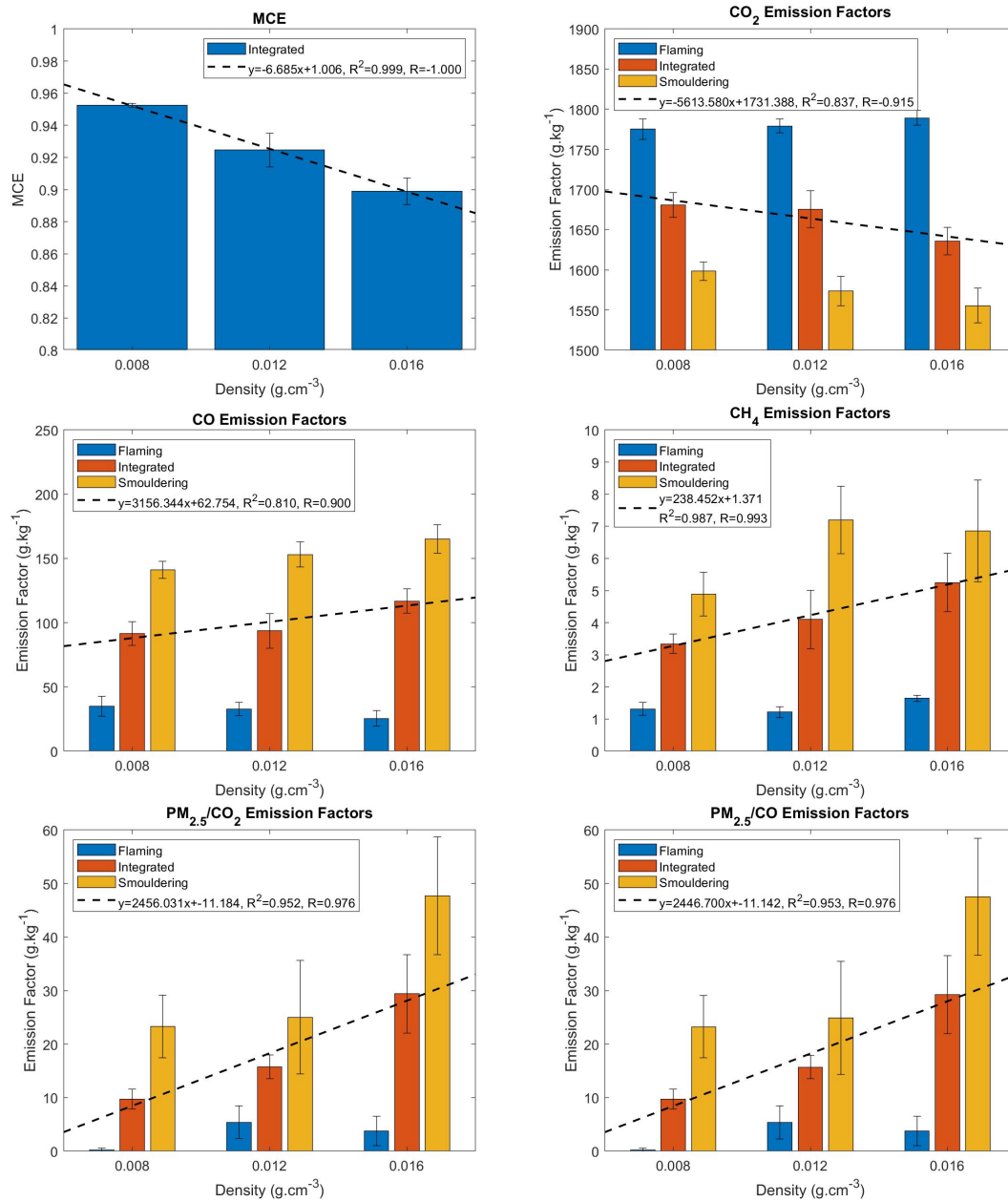


Figure 3.6: Weighted average MCE for integrated phases and weighted average EFs of trace gases and PM_{2.5} (g·kg⁻¹) with standard deviations in different combustion phases, including integrated, flaming (FL), and smouldering (SM) phases, calculated from burning rice straw with different packing densities, including low, medium and high density (LD, MD and HD). A least-squares linear trend line based on the results from integrated combustion is shown in each subplot, along with the coefficient of variation (R^2) and correlation coefficient (R).

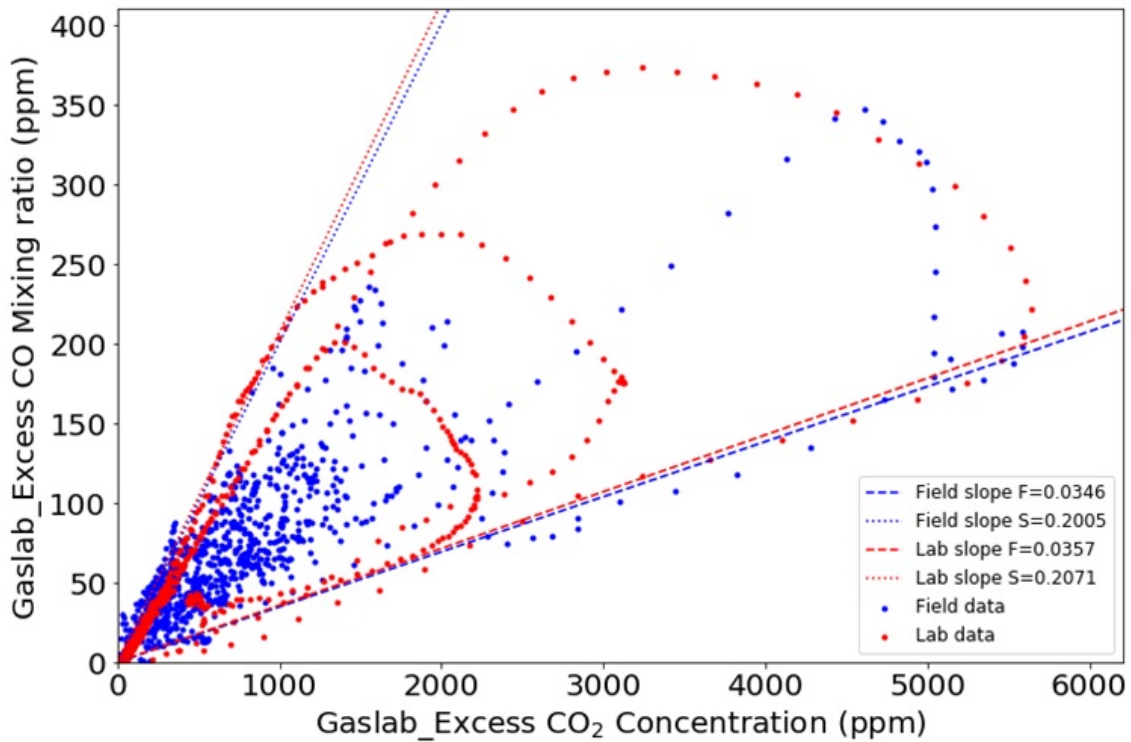


Figure 3.7: Measured mixing ratios of CO and CO₂ from rice straw burning in the actual agricultural land (blue dots) and from the burning 100 g of rice in the ambient condition as bonfires in the laboratory (red dots). ERs between CO and CO₂ for pure flaming and smouldering phases of the two combustions are presented by blue and red lines, respectively.

(see Figure 3.7). It shows that the blue slopes representing the ER_{CO/CO_2} in flaming and smouldering combustion phases from the field measurements - are very close to the red slopes representing the ER_{CO/CO_2} from the laboratory. This suggests that two combustions were very similar and their EFs should also be similar (Reisen et al., 2018; M. J. Wooster et al., 2018; M. Wooster et al., 2011). To precisely estimate the EFs of trace gases and aerosol from *in situ* experiment, the integrated MCE from the field was compared to that from the laboratory work. According to the linear relationship fitted between MCE and EFs of all data samples from rice straw burning in the laboratory (Figure 3.8), the EFs of CO₂, CO, CH₄, PM_{2.5}/CO₂ and PM_{2.5}/CO from rice straw burning in the field are estimated as 1607 g·kg⁻¹, 133.32 g·kg⁻¹, 6.38 g·kg⁻¹, 42.53 g·kg⁻¹, and 42.53 g·kg⁻¹ as MCE of the field fires was 0.89.

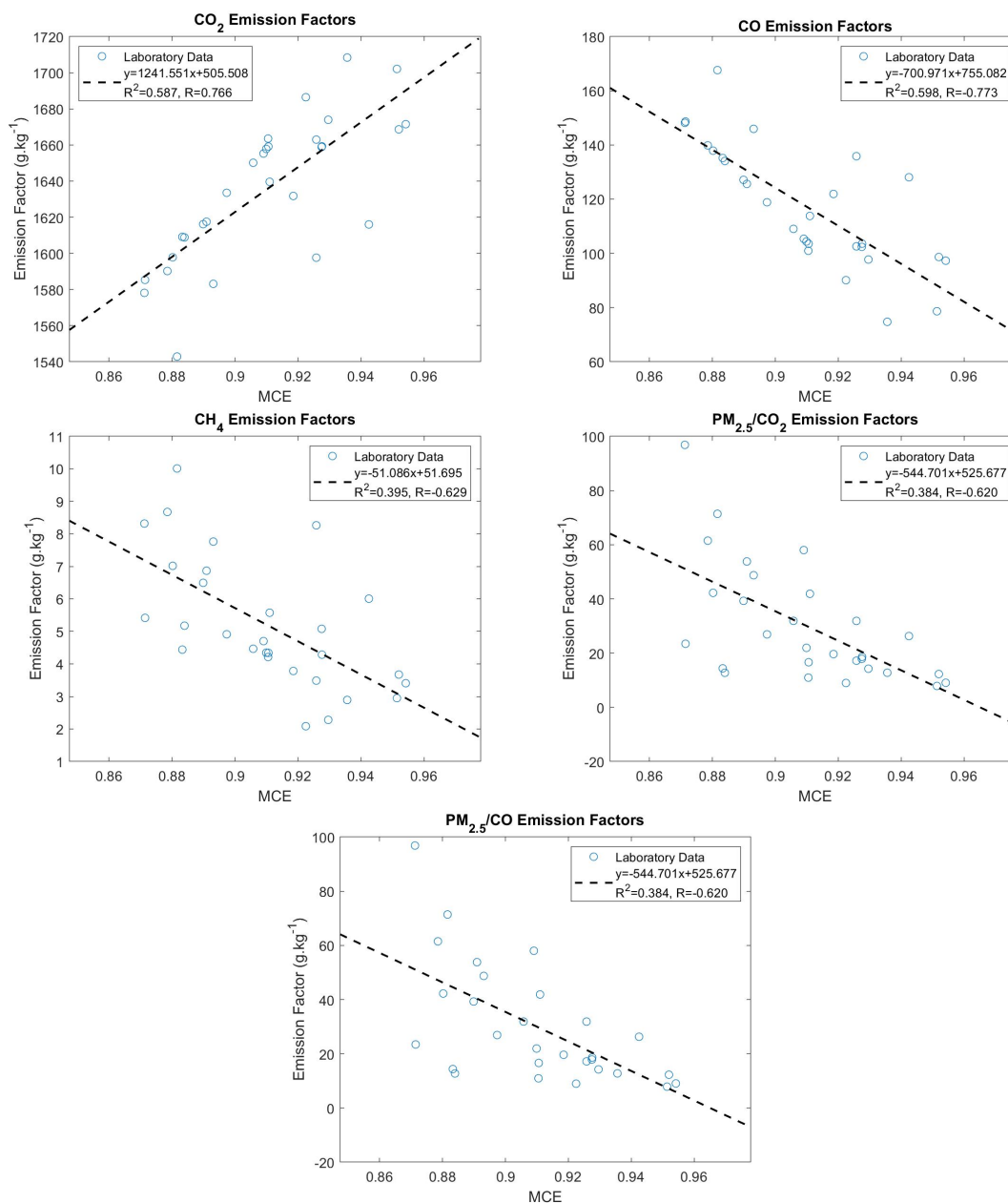


Figure 3.8: Scatterplots of weighted average EFs of trace gases ($\text{g}\cdot\text{kg}^{-1}$) and MCE of all rice straw burning in the laboratory. Dashed line in each subplot represents the OLS best-fitting to the data, whose equation is shown along with the coefficient of variation (R^2) and correlation coefficient (R).

Table 3.3: PM_{2.5} concentration statistics of the two different smoke treatments created in the combustion chamber. Ignition of the straw occurred at time T₁. Total time-integrated PM_{2.5} concentration and mean PM_{2.5} concentration are given, both for the period from T₁ up to 10 minutes after straw ignition (T₁ + 10 minutes) and also up to 20 minutes after ignition (T₁ + 20 minutes).

Smoke Treatment	Replicates	(T ₁ + 10 minutes)		(T ₁ + 20 minutes)	
		Integrated total (mg·m ⁻³ ·s)	Mean (mg·m ⁻³)	Integrated total (mg·m ⁻³ ·s)	Mean (mg·m ⁻³)
30 g wheat straw	3	5665	11	10227	9
60 g wheat straw	3	33438	64	63560	57

3.5 Incense Stick Burning

In order to explore the effects of smoke on migratory insects, we now need to consider a suitable source that can create a smoky environment similar to that of agricultural residue burning. However, directly burning agricultural residues in the laboratory is not a good choice. One of the reasons is that the combustion of agricultural straw ends too quickly to create a stable smoky environment. For example, two smoke treatments were generated by burning 30g and 60g of wheat straw, with three replicates per treatment (Table 3.3). The temporal variation of PM_{2.5} concentration recorded from the two treatments is shown in Figure 3.9. The PM_{2.5} concentration raised rapidly, reaching the maximum about two minutes after igniting. After that, it gradually reduced within 20 minutes, especially in the case of burning 60g of wheat straw. More importantly, burning agricultural residues in the laboratory could create too high PM_{2.5} concentration, which is different from that recorded in real agricultural burning where the maximum PM_{2.5} concentration recorded was only about 1.5 mg·m⁻³ by R. Jiang and Bell (2008). This is because the space of the combustion chamber is limited and there is no natural air flow like in the open scenario, which allows the smoke to disperse. Therefore, we cannot use agricultural straw burning in the actual experiment.

The unscented incense sticks were considered as an alternative fuel to generate different smoke conditions as the literature suggested that they are made of biomass

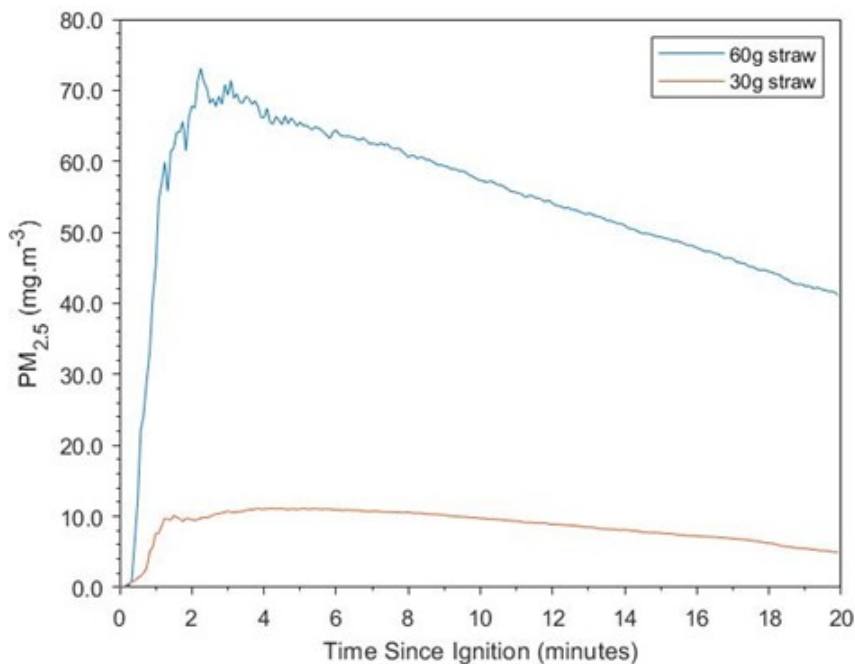


Figure 3.9: Mean atmospheric PM_{2.5} concentration timeseries calculated from the three replicates performed for each of the two different experimental smoke treatments made by 30 g and 60 g wheat straw in ambient conditions. Data are shown from the time of straw ignition (T_1) to $T_1 + 20$ minutes. See Table 3.3 for the total time-integrated and mean PM_{2.5} concentrations for each treatment recorded over the same time periods.

and release similar smoke emissions (Jetter et al., 2002; S.-C. Lee and Wang, 2004). More importantly, they can create a relatively stable smoky environment, which is easier to use in further experiments. Before using them, we need to validate that the smoke emissions from burning incense sticks are similar to those of real agricultural residue burning. The mixing ratios of CO₂, CO, CH₄ and PM_{2.5} concentration emitted from different numbers of incense sticks were measured. The incense sticks were placed on the burning tray, as indicated in Figure 3.10, and a tube was placed on top of the incense stick, connected with Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyser and TSI Dusttrak II Aerosol monitor 8530.

Figure 3.11 shows the ER between CO and CO₂ from incense stick burning, which indicates a constant combustion phase given the linear nature of the relationship. The EFs of trace gases and PM_{2.5} from burning different numbers of incense stick have been summarised in Table 3.4. The EFs of CO₂, CO and CH₄ from our



Figure 3.10: Measurement of burning one incense stick on the burning tray.

experiment are aligned with the EFs reported in the literature (S.-C. Lee and Wang, 2004). They showed that the EFs of CO_2 varied between $4.7 \text{ g}\cdot\text{kg}^{-1}$ and $2251.7 \text{ g}\cdot\text{kg}^{-1}$, EFs of CO changed between $110 \text{ g}\cdot\text{kg}^{-1}$ and $461 \text{ g}\cdot\text{kg}^{-1}$, and EFs of CH_4 were from $1.8 \text{ g}\cdot\text{kg}^{-1}$ to $28.3 \text{ g}\cdot\text{kg}^{-1}$ from traditional incense burning (S.-C. Lee and Wang, 2004). However, these EFs of trace gases from our incense stick burning experiment are similar to the EFs of trace gases for the smouldering phase of burning 100 g of wheat straw with 20% moisture contents as bonfire, which are $1396 \pm 15.96 \text{ g}\cdot\text{kg}^{-1}$ for CO_2 , $245 \pm 11.28 \text{ g}\cdot\text{kg}^{-1}$ for CO and $19.28 \pm 0.75 \text{ g}\cdot\text{kg}^{-1}$ for CH_4 .

For the EFs of $\text{PM}_{2.5}$ from incense sticks burning, they were reasonably similar to those reported in Jetter et al. (2002) but were lower than those from aromatic incense sticks, varied from $10 \text{ g}\cdot\text{kg}^{-1}$ to $85 \text{ g}\cdot\text{kg}^{-1}$ (S.-C. Lee and Wang, 2004) and ‘Chih-Chen’, varied from $19 \text{ g}\cdot\text{kg}^{-1}$ to $45 \text{ g}\cdot\text{kg}^{-1}$ (Lung and Hu, 2003). However, compared with straw burning, EFs of $\text{PM}_{2.5}$ from incense sticks burning are slightly

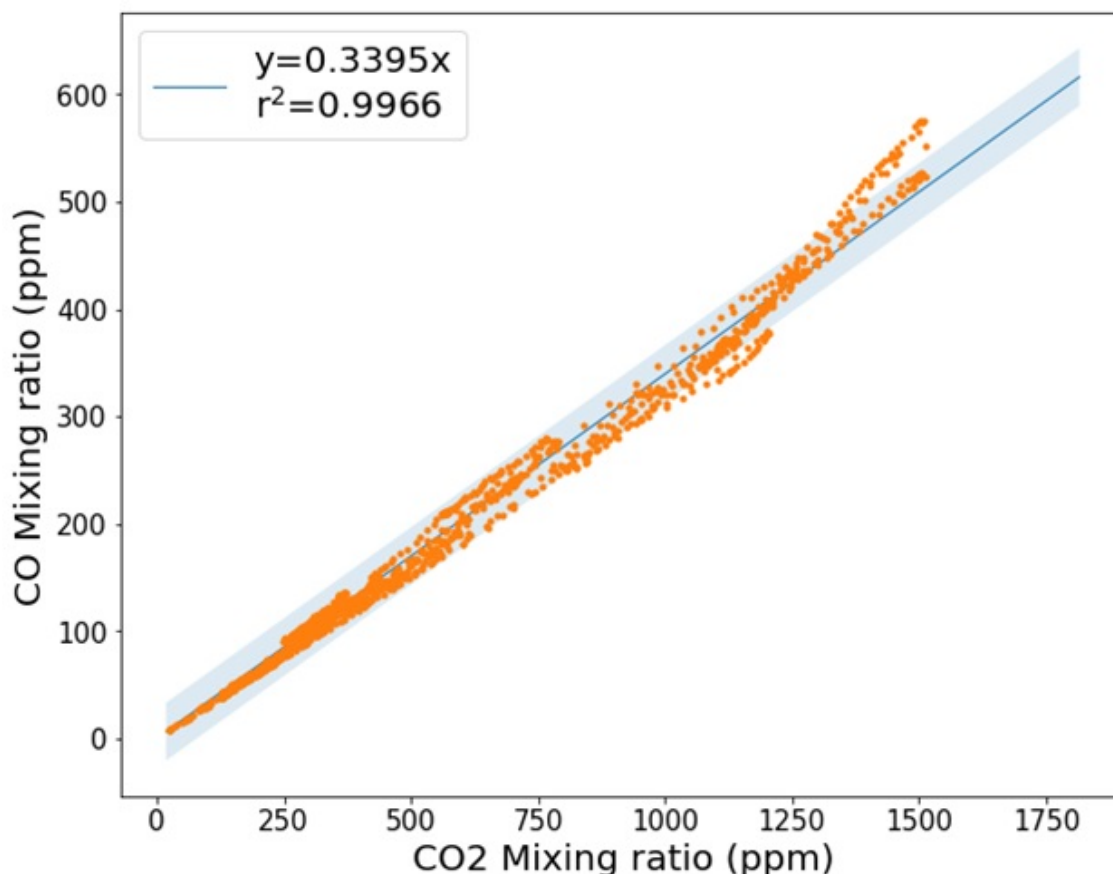


Figure 3.11: Measured mixing ratios of CO and CO₂ from incense stick burning are plotted in orange spots. The slope of the least squares linear best fit to these data (blue dashed line) along with 95% confidence interval (blue shaded area) is used to derive the ER_{CO/CO_2} .

lower to those from smouldering phases of burning 100 g of millet straw as bonfire in completely dry conditions, which are $1.19 \pm 1.08 \text{ g}\cdot\text{kg}^{-1}$ with CO₂ as reference and $1.18 \pm 1.07 \text{ g}\cdot\text{kg}^{-1}$ with CO as reference. This proved that incense sticks have similar EFs of trace gases and PM_{2.5} as biomass burning in the real world and therefore using incense sticks to simulate the environment of biomass burning is feasible and meaningful.

3.6 Summary

This chapter reports the EFs of CO₂, CO, CH₄, and PM_{2.5} calculated for integrated burning, flaming phase and smouldering phase of burning five different agricultural residues, including rice, wheat, soybean, millet, and corn straw. These are based on

Table 3.4: Weighted average MCE and weighted average EFs of trace gases and PM_{2.5} (g·kg⁻¹) from burning different numbers of incense sticks.

Parameter	Smoke component	Incense stick		
		No. = 1	No. = 2	No. = 3
MCE		0.76	0.78	0.77
EF	CO ₂	1354	1404	1379
	CO	271	248	257
	CH ₄	19.52	14.55	18.75
	PM _{2.5} /CO ₂	1.19	1.28	7.55
	PM _{2.5} /CO	1.19	1.28	10.93

measurements made on laboratory fires. Among the five types of straw, millet straw has the highest EFs of CO₂ at 1683 g·kg⁻¹, while the lowest CO at 89.86 g·kg⁻¹ and CH₄ at 3.42 g·kg⁻¹; and soybean straw has the lowest EFs of PM_{2.5}/CO₂ and PM_{2.5}/CO at 3.07 g·kg⁻¹, and 3.49 g·kg⁻¹ respectively. The EFs of CO₂ for all types of straw burning were higher in the flaming phases than those in the smouldering phases, while the EFs CO and CH₄ showed the opposite trend. The EFs of PM_{2.5} from burning all types of straw were dominated by the flaming phases except the wheat straw.

In addition, the impacts of potential factors on EFs of trace gases and particles for integrated burning, flaming, and smouldering phases have been studied, including moisture content, combustion type, and packing density. As moisture content increases, the EF of CO₂ decreases whilst those of CO, CH₄, and PM_{2.5} increase. In particular, there is a negative relationship between MCE and moisture content. In terms of two combustion types, EFs of CO₂ have higher values for the spreading fire compared with bonfire fire, while EFs of other trace gases and PM_{2.5} have lower values. According to the results of EFs from burning rice straw with three different packing densities, we found that the EFs of CO₂ decreased while EFs of CO and PM_{2.5} increased as packing density increased.

We have applied a method to estimate the emission factors of trace gases (CO₂, CO,

CH₄) and PM_{2.5} from actual agricultural fires by comparing the ER_{CO/CO_2} obtained from both laboratory work and fieldwork. When the ER_{CO/CO_2} have been collected from the fieldwork are very close to those collected in the laboratory work, we can reasonably predict the emissions factors of other gases as the EFs of trace gases and particulates based on the precise measurements in the laboratory work. Finally, the EFs of trace gases and PM_{2.5} from burning incense sticks were investigated and found close to those from agricultural residue burning, validating that they are good smoke-source for further experiments.

Chapter 4

Impact of dense smoke conditions on butterfly flight performance

4.1 Introduction

As described in Chapter 2, although there is substantial evidence showing that smoke pollution from landscape fires impacts insects, the impact of smoke pollution on insect migration has rarely been known. Therefore, this chapter focuses on determining whether dense smoke pollution from landscape fires affects migratory insects. To achieve this objective, we identified a suitable migratory insect species as a research target and conducted a series of experiments to quantitatively study the insect response to smoke conditions created by burning appropriate biomass.

This chapter comprises a published paper in Section 4.2, describing the first measurement of smoke pollution from biomass burning on the flight behaviour of insects (Y. Liu et al., 2021). *Vanessa cardui* L. (Painted lady butterfly) was chosen as the research target, and a tethered flight mill system was used to quantify the flight performance of individual insects exposed to different smoke conditions generated by burning incense sticks. Section 4.3 describes the reason for the selection of *Vanessa*

cardui (Painted lady butterfly). Section 4.4 provides more details about the TFM and flight performance accuracy tests. Section 4.5 provides more details on preliminary experiments undertaken to understand the smoke condition produced in the combustion chamber. The study in this chapter explored how the flight behaviour of butterflies (including total flight distance, flight speed and flight duration) was affected by exposure to different smoke conditions. Therefore, it also provided some of the first evidence of how smoke from fires might potentially impact insect migration.

The author of this PhD thesis is the first author of this paper and undertook the whole experiment, with advice from M. Wooster and K. Lim on protocols and experimental design. K. Lim was involved in designing the tethered flight mill systems. The author of this PhD conducted all the data processing and analyses presented in the manuscript. M. Wooster, M. Grosvenor, K. Lim and R. Francis provided advice on data analyses. The author drafted the first version of the paper and updated the versions of the paper with the co-authors' editorial suggestions.

4.2 Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)



Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)

YANAN LIU,^{1,2} MARTIN J. WOOSTER,^{1,2,3,4} MARK J. GROSVENOR,^{1,2,3,4} KAS. LIM² and ROBERT A. FRANCIS¹

¹Department of Geography, King's College London, London, UK, ²Rothamsted Research, Harpenden, UK, ³Leverhulme Centre for Wildfires, Environment and Society, King's College London, London, UK and ⁴NERC National Centre for Earth Observation, King's College London, London, UK

Abstract. 1. A major component of biomass burning smoke is fine particulate matter (PM_{2.5}), which has been shown to generate impacts on insect population dynamics and development. However, little is known about its effect on insect flight behaviour, even though this will influence insect dispersal and distribution, and potentially migration and ecosystem services such as pollination.

2. Here we use a tethered flight mill setup to examine the behaviour of adult painted lady butterflies (*Vanessa cardui* L.) flying in different levels of combustion-generated airborne PM_{2.5}, comparison this to TFM flying under 'clean air' conditions.

3. Descriptive statistics and paired sample *t*-tests indicate that the smoke had a significantly deleterious impact on flight behaviour, with for example total flight distance covered declining by 65% during the first 20 min of flying in the least smoke contaminated air compared to 'clean air' control conditions, whilst average speed declined by 54% and flight duration by 32%. A strongly negative and highly significant linear correlation between flight speed and PM_{2.5} concentration was also observed.

4. This study represents the first time that smoke effects on insect flight behaviour have been experimentally tested, and the longer the butterflies were exposed to the elevated PM_{2.5} concentrations the more obviously their flight behaviour declined. We conclude that the month(s)-long episodes of air pollution often associated with agricultural burning and deforestation fires in the tropics may well be significantly affecting the behaviour of the flying insects living in those regions and/or who migrate through them.

Key words. smoke pollution, fires, *Vanessa cardui* L., flight behaviour, tethered flight mill, insect.

Introduction

Landscape fires burn across millions of square km of Earth's landscapes annually (Giglio *et al.*, 2010), and human-driven fires associated with land clearance and agricultural management are particularly prevalent as a seasonal occurrence across many developing nations of Asia, Africa, and Latin America (Korontzi *et al.*, 2006; Yadav & Devi, 2018). Agricultural residue burning is a seasonal practice in many of these nations

for example, burning wheat stubble, rice straw, and other vegetative waste before and/or after harvest (Scholes *et al.*, 1996; Streets *et al.*, 2003; Toledo *et al.*, 2005; Gadde *et al.*, 2009; Mahmud, 2013; Jain *et al.*, 2014; Zhang *et al.*, 2016). Though each of these residue fires maybe individually small (Randerson *et al.*, 2012; Zhang *et al.*, 2017), the very large numbers of fires burning simultaneously can seriously degrade local and regional air quality (Li *et al.*, 2014; Liu *et al.*, 2020) by releasing a complex mixture of gases and aerosols (Li *et al.*, 2007; Gadde *et al.*, 2009; Shi *et al.*, 2014; Zhang *et al.*, 2015). At these times, atmospheric concentrations of fine particulate matter (PM_{2.5}) can sometimes exceed 1 mg m⁻³ in heavily affected areas of China for example (Zhang *et al.*, 2017), and elsewhere in

Correspondence: Martin J. Wooster, Department of Geography, King's College London, Bush House, 30 Aldwych, London, WC2B 4BG, UK. E-mail: martin.wooster@kcl.ac.uk

© 2020 The Authors. *Ecological Entomology* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society

195

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Asia extremes even exceeding 3 mg m^{-3} have been seen during very large fire events associated with large scale land clearance and drought (Wooster *et al.*, 2018). In addition to the significant effects on human health – particularly from the fine particulate matter (Johnston, 2017) – animals are very likely also affected by this air pollution. This includes insects, which have important ecological functions, facilitating plant pollination (Chapman *et al.*, 2010; Ollerton, 2017), seed dispersal (Willson & Traveset, 2000), and soil ventilation (Wardlaw *et al.*, 1998), for example, as well as roles in maintaining important trophic relationships (Belovsky & Slade, 2000). However, whilst a few studies have explored the impact of smoke pollution on insect development (Tan *et al.*, 2018; Wang *et al.*, 2017), there have been no quantitative studies of how it might affect insect flight behaviour. In this context we have designed and performed a series of laboratory experiments to investigate this issue for the first time, focusing on *Vanessa cardui*, the painted lady butterfly, which is an important indicator species because of their sensitivity to ecosystem conditions (Griffis *et al.*, 2001).

The smoke released from agricultural residue fires and other types of landscape burning includes trace gases such as CO_2 , CO , NH_3 , CH_4 , SO_2 , NO_x (Radojevic, 2003; Ding *et al.*, 2013; Zhang *et al.*, 2015), but it is the fine $\text{PM}_{2.5}$ particles of black carbon (BC) and organic carbon (OC) that pose the most serious risk to air quality (Li *et al.*, 2007; Cao *et al.*, 2008; Zhang *et al.*, 2017). Such fine particles dominate the aerosols present in vegetation fire smoke (Dennis *et al.*, 2002; Zhang *et al.*, 2016; Ni *et al.*, 2017), and when emitted in large quantities by very large and/or long-lived fires (Wooster *et al.*, 2018) or by huge numbers of smaller burns (Zhang *et al.*, 2017), they can dramatically increase the extent and severity of regional haze and smog episodes (Othman *et al.*, 2014; Koplitz *et al.*, 2016; Chen *et al.*, 2017). In humans these fine particles can enter the respiratory system in sufficient numbers to cause serious morbidity and even mortality (Chen & Kan, 2008; Li *et al.*, 2013; Koplitz *et al.*, 2016), with consequential economic impacts on healthcare (Othman *et al.*, 2014) and tourism (Anaman & Looi, 2000). However, few studies have examined the consequences of such pollution for other animal species. A few have indicated effects on insect development and thus population dynamics (Ginevan & Lane, 1978; Alstad *et al.*, 1982; Führer, 1985), including for example impairing the development of insect larvae, such as was shown by Tan *et al.*'s (2018) observations of smoke haze prolonging development time and decreasing pupal weight of *Bicyclus anynana* (squinting bush brown butterfly). Even the smoke caused the decline of five butterfly species (Lepidoptera: Rhopalocera) in Epping forest (Corke, 1999). However, the impact of smoke on insect flight behaviour has rarely been considered, despite flight performance largely determining dispersal capacity, which then profoundly influences metapopulation dynamics and ultimately population viability, species persistence, gene flow, and processes of natural selection (Bowler & Benton, 2005; Lester *et al.*, 2007; Berg *et al.*, 2010; Dantharayanan, 1986). Certain of the seasonal biomass burning patterns in Asia (Vadrevu *et al.*, 1986) coincide with the period in which many insects start to migrate (Huang *et al.*, 2012; Jones *et al.*, 2016; Fang *et al.*, 2019), and this is likely to be the case in other continents as well. Increasing our understanding of

insect flight performance in smoke-contaminated air may ultimately help elucidate whether the air pollution associated with these fires might affect insect migration, and all the consequent impacts that stem from any such effect.

Butterflies are a predominant insect group present in agricultural lands and are known to be sensitive to environmental changes (Hill *et al.*, 1995; Cleary & Grill, 2004). Cleary & Grill (2004) showed that the richness of *Jamides celeno* (Common cerulean) has increased over 50% in response to El Niño Southern Oscillation induced fires events as an example and in Indonesia, where vegetation fire smoke contaminated air is an annual occurrence (Wooster *et al.*, 2018), the richness and biodiversity of butterflies are linked to human activities such as forest logging and fires, presumably by directly destroying their habitat (Hill *et al.*, 1995; Cleary & Grill, 2004). The butterflies used herein, therefore, represent a good organism with which to start to explore the impact of smoke pollution on flying insects.

Materials and methods

Study species

Adult (imago) *V. cardui* were chosen as the experimental subject for this work. *V. cardui* has a wide global distribution and is found in temperate areas and tropical areas across all continents apart from South America and Antarctica (Ecuador, 1992; Stefanescu *et al.*, 2017; Talavera & Vila, 2017). *V. cardui* generally maintains a large population through multi successive generations every year (Stefanescu *et al.*, 2013; Talavera & Vila, 2017). *V. cardui* have excellent flight capacities, reflected in their annual mass migration between Africa and Europe (Talavera *et al.*, 2018; Menchetti *et al.*, 2019; Suchan *et al.*, 2019). Normally, they migrate from Europe to the Afrotropics in autumn and also evidence proved that they had a reverse northwards trans-Saharan migration in Spring (Talavera & Vila, 2017; Talavera *et al.*, 2018). Adults arriving in Britain in May and June are thought to arrive directly from North Africa (Asher *et al.*, 2001; Nesbit *et al.*, 2009). Massive breeding starts immediately after the arrival of migrants. The offspring appear in the UK in the late summer, such that the population greatly increases at this time (Stefanescu *et al.*, 2013, 2016). The flight capacities of *V. cardui* depend in part on wing power, with wing size being considered a significant factor on flight performance (Rayner, 1979; Elington, 1984; Steyn *et al.*, 2016). The wingspan of the male is normally 58–70 mm, and that of the female 62–74 mm (Ukbutterflies.co.uk, 2020). Adult *V. cardui* live for 3–4 weeks, often up to 5 (Talavera & Vila, 2017; Stefanescu *et al.*, 2020), providing enough time for experimental treatments such as those detailed here to be completed while the butterflies are in robust health.

To standardise the flight ability of the selected *V. cardui* subjects as far as possible in the current study, individual differences in *V. cardui* individuals such as age, wingspan, and body size were minimised by obtaining 20 butterfly pupae of the same age from *Gribblybugs LLP*, a UK entomological supplier. Pupae were placed in a greenhouse and adults of mixed sexes emerged from the pupae over a one-week period

4.2. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)

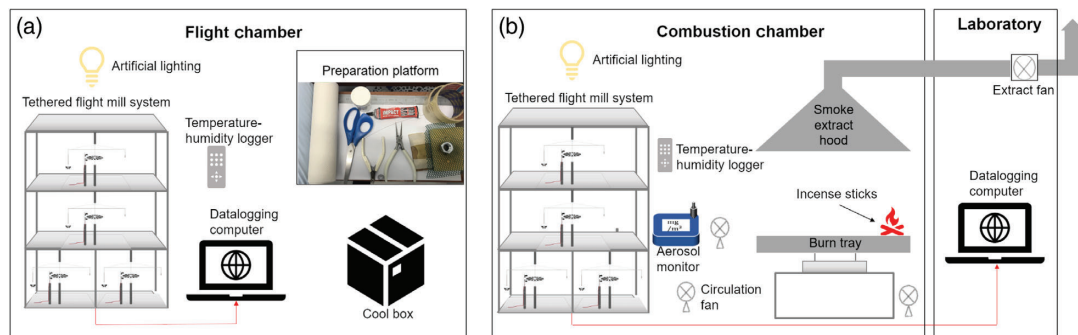


Fig. 1. Experimental setup of (a) the flight chamber and (b) the combustion chamber. The two chambers both contain artificial lighting, a temperature and humidity logger, and four tethered flight mills (TFMs) each of which had a single butterfly subject attached. Different experimental smoke treatments were created in the combustion chamber by burning incense sticks after an initial pre-treatment flight period of 10 min, whilst clean-air 'control' conditions were always maintained in the flight chamber. [Colour figure can be viewed at wileyonlinelibrary.com].

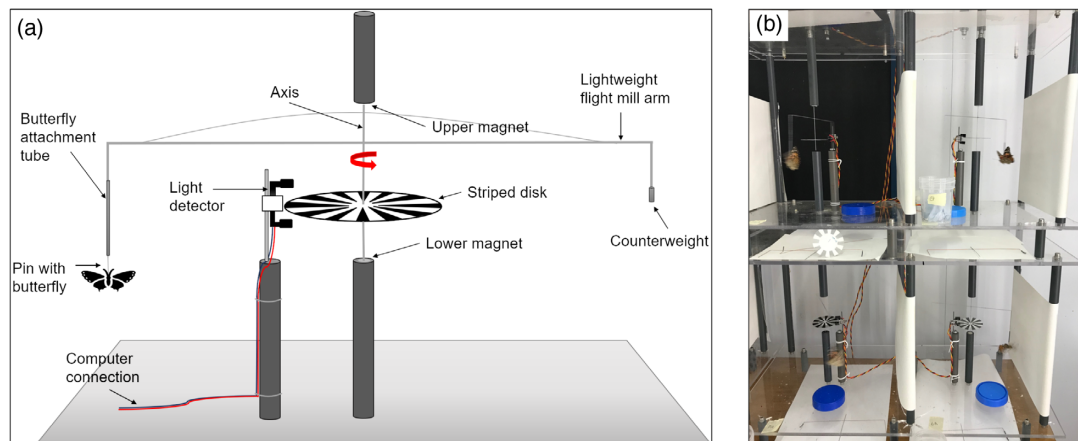


Fig. 2. Tethered flight mill details. (a) An individual TFM (adapted from Jones *et al.*, 2016; Patent: Lim *et al.*, 2013), four of which were used in each chamber as depicted in Fig. 1a,b. (b) Photograph of the TFM configuration used in each chamber, showing four TFMs with a butterfly attached to each. [Colour figure can be viewed at wileyonlinelibrary.com].

and had similar weights (mean = 0.31 ± 0.01 g) and wingspans (mean = 60.0 ± 0.1 mm) at the time of experiments.

Experimental overview

Two test chambers having almost identical ambient environments were used as the location for the experiment, both were located at Rothamsted Research in Southern England and sited within 10 m of one another. The 'flight chamber' (Fig. 1a) was always maintained with a neutral ambient 'clean-air' environment ($PM_{2.5} < 0.015$ mg m⁻³), whilst the nearby 'combustion chamber' (Fig. 1b) had a series of smoke treatments applied by burning unscented incense sticks to increase its $PM_{2.5}$ atmospheric concentration. The butterfly subjects were attached to flight-recording tethered flight mill (TFM) systems (Fig. 2a) in both the flight chamber and the combustion chamber, and in

the former always flew in clean air conditions whilst in the latter the flew in clean air conditions for a period prior to the incense stick ignition time, and after this in 'smoke polluted' conditions. Three different treatments were used in the combustion chamber, classified as Low, Medium, and High Smoke (LS; MS; HS) based on the number of incense sticks burned simultaneously to create the polluted air conditions (see Table 1). A laser-based particulate matter measurement device (TSI Dust-Trak II Desktop Aerosol Monitor 8530) was used to record the $PM_{2.5}$ concentration timeseries in the combustion chamber throughout each experiment. The instrument provides $PM_{2.5}$ concentration on the basis of laser backscattering, and is factory calibrated using Arizona road dust. We applied the adjustment factor of 0.61 from McNamara *et al.* (2011) to deliver concentrations of smoke $PM_{2.5}$ which have a lower density than road dust. Wooster *et al.* (2018) provides details of a similar

Table 1. PM_{2.5} concentration statistics of the three different smoke treatments created in the combustion chamber. Ignition of the incense sticks occurred at time T₁, 10 min after the butterflies were placed on the TFMs at time T₀. Total time-integrated PM_{2.5} concentration and mean PM_{2.5} concentration are given, both for the period from T₁ up to 10 min after incense stick ignition (i.e. T₁ + 10 min) and also up to 20 min after ignition (T₁ + 20 min).

Smoke Treatment	Replicates	(T ₁ + 10 min)		(T ₁ + 20 min)	
		Integrated Total (mg m ⁻³ s)	Mean (mg m ⁻³)	Integrated Total (mg m ⁻³ s)	Mean (mg m ⁻³)
Low smoke (LS)	3	54	0.15	208	0.18
Medium smoke (MS)	3	231	0.38	723	0.61
High smoke (HS)	3	449	0.75	1544	1.28

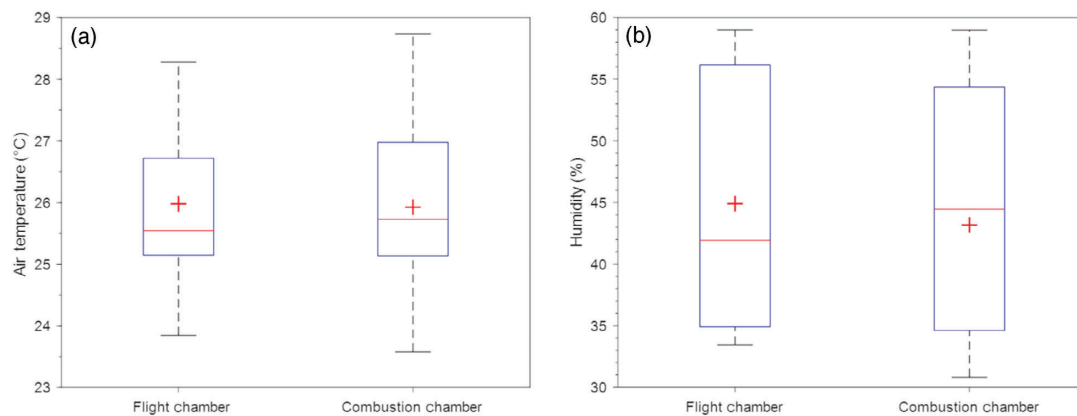


Fig. 3. Atmospheric conditions in the flight chamber and combustion chamber, measured across all experiments for (a) air temperature and (b) relative humidity. The higher and lower bars of the plots are the maximum and minimum values respectively, while the rectangle illustrates the first quartile, the median, and the third quartile (bottom to top). The red plus is the mean. [Colour figure can be viewed at wileyonlinelibrary.com].

calibration adjustment for smoke particulates recorded by this sensor. Each experimental treatment involved four butterflies obtained from a total pool of 20 and flown in the combustion chamber, as did the control treatment based in the flight chamber (Fig. 2b). Whilst the PM_{2.5} concentration of the flight chamber was strongly influenced by the smoke produced by the burning incense sticks, the other atmospheric characteristics of the chambers (air temperature and relative humidity) were statistically similar throughout the experiments (Fig. 3). All experiments were conducted under the artificial lights, with the lighting homogenous in the different mills within the two chambers.

Using the setup described above we investigated the following: (i) whether and for how long butterflies keep a constantly stable flight behaviour when flying under ‘clean air’ conditions; (ii) whether smoke causes a significant change in this flight behaviour; and (iii) how any change is affected by increasing smoke PM_{2.5} concentration.

Details of the tethered flight mill technique

The TFM (Fig. 2) is quite widely used to measure insect flight speed and duration across a wide range of insect body sizes

and types (Jones *et al.*, 2016; Dällenbach *et al.*, 2018; Minter *et al.*, 2018). A lightweight arm, secured and balanced using a counterweight, is suspended between upper and lower magnets, and an axis between the two magnets allows even an insect with relatively limited flight power to turn the mill successfully when attached to the mill arm. When the insect flies, the mill arm turns in a circular trajectory with a circumference of 50 cm, and a black and white striped disk attached to the axis rotates with the arm. A light detector detects the movements of the banded pattern on the disk, using this to record the flight distance to a precision of 10 cm at a 5-s temporal resolution. In a 5-s period, the *V. cardui* studied herein covered an averaged flight distance of 300 cm when attached to the TFM system. Four TFMs were used in the flight chamber and four in the combustion chamber, as shown in Fig. 1.

Subject preparation

Several preparatory steps were necessary prior to placing the butterflies on the TFM systems in both chambers. Special pins were constructed to connect the subjects to the TFMs, each made by bending a small length (around 3 cm) of steel wire into a small loop to which the butterflies could be firmly glued (Nesbit

4.2. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)

et al., 2009). Because of the fragility of the butterfly wings, all subjects were kept chilled and in a torpid state in refrigeration units prior to this procedure, minimising the risk of damaging their wings and ensuring they were not too active too soon. Each butterfly in its chilled state was placed on a sponge mat and secured with a net and two small weights to avoid it being damaged or escaping during attachment of the pin. The scales on the surface of the butterfly thorax were cleared to make sure the pin could be firmly glued to the butterfly. The pin facilitates weighing, feeding, and minimizes stress to the butterfly during preparation for flight. Before placing the butterflies on the TFM system, they were fed with a mixture of cool water and honey in the ratio of 9:1 by weight by letting them drink from pieces of paper tissue dipped in the liquid. Each butterfly was then mounted on its TFM system at an appropriate angle to ensure normal flight.

Smoke treatments

The unscented incense sticks used to create the smoke within the combustion chamber consisted of a wooden base with incense compounds attached at one end (Jetter *et al.*, 2002). They were considered a suitable medium for generating the smoke for this experiment since they can sustain combustion for around 1 h and the smoke released is similar in composition to that from standard biomass burning, including gases (CO and volatile organic compounds, as well as aldehydes and polycyclic aromatic hydrocarbons (PAHs) (Jetter *et al.*, 2002; Lee & Wang, 2004; Lin *et al.*, 2008; Shi *et al.*, 2014). The incense sticks were positioned close to the ground in one corner of the combustion chamber, well away from the butterflies to avoid any direct increase in their temperature. The three experimental treatments of LS, MS, and HS (Table 1) were generated by burning different quantities of incense sticks simultaneously. The aerosol monitor was placed next to the TFM systems in the combustion chamber to record the airborne PM_{2.5} concentration, and the temporal variation of PM_{2.5} associated with the three different treatments are shown in Fig. 4. There were other substances being created during the smoke treatments, but they were not measured in the experiment. The PM_{2.5} concentration were recorded to represent the smoke conditions during the whole experiment.

Experimental procedure

To conduct the experiments, the available pool of 20 butterflies was divided into five groups of four individuals, and two groups of four in good physical condition were chosen for each run of each experimental treatment. Each treatment was replicated three times to provide more robust statistics, using different butterflies each time. In each case, one group of four butterfly subjects was placed on the TFMs in the combustion chamber and immediately started flying (at time T_0), and this 'experimental group' flew for a pre-treatment period of 10 min in the clean-air condition before ignition of the incense sticks at T_1 and a total treatment period of around 1 h flying in smoke polluted air. Once the incense sticks were burned out after around 1 h, an extractor

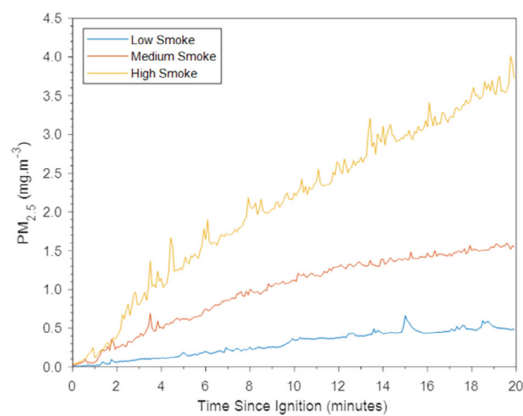


Fig. 4. Mean atmospheric PM_{2.5} concentration timeseries for the combustion chamber, calculated from the three replicates performed for each of the three different experimental smoke treatments (LS, MS, and HS). Data are shown from the time of incense stick ignition (T_1) to $T_1 + 20$ min. See Table 1 for the total time-integrated and mean PM_{2.5} concentrations for each treatment recorded over the same time periods. [Colour figure can be viewed at wileyonlinelibrary.com].

fan was activated to remove all the smoke in the combustion chamber and the butterflies were removed from the TFM system. Another 'control group' set of subjects were placed on the TFMs in the flight chamber and flown in permanently clean-air conditions for the same period, providing a comparison to those flown in the polluted conditions. The collected TFM data of distance flown every 5 s was processed using a script written in MATLAB (version R2019a) to obtain the different flight behaviour variables. These were total flight distance (m), average speed (m s^{-1}), maximum speed (m s^{-1}), and time spent flying (minutes), each calculated over different durations as detailed below. The means (with SD), median (with Interquartile Range, IQR), minimum and maximum values were also derived. Because butterflies showed signs of fatigue after flying 30 min in the clean-air environment of the flight chamber (i.e. flew more slowly or even stopped flying completely; see Results section), time periods shorter than this were selected for calculation of the flight variables, such that we could isolate the influence of the smoke from that of fatigue. The two periods were (i) the initial 10 min of flying in the combustion chamber following ignition of the incense sticks ($T_0 + 10$) and (ii) the full 20 min of flying in the combustion chamber following ignition ($T_1 + 20$). Data for the control group flying in the flight chamber were selected for the same periods. We also compared flight data from the combustion chamber taken during the initial 10 min of flying in the clean-air conditions, and in the subsequent polluted conditions post-ignition.

Results

Data were analysed using a variety of statistical techniques, and prior to this the univariate normalities of all data were

Table 2. Results of the tests to determine whether a significant difference exists in total flight distance covered by the butterflies in 10-min blocks of time, starting from when flight commenced on the tethered flight mill (TFM) system in the flight chamber at T_0 . Differences were evaluated using paired sample t -tests. *Vanessa cardui* L. flew for 40 min in total. n is number of different data used for the comparison, and the P value of <0.05 seen for the comparison of the first and fourth 10-min periods means there is a significant difference between total flight distance covered in these two periods (but not between the other periods that are compared). The conclusion is that after 30 min the *Vanessa cardui* L. start to become too fatigued to fly in the same way as they did during the first 30 min of flight, but prior to this period they fly consistently.

Comparison Flight Periods	n	P value	Significant Difference
1st versus 4th 10-min period (T_0 to $T_0 + 10$ vs. $T_0 + 10$ to $T_0 + 20$)	36	0.815	No significant difference
1st versus 3rd 10-min period (T_0 to $T_0 + 10$ vs. $T_0 + 20$ to $T_0 + 30$)	36	0.357	No significant difference
1st versus 4th 10-min period (T_0 to $T_0 + 10$ vs. $T_0 + 30$ to $T_0 + 40$)	36	0.049	Significant difference
2nd versus 3rd 10-min period ($T_0 + 10$ to $T_0 + 20$ vs. $T_0 + 20$ to $T_0 + 30$)	36	0.296	No significant difference
2nd versus 4th 10-min period ($T_0 + 10$ to $T_0 + 20$ vs. $T_0 + 30$ to $T_0 + 40$)	36	0.059	No significant difference
3rd versus 4th 10-min period ($T_0 + 20$ to $T_0 + 30$ vs. $T_0 + 30$ to $T_0 + 40$)	36	0.071	No significant difference

The bold text shows the P value is lower than 0.05 at 95% confidence interval.

confirmed using the Shapiro–Wilk test in the Statistical Package for the Social Sciences (SPSS), version 26, which determined that the data were normally distributed ($P \geq 0.091$). The following suites of analyses were then performed:

Determining the analytical time period

To determine the duration of the analysis periods, data from the ‘control group’ were first used to understand the length of time that *V. cardui* typically fly in a consistent way. For this we used data on total flight distance, because average flight speed is dependent on the total distance flown in a certain period, and maximum speed was found to be too random to be statistically representative. Total flight distance data from the flight chamber was analysed in 10-min blocks using paired sample t -tests across a total of 40 min, so in the periods T_0 to $T_0 + 10$, $T_0 + 10$ to $T_0 + 20$, $T_0 + 20$ to $T_0 + 30$, and $T_0 + 30$ to $T_0 + 40$. Total flight distance covered in the different time periods were confirmed as normally distributed ($P > 0.80$) and the null hypothesis (H_0) was that no significant difference would be observed between each of the four different flight periods, whilst the alternative (H_1) was that a difference would be observed.

Results in Table 2 show that the total flight distance covered in the fourth 10 min period of flying in clean air ($T_0 + 30$ to $T_0 + 40$) was significantly lower than that in first 10 min period (T_0 to $T_0 + 10$) ($P = 0.049$, $n = 36$), but that between all other periods the total flight distance covered is statistically similar. This indicates that *V. cardui* can keep consistent flight behaviour for 30 min ($P \geq 0.296$), after which flight behaviour begins to change – presumably due to fatigue. This 30 min threshold was, therefore, used to determine our total experimental duration, meaning that we (i) subsequently compared flight data from the combustion chamber pre-treatment (pre-ignition) period ($T_0 + 10$) to the that from the treatment period (T_1 to $T_1 + 10$ and T_1 to $T_1 + 20$); and (ii) compared the control group in the flight chamber to that in the combustion chamber with no analysis of data from beyond 30 min of flying time.

Comparisons of flying in the pre-treatment and treatment conditions

The first determination of whether subject flight behaviour changed in response to smoke exposure was made by comparing the total flight distance covered by the experimental group flown for 10 min in the combustion chamber pre- and post-treatment. Specifically, for each different smoke treatment (LS, MS, and HS) we compared the flight variables for the pre-treatment period (T_0 to $T_0 + 10$ min) prior to incense stick ignition to those recorded for the same butterflies in the period (T_1 to $T_1 + 10$ min) immediately after ignition. Paired sample t -tests were used and the null hypothesis (H_0) was that no significant difference would be observed between these two flight periods, whilst the alternative hypothesis (H_1) was that a difference would be observed.

Descriptive data of each of the flight behaviour variables for the pre-treatment and post-treatment periods are shown in Table 3. During the pre-treatment period, the subjects showed similar flight behaviour characteristics, with average distance flown being 208 m in the 10 min of measurement at an average speed of 0.34 m s^{-1} . However, flight behaviour changed in the 10 min that they flew in the smoke conditions, and some butterflies stopped flying on occasion, especially in the MS treatments (highlighted in Table 3). Total flight distance covered was 25% less in the 10 min of the MS smoke treatment than in the subsequent treatment period, and average speed 26% lower. Also, the maximum speed in the MS condition was lower than that in the pre-treatment period by 43%, though the average flight duration was similar. Paired sample t -tests comparing total flight distance in both pre-treatment and treatment periods identified significant differences between the two flight periods for the MS treatments ($P = 0.024$, $n = 12$); while no significant difference was found for either the LS treatment ($P = 0.936$, $n = 12$) nor the HS treatment ($P = 0.832$, $n = 12$).

Flight comparisons between control and treatment conditions

To further determine whether flight behaviour during smoke exposure was different to that seen under control conditions,

4.2. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)

Table 3. Descriptive statistics of flight behaviour variables (total flight distance, average speed, maximum speed, and flight duration) for the pre-treatment flight period in the combustion chamber (T_0 to $T_0 + 10$ min; *Vanessa cardui* L. was put on TFM at T_0) and in the post-treatment period (T_1 to $T_1 + 10$ min; Ignition of the incense sticks occurred at T_1). Data shown here only come from subjects flown in the combustion chamber, with each flown in the pre-treatment condition for 10 min prior to ignition of the incense stick(s).

Flight Variables	Smoke Conditions	Pre-treatment ('Clean Air') Period (T_0 to $T_0 + 10$ min)				Post-treatment ('Smoke Polluted Air') Period (T_1 to $T_1 + 10$ min)			
		Mean (SD)	Median (IQR)	Min	Max	Mean (SD)	Median (IQR)	Min	Max
Total flight distance (m)	LS	208 (± 134)	201 (208)	35	445	198 (± 155)	221 (226)	0	471
	MS	211 (± 117)	220 (190)	4	407	159 (± 108)	167 (107)	0	412
	HS	206 (± 97)	199 (138)	66	401	199 (± 91)	205 (128)	0.04	289
Average speed ($m s^{-1}$)	LS	0.34 (± 0.22)	0.33 (0.34)	0.06	0.73	0.33 (± 0.25)	0.33 (0.37)	0	0.78
	MS	0.35 (± 0.19)	0.37 (0.32)	0.01	0.68	0.26 (± 0.18)	0.27 (0.17)	0	0.68
	HS	0.34 (± 0.16)	0.33 (0.22)	0.12	0.66	0.33 (± 0.15)	0.34 (0.21)	0.01	0.48
Maximum speed ($m s^{-1}$)	LS	0.74 (± 0.42)	0.69 (0.41)	0.06	1.70	0.62 (± 0.32)	0.66 (0.61)	0	1.04
	MS	0.70 (± 0.28)	0.62 (0.45)	0.28	1.20	0.40 (± 0.21)	0.36 (0.18)	0	0.80
	HS	0.52 (± 0.19)	0.53 (0.24)	0.18	0.88	0.53 (± 0.23)	0.56 (0.21)	0.04	0.94
Flight duration (min)	LS	9 (± 2)	10 (0)	4	10	8 (± 3)	10 (4)	0	10
	MS	9 (± 3)	10 (3)	1	10	9 (± 3)	10 (0)	0	10
	HS	10 (± 0)	10 (0)	9	10	8 (± 4)	10 (2)	0	10

Bold text identifies a significant difference between pre-treatment and treatment period.

Table 4. Descriptive statistics of flight behaviour variables (total flight distance, average speed, maximum speed, and flight duration) between the pre-treatment flight period ($T_0 + 10$ min to $T_0 + 30$ min; *Vanessa cardui* L. was put on TFM at T_0) and post-treatment flight period (T_1 to $T_1 + 20$ min; Ignition of the incense sticks occurred at T_1). Data for the control group were collected in the flight chamber, and for the smoke treatment group in the combustion chamber. The two groups contained the same butterfly subjects.

Flight Variables	Smoke Conditions	Control Group ($T_0 + 10$ min to $T_0 + 30$ min)				Smoke Treatment Group (T_1 to $T_1 + 20$ min)			
		Mean (SD)	Median (IQR)	Min	Max	Mean (SD)	Median (IQR)	Min	Max
Total flight distance (m)	LS	887 (± 325)	937 (546)	314	1256	312 (± 314)	251 (422)	0	947
	MS	745 (± 218)	735 (404)	415	1085	312 (± 212)	318 (232)	8	818
	HS	866 (± 315)	878 (1100)	186	1286	381 (± 183)	380 (264)	27	610
Average speed ($m s^{-1}$)	LS	0.74 (± 0.27)	0.78 (0.45)	0.26	1.05	0.34 (± 0.34)	0.29 (0.56)	0	1.04
	MS	0.62 (± 0.18)	0.62 (0.35)	0.35	0.90	0.26 (± 0.17)	0.27 (0.19)	0.04	0.68
	HS	0.72 (± 0.26)	0.73 (0.42)	0.16	1.07	0.32 (± 0.15)	0.32 (0.22)	0.02	0.51
Maximum speed ($m s^{-1}$)	LS	1.06 (± 0.37)	1.05 (0.78)	0.56	1.58	0.60 (± 0.36)	0.62 (0.64)	0	1.04
	MS	0.79 (± 0.25)	0.78 (0.41)	0.52	1.34	0.46 (± 0.22)	0.37 (0.25)	0.10	0.88
	HS	0.92 (± 0.33)	0.99 (0.50)	0.30	1.52	0.55 (± 0.23)	0.56 (0.21)	0.06	0.94
Flight duration (min)	LS	19 (± 2)	20 (0)	14	20	13 (± 8)	17 (17)	0	20
	MS	20 (± 0)	20 (0)	20	20	17 (± 6)	20 (5)	4	20
	HS	20 (± 0)	20 (1)	19	20	18 (± 3)	20 (5)	11	20

total flight distance covered was compared between the treatment flight periods of the experimental group (T_1 to $T_1 + 20$ min) flying in the polluted air of the combustion chamber and the same butterflies flying in the clean air of the flight chamber.

Compared to the prior comparison of the butterflies flying in the pre-treatment and treatment conditions, the disadvantage here was that the control run and experimental run with the same butterfly could not be conducted immediately after each other (so the ambient temperature and humidity may have differed) since each subject had to be fed, rested and moved between the two chambers. However, the advantage was that flight periods of 20 min under clean air and polluted air conditions could be compared, and were twice as long as the 10 min possible with the flights conducted in the pre-treatment and treatment conditions (Table 3). The period up to 20 min after incense stick ignition

also allowed the mean $PM_{2.5}$ concentrations to increase to higher values compared to just the first 10 min (Table 1).

The analysis was again performed using paired sample *t*-tests, and the null hypothesis (H_0) was that no significant difference would be observed between the two, whilst the alternative hypothesis (H_1) was that a difference would be observed.

Results (Table 4) show that the control group flew an average total flight distance of 833 m in the 20 min period, while in smoke treatments the average was far lower at 335 m. Total flight distance covered in the three smoke treatments (LS, MS, and HS) decreased by 65%, 58%, and 56%, respectively compared to that in the control treatments performed using the same butterflies, whilst the average speed declined by 54%, 58%, and 56%, respectively. Maximum speed was also lower than that in control treatments, by 43%, 42%, and 40%, respectively, as

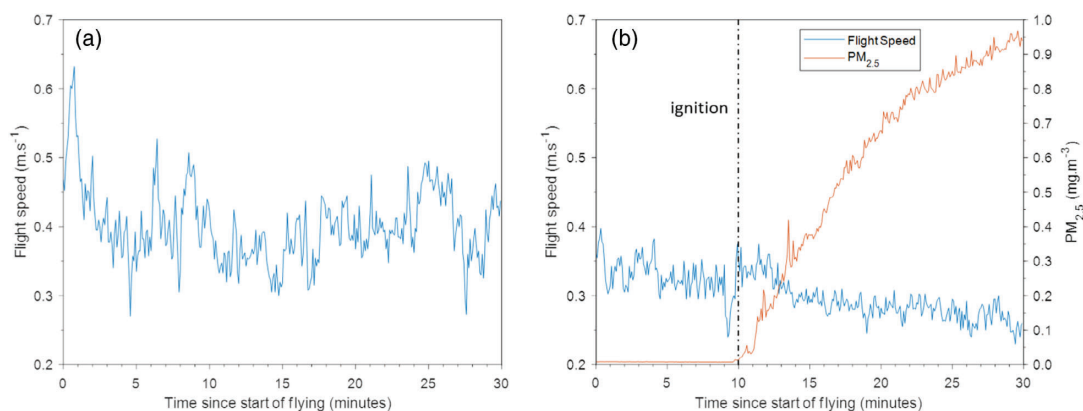


Fig. 5. Exemplar data from four butterflies flown under (a) control conditions in the flight chamber and (b) under the medium smoke (MS) treatment in the combustion chamber. Mean flight speeds from all four subjects are shown, and in (a) the flights under control conditions (T_0 to $T_0 + 30$ min) in the flight chamber show no discernible trend, as do those in (b) collected under the pre-treatment conditions (T_0 to $T_0 + 10$ min) in the combustion chamber. However also in (b) after the smoke treatment is applied 10 min into the flight time (via ignition of the incense sticks) the flight speed shows a steady reduction. Also shown in (b) is the mean $PM_{2.5}$ atmospheric concentration recorded in the flight chamber by the TSI DustTrak II Desktop Aerosol Monitor. [Colour figure can be viewed at wileyonlinelibrary.com].

was flight duration which respectively declined by 32%, 15%, and 10% under the LS, MS, and HS conditions. An example to show how flight speed changed is shown in Fig. 5. Butterflies in the control group (Fig. 5a) flew in a relatively continuous and uniform manner during the first 30 min of flight (supporting the findings in Table 2), whilst Fig. 5b shows that the experimental group also showed a similar pattern during the pre-treatment period (T_0 to $T_0 + 10$ min) but after smoke was introduced 10 min into the experiment the flight speed gradually reduced until $T_0 + 30$ min.

Additionally, paired t sample tests showed that total flight distance for all three treatments (LS, MS, and HS) was significantly reduced compared to the control in the 20 min ($P = 0.001$, 0.002, 0.001, respectively). However, paired t sample tests indicated that total flight distance only for the MS treatments was significantly decreased compared to the pre-treatment in the 10 min ($P = 0.024$, $n = 12$). This illustrated that the longer butterflies stayed in the smoke polluted conditions, the greater the differences in flight behaviour were to that seen in the clean-air conditions.

Relationships between flight speed and $PM_{2.5}$ concentration

The previous sections have already shown flight distance to be clearly influenced by the presence of smoke, so ordinary least squares (OLS) linear regression was used to further investigate relationships between flight speed and $PM_{2.5}$ concentration. Calculations were performed at the 5-s maximum resolution of the flight mill data, with the null hypothesis (H_0) being that no significant relationship would be observed, whilst the alternative hypothesis (H_1) was that a significant relationship would be observed.

The data were divided into 10 groups of increasing $PM_{2.5}$ concentration, and flight speeds corresponding to each group

were extracted and displayed using boxplots (Fig. 6a). The first boxplot in both Fig. 6a,b ($PM_{2.5}$ concentration = 0) contains data from both the control runs in the flight chamber and the pre-treatment period (i.e. first 10 min flying) of the experimental groups in the combustion chamber. These $PM_{2.5}$ concentration = 0 data highlight that under clean air conditions, maximum flight speed can reach 1.7 m s^{-1} . The remaining nine boxplots incorporate flight speed data collected under various smoke concentrations in the combustion chamber, and it can be seen that as $PM_{2.5}$ concentration increased the median of the flight speeds first decreased slightly, then increased up to 1.6 mg m^{-3} , after which the median flight speeds once again decreases somewhat. Maximum flight speed also continuously decreased as $PM_{2.5}$ concentration increased.

For $PM_{2.5}$ concentrations less than 1.2 mg m^{-3} (first four boxplots of Fig. 6a) the flight speeds have a larger dynamic range and more values in the outliers. However, at concentrations higher than 1.2 mg m^{-3} the boxplots show a smaller dynamic range and no outliers. Even though more flight speed data were obtained at low $PM_{2.5}$ concentrations compared to high $PM_{2.5}$ concentrations, the far narrower range of flight speeds seen as $PM_{2.5}$ concentration increases (Fig. 6a) indicates that flight speed may be impacted by smoke concentration. Figure 6b shows the same data as in Fig. 6a, but excluding the zero flight speed values when the *V. cardui* subjects stopped flying altogether. These Fig. 6b data, therefore, represent the actual speed when the butterflies were in flight, rather than including the data when they were paused, though the trends are essentially the same as in Fig. 6a which included both types of behaviour.

Figure 7 shows the OLS linear best fit relationships between subject flight speed and airborne $PM_{2.5}$ concentration, and as with Fig. 6 we show the data both with (Fig. 7a) and without (Fig. 7b) the zero (i.e. non-flying) values included. In Fig. 7a the data points trace out an 'S' curve, with a $PM_{2.5}$ concentration of

4.2. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)

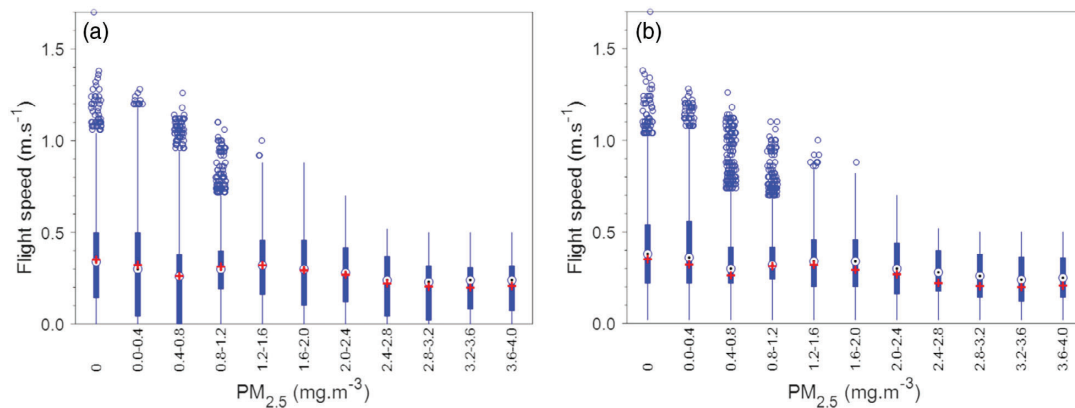


Fig. 6. Boxplots showing the flight speed of butterflies separated into 10 different $PM_{2.5}$ concentration classes. Data for the lowest $PM_{2.5}$ concentration class come from the pre-treatment period of the experimental group flown in the combustion chamber, and for the other (higher $PM_{2.5}$) classes from all smoke treatments applied in the combustion chamber up to 20 min after ignition of the incense sticks ($T_1 + 20$ min). (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying completely. The higher and lower bars of the plots are the maximum and minimum values respectively, whilst the rectangle illustrates the first quartile and the third quartile (bottom to top). The median value of flight speed in each group are represented by the blue circle with centre of the box, whereas the red plus is the mean. Beyond these ranges, outliers are plotted as blue circles. [Colour figure can be viewed at wileyonlinelibrary.com].

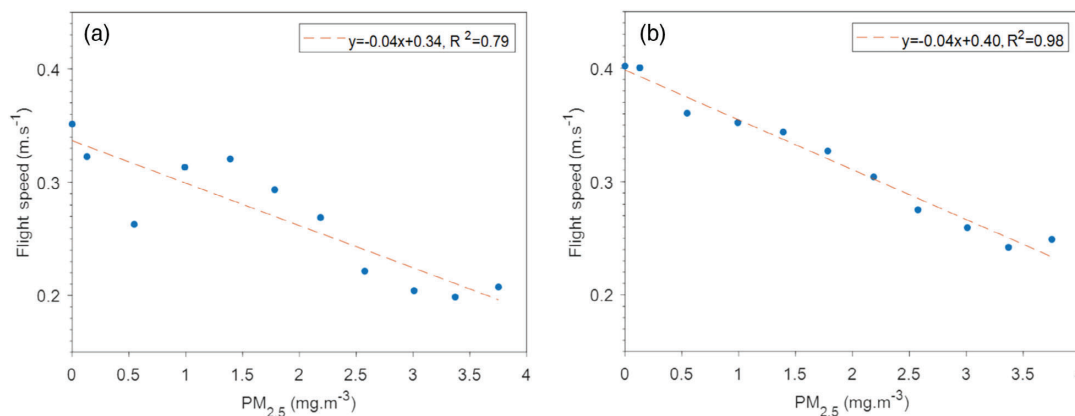


Fig. 7. Scatterplots of mean flight speed against mean $PM_{2.5}$ concentration ($mg\ m^{-3}$) calculated (a) from all data as and (b) with the zero value flight speeds removed as was the case with Fig. 6b. Dashed lines represent the OLS linear best-fit to the data, the equation for which is shown along with the coefficient of variation (r^2). [Colour figure can be viewed at wileyonlinelibrary.com].

around $2\ mg\ m^{-3}$ seeming to be the approximate middle point, whilst in Fig. 7b this shape is damped, and the relationship appears more linear. Overall, both Fig. 7a,b (both $P < 0.001$) demonstrate a clear and strongly negative linear correlation between flight speed and $PM_{2.5}$, backing up the interpretation of the data shown in Fig. 6.

Discussion

Smoke from landscape fires is the greatest single source of airborne fine particulate matter ($PM_{2.5}$) in Earth's atmosphere, and

one that is particularly prevalent in many developing nations (Huang *et al.*, 2014). Local atmospheric concentrations of $PM_{2.5}$ can sometimes exceed $1\ mg\ m^{-3}$ during intense agricultural burning seasons (Zhang *et al.*, 2017), and even higher values have been seen to persist for weeks over some regions affected by extreme landscape fire events (Wooster *et al.*, 2018). Previous studies have demonstrated that exposure to $PM_{2.5}$ can have a significant impact on insects. Tan *et al.* (2018) demonstrated that a $PM_{2.5}$ concentration of $0.05\ mg\ m^{-3}$ can restrict butterfly development, whilst Wang *et al.* (2017) showed that exposure to concentrations of $0.08\ mg\ m^{-3}$ shortened the lifespan of *Drosophila melanogaster* from 48 to 20 days. Here for

the first time we have explored the effect of atmospheric PM_{2.5} on insect flight behaviour, choosing *V. cardui* butterflies as our test subjects. The experimental treatments detailed herein exposed subjects to different levels of PM_{2.5} smoke pollution from burning incense sticks, and over the first 10 min from the ignition point (T₁ + 10 min) concentrations were found to be an average of 0.15 mg m⁻³ in the LS treatment, 0.38 mg m⁻³ in the MS treatment, and 0.75 mg m⁻³ in the HS treatment. In all cases, PM_{2.5} concentrations increased further after the first 10 min of burning, and so for 20 min tests (T₁ + 20 min) concentrations were often even higher (averaging 0.18 mg m⁻³ for LS, 0.61 mg m⁻³ for MS and 1.28 mg m⁻³ for HS). These concentrations are well within the levels found in the ambient atmosphere in areas affected by smoke from biomass burning. In Northern India for example, the post-monsoon agricultural burning season in the NW Indian States of Punjab and Haryana, added to local urban sources within Delhi, quite often results in levels of PM_{2.5} frequently exceeding 0.3 mg m⁻³ (Pant *et al.*, 2015).

We used TFM to fly *V. cardui* in smoke polluted air, and have shown this to be an effective way of quantifying flight behaviour. It is known that TFMs can limit natural flight behaviour somewhat by potentially hindering wing-flapping (Jones *et al.*, 2016), including in butterflies such as *V. cardui* which have a 'clap-and-flapping' style of flight (Srygley & Thomas, 2002). The tethered and screened position of the butterfly in the flight mill, along with an absence of appropriate visual cues for take-off and flight, could for example have prolonged flight duration and delayed 'landing' (Gatehouse & Hackett, 1980; Jones *et al.*, 2016). For these reasons, in addition to the smoke treatments that the subjects were exposed to during each experimental run, we also flew the same butterflies in clean air on the same TFM system and for the same 30 min time period to provide a control dataset for assessing flight performance effects of the smoke. We also flew each butterfly for an initial 10-min period in clean air prior to application of each smoke treatment, so as to have a pre-treatment performance period for comparison purposes.

Our results show that the flight variables of speed, duration, and distance were all significantly reduced when flying for 20 min under the smoke contaminated conditions compared to the clean air conditions of the control group, highlighting the deleterious effect that the smoke had on the flight performance. In terms of flight duration, for example, we found this to be shortened by 32% in the LS conditions, 15% in MS and 10% in HS conditions respectively during the first 20 min of flying compared to the control ('clean air') conditions. Some studies have suggested that certain insect species may become disorientated under smoky atmospheric conditions due to changes in the polarisation of sunlight (Hegedüs *et al.*, 2007), however, the distance between the light source and the butterflies in our experiment was only a few meters and the smoke concentrations such that the effect of the particulates on the light was certainly not observable by eye. Thus, whilst in natural conditions smoke can darken the skies and change the polarisation field of incoming sunlight (Johnson *et al.*, 2005; Hegedüs *et al.*, 2007) we do not believe that changes in the light field were responsible for our findings. Rather we think the direct presence of the smoke is what is affecting the butterfly

performance. Our data show that as smoke conditions worsened from MS to HS conditions, flight duration actually increased again, becoming closer to that under clean air conditions. One explanation is that the increasingly polluted environment stimulates an escape response, resulting in an increase in flight duration. It is not uncommon for insects to respond to a change in environmental conditions; for example, mosquitos can use a flutter stroke to double the wingbeat frequency of normal flight, in order to remove drops of water on their wings before taking off (Dickerson & Hu, 2014). Although the butterflies may have increased their flight duration to 'escape' the smoke, their flight speed remained significantly lower than under the clean air control conditions. This effect could be related to the fine particulate matter attaching to their wings and causing a decrease in flight speed; in the same way that water can accumulate on mosquito wings and bend them out of shape, eventually preventing flight in foggy conditions (Dickerson & Hu, 2014; Dickerson *et al.*, 2015).

When the 10 min flight data for the pre-treatment ('clean air') conditions were examined and compared to the first 10 min of the subsequent 'smoke contaminated' period, the flight distance and flight speed were both reduced, but this was only statistically significant in the MS conditions. The flight duration of butterflies under MS conditions was similar to that under the pre-treatment conditions, but the average flight speed reduced by 26%, resulting in a 25% shorter flight distance. We found, however, that the differences between butterfly flight behaviour pre-treatment and post-treatment, under both the LS and HS treatments, were relatively small compared to that under the MS treatment. They were also less significant than the differences found between the longer control and experimental treatment runs. This suggests that longer periods of smoke exposure are required to produce significant differences in flight behaviour under the lower and higher PM_{2.5} concentrations. It may also be the case that impacts manifest themselves more obviously (or earlier) in the MS conditions, perhaps because whilst the MS conditions are detrimental to flight, the butterflies are still able to fly quite well and are thus, effectively trying to escape the polluted conditions. Higher mean PM_{2.5} concentrations were also reached in each experimental smoke treatment after 20 min of smoke production compared to the first 10 min (Table 1), thus providing more contrast in the control versus treatment comparisons than in the pre-treatment versus treatment comparisons.

Our data show a clear and significantly negative linear correlation between mean flight speed and PM_{2.5} concentration, indicating that the higher the pollution level the lower the mean flight speed becomes (Fig. 7). However, the data in Fig. 7a also suggest a possible change in relationship at around 2 mg m⁻³, and that when concentrations rise above this level the butterflies may react by reducing flight speed, possibly as an attempt to seek escape or shelter from the polluted conditions. Once PM_{2.5} concentrations reach approximately 3.4 mg m⁻³, the mean flight speed increases again slightly with increasing PM_{2.5} concentration. This may reflect a more 'panicked' attempt to move faster to escape the smoke conditions. These potential behavioural explanations are only hypotheses, and remain to be rigorously tested in future work.

4.2. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)

Smoke effects on butterfly flight behaviour 205

It is also possible that beyond fine particulates, combustion gases may also influence the flight behaviour of *V. cardui*. Ginevan *et al.* (1980) found that *Lasioglossum zephyrum* (Sweat bee) exposed to a polluted environment with SO₂ levels at 0.14–0.28 ppm for 16–29 days demonstrated reduced flight activity compared to a control population for example. Such poor air quality could cause insects to close their spiracle valves longer, decrease oxygen intake and reduce metabolism (Tan *et al.*, 2018). Toxic compounds may also influence butterfly flight performance by affecting the insects' body functions. For instance, muscles of *Cecropia* moths are sensitive to CO₂ (and O₂) levels, with changes in concentration causing spiracle closures (Burkett & Schneiderman, 1974). Since the smouldering combustion style of the incense sticks used as the source was constant across the period of burning, CO₂ is released in direct proportion to PM_{2.5} (Zhang *et al.*, 2015), it is possible in our experiments that an increase in CO₂ concentration, and perhaps in some of the other gases compounds released by burning, could have induced longer closure of the insect spiracle valves and contributed to the decreased flight performance seen. This remains to be tested in future experiments taking into account more pollutant species, as does any effect of the particulates on the incoming light field even over the very short optical paths involved, but smoke (as assessed here via PM_{2.5}) clearly has a negative impact on *V. cardui* flight behaviour, even at concentration ranges significantly lower than that found 'naturally' in some biomass burning affected regions. More research is required to show how the specific behavioural and physiological mechanics of butterfly flight respond to increasing concentrations of different smoke constituents.

The work presented herein is the first to experimentally quantify the impact of smoke pollution on butterfly flight performance, and highlights the deleterious impact on both the flight speed and flight duration of adult butterflies. Although the effect was demonstrated in a controlled experiment where insects were flown on a TFM, and was based on non-natural populations that can sometimes suffer inbreeding, it is an indication of the potentially harmful effect of smoke pollution on flight behaviour in the real world. It is a first step towards understanding the impact of smoke on natural flight performance, and ultimately on issues such as insect migration in regions affected by biomass burning smoke. A reduction in flight speed due to smoke pollution could have a substantial impact on the ability of butterflies to migrate successfully, as slower flying speeds will reduce the distance it is possible to fly in a single flight. This could have serious consequences if the insects must fly over large water bodies in such a flight for example, where a diminished flight capability during polluted conditions might mean insects being unable to make the necessary distance. Since smoke from fires can be released into the boundary layer or lofted high into the atmosphere (e.g. Paugam *et al.*, 2016), particulate matter concentrations can vary widely with altitude, meaning that insects could encounter them at different altitudes or even possibly make adjustments in their behaviour to avoid the highest concentrations. Further studies are required to determine if the fine particulates focused on here are those controlling all the impact on the insects flight behaviour during the polluted conditions, or whether some of

the gaseous compounds released by burning might also have a detectable affect.

Acknowledgements

We extend thanks to Ceri Watkins and Rebecca Nesbit for training and advice on the TFM and on butterfly handling, James Johnson and Bruce Main for additional assistance with the experiment, and Su Yan for assistance with coding. Aspects of this work were supported by National Capability funding awarded by NERC to the National Centre for Earth Observation (NERC grant no. NE/R016518/1). Certain aspects of this research were supported by funding from the Leverhulme Centre for Wildfires, Environment, and Society through the Leverhulme Trust, grant number RC-2018-023. This work forms part of the outcome of the UKRI projects ST/S003029/1, ST/R00286X/1, and EP/P510804/1. The contribution from K.S.L. (Rothamsted) forms part of the Smart Crop Protection (SCP) strategic programme (BBS/OS/CP/000001) funded through the Biotechnology and Biological Sciences Research Council's Industrial Strategy Challenge Fund. The authors declare that they have no conflict of interest. The data that support the findings of this study are available from the corresponding author upon reasonable request.

Author contributions

M.J.W. and K.S.L. proposed the project and designed the plan. Y.L. and M.J.G. designed the experimental details. Y.L., M.J.G., M.J.W., and R.A.F. conducted the experiment. Y.L. analysed the data using scripts in part written by Y.L. All authors contributed to writing and revising the manuscript.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

- Alstad, D.N., Edmunds, G.F. Jr. & Weinstein, L.H. (1982) Effects of air pollutants on insect populations. *Annual Review of Entomology*, **27**, 369–384.
- Anaman, K.A. & Looi, C.N. (2000) Economic impact of haze-related air pollution on the tourism industry in Brunei Darussalam. *Economic Analysis and Policy*, **30**, 133–144.
- Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. (2001) *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford.
- Belovsky, G.E. & Slade, J.B. (2000) Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences*, **97**, 14412–14417.
- Berg, M.P., Kiers, E.T., Driessen, G., Van Der Heijden, M., Kooi, B.W., Kuenen, F. *et al.* (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, **16**, 587–598.

- Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205–225.
- Burkett, B.N. & Schneiderman, H.A. (1974) Roles of oxygen and carbon dioxide in the control of spiracular function in *Cecropia* pupae. *The Biological Bulletin*, **147**, 274–293.
- Cao, G., Zhang, X., Wang, Y. & Zheng, F. (2008) Estimation of emissions from field burning of crop straw in China. *Chinese Science Bulletin*, **53**, 784–790.
- Chapman, J.W., Nesbit, R.L., Burgin, L.E., Reynolds, D.R., Smith, A.D., Middleton, D.R. et al. (2010) Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science*, **327**, 682–685.
- Chen, B. & Kan, H. (2008) Air pollution and population health: a global challenge. *Environmental Health and Preventive Medicine*, **13**, 94–101.
- Chen, J., Li, C., Ristovski, Z., Milic, A., Gu, Y., Islam, M.S. et al. (2017) A review of biomass burning: emissions and impacts on air quality, health and climate in China. *Science of the Total Environment*, **579**, 1000–1034.
- Cleary, D.F. & Grill, A. (2004) Butterfly response to severe ENSO-induced forest fires in Borneo. *Ecological Entomology*, **29**, 666–676.
- Corke, D. (1999) Are honeydew/sap-feeding butterflies (Lepidoptera: Rhopalocera) affected by particulate air-pollution? *Journal of Insect Conservation*, **3**, 5–14.
- Dällenbach, L.J., Glauser, A., Lim, K.S., Chapman, J.W. & Menz, M.H. (2018) Higher flight activity in the offspring of migrants compared to residents in a migratory insect. *Proceedings of the Royal Society B*, **285**, 20172829.
- Danthanarayana, W. (1986) Insect Flight: Dispersal and Migration. *Proceedings in Life Sciences*. Berlin Heidelberg: Springer-Verlag.
- Dennis, A., Fraser, M., Anderson, S. & Allen, D. (2002) Air pollutant emissions associated with forest, grassland, and agricultural burning in Texas. *Atmospheric Environment*, **36**, 3779–3792.
- Dickerson, A.K. & Hu, D.L. (2014) Mosquitoes actively remove drops deposited by fog and dew. *Integrative and Comparative Biology*, **54**, 1008–1013.
- Dickerson, A.K., Liu, X., Zhu, T. & Hu, D.L. (2015) Fog spontaneously folds mosquito wings. *Physics of Fluids*, **27**, 021901.
- Ding, A.J., Fu, C.B., Yang, X.Q., Sun, J.N., Petäjä, T., Kerminen, V.M. et al. (2013) Intense atmospheric pollution modifies weather: a case of mixed biomass burning with fossil fuel combustion pollution in eastern China. *Atmospheric Chemistry and Physics*, **13**, 10545–10554.
- Ecuador, G.I. (1992) World distribution of the *Vanessa cardui* group (Nymphalidae). *Journal of the Lepidopterists' Society*, **46**, 235–238.
- Elington, C.P. (1984) The aerodynamics of hovering insect flight iii kinematics philos. *Trans. R. Soc. Lond. Biol. Sci.* **305** 79–113.
- Fang, L., Zhang, Y., Gao, K., Ding, C. & Zhang, Y. (2019) Butterfly communities along the Heihe River basin in Shaanxi Province, a biodiversity conservation priority area in China. *Journal of Insect Conservation*, **23**, 873–883.
- Führer, E. (1985) Air pollution and the incidence of forest insect problems. *Zeitschrift für Angewandte Entomologie*, **99**, 371–377.
- Gadde, B., Bonnet, S., Menke, C. & Garivait, S. (2009) Air pollutant emissions from rice straw open field burning in India, Thailand and the Philippines. *Environmental Pollution*, **157**, 1554–1558.
- Gatehouse, A.G. & Hackett, D.S. (1980) A technique for studying flight behaviour of tethered *Spodoptera exempta* moths. *Physiological Entomology*, **5**, 215–222.
- Giglio, L., Randerson, J.T., Van der Werf, G.R., Kasibhatla, P.S., Collatz, G.J., Morton, D.C. et al. (2010) Assessing variability and long-term trends in burned area by merging multiple satellite fire products. *Biogeosciences*, **7**, 1171–1186.
- Ginevan, M.E. & Lane, D.D. (1978) Effects of sulfur dioxide in air on the fruit fly, *Drosophila melanogaster*. *Environmental Science & Technology*, **12**, 828–831.
- Ginevan, M.E., Lane, D.D. & Greenberg, L. (1980) Ambient air concentration of sulfur dioxide affects flight activity in bees. *Proceedings of the National Academy of Sciences*, **77**, 5631–5633.
- Griffis, K.L., Mann, S.S. & Wagner, M.R. (2001) The suitability of butterflies as indicators of ecosystem condition: a comparison of butterfly diversity across stand treatments in northern Arizona. *Proceedings of the 5th Biennial Conference of Research on the Colorado Plateau*, pp. 125–135. US Geological Survey, Forest and Rangeland Ecology Science Center.
- Hegedüs, R., Åkesson, S. & Horváth, G. (2007) Anomalous celestial polarization caused by forest fire smoke: why do some insects become visually disoriented under smoky skies? *Applied Optics*, **46**, 2717–2726.
- Hill, J.K., Hamer, K.C., Lace, L.A. & Banham, W.M.T. (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology*, **32**, 754–760.
- Huang, X., Li, M., Li, J. & Song, Y. (2012) A high-resolution emission inventory of crop burning in fields in China based on MODIS thermal anomalies/fire products. *Atmospheric Environment*, **50**, 9–15.
- Huang, Y., Shen, H., Chen, H., Wang, R., Zhang, Y., Su, S. et al. (2014) Quantification of global primary emissions of PM_{2.5}, PM₁₀, and TSP from combustion and industrial process sources. *Environmental Science & Technology*, **48**, 13834–13843.
- Jain, N., Bhatia, A. & Pathak, H. (2014) Emission of air pollutants from crop residue burning in India. *Aerosol and Air Quality Research*, **14**, 422–430.
- Jetter, J.J., Guo, Z., McBrien, J.A. & Flynn, M.R. (2002) Characterization of emissions from burning incense. *Science of the Total Environment*, **295**, 51–67.
- Johnson, D.L., Naylor, D. & Scudder, G. (2005) March. Red sky in day, bugs go astray. *Meeting of the Canadian Association of Geographers*, Placeholder Textp. 145. Western Division.
- Johnston, F.H. (2017) Understanding and managing the health impacts of poor air quality from landscape fires. *Medical Journal of Australia*, **207**, 229–230.
- Jones, H.B., Lim, K.S., Bell, J.R., Hill, J.K. & Chapman, J.W. (2016) Quantifying interspecific variation in dispersal ability of noctuid moths using an advanced tethered flight technique. *Ecology and Evolution*, **6**, 181–190.
- Kopplitz, S.N., Mickley, L.J., Marlier, M.E., Buonocore, J.J., Kim, P.S., Liu, T. et al. (2016) Public health impacts of the severe haze in equatorial Asia in September–October 2015: demonstration of a new framework for informing fire management strategies to reduce downwind smoke exposure. *Environmental Research Letters*, **11**, 094023.
- Korontzi, S., McCarty, J., Loboda, T., Kumar, S. & Justice, C. (2006) Global distribution of agricultural fires in croplands from 3 years of moderate resolution imaging Spectroradiometer (MODIS) data. *Global Biogeochemical Cycles*, **20**, GB2021.
- Lee, S.C. & Wang, B. (2004) Characteristics of emissions of air pollutants from burning of incense in a large environmental chamber. *Atmospheric Environment*, **38**, 941–951.
- Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters*, **10**, 745–758.
- Li, X., Wang, S., Duan, L., Hao, J., Li, C., Chen, Y. et al. (2007) Particulate and trace gas emissions from open burning of wheat straw and corn Stover in China. *Environmental Science & Technology*, **41**, 60526058.
- Li, T.T., Du, Y.J., Mo, Y., Xue, W.B., Xu, D.Q. & Wang, J.N. (2013) Assessment of haze-related human health risks for four Chinese cities

4.2. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)

Smoke effects on butterfly flight behaviour 207

- during extreme haze in January 2013. *Zhonghua Yi Xue Za Zhi*, **93**, 2699–2702.
- Li, J., Song, Y., Mao, Y., Mao, Z., Wu, Y., Li, M. *et al.* (2014) Chemical characteristics and source apportionment of PM_{2.5} during the harvest season in eastern China's agricultural regions. *Atmospheric Environment*, **92**, 442–448.
- Lim, K.S., Wolf, M., Jones, H. & Black, I. (2013) Flight mill. Patent number: PCT/GB2014/052466.
- Lin, T.C., Krishnaswamy, G. & Chi, D.S. (2008) Incense smoke: clinical, structural and molecular effects on airway disease. *Clinical and Molecular Allergy*, **6**, 3.
- Liu, T., He, G. & Lau, A.K.H. (2020) Statistical evidence on the impact of agricultural straw burning on urban air quality in China. *Science of the Total Environment*, **711**, 134633.
- Mahmud, M. (2013) Assessment of atmospheric impacts of biomass open burning in Kalimantan, Borneo during 2004. *Atmospheric Environment*, **78**, 242–249.
- McNamara, M.L., Noonan, C.W. & Ward, T.J. (2011) Correction factor for continuous monitoring of wood smoke fine particulate matter. *Aerosol and Air Quality Research*, **11**, 315–322.
- Menchetti, M., Guéguen, M. & Talavera, G. (2019) Spatio-temporal ecological niche modelling of multigenerational insect migrations. *Proceedings of the Royal Society B*, **286**, 20191583.
- Minter, M., Pearson, A., Lim, K.S., Wilson, K., Chapman, J.W. & Jones, C.M. (2018) The tethered flight technique as a tool for studying life-history strategies associated with migration in insects. *Ecological Entomology*, **43**, 397–411.
- Nesbit, R.L., Hill, J.K., Woivod, I.P., Sivell, D., Bensusan, K.J. & Chapman, J.W. (2009) Seasonally adaptive migratory headings mediated by a sun compass in the painted lady butterfly, *Vanessa cardui*. *Animal Behaviour*, **78**, 1119–1125.
- Ni, H., Tian, J., Wang, X., Wang, Q., Han, Y., Cao, J. *et al.* (2017) PM_{2.5} emissions and source profiles from open burning of crop residues. *Atmospheric Environment*, **169**, 229–237.
- Ollerton, J. (2017) Pollinator diversity: distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*, **48**, 353–376.
- Othman, J., Sahani, M., Mahmud, M. & Ahmad, M.K.S. (2014) Trans-boundary smoke haze pollution in Malaysia: inpatient health impacts and economic valuation. *Environmental Pollution*, **189**, 194–201.
- Pant, P., Shukla, A., Kohl, S.D., Chow, J.C., Watson, J.G. & Harrison, R.M. (2015) Characterization of ambient PM_{2.5} at a pollution hotspot in New Delhi, India and inference of sources. *Atmospheric Environment*, **109**, 178–189.
- Paugam, R., Wooster, M., Freitas, S. & Val Martin, M. (2016) A review of approaches to estimate wildfire plume injection height within large-scale atmospheric chemical transport models. *Atmospheric Chemistry and Physics*, **16**, 907–925.
- Radojevic, M. (2003) Chemistry of forest fires and regional haze with emphasis on Southeast Asia. *Pure and Applied Geophysics*, **160**, 157–187.
- Randerson, J.T., Chen, Y., Van Der Werf, G.R., Rogers, B.M. & Morton, D.C. (2012) Global burned area and biomass burning emissions from small fires. *Journal of Geophysical Research: Biogeosciences*, **117**, G04012.
- Rayner, J.M. (1979) A new approach to animal flight mechanics. *Journal of Experimental Biology*, **80**, 17–54.
- Scholes, R.J., Ward, D.E. & Justice, C.O. (1996) Emissions of trace gases and aerosol particles due to vegetation burning in southern hemisphere Africa. *Journal of Geophysical Research: Atmospheres*, **101**, 23677–23682.
- Shi, T., Liu, Y., Zhang, L., Hao, L. & Gao, Z. (2014) Burning in agricultural landscapes: an emerging natural and human issue in China. *Landscape Ecology*, **29**, 1785–1798.
- Srygley, R.B. & Thomas, A.L.R. (2002) Unconventional lift-generating mechanisms in free-flying butterflies. *Nature*, **420**, 660–664.
- Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T. *et al.* (2013) Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palaearctic. *Ecography*, **36**, 474–486.
- Stefanescu, C., Soto, D.X., Talavera, G., Vila, R. & Hobson, K.A. (2016) Long-distance autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses in the tropical savannah. *Biology Letters*, **12**, 20160561.
- Stefanescu, C., Puig-Montserrat, X., Samraoui, B., Izquierdo, R., Ubach, A. & Arrizabalaga, A. (2017) Back to Africa: autumn migration of the painted lady butterfly *Vanessa cardui* is timed to coincide with an increase in resource availability. *Ecological Entomology*, **42**, 737–747.
- Stefanescu, C., Ubach, A. and Wiklund, C. (2020) Timing of mating, reproductive status and resource availability in relation to migration in the painted lady butterfly, *Vanessa cardui*, *bioRxiv*.
- Steyn, V.M., Mitchell, K.A. & Terblanche, J.S. (2016) Dispersal propensity, but not flight performance, explains variation in dispersal ability. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160905.
- Streets, D.G., Yarber, K.F., Woo, J.H. & Carmichael, G.R. (2003) Biomass burning in Asia: annual and seasonal estimates and atmospheric emissions. *Global Biogeochemical Cycles*, **17**, 1099.
- Suchan, T., Talavera, G., Sáez, L., Ronikier, M. & Vila, R. (2019) Pollen metabarcoding as a tool for tracking long-distance insect migrations. *Molecular Ecology Resources*, **19**, 149–162.
- Talavera, G. & Vila, R. (2017) Discovery of mass migration and breeding of the painted lady butterfly *Vanessa cardui* in the sub-Saharan: the Europe–Africa migration revisited. *Biological Journal of the Linnean Society*, **120**, 274–285.
- Talavera, G., Bataille, C., Benyamini, D., Gascoigne-Pees, M. & Vila, R. (2018) Round-trip across the Sahara: afro-tropical painted lady butterflies recolonize the Mediterranean in early spring. *Biology Letters*, **14**, 20180274.
- Tan, Y.Q., Dion, E. & Monteiro, A. (2018) Haze smoke impacts survival and development of butterflies. *Scientific Reports*, **8**, 15667.
- Toledo, T.E., Pohlman, H.A.J., Gehrke, V.M.R. & Leyva, G.A. (2005) Green sugarcane versus burned sugarcane—results of six years in the Soconusco region of Chiapas, Mexico. *Sugar Cane International*, **23**, 20–27.
- Ukbutterflies.co.uk. (2020) UK Butterflies - Painted Lady - *Vanessa cardui* [online]. <https://www.ukbutterflies.co.uk/species.php?species=cardui> (accessed 28 January 2020).
- Vadrevu, K.P., Lasko, K., Giglio, L. & Justice, C. (2015) Vegetation fires, absorbing aerosols and smoke plume characteristics in diverse biomass burning regions of Asia. *Environmental Research Letters*, **10**, 105003.
- Wang, X., Chen, M., Zhong, M., Hu, Z., Qiu, L., Rajagopalan, S. *et al.* (2017) Exposure to concentrated ambient PM_{2.5} shortens lifespan and induces inflammation-associated signalling and oxidative stress in *Drosophila*. *Toxicological Sciences*, **156**, 199–207.
- Wardlaw, J.C., Elmes, G.W. & Thomas, J.A. (1998) Techniques for studying *Maculinea* butterflies: I. Rearing *Maculinea* caterpillars with *Myrmica* ants in the laboratory. *Journal of Insect Conservation*, **2**, 79–84.
- Willson, M.F. & Traveset, A. (2000) The ecology of seed dispersal. *Seeds: The Ecology of Regeneration in Plant Communities*, **2**, 85–110.
- Wooster, M.J., Gaveau, D., Salim, M.A., Zhang, T., Xu, W., Green, D.C. *et al.* (2018) New tropical peatland gas and particulate emissions factors indicate 2015 Indonesian fires released far more particulate

208 Yanan Liu et al.

- matter (but less methane) than current inventories imply. *Remote Sensing*, **10**, 495.
- Yadav, I.C. & Devi, N.L. (2018) Biomass burning, regional air quality, and climate change. *Earth Systems and Environmental Sciences. Edition: Encyclopedia of Environmental Health*. Waltham, MA, United States: Elsevier.
- Zhang, T., Wooster, M.J., Green, D.C. & Main, B. (2015) New field-based agricultural biomass burning trace gas, PM_{2.5}, and black carbon emission ratios and factors measured in situ at crop residue fires in eastern China. *Atmospheric Environment*, **121**, 22–34.
- Zhang, L., Liu, Y. & Hao, L. (2016) Contributions of open crop straw burning emissions to PM_{2.5} concentrations in China. *Environmental Research Letters*, **11**, 014014.
- Zhang, H., Hu, J., Qi, Y., Li, C., Chen, J., Wang, X. *et al.* (2017) Emission characterization, environmental impact, and control measure of PM_{2.5} emitted from agricultural crop residue burning in China. *Journal of Cleaner Production*, **149**, 629–635.

Accepted 6 September 2020
First published online 2 October 2020
Associate Editor: Simon Leather

4.3 *Vanessa cardui*(*Painted lady butterfly*)

Butterflies have been at the forefront of research on insect migration since the beginning of such studies (Tutt, 1902; C. B. Williams et al., 1930), providing valuable insights into migration mechanisms, patterns, and ecological significance (Reppert and de Roode, 2018; Zhan et al., 2011). *Vanessa cardui* stands out as a globally distributed species, making it an ideal subject for studying migration. It can be found on every continent across the world, with the exception of South America and Antarctica (Ecuador, 1992). Its wide distribution not only indicates the capacity of *Vanessa cardui* to adapt to diverse environmental conditions (Nesbit et al., 2009; Talavera et al., 2023) but also indicates a tight link to the distribution of host-plants as *Vanessa cardui* can utilize a wide range of plants for feeding and reproduction (Celorio-Mancera et al., 2016; Talavera et al., 2023). This flexibility in food sources contributes to its ability to migrate across different ecosystems and environments.

Vanessa cardui is renowned for its migratory behavior, particularly between Africa and Europe, which has been extensively studied over the past two decades (Comay et al., 2020; Pollard, 1998; Stefanescu, 2011; Stefanescu et al., 2013; Stefanescu et al., 2016; Talavera et al., 2018; Talavera and Vila, 2017). The annual migratory loop between tropical West Africa and Scandinavia is recognized as the longest known regular insect migration circuit, spanning approximately 14,000 km (Hu et al., 2021; Menchetti et al., 2019; Stefanescu et al., 2013), which demonstrates its ability to traverse vast distances across different landscapes and habitats. Moreover, a similar multi-generational pattern is likely observed in North America, where *Vanessa cardui* migrates on an annual basis from Mexico to the northern regions of the United States and Canada (Shapiro, 2019; Talavera and Vila, 2017).

During their migration, *Vanessa cardui* exhibits a broad altitude range, with flights occurring between 150m and 1200m above ground level. However, it is most common for the butterflies to migrate at altitudes of several hundred meters above the ground during both spring and autumn migrations. In spring migration, the peak densities are recorded in the lowest radar range gate, specifically between 150m and 195m,

indicating that the majority of migrants tend to fly at lower altitudes. Conversely, during the autumn migration, over 60% butterflies are observed between 200m and 600m, with the highest density occurring between 350m and 400 above the ground (Stefanescu et al., 2013).

The migratory nature of *Vanessa cardui* makes it an excellent species for investigating the impact of LFS and weather conditions on migratory insects. Given the occurrence of fires in Africa and the potential encounters during migration, studying the impact of smoke becomes relevant. The altitude at which smoke from landscape fires reaches varies depending on several factors, including fire size, intensity, weather conditions, and vegetation type (Pausas and Keeley, 2021). It has been observed that aerosols from Canada forest fires can reach heights ranging from 50m to 1400m or even higher (Stefanescu et al., 2013), indicating the potential for *Vanessa cardui* to experience smoke exposure during their migration, particularly when they are near ground level. Therefore, investigating the influence of LFS and weather conditions on *Vanessa cardui* migration can provide valuable insights into the interactions between migratory behavior and environmental factors, including smoke exposure.

Although the abundance of *Vanessa cardui* in Britain varies greatly between years and their abundance in the UK, it remains one of the most common immigrant species in the region (Asher et al., 2001), particularly during the summer period, facilitating its accessibility for research purposes. In our study, *Vanessa cardui* were acquired from *Gribblybugs LLP*, a UK entomological supplier. Although the specific information regarding the origin and history of these *Vanessa cardui* is not available, all the butterflies used in our comparative experiments were sourced from the same supplier.

Overall, *Vanessa cardui* has been chosen as our study species and also their flight behavior is considered representative of a broad range of migrants due to its extensive distribution, adaptability, and ability to undertake long-distance migrations.

4.4 Tethered Flight Mill Techniques

As mentioned in Section 4.2, a tethered flight mill (TFM) system was applied to quantitatively study the flight performance of butterflies. Since the 1950s, TFMs were initially used to study insect flight behavior, which was introduced by (Hocking et al., 1953), with stainless steel hypodermic tubing arms, Teflon bearings with magnetic levitation, and infrared sensors. It is one of the most adaptable techniques that has been extensively used in the laboratory (Attisano et al., 2015), which can measure migratory insects in size varying between aphids and butterflies (H. B. Jones et al., 2016; Minter et al., 2018). For example, TFMs were used to measure the flight capacity of *Cerotoma trifurcate* (Bean leaf beetle) (Krell et al., 2003), *Chrysoperla sinica* (The green lacewing) (Z. Liu et al., 2011), and *Bactrocera oleae* (The olive fruit fly) (X.-G. Wang et al., 2009). Compared with entomological radars to track insect migrations, TFMs are far more economical as it is constructed by using small low cost components (Okada et al., 2018). Moreover, the TFM technique is capable of continuously measuring the flight parameters of insects over a long period of time during insect dispersal and migration, including flight speed, distance, and duration. For instance, *Sitodiplosis mosellana* (Orange Wheat Blossom Midge) has been studied on a flight mill system for 24 hours to explore their flight performance and it was found that the average flight speed of female *S. mosellana* was $0.17 \text{ m}\cdot\text{s}^{-1}$, while the average speed of males was $0.15 \text{ m}\cdot\text{s}^{-1}$ (Hao et al., 2013; Lopez et al., 2014).

4.4.1 Butterfly preparation for TFMs

Before we quantitatively studied flight performance of butterflies, there are several steps to complete before putting them on the TFMs, as can be seen in Figure 4.1. Special pins were constructed to connect the subjects to the TFMs, each made by bending a small length (around 3 cm) of steel wire (Figure 4.1a) into a small loop (Figure 4.1b) to which the butterflies could be firmly glued (Nesbit et al., 2009). Because of the fragility of the butterfly wings, all subjects were kept chilled so they would be in a torpid state in prior to this procedure, minimising the risk of damaging

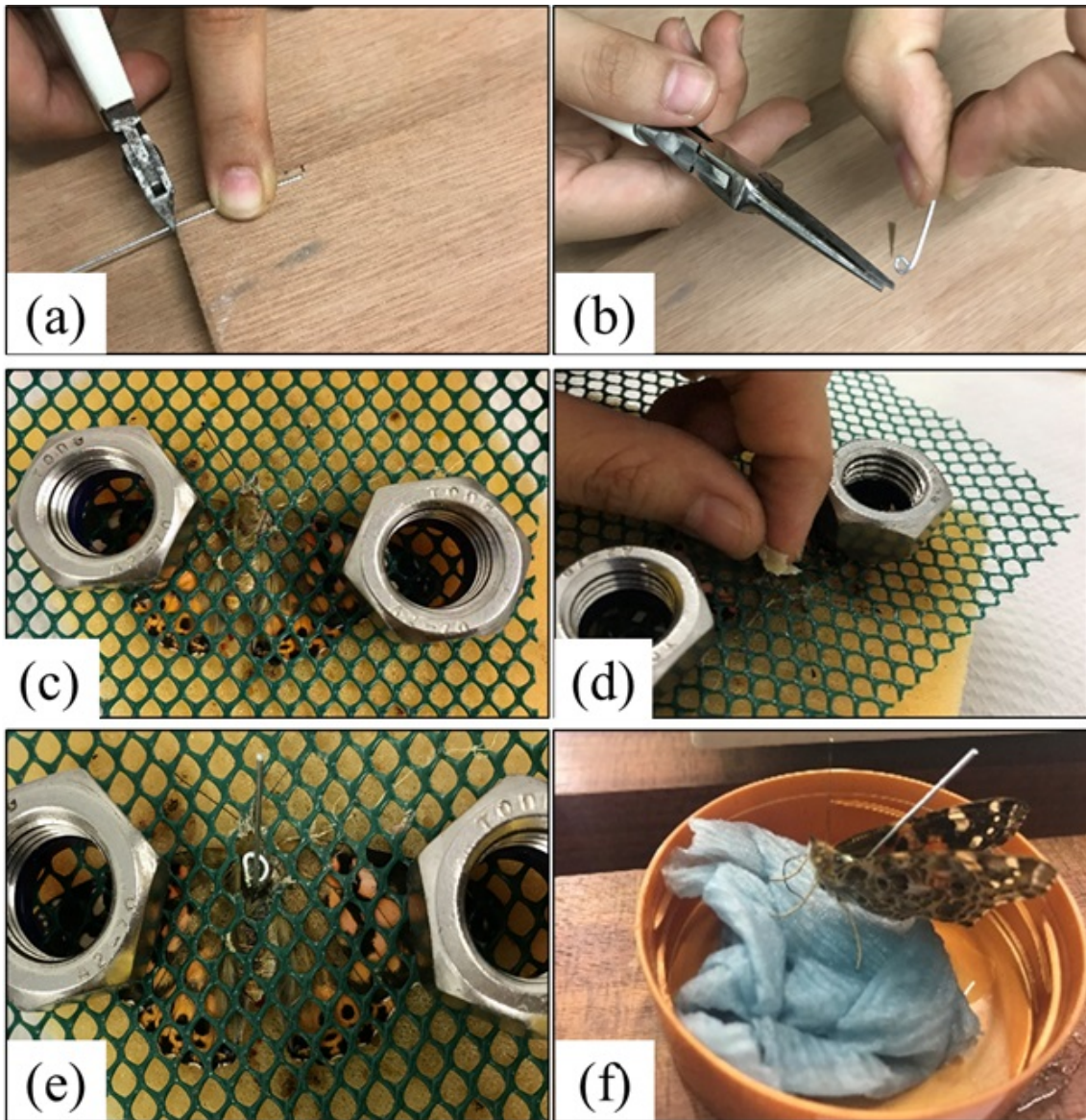


Figure 4.1: Preparation of processed *Vanessa cardui* L. in the preparation stage before putting *Vanessa cardui* L. on the tethered flight mill technique (a) cutting a 3 cm length of steel wire; (b) making a pin by bending the end into a loop; (c) secured butterfly with net; (d) removing the surface of thorax (e) pin glued to the surface of thorax; (f) fed with honey water.

their wings and ensuring they were not too active too soon. Each butterfly in its chilled state was placed on a sponge mat and secured with a net and two small weights to avoid it being damaged or escaping during the attachment of the pin (Figure 4.1c). The scales on the surface of the butterfly thorax were cleared (Figure 4.1d) to make sure that the pin could be firmly glued to the butterfly (Figure 4.1e). The pin facilitates weighing, feeding, and minimizes stress to the butterfly during preparation for flight. Before placing the butterflies on the TFM system, they were fed with a mixture of cool water and honey in a ratio of 9:1 by weight by letting them drink from pieces of paper tissue dipped in the liquid (Figure 4.1f). Each butterfly was then mounted on its TFM system at an appropriate angle to ensure normal flight.

4.4.2 TFM accuracy test on flight performance

Before starting the experiments to study the impact of smoke pollution on insect flight behaviour, moths from the family of Noctuidae were used to practice the TFM operation and check the accuracy on flight performance. These were selected as they are common within the British Isles with over 400 species and easy to capture during night (Bates et al., 2013; Yela and Holyoak, 1997). Moreover, their size and flight speed are similar to that of butterflies (H. B. Jones et al., 2016; Minter et al., 2018), and they also lead a seasonal migration between summer and winter (Alerstam et al., 2011).

4.4.2.1 Nocturnal moth species used for TFM testing

A light trap was placed at Rothamsted Research Institution, Harpenden, UK (located at $51^{\circ}48'38''\text{N}$, $0^{\circ}22'36.5''\text{W}$) on selected nights between June to July 2019 (Figure 4.2) as large noctuid moths migrate over UK during summer periods (Wood et al., 2009). The light bulb was switched on from 9 p.m. to 4 a.m. local time every day, and some cardboard egg boxes were placed in the base of the light trap to provide a more enclosed environment for any captured moths to rest on. In total, forty-three moths were captured in one month.



Figure 4.2: A light trap for capturing nocturnal moths. The white sheet is used to reflect the light and increase the overall light intensity.

Different types of nocturnal moth moths (Family Noctuidae) were captured, including *Autographa gamma* (Sliver Y), *Noctua pronuba* (Large yellow underwing), *Phlogophora meticulosa* (Angle shades), *Xestia c-nigrum* (Setaceous Hebrew Character), *Agrotis exclamationis* (Heart and dart), *Apamea monoglypha* (Dark arches), *Amphipyra pyramidea* (Copper underwing). The method of mounting the moths on the TFM is identical to that described in Section 4.4.1.

4.4.2.2 Characterising flight ability of noctuid moths with TFMs

There were totally 28 noctuid moths flown on the TFM. Although the number of insects caught varied for each species, the average of all flight variables of different moth species recorded with TFM over one-hour time duration was calculated (Table 4.1), including total flight distance (m), average speed ($\text{m}\cdot\text{s}^{-1}$), maximum speed ($\text{m}\cdot\text{s}^{-1}$), and flight durations (minutes). Approximately 71% moth species could fly

on TFMs over 30 minutes, and 57% of moth species had an average flight speed greater than or equal to $0.37 \text{ m}\cdot\text{s}^{-1}$. In terms of flight distance, four insect species containing, *Xestia c-nigrum*, *Phlogophora meticulosa*, *Autographa gamma*, and *Noctua pronuba* had similar flight distance with average value of 1356 m, and *Amphipyra pyramidea* and *Apamea monoglypha* had similar flight distance with average value at 740 m. However, *Agrotis exclamatoris* had the slowest flight speed although it can almost fly for one hour.

Besides, H. B. Jones et al. (2016) also quantified the dispersal ability of noctuid moths using a TFM by comparing the maximum speed and total flight distance measured for the whole night (from 21:00 BST until morning). Thus, the flight distance and maximum speed collected by H. B. Jones et al. (2016) from the same species were also put in Table 4.1. We found that noctuid moths were ranked similarly in terms of maximum speed in both experiments. The data collected from this experiment suggests that the TFMs appear to be functioning correctly. Although the maximum speed of the noctuid moths was slight lower in the pilot experiment, which may be due to the different numbers of insects and flight duration, the TFMs used in the pilot experiment is still trustworthy we therefore have applied it to the formal butterfly experiment (See Section 4.2).

4.5 Smoke Consistency Measurements

As well as finding a fuel that produced a steady output of smoke, it was also important to understand the distribution of smoke within the combustion chamber to ensure that all butterflies on each of the TFMs would be exposed to the same concentrations. An experiment was conducted to produce smoke within the combustion chamber and measure its concentration at various locations within the chamber using a series of instruments.

To determine the consistency of smoke concentration in the combustion chamber, five laser-based particulate matter measurement devices (TSI SidePak Personal Aerosol

Table 4.1: Descriptive statistics of flight behaviour variables (total flight distance, average speed, maximum speed, and flight duration) from six moth species (Family: Noctuidae) within one hour on tethered flight mill (TFM) collected from our pilot experiment, and flight behaviour variables (total flight distance and maximum speed) collected from H. B. Jones et al. (2016). Maximum speeds recorded from both experiments are in bold for comparison.

Moth species	Our pilot experiment				H. B. Jones et al., 2016			
	Number of insects	Total flight distance (m)	Average speed (m·s ⁻¹)	Maximum speed (m·s ⁻¹)	Flight duration (min)	Number of insects	Total flight distance (m)	Maximum speed (m·s ⁻¹)
<i>Xestia c-nigrum</i>	5	1389	0.47	0.94	49	59	5039	1.17
<i>Agrotis exclamatoris</i>	8	167	0.05	1.26	57	18	6935	1.46
<i>Autographa gamma</i>	4	1321	0.65	1.37	34	13	5168	1.54
<i>Amphipyra pyramidea</i>	4	718	0.66	1.42	18	14	12352	1.80
<i>Noctua pronuba</i>	2	1338	0.66	1.53	34	37	111596	1.62
<i>Apamea monoglypha</i>	3	762	0.79	1.69	16	39	9039	2.06

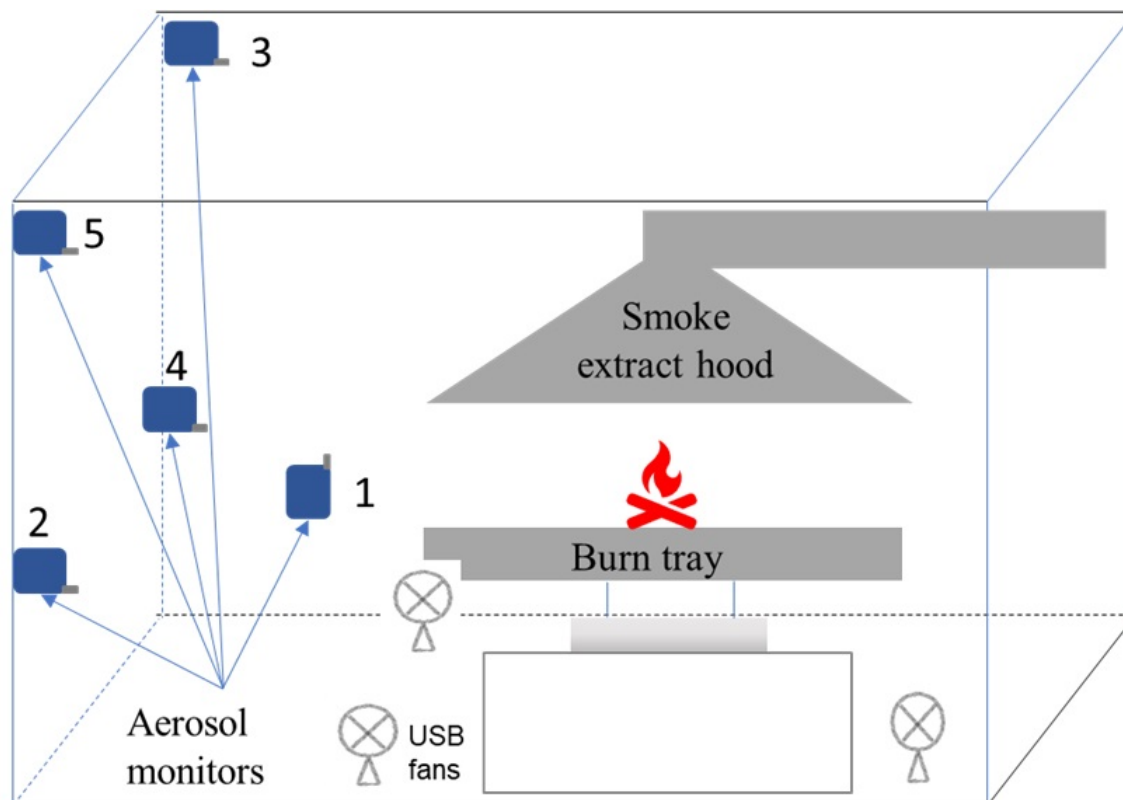


Figure 4.3: TSL SidePak Aerosol Monitors were put in different heights and positions in the combustion chamber to record $\text{PM}_{2.5}$ concentrations, which were created by burning straw in the burn tray (SidePak 1 in the middle of the empty space; SidePak 2 is the bottom left, SidePak 3 is on the top right, SidePak 4 is on the bottom right and SidePak 5 is on the top left). Three small fans were put next to the burn tray to make the distribution of particles uniform in the whole chamber.

Monitor AM520) were placed in the area where the TFMs were placed, allowing these sensors to cover as much of the general area occupied by the TFMs as possible, see Figure 4.3. The maximum limitation of $\text{PM}_{2.5}$ concentrations recorded by the AM520 was $100 \text{ mg}\cdot\text{m}^{-3}$, and we applied an optimal calibration factor of 0.27 from (Vernooij et al., 2022). Different weights of straw were burned in the burning tray to create different smoke conditions, including 15 g, 30 g, and 60 g. Small fans were used within the chamber to encourage mixing of the smoke within the space. Time-series $\text{PM}_{2.5}$ concentrations generated from burning 15 g, 30 g, 60 g were recorded by the five aerosol monitors at different locations, which is shown in Figure 4.4. The variation in $\text{PM}_{2.5}$ concentrations over time is very similar from the different positions which indicated that the smoke concentration was relatively uniform throughout the entire combustion chamber.

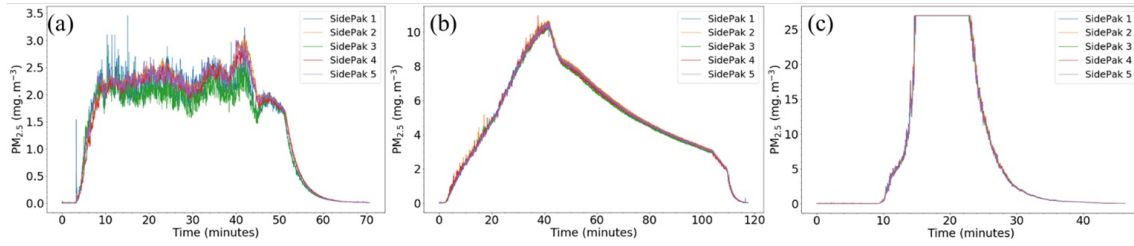


Figure 4.4: Time-series $PM_{2.5}$ concentrations recorded by the five SidePak Aerosol Monitors shown in Figure 4.3 when burning (a) 15 g straw, (b) 30 g straw, (c) 60 g straw. The instrument becomes saturated at $PM_{2.5}$ concentrations above $27 \text{ mg}\cdot\text{m}^{-3}$ after applying calibration factor of 0.27.

4.6 Summary

In this chapter, we firstly quantitatively tested the impact of smoke conditions from biomass burning on flight behaviour of *V. cardui* including total flight distance, average flight speed, maximum flight speed, and flight duration. *V. cardui* has been determined as the research target as they have a strong flight ability, are easy to acquire identical individuals, and are sensitive to environmental change. The incense sticks have been used to create different smoke concentrations as they create similar smoke components as biomass burning and are easy to control. A suitable technique - TFM was applied to record the flight performance of migratory insects, which allows us to quantitatively compared the flight behaviour of butterflies in different smoke conditions. Although the total test only lasted for 1 hour, it determined that dense smoke conditions negatively impact the flight behaviour of *V. cardui*, both in flight speed, duration, and ultimately flight distance.

Chapter 5

Impacts of light smoke conditions on butterfly flight performance over long flight periods

5.1 Introduction

In chapter 4, butterflies were exposed to three increased dense smoke conditions in which the PM_{2.5} concentrations achieved 4000 $\mu\text{g}\cdot\text{m}^{-3}$ in the first 20 minutes. And only the flight behaviour of butterflies in the first 30 minutes on the tethered flight mill (TFM) was studied. The results showed that butterfly flight speed decreases significantly when smoke concentration exposure increases, as did other flight variables. In the real world, *Vanessa cardui* was observed that could fly around 7-8 hours per day during migration (Abbott, 1951; Stefanescu et al., 2013). Thus, to comprehensively understand butterfly response to various smoke conditions during their migration, following Chapter 4, we continue our exploration of smoke pollution from landscape fires on the flight performance of *Vanessa cardui*.

In this chapter, butterfly individuals were exposed to three smoke conditions (with

PM_{2.5} concentrations at 120 $\mu\text{g}\cdot\text{m}^{-3}$, 371 $\mu\text{g}\cdot\text{m}^{-3}$ and 832 $\mu\text{g}\cdot\text{m}^{-3}$) from biomass burning for a longer period - 6 hours. This period was determined by a pilot experiment investigating the maximum flight duration of *Vanessa cardui*, during which 16 representative butterflies were selected and put on the TFM for a 24-hour flight test. The flight behaviours of butterflies in the smoke conditions are then compared with the ones in clean-air conditions. Then, we designed another experiment to specifically explore which smoke substances might affect the flight behaviour of butterflies, especially particles. Furthermore, scanning electronic microscopy was applied to check whether any particles were on the body of the butterflies - and if so what might this mean for how the smoke physically affects the butterfly behaviour.

5.2 Background

Some evidence has been presented in Chapter 4 to show that smoke negatively influenced butterfly flight performance, but the smoke conditions created were very high (with a PM_{2.5} concentration up to 4000 $\mu\text{g}\cdot\text{m}^{-3}$), the flight duration of butterflies was limited to only 30 minutes in the designed experiments, and some butterflies were re-flown on the instrument. Whilst a link between flight performance and PM_{2.5} concentration could be demonstrated, more evidence is still needed to clarify how realistic smoke concentrations may influence the long-term movement of insects. Based on the previous limitations, this study aims to evaluate the effect of actual concentrations of smoke from biomass burning on insects over a more extended flight period and understand how butterflies might respond to the biomass smoke polluted conditions when exposed for the first time, and also explore whether particulate matter or gaseous compounds from smoke are the primary factors to affect flight behaviour. We hypothesised that biomass smoke has a detrimental effect on flight behaviour, either via damage to eyes, respiratory blockages, an increase of body weight by particulate matter, or via gas toxicity.

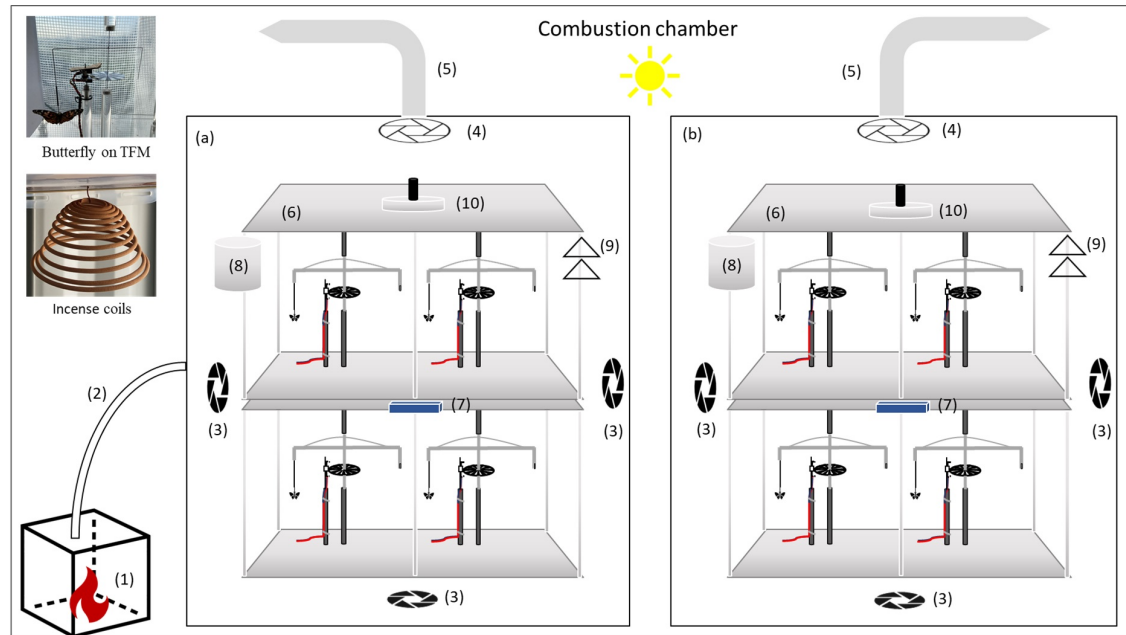


Figure 5.1: A diagram of the experimental setup. Individuals were put in (a) smoke enclosure or (b) control enclosure. Smoke was released from burning incense coils in a smoke box (1) and transported to the smoke enclosure by tube (2). Three axial fans (3) were placed in right, left, and underneath the enclosure to promote air circulation, exhaust fan (4) and extract duct was to remove excess smoke. The TFM equipment (6) was used to record the butterfly flight performance. A particulate sensor (7) and PurpleAir PA-II SD air quality sensor (8) were to record $PM_{2.5}$ concentration. A temperature-humidity sensor (9) and light intensity sensor (10) recorded the environmental factors.

5.3 Methodology

5.3.1 Experiment setup

All experiments were carried out in the King's Combustion Chamber indicated in Figure 5.1, located at Rothamsted Research, Harpenden, UK, from September to November 2020. This season coincides with the autumn migration period of *Vanessa cardui* (Stefanescu et al., 2017). One side of the chamber (facing 296° , northwest) was open externally and covered with a transparent tarpaulin, which allowed natural light to enter directly while not being affected by adverse environmental conditions (e.g. rain, wind).

Within the combustion chamber space, two further enclosures (one for containing

the smoke, and one for control conditions) were constructed using a frame covered with transparent plastic sheeting. Both enclosures were placed near to the open side of the chamber to allow natural light in. A butterfly was attached to a tethered flight mill (TFM) instrument, which allows them to fly around in a circle to assess maximum flight duration and distance within a set period (H. B. Jones et al., 2016; Minter et al., 2018), for a diagram of the TFM set-up, see Y. Liu et al. (2021). Four butterflies can fly simultaneously as four tethered flight mills (TFMs) were placed in each enclosure and were separated by white paper to act as a visual barrier to minimise mutual influence between butterflies.

Particulate sensors (Plantower PMS5003) and PurpleAir PA-II SD air quality sensors were placed in the middle of the enclosures to record the $PM_{2.5}$ concentration timeseries throughout each experiment. Three axial fans were placed in each enclosure (two at the sides and one at the bottom) to ensure even particle distribution and airflow. The speed and positioning of the fans were adjusted to ensure that they gently mixed the smoke but did not cause turbulence that would affect the flight performance of butterflies. The solenoid control system is used to control the smoke concentration, where the smoke detection sensor and the control panel are connected via a wireless network. The detected smoke level is transmitted to the control panel. When the detected smoke level exceeds the set threshold on the control panel, the excess smoke is vented to the outside to as best as possible ensure that the smoke concentration in the smoke enclosure remains within a set range. A photosynthetically active radiation (PAR) light sensor (SQ-100X) was placed on the top of the TFM to record the sunlight intensity (wavelength 400-700 nm), aiming at checking whether the light intensity in the two enclosures is similar. A temperature & humidity sensor (BME280) was put to the right side of the TFM. An extractor fan was activated to remove all smoke in the two enclosures once the experiment was completed and to maintain consistent airflow through each of the enclosures. Replacement air was allowed into the enclosure either through the smoke inlet, or through a small opening at the base for the control enclosure. All sensors were connected to an Arduino controller (an open-source electronics platform based on

easy-to-use hardware and software) to record data every five seconds.

5.3.2 Determination of butterfly flight duration on TFM

Vanessa cardui was observed by vertical-looking radar to fly for around 7-8 hours during their migration on most days (Abbott, 1951; Stefanescu et al., 2013), however, we do not know the flight duration of *Vanessa cardui* on a TFM. Thus, a pool of 20 adult *Vanessa cardui* that freshly emerged from pupae with average wingspan length at 62 mm was chosen to check the flight duration on TFM. To figure out the maximum flight duration of *V. cardui* for one day on TFMs, a pilot experiment was performed, where 16 butterflies in good condition were selected from the whole pool of 20 butterflies to fly on the TFM under clean-air conditions. Those butterflies were put on the TFM for 24 hours (12 hours daytime and 12 hours night-time) in August 2020. Artificial light was used in the first 12 hours to simulate daytime conditions. During the experiment, the butterfly individuals were fed once with honey water (water:honey=9:1) before being placed on the TFM each time, to provide substantial energy for flying. An air conditioner was applied to keep the temperature in the flight chamber at 25°C.

Figure 5.2 shows an example of a group of eight butterflies' flight speed and how it varied over 24 hours. We found that most of the butterflies flew in the first 8 hours (daytime). The total flight duration of the butterflies in 24 hours has been calculated, with an average of 3.5 hours and a maximum of 5.8 hours. In response to this flight behaviour, butterflies in the main experiment were put on the TFM for 6 hours during daytime conditions. The aim being to further investigate the smoke impact on butterfly flight performance, in a way that is expected to replicate natural conditions more closely than the experiment in Chapter 4 (i.e. with lower smoke concentrations, more comparable to the natural environment, and a longer flight duration more akin to what might be experienced during migration).

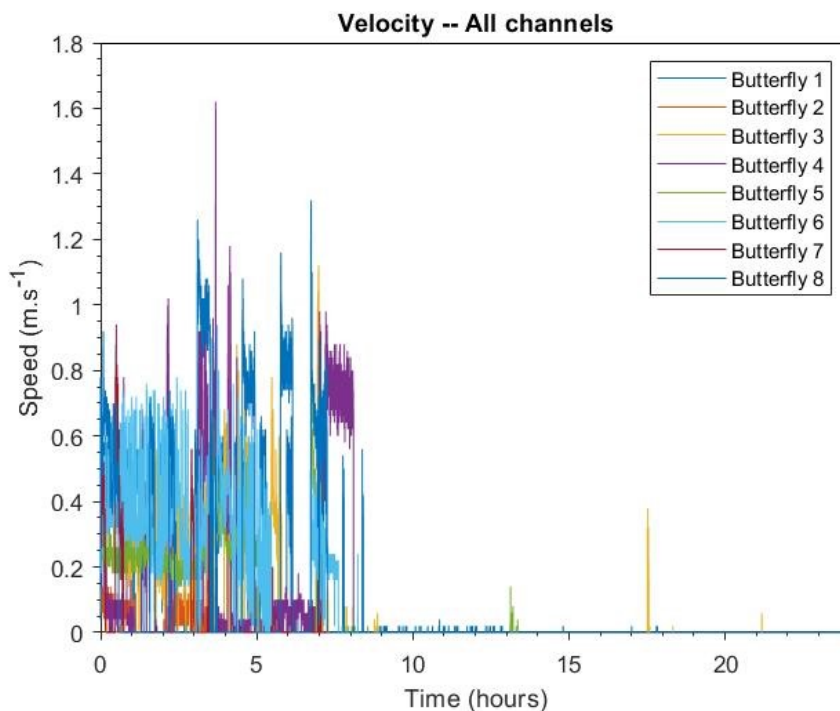


Figure 5.2: Flight speed of eight sample butterflies flown under clean-air conditions for 24 hours. Most have ceased flying by 8 hours.

5.3.3 Experiment design

There were two new experiments - building on that in Chapter 4 - each designed to further investigate how smoke from biomass burning impacts the flight behaviour of *Vanessa cardui*, summarised in Table 5.1. Experiment A compared the flight performance of the butterflies in smoke and clean-air conditions. Experiment B investigated what smoke components (trace gases or particulates) might affect the butterflies. In both Experiment A and B, butterflies were put on the TFM for six hours as *Vanessa cardui* demonstrated that they can continuously fly for around six hours or more on the TFM in the pilot experiment. The total flight distance (m), average flight speed (m.s⁻¹), maximum flight speed (m.s⁻¹), flight duration (minutes), and percentage of flight duration (%) have been calculated in both enclosures for the further analysis. After exposure to smoke, we then conducted an analysis on a proportion of the butterflies to determine whether there was any evidence of the particles coating their bodies using scanning electron microscopy (SEM).

Table 5.1: Summary of experiment design, indicating the number of butterflies used in Experiments A and B, where CC represents control condition, LS represents low smoke, MS represents medium smoke and HS represents high smoke.

Replicate	Experiment A				Experiment B			
	CC	LS	CC	MS	CC	HS	Gas	HS
i	4	4	4	4	4	4	4	4
ii	4	4	4	4	4	4	4	4
iii	4	4	4	4	4	4	4	4
iv	4	4	4	4	4	4	4	4
Replacement	8		8		8		8	

5.3.3.1 Experiment A: Investigating flight performance of *V. cardui* in smoke and clean-air conditions

The aim of this experiment was to compare the flight behaviour of butterflies in different smoke concentrations - low, medium and high smoke (LS, MS, and HS) - based on the $\text{PM}_{2.5}$ concentrations in the smoke enclosure compared to the clean air conditions (control enclosure). The concentrations selected were substantially lower than those used in Chapter 4, and more akin to what might be experienced in the natural environment in heavily smoke-polluted areas. As planned in Table 5.1, three comparative sub-experiments were conducted in total and each of them has four replicates with four butterflies in the smoke condition and four butterflies in the control condition per replicate.

One reason that $\text{PM}_{2.5}$ concentrations are used to demonstrate the severity of the smoke is that it is easy to measure with low-cost sensors that react quickly to changing concentrations (since they use laser-based measurement techniques) PM is also the dominant health-impacting component of landscape fire smoke, that also has a visible effect on the opacity of the atmosphere (Nguyen et al., 2021; Roberts and Wooster, 2021). We set the LS, MS, and HS conditions as $150 \mu\text{g}\cdot\text{m}^{-3}$, $450 \mu\text{g}\cdot\text{m}^{-3}$, and $900 \mu\text{g}\cdot\text{m}^{-3}$ of $\text{PM}_{2.5}$ respectively, selected because $\text{PM}_{2.5}$ concentrations varied between $10 \mu\text{g}\cdot\text{m}^{-3}$ and $1000 \mu\text{g}\cdot\text{m}^{-3}$ from 1200 m altitude to the surface during intense burning seasons according to data in the WACCM global Chemistry

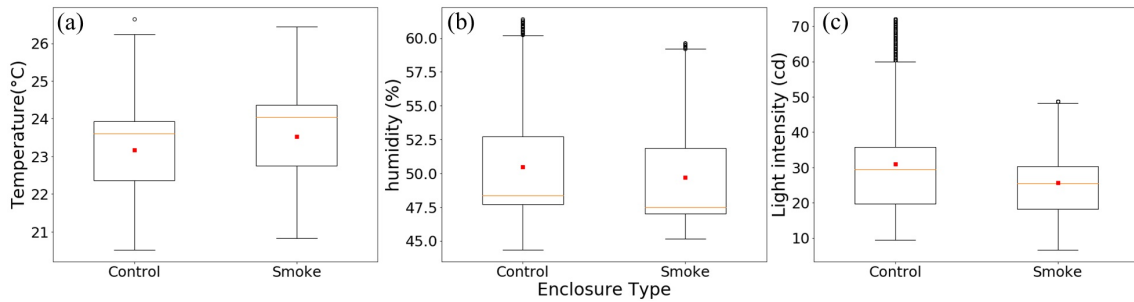


Figure 5.3: Atmospheric conditions in the smoke enclosure and control enclosure, measured across all experiments for (a) air temperature, (b) relative humidity, and (c) light intensity. Box plots illustrate the upper quartile (75th percentile), the median (50th percentile) and the lower quartile (25th percentile), with upper whiskers reaching $Q_3 + 1.5 \times \text{interquartile range (IQR)}$ and lower whiskers $Q_1 - 1.5 \times \text{IQR}$. The red square is the mean.

model (WACCM 2021). $\text{PM}_{2.5}$ concentrations were considered in this altitude range because *V. cardui*, typically fly in a wide altitude range between 150 m to 1200 m during large-scale migration (Stefanescu et al., 2013).

Smoke conditions were created by burning unscented incense coils in a large-sealed box - as this could generate smoke at a consistent rate for over 6 hours. As shown in Chapter 3, the composition of the smoke from burning incense is similar to that from standard biomass burning (W.-H. Cheng et al., 2015; Jetter et al., 2002; Lui et al., 2016). To ensure that the incense coils burn at a relatively constant rate, an air pump was used to supply a steady supply of fresh air to the smoke box. Moreover, the smoke box was connected with another two pumps, one was to deliver a constant smoke concentration to the smoke enclosure that was controlled via solenoids, while the other one was responsible for discharging the excess smoke into the filter. The solenoids were controlled using an Arduino controller linked to a particulate sensor (Plantower PMS5003) inside the smoke enclosure, which allowed a target $\text{PM}_{2.5}$ concentration to be set and ideally maintained. Apart from the presence of smoke, the other environmental factors were similar in the two enclosures, including temperature, humidity, and light intensity, as shown in Figure 5.3.

5.3.3.2 Experiment B: Investigating flight performance of *V. cardui* in smoke conditions with and without particles

In this experiment, we compared the flight performance of *V. cardui* in HS condition (smoke enclosure) and gas (only) condition (control enclosure). The gas condition is the same as in the HS condition, but with the particulates filtered out. The aim was to investigate whether it is particles or trace gases in the smoke that affect the butterfly flight performance. One comparative sub-experiment was planned, which included four replicates with four butterflies in both HS and gas conditions per replicate.

To generate the HS and gas conditions, a pump with two pipes was connected to the smoke box, and two pipes were connected to the smoke enclosure and control enclosure respectively. Smoke was transported to the smoke enclosure directly by one pipe while gaseous emissions were transported to the control enclosure by another pipe where the smoke passed through a filter to remove all particulates. The most significant gas compounds present in biomass burning (and incense stick burning) are CO₂, CO, CH₄ (Akagi et al., 2011). These three compounds were measured using a Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyser during experiment B. Two tubes were connected to the gas analyser via a valve to allow measurement of either smoke or gas conditions. The concentrations of three gases were similar in two enclosures during the experiment, including CO₂, CO, CH₄, as shown in Figure 5.4.

5.3.4 Post-exposure examination using scanning electron microscopy (SEM)

To investigate the possible impact of particulate matter on the body of the exposed butterfly, SEM was used to observe the distribution and number of particles (PM₁/PM_{2.5}/PM₁₀) stuck to the butterfly after their exposure to different smoke conditions (control, LS, MS, and HS conditions). The forewing, hindwing, antenna, head, eye, and abdomen were all examined.

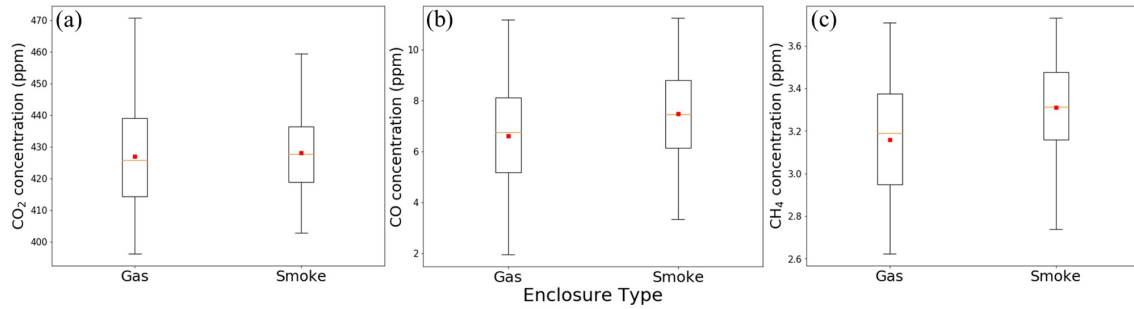


Figure 5.4: Boxplots showing gaseous emissions from high smoke conditions in smoke enclosure and gas conditions in control enclosure, measured across all experiment B for (a) CO₂ concentration (b) CO concentration and (c) CH₄ concentration. Box plots illustrate the upper quartile (75th percentile), the median (50th percentile) and the lower quartile (25th percentile), with upper whiskers reaching $Q_3 + 1.5 \times$ interquartile range (IQR) and lower whiskers $Q_1 - 1.5 \times$ IQR. The red square is the mean and outliers beyond these limits are plotted as black circle.

Butterfly specimens were frozen at -20°C for 48-72 hours and transferred to a desiccator upon arrival. Specimens were dissected to remove wings, head, antennae, and abdomen then mounted on SEM stubs. Wing and antenna were placed on sticky carbon tape and covered with another layer of carbon. However, the head and abdomen parts were glued onto SEM stubs with silver paint, and specimens were sputter coated with gold. All samples were then imaged at Rothamsted Research's Bioimaging Facility using a JEOL JSM-6360LV SEM with 3.0 nm resolution and 20 mm observation distance. For each body part we selected three areas ($100 \times 90 \mu\text{m}^2$) randomly and $1500\times$ magnification was used to observe PM₁, PM_{2.5}, PM₁₀.

5.3.5 Statistical analysis

The data of each butterfly mounted on the TFM was analysed every 5 seconds using a script written in MATLAB (version R2019a) to obtain a series of flight variables, including total flight distance (m), average speed ($\text{m}\cdot\text{s}^{-1}$), maximum speed ($\text{m}\cdot\text{s}^{-1}$), and time spent flying (minutes). The descriptive statistics have been driven to understand the flight performance of butterflies, including mean value and standard deviation (SD). Moreover, Univariate Analysis of Variance (ANOVA) is also used to check if the significant difference of average flight speed of each butterfly among three control groups in the sub-experiments in Experiment A. The univariate normality

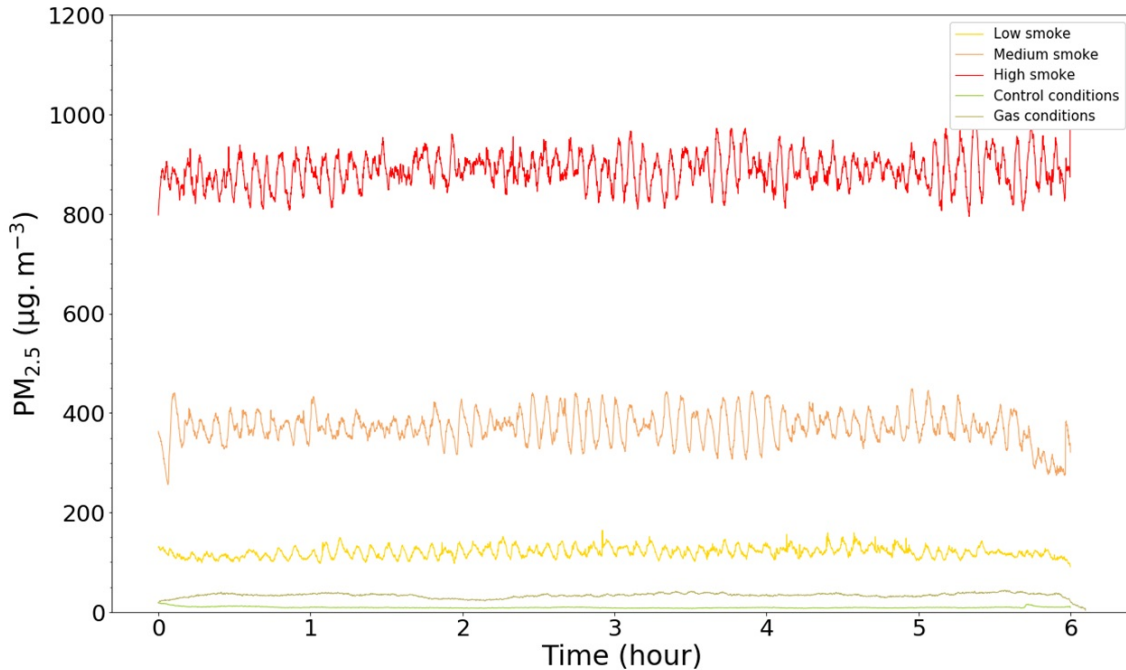


Figure 5.5: Timeseries of mean atmospheric $\text{PM}_{2.5}$ concentration of different smoke conditions calculated from the four replicates in five different conditions, including control, LS, MS, HS, and gas conditions. Data are shown from the time of incense stick ignition (T_1) to $T_1 + 6$ hours. $\text{PM}_{2.5}$ concentration data was collected from the particulate sensors and oscillates within a certain range for each condition.

was tested using a Shapiro-Wilk test (Hanusz and Tarasińska, 2015). Since average flight speed of butterflies in gas and HS conditions are not normally distributed as shown in following results, a Mann-Witney U test which is the non-parametric counterpart to the T-test for independent samples was used to compare whether the average flight speed of individual butterflies is significantly different in Gas and HS conditions from Experiment B.

5.4 Results

5.4.1 Incense coils successfully created three smoke conditions

Three stable smoke conditions with different $\text{PM}_{2.5}$ concentrations were created in the smoke enclosure, termed as LS, MS, and HS. Although the real smoke concentrations are a bit lower than the set value, they are reasonable with means of

120 $\mu\text{g}\cdot\text{m}^{-3}$, 371 $\mu\text{g}\cdot\text{m}^{-3}$ and 832 $\mu\text{g}\cdot\text{m}^{-3}$ respectively. These concentrations are all values that realistically could occur in smoke-affected regions. For example, in Palangkaraya Indonesia in 2015 during an extreme fire episode, atmospheric concentrations of $\text{PM}_{2.5}$ were likely above 2000 $\mu\text{g}\cdot\text{m}^{-3}$ (based on the PM_{10} measurements available and the fact that most PM in biomass burning smoke is $\text{PM}_{2.5}$ or smaller (M. J. Wooster et al., 2018)). Meanwhile, the average $\text{PM}_{2.5}$ concentration in the control condition was maintained at 9 $\mu\text{g}\cdot\text{m}^{-3}$, and the smoke concentrations in MS and HS conditions are roughly double that of the LS. Although the filter was applied to remove particles in the “gas only” condition, some particles also entered the chamber. Thus, the $\text{PM}_{2.5}$ concentration in the “gas only” condition was a bit higher than in the control conditions, as shown in Figure 5.5. The analysis of variance indicated that $\text{PM}_{2.5}$ concentrations in five smoke conditions are significantly different (ANOVA, P value < 0.001).

5.4.2 Flight speed change in smoke condition

5.4.2.1 Flight performance in clean-air conditions

To understand the flight performance of butterflies under clean-air conditions for six hours, the datasets collected from the three control groups in Experiment A were analysed. The six-hour flight speed data from control enclosure in each experiment were divided into 36 timesteps of 10-minute data to plot one boxplot. The mean value of flight speed data in each group is also calculated and shown as the blue squares in Figure 5.6a. The mean values show that the flight speed of butterflies decreases as time increases in clean-air conditions. However, these mean values were not representative of the actual flight status because they were calculated based on the flight data recorded during not only ‘flying’ status but also ‘resting’ status within each 10-minute. As butterflies freely fly and stop on TFMs, to understand the ratio of ‘flying’ and ‘resting’ time of butterflies in six hours, the percentage of time that butterflies were ‘flying’ and ‘resting’ in every 10-minute timestep was calculated and plotted in Figure 5.7. This demonstrates that as time goes by, butterflies took longer rests, which leads to a downward trend in the overall flight speed.

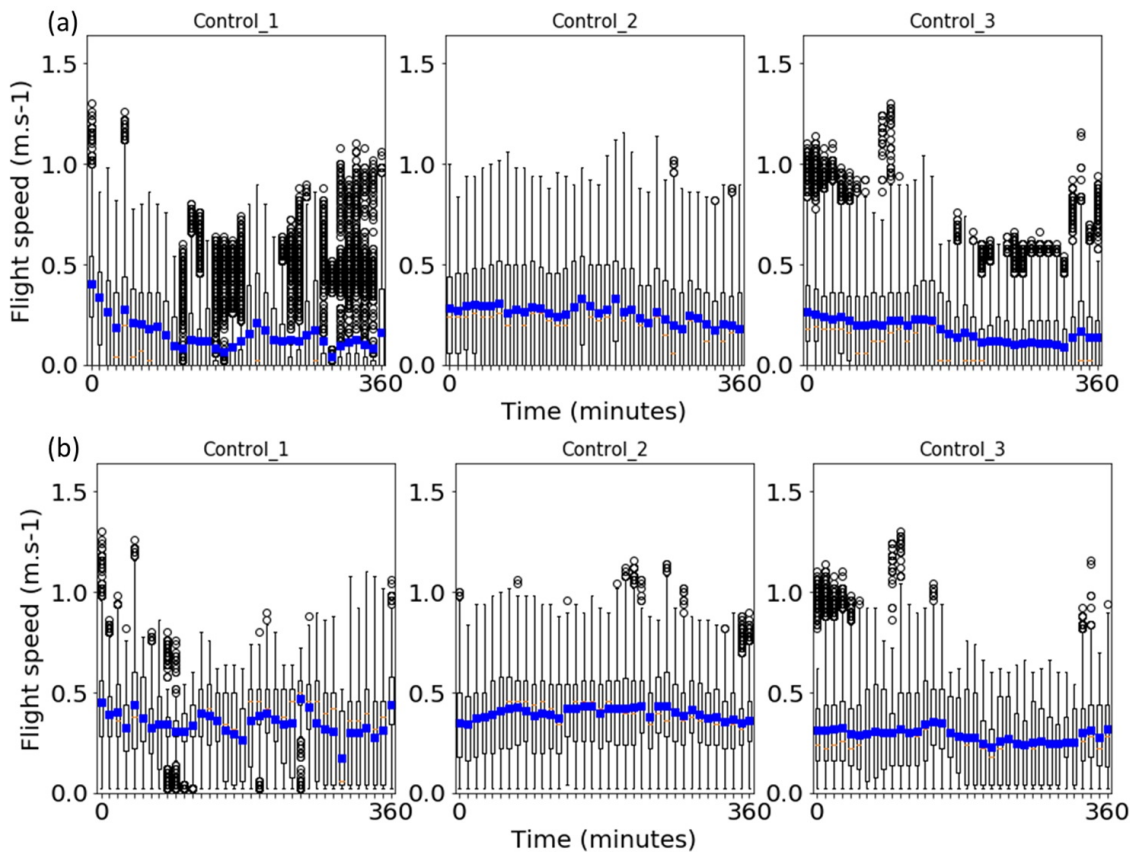


Figure 5.6: Boxplots showing the flight speed of butterflies from control conditions separated into 36 10-minute timesteps, collected from Experiment A. (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying completely. The higher and lower bars of the plots are the maximum and minimum values respectively, while the rectangle illustrated the first quartile, the median, and the third quartile (bottom to top). The blue square is the mean and black circle is outliers.

Thus, to further understand the actual speed changes when the butterflies were in flight, the speed and time where the butterflies were resting are excluded. Figure 5.6b shows the same data as in Figure 5.6a but excluding the zero flight speed values when the *V. cardui* subjects stopped flying altogether. This shows that there is a much smaller change in speed over time. The mean value in each boxplot is calculated from data when the butterflies were flying.

Different flight variables were obtained during the 6-hour experiments for the three control groups in Experiment A. Results in Table 5.2 show that the three control groups have different mean values of total flight distance with 3650 m, 4106 m, 4195

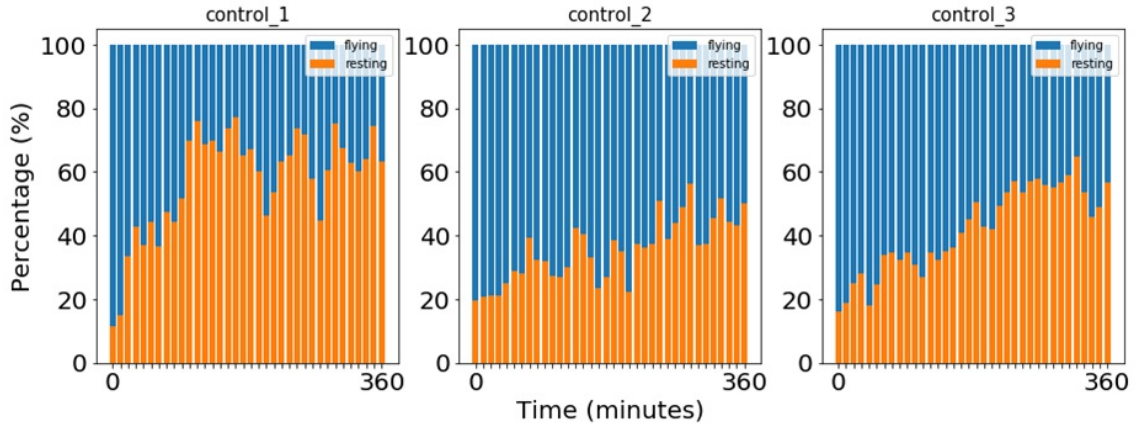


Figure 5.7: Bar charts showing percentage of flying for 36 10-minutes timesteps in control conditions calculated from Experiment A.

Table 5.2: The mean value of flight behaviour variables, including total flight distance, average flight speed, maximum speed, and flight duration, in the control conditions in six hours with standard deviation (SD). The data was collected from Experiment A.

Flight variables	Mean (\pm SD)		
	Control 1 $N = 16$	Control 2 $N = 16$	Control 3 $N = 16$
Total flight distance (m)	3650 (\pm 3170)	4106 (\pm 3397)	4195 (\pm 3956)
Average speed ($\text{m}\cdot\text{s}^{-1}$)	0.25 (\pm 0.16)	0.26 (\pm 0.14)	0.23 (\pm 0.18)
Maximum speed ($\text{m}\cdot\text{s}^{-1}$)	0.78 (\pm 0.24)	0.58 (\pm 0.25)	0.59 (\pm 0.27)
Flight duration (minutes)	177 (\pm 101)	207 (\pm 120)	218 (\pm 126)

m in Control 1, Control 2 and Control 3 respectively. The average speed is quite similar in three control groups with $0.25 \text{ m}\cdot\text{s}^{-1}$, $0.26 \text{ m}\cdot\text{s}^{-1}$ and $0.23 \text{ m}\cdot\text{s}^{-1}$. The flight speed between the different batches of butterflies in clean-air conditions is similar with flight speed at $0.24 \text{ m}\cdot\text{s}^{-1}$. However, the total flight distance is different mainly due to the different flight durations. The butterflies in the control groups in Experiment A have gradually increased flight durations. ANOVA was used to determine whether the means of average flight speed in the three control groups are same or not. The null hypothesis (H_0) was that no significant difference would be observed in the mean value of flight speed among three groups, whilst the alternative hypothesis (H_1) was that a difference would be observed. The resulting P value = 0.33 shows no significant difference among the three groups. Similarly, P value = 0.60 calculated with ANOVA among the average flight durations in the three control

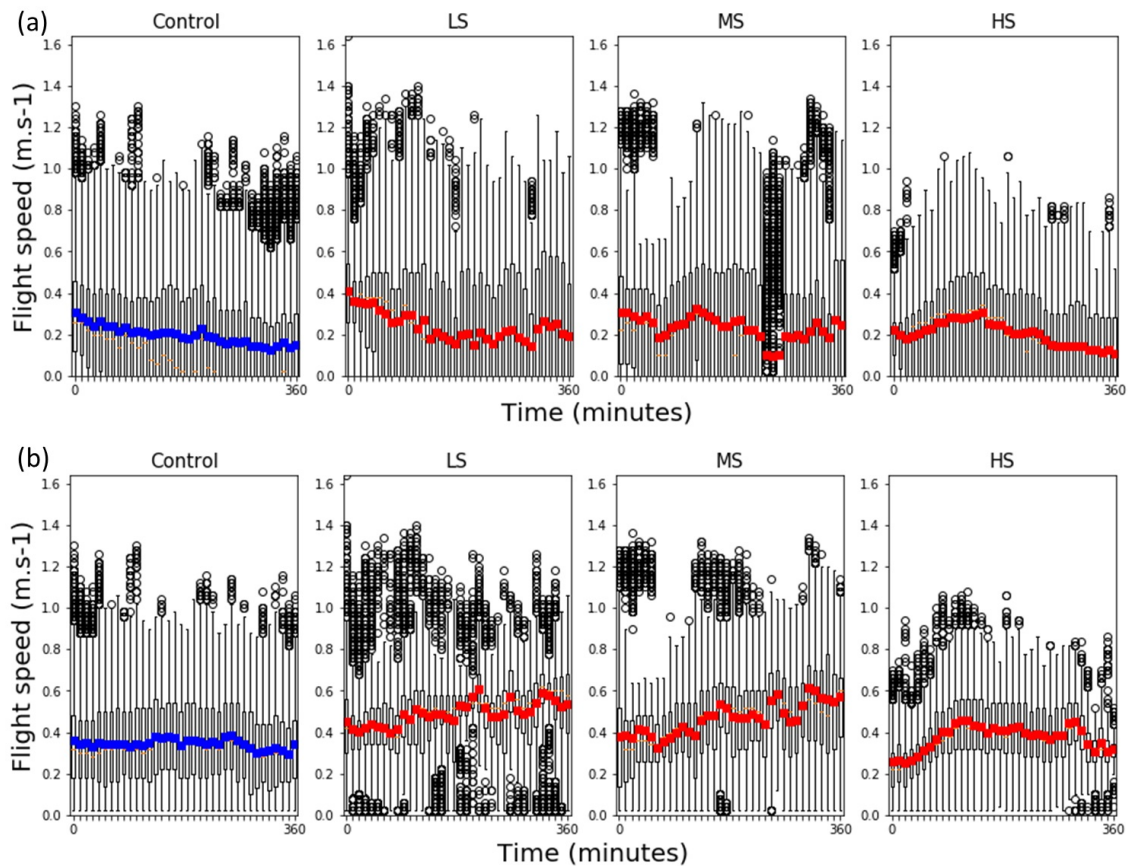


Figure 5.8: Boxplots showing the flight speed of butterflies from different smoke conditions (red) and control conditions (blue) separated into 36 10-minute periods, collected from Experiment A. (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying completely. The higher and lower bars of the plots are the maximum and minimum values respectively, while the rectangle illustrates the first quartile, the median, and the third quartile (bottom to top). The red square is the mean and black circle is outliers.

groups shows that there are not significant differences among the three groups.

5.4.2.2 Flight performance comparisons between control and smoke conditions

To determine whether the flight behaviours of butterflies in smoke exposure are different from those under control conditions, the datasets collected from the smoke conditions in Experiment A are compared with the ones from the control conditions. Since the flight performance of butterflies in control conditions is similar, they are pooled together to be analysed (see Table 5.3). It is shown that butterflies in ambient-clean air conditions have a mean total flight distance of 3984 m, flight speed

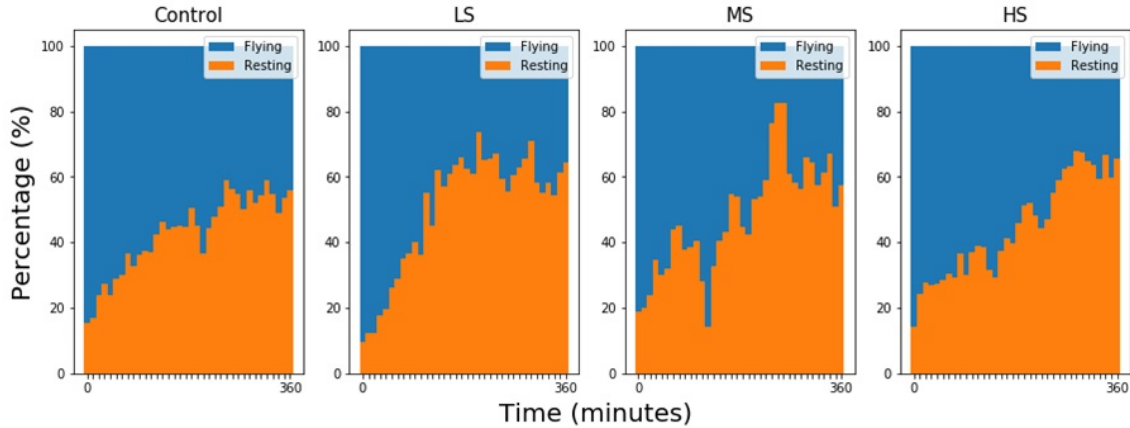


Figure 5.9: Bar charts showing percentage of flying for 36 10-minutes timestep in different smoke conditions (LS, MS, and HS) and control conditions calculated from Experiment A.

Table 5.3: The mean value of flight behaviour variables, including total flight distance, average flight speed, maximum speed, and flight duration, in the control conditions and three smoke conditions (LS, MS, and HS) in six hours with standard deviation (SD). Data was collected from Experiment A.

Flight variables	Mean (\pm SD)			
	Control $N = 48$	LS $N = 16$	MS $N = 16$	HS $N = 16$
Total flight distance (m)	3984 (\pm 3466)	5035 (\pm 3848)	5048 (\pm 4349)	4908 (\pm 4162)
Average speed ($\text{m}\cdot\text{s}^{-1}$)	0.25 (\pm 0.16)	0.38 (\pm 0.21)	0.36 (\pm 0.23)	0.34 (\pm 0.18)
Maximum speed ($\text{m}\cdot\text{s}^{-1}$)	0.65 (\pm 0.26)	0.94 (\pm 0.26)	0.84 (\pm 0.34)	0.70 (\pm 0.23)
Flight duration (minutes)	201 (\pm 115)	175 (\pm 103)	187 (\pm 99)	202 (\pm 135)

of $0.25 \text{ m}\cdot\text{s}^{-1}$, maximum speed of $0.65 \text{ m}\cdot\text{s}^{-1}$ and flight duration of 201 minutes.

The flight data in LS, MS, and HS have been processed with the same analysis method as used for the control group data and the results are plotted in Figure 5.8a. The overall butterfly flight performance in the three smoke conditions shows a similar decrease through time as that in control conditions. As such, the percentage of time that the butterflies were ‘flying’ and ‘resting’ in every 10 minutes has a similar trend as that in control conditions (Figure 5.9).

However, when the resting time is removed, the actual flight speed indicates an upward movement in all smoke conditions. As seen in Figure 5.8b, the real flight speed when resting is excluded shows an increasing trend in all three smoke conditions.

To understand the relationship between flight speed and time, the mean value in each boxplot is extracted from Figure 5.8b and a linear best fit is applied to understand the trend of flight speed thorough time variation (Figure 5.10). Compared to the slight decrease in flight speed of butterfly in the control conditions, an upward tendency of butterfly flight speed over six hours in different smoke conditions can be clearly seen, especially in LS and MS conditions. However, in the HS conditions, the relationship appears to be non-linear with an increase in the roughly first two hours and decrease in the next four hours.

To understand the difference of flight speed of butterflies under ‘flying’ status between different smoke groups and control groups, the difference is calculated by subtracting the data in the control groups from the data in the smoke groups. The flight data from the control group is regarded as zero, it gives a positive value when butterflies in smoke conditions are going faster, or a negative value if they are going slower. It can be clearly seen that the butterfly flight speed shows a gradual increase in the LS and MS conditions. However, butterflies in the HS conditions did not fly faster at all times. The negative values in first 1.5 hours appears that the butterflies start off flying much slower than they would in control conditions, but they increase their speed quite quickly. In the resting time periods, although butterflies flew faster than that in control conditions, they were much slower than in the other smoke conditions yet never reached the speeds seen in the other smoke conditions (LS and MS conditions) (Figure 5.11). Although the butterflies showed an increase in flight speed in all three smoke environments, the magnitude of the increase and the duration of the accelerated flight were different. When the butterfly was in an increasingly severe smoke environment, the butterfly’s flight speed increased less and less, and even slowed down.

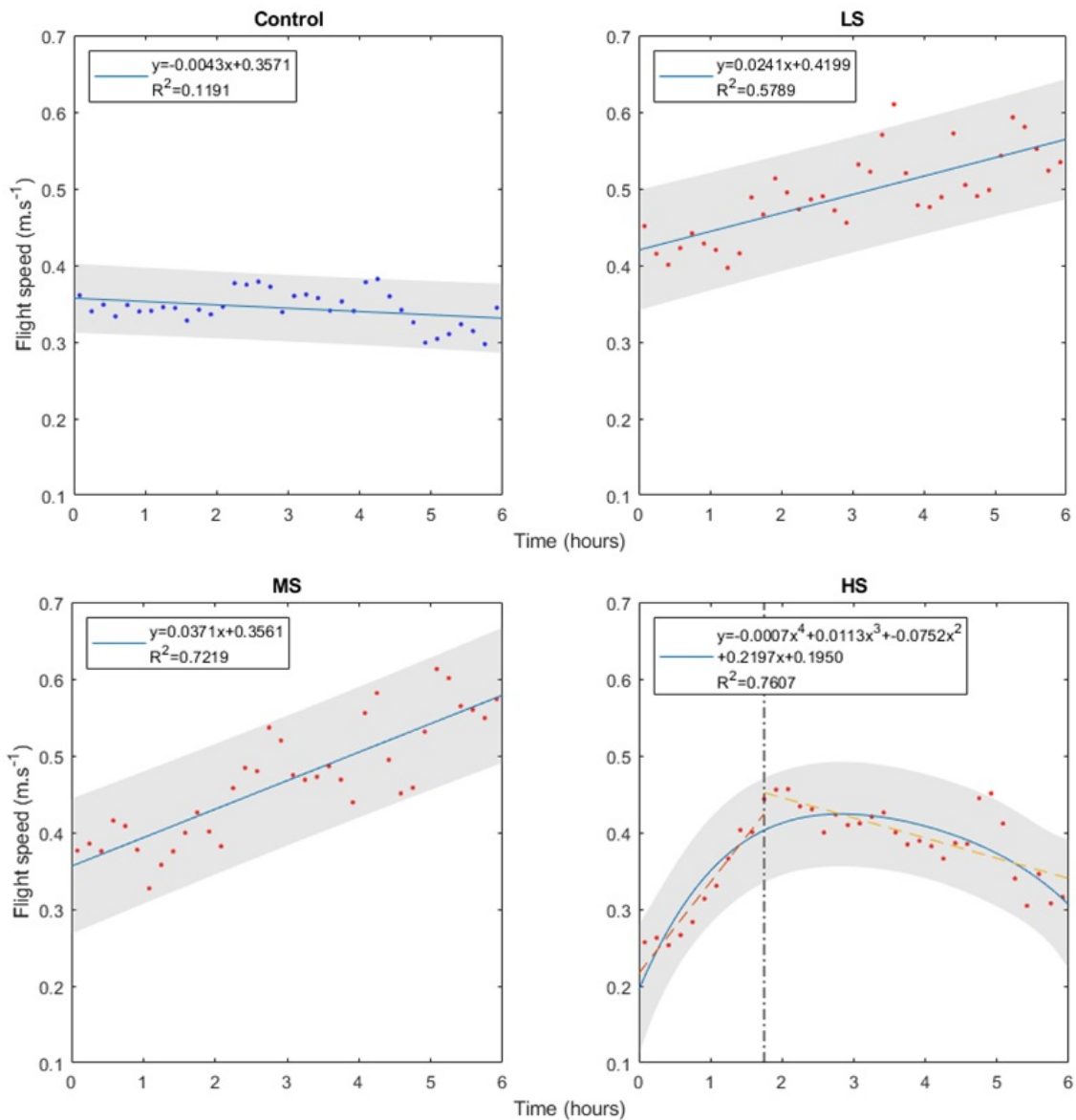


Figure 5.10: Scatterplots of mean flight speed changes over time extracted from data without the zero value flight speeds as was the case with Figure 5.8b in different smoke conditions (LS, MS, and HS) and control conditions. The blue line represents the least squares linear best-fit for control, LS, and MS conditions and nonlinear best-fit for HS conditions, along with the 95% confidence intervals on the slope (light blue area). The equations for which is shown along with the coefficient of variation (R^2). The dashed line showed the flight speed variance thresholds, which divided the flight speed variance into two parts-increasing trend and decreasing trend.

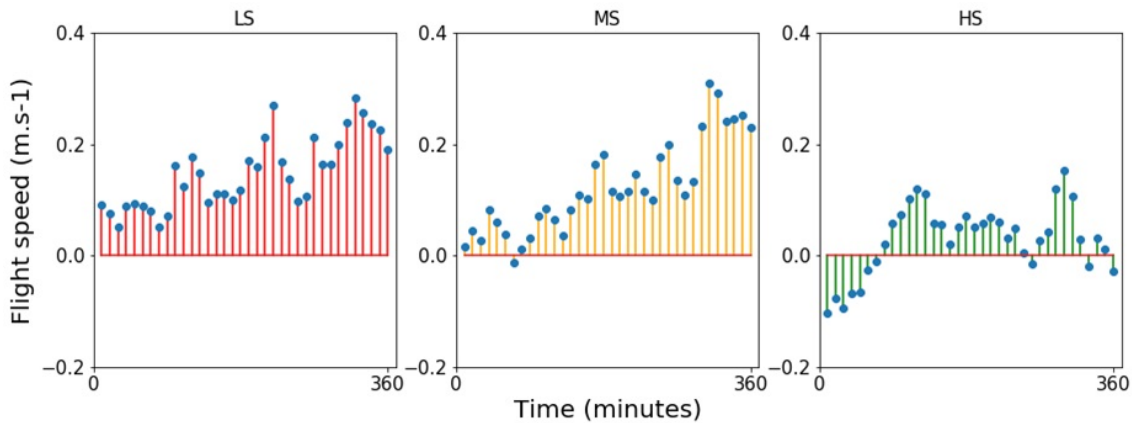


Figure 5.11: Stem plots show the difference of mean flight speed between (a) LS conditions (Red line), (b) MS conditions (Yellow line) and (c) HS conditions (Green line) and control conditions calculated from all data with the zero value flight speeds removed as was the case with Figure 5.8b. The flight value without zero value in control conditions are regarded as baseline.

Compared with flight variables obtained from control conditions, the total flight distance of butterflies in three smoke conditions increased by 26%, 27%, and 23% in LS, MS, and HS conditions individually. The increased flight distance mainly due to increased flight speed, which the average speed in the three smoke conditions was improved by 52%, 44%, and 36% respectively and maximum speed was increased by 45%, 29%, 8%. However, Flight duration declined by 13% and 7% in LS and MS conditions respectively, whereas the flight duration in HS conditions was similar to that in control conditions.

5.4.3 Flight performance comparison between gas and smoke conditions

The results in Section 5.4.2 have shown that butterflies increased their flight speed in smoke conditions. To further explore the effects of the constituents in the smoke that may affect flight behaviour, butterflies were exposed to HS conditions and gas conditions in Experiment B. The difference in the two enclosure conditions is particulate concentration as the smoke was passed through filters to leave only the combustion gases entering the enclosure. The concentrations of gases in the two conditions are similar as already shown in Figure 5.4. The flight data collected from

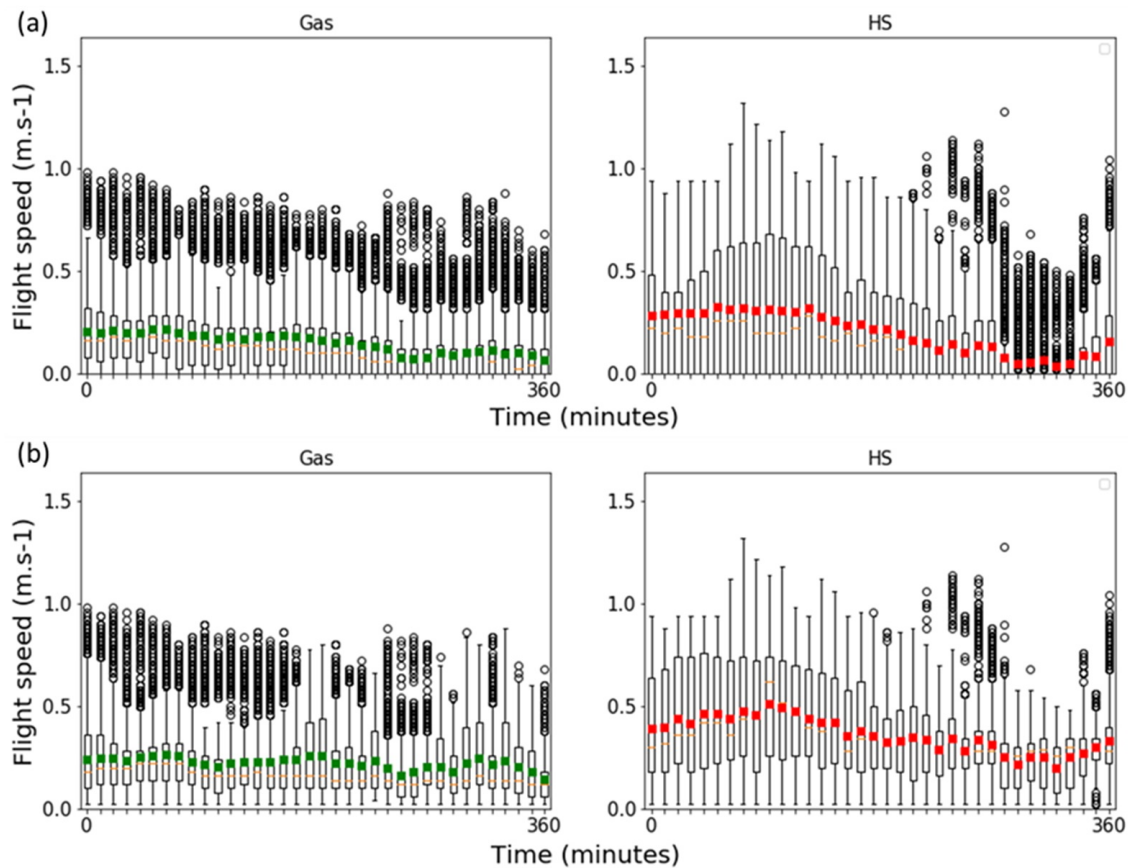


Figure 5.12: Boxplots showing the flight speed of butterflies from different smoke conditions (red) and gas conditions (green) separated into 36 10-minute, collected from experiment B. (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying completely. The higher and lower bars of the plots are the maximum and minimum values respectively, while the rectangle illustrated the first quartile, the median, and the third quartile (bottom to top). The red square is the mean and black circle is outliers.

experiment B has been processed using the same methods as previous analysis. Boxplots in Figure 5.12a show that the flight speed decreased in both gas and HS conditions over six hours. The percentage of ‘flying’ and ‘resting’ status in every 10 minutes also has been calculated, which shows a similar increasing trend in ‘resting’ periods in both HS conditions and gas conditions (Figure 5.13). Compared to the resting periods in gas conditions, butterflies in HS conditions had longer resting periods.

After removing the flight data in ‘resting’ periods, Figure 5.12b demonstrated a more stable flight speed change over six hours in gas conditions and HS conditions.

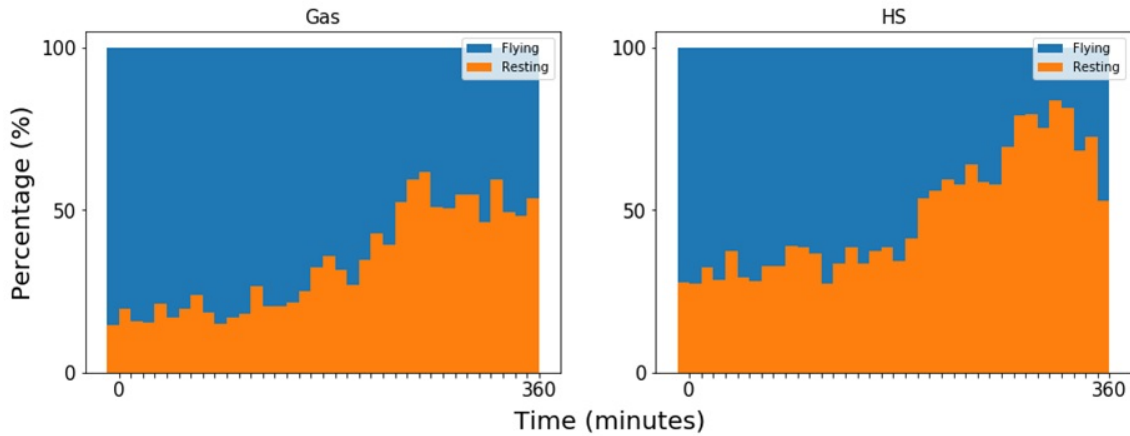


Figure 5.13: Bar charts showing percentage of flying for 36 10-minutes timestep in HS conditions and gas conditions calculated from experiment B with four replicates.

The mean value in each boxplot has been extracted from Figure 5.12b and a linear best fit is applied to the flight speed data. This showed a slightly decreasing trend over time in gas conditions, while the flight speed increased dramatically in the previous 1.8 hours and it decreased sharply in the resting time periods in the HS conditions (Figure 5.14). The change in flight speed between the two HS conditions was relatively close, and the trend in flight speed was closer in the Gas conditions and in control conditions.

Results in Table 5.4 show that butterflies in HS conditions have average flight distance of 4924 m, while their average flight distance in gas conditions is 3643 m (35% longer flight distance in HS conditions). The average speed in gas conditions is $0.16 \text{ m}\cdot\text{s}^{-1}$ while the speed in HS conditions is nearly doubled which is $0.30 \text{ m}\cdot\text{s}^{-1}$. Their flight duration is 211 minutes in HS conditions and 263 minutes in gas conditions (20% less flight duration in HS conditions). The data of average flight speed collected from both HS conditions and Gas conditions is not normal distributed ($P = 0.016$). As the data from two groups did not meet the tests for a normal distribution, a Mann-Witney U test was applied to show that the average flight speeds from the two groups are significantly different ($P = 0.043$, $n = 16$). The results indicated that butterflies in HS conditions have a faster flight speed, indicating that particles may be a cause of the accelerated flight of butterflies.

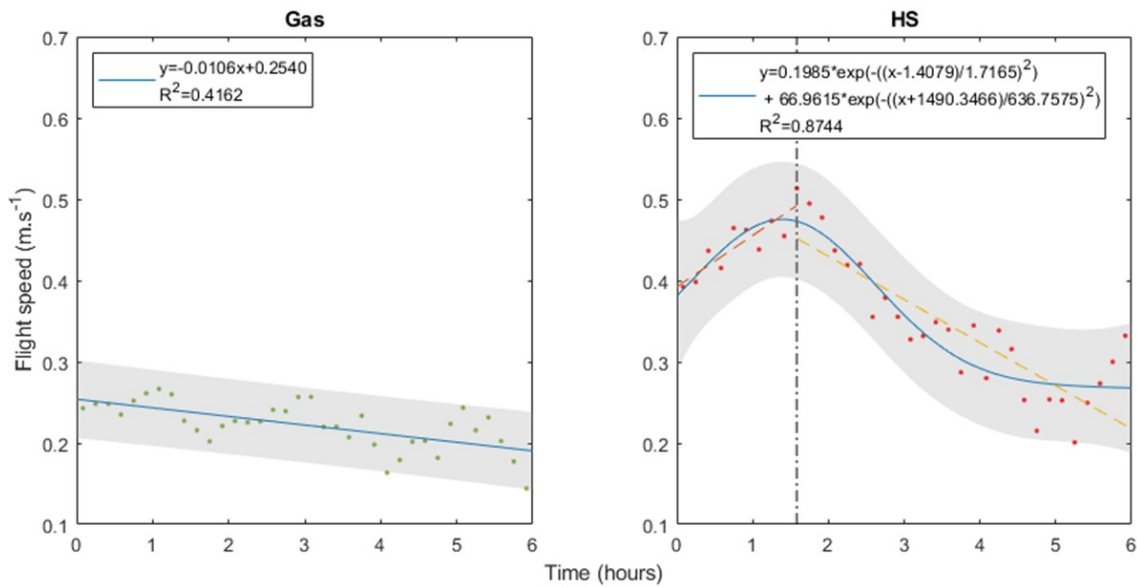


Figure 5.14: Scatterplots of mean flight speed changes over time extracted from data without the zero value flight speeds as was the case with Figure 5.12b in HS conditions and gas conditions. The blue line represents the least squares linear best-fit for gas conditions and non-linear best fit for HS conditions, along with the 95% confidence intervals on the slop (light blue area). The equations for which is shown along with the coefficient of variation (R^2). The dashed line showed the flight speed variance thresholds, which divided the flight speed variance into two parts-increasing trend and decreasing trend.

5.4.4 Scanning electron microscopy of butterfly body

Images collected with the scanning electron microscope (SEM) shows that there were some particles with diameters of 1 μm , 2.5 μm , and 10 μm observed on the antennae and abdomen of butterfly in the smoke conditions, while no obvious particles were found in other body parts, including eyes, forewing, and hindwing. Where present, particles are not homogenously distributed (Figure 5.15). Furthermore, the observations did not show a significant increase in the number of particles as the smoke concentration increased (from LS to HS).

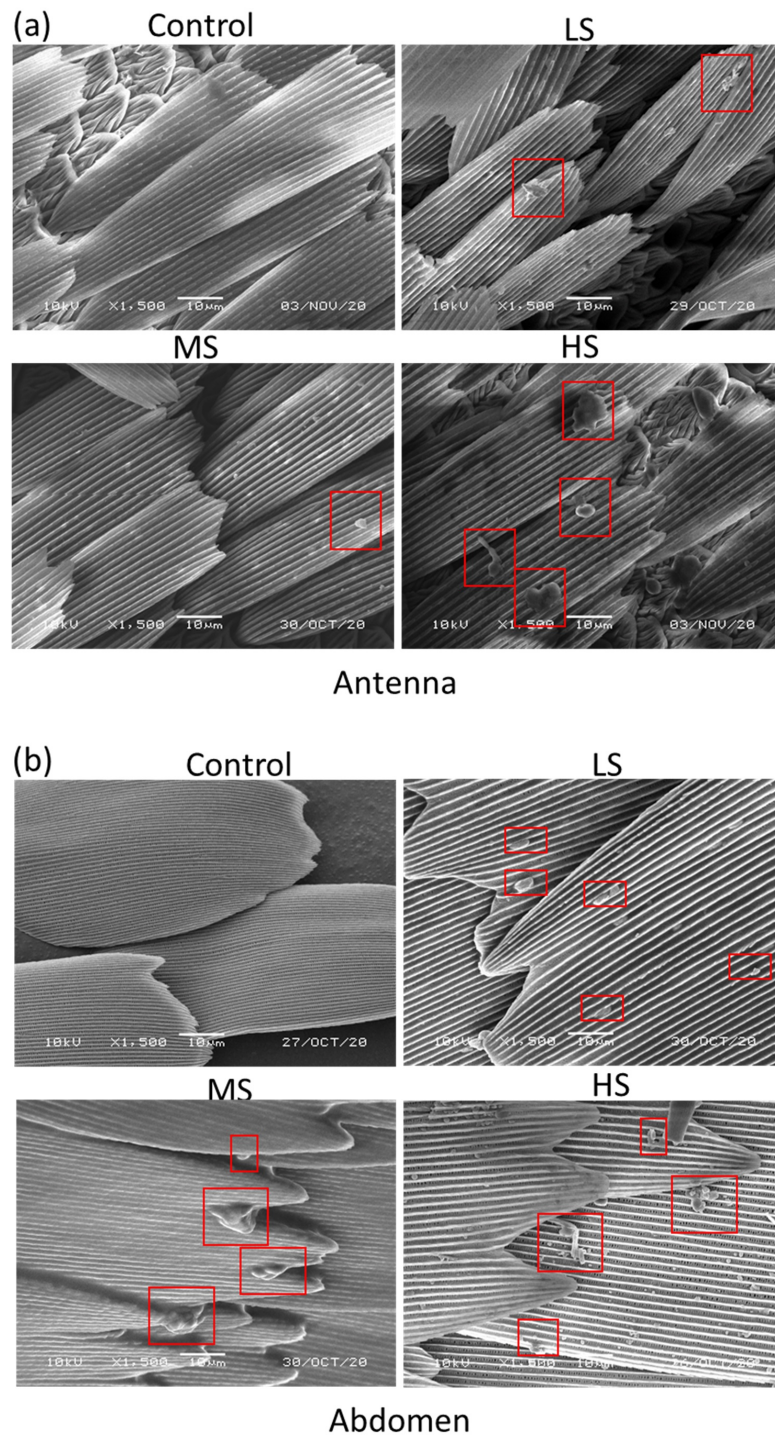


Figure 5.15: Scanning electron microscopy images of (a) antenna (b) abdomen in butterfly with $\times 1500$ magnification to show the presence of $PM_1/PM_{2.5}/PM_{10}$ from (i) control condition; (ii) LS condition; (iii) MS condition; and (iv) HS condition. The red square shows the area where the particles potentially appeared.

Table 5.4: The mean value of flight behaviour variables, including total flight distance, average flight speed, maximum speed, and flight duration, in the gas conditions and HS conditions in six hours with standard deviation (SD). Data was collected from experiment B.

Flight variables	Mean (\pm SD)	
	Gas $N = 16$	HS $N = 16$
Total flight distance (m)	3643 (\pm 2610)	4924 (\pm 3456)
Average speed ($\text{m}\cdot\text{s}^{-1}$)	0.16 (\pm 0.09)	0.30 (\pm 0.20)
Maximum speed ($\text{m}\cdot\text{s}^{-1}$)	0.52 (\pm 0.23)	0.76 (\pm 0.39)
Flight duration (minutes)	263 (\pm 74)	211 (\pm 97)

5.5 Discussion

5.5.1 Incense coils burning generated different $\text{PM}_{2.5}$ concentrations that simulated real landscape fire smoke exposure

Although the $\text{PM}_{2.5}$ concentrations were slightly lower than the pre-set, the concentrations in the experiments were still representative of what a butterfly might encounter in the real world. Some studies of the vegetation fires in Africa measured $\text{PM}_{2.5}$ concentrations between $40 \mu\text{g}\cdot\text{m}^{-3}$ and $1620 \mu\text{g}\cdot\text{m}^{-3}$ during the dry season (early June-early August). These studies also measured CO_2 concentrations consumed by fires between 2 ppm and 1043 ppm, and CO concentrations between 0.18 ppm and 92 ppm, and CH_4 concentrations between 0.026 ppm and 5.8 ppm (Korontzi et al., 2003; Ward et al., 1996). Roberts and Wooster (2021) also reported that some of the people in central and western Africa are affected by the landscape fire smoke, in which the $\text{PM}_{2.5}$ concentrations can be higher than $250 \mu\text{g}\cdot\text{m}^{-3}$. Besides, fire incidence may increase around the world in certain regions because of climate change (Dupuy et al., 2020; M. W. Jones et al., 2022), which will increase the risk of the butterflies being exposed to smoke emissions during their migration.

In addition to variables measured in the particulate concentrations through control, LS, MS and HS conditions across two enclosures, it is possible that there is an

other unquantified difference among the five conditions across the two enclosures. However, the ambient temperature, relative humidity, and light intensity are quite similar between the two enclosures throughout the experiments, thus, it is unlikely that these environmental factors cause the differences in butterfly flight performance across various smoke treatments.

5.5.2 Smoke conditions impact butterfly flight performance

The average flight speed of *V. cardui* under clean-air conditions was $2.4 \text{ m}\cdot\text{s}^{-1}$ on TFM. However, the mean flight speed of butterflies when they are flying downwind was $6 \text{ m}\cdot\text{s}^{-1}$ during their spring migration (Stefanescu et al., 2013). It indicated that TFMs potentially limit a butterfly's natural flight performance. As H. B. Jones et al. (2016) represented that TFM may impact wing flapping. Besides, the differences between different batches of butterflies in control conditions could be due to the period within the season that the butterflies were bred even though all experiments were conducted within the season for their autumn migration which normally starts at the beginning of August and ends by early November, with a peak from mid-September to mid-October (Stefanescu et al., 2017; Stefanescu et al., 2013). It is also possible that the flight durations of the three control groups differed because the butterflies were hatched in three batches and there were individual differences. Brown and Crone (2016) showed that individual variation of butterfly species such as *Euphydras phaeton* (Baltimore checkerspot butterfly) leads to great variability in dispersal distance and habitat patch size. Furthermore, another study demonstrated that butterflies not from the same generation may have significant differences in flight performance and energy metabolism under experimental, standardized conditions (Lebeau et al., 2016). The slight downward trend in flight speed in control conditions (Figure 5.6) could possibly be due to the butterflies having been fed prior to being placed on the TFM but then use all this energy throughout the experimental period without an opportunity to feed.

The results in Table 5.3 clearly demonstrate that butterflies had higher flight speed in smoke conditions in Experiment A, compared to the control groups, although the

flight variance tendency is different in LS, MS, and HS conditions. These indicate that smoke stimulates butterflies to speed up their flight, especially in LS and MS conditions. This may be because when butterflies are in a light smoke condition, they want to speed up to escape this unfavourable environment. For example, the number of *Apis mellifera* (western honey bees) increased at the entrance of hives when it is affected by smoke and they flee quickly, which is a form of absconding behaviour (Gage et al., 2018; Tribe et al., 2017). Also, six *Exyra semicrocea* (Pitcher plant mining moths) were observed in five tubular leaves of *S. flava*, and every moth almost immediately left its plant when they were exposed to smoke from periodic fire in pine savannas. Although the flight speed of those moths has not been quantified, the average time in which it took them to leave is 6.5 seconds (J. Lee et al., 2016). However, although the flight speed in HS conditions is higher than that in clean-air conditions, in the first two hour, the flight speed is lower than that in the control conditions, Y. Liu et al. (2021) put the butterflies in thick smoke for 30 minutes and found that flight speed have significantly decreased in the thick smoke conditions. in the following four hours, although the flight speed is higher in HS conditions, there is a decreasing trend. These results suggest that butterflies increased their flight speed in some stable smoke conditions, but the pattern of flight speed change depends on the smoke concentrations; if they are in light smoke conditions, butterflies will continue to accelerate for a relatively long period, while as the smoke concentrations become thicker, the range of acceleration will decrease.

In terms of flight duration, compared with that in control conditions from individual sub-experiments in Experiment A, flight duration decreased by 13% and 7% in LS and MS conditions respectively. The lower flight duration in smoke conditions may be the case that butterflies consume more energy in smoke conditions. Grasshoppers and seed bugs have been observed to reduce straight-line flight to short distances, and delay flight/migration behaviour when they were stuck in the forest fire smoke conditions (Hegedüs et al., 2007; Johnson et al., 2005). Total flight distance depends on flight duration and flight speed, although there is a slight decrease in flight duration, the overall flight distance has increased by around 25% in smoke conditions

due to the significant increase in flight speed.

5.5.3 Particles may be the main cause of the accelerated flight of butterfly

The results in Table 5.4 clearly showed that *Vanessa cardui* flew twice as fast with 25% shorter flight duration in HS conditions, compared to gas conditions, from Experiment B. *Vanessa cardui* in HS conditions from Experiment A and B have similar flight performance, reflected in all flight variables. Moreover, butterflies in gas conditions have a similar flight distance compared to control conditions. However, butterflies in gas conditions have a slower flight speed (decreased by 33%) and longer flight duration (increased by 32%). The gases in the smoke may have stimulated the butterfly to reduce its flight speed and prolong their flight duration. As the gas concentrations are close in both gas and HS conditions, this suggests that particulate matter is the main reason that butterflies increased their flight speed. (Lukowski et al., 2018) indicated that particulate matter negatively impacted the mass and the efficiency of conversion of ingested food of adult *Gonioctena quinquepunctata* (Coleoptera: Chrysomelidae). Tan et al. (2018) demonstrated that larvae of *Bicyclus anynana* (Lepidoptera: Nymphalidae) had a low survival rate, low weight mass, and long development period when exposed to smoke with a PM_{2.5} concentration of 120 µg·m⁻³. This evidence shows that particulate matter has significant impacts on insects. Therefore, it is possible that the disturbance of particulate matter irritated the butterfly, causing them to speed up their flight in an attempt to escape the smoke conditions.

5.5.4 Particles distributed on the antennae may be the main cause of changes in butterfly flight performance

The SEM was utilized to examine the particle distribution on butterfly bodies. Our finding revealed that particles were not homogenously distributed across the whole body, but were mainly distributed in the antenna and abdomen of *Vanessa cardui* and absent from the eyes, hindwing, and forewing on individuals exposed to smoke.

This non-homogeneous distribution suggests that the flapping motion of the wings may hinder the settling of particles, while the relatively stationary nature of the abdomen and antennae during flight allows for more particle accumulation in these areas (G. K. Taylor, 2001).

It is highly probable that the particles landing on the antennae stimulated the butterflies and influenced their flight acceleration. Insects' antennae serve as complex sensory organs that contribute to flight performance (G. J. Donley, 2022; Gewecke, 1970; Sane, 2016; Sane et al., 2007). G. Donley et al. (2022) indicated that the antennae of *Vanessa cardui* consists of long, thin flagella connected by membranes, with scales distributed along their entire length, which can sense many chemicals. Smoke as a special chemical can possibly stimulate the antennae of butterflies, causing *Vanessa cardui* to change their flight behavior. More specifically, smoke particles might adhere to the antenna and simply block access of the pheromones to chemoreceptors (Visscher et al., 1995).

Furthermore, the antennae of *Manduca sexta* (Hawk moth) plays a critical role in ensuring flight stability. This is achieved through the proper functioning of the antennal flagellum, which impacts the normal loading of the mechanosensor located at the base of the antennae. The intact and functioning antennal flagellum is essential for maintaining the balance and stability of flight in *Manduca sexta*, as it enables accurate sensory input and response to external stimuli (Sane et al., 2007).

In various species, including *Triatoma infestans* (Winchuka), the antennae play a crucial role in gathering information and facilitating accurate orientation toward a stimulus source. Specifically, in *Triatoma infestans*, impaired or damaged antennae result in significant alterations in movement patterns, characterized by sudden changes in direction. This highlights the antennae's crucial function in guiding insects toward thermal sources and their ability to respond to specific stimuli (Flores and Lazzari, 1996). The disturbance of the antennae by particulate matter might largely have a significant impact on the flight performance of insects. Not only

particulate matter, but other chemical compounds may also stimulate the sensory receptors in the antennae of insects, triggering specific behavioral responses. For example, The antennae of jewel beetles can detect substances emitted in smoke from burning wood, providing sensory cues to these insects (Schütz et al., 1999).

5.5.5 Particles may impact butterfly flight performance from other aspects

While the presence of particulates on the antennae of butterflies could potentially impact their flight performance, it may not be the sole factor involved. Our examination focused on the surface particulate distribution on butterflies, rather than internal factors. It is important to note that the impact of particulate matter (PM_{2.5}) injection is well-documented in human respiratory systems, causing direct effects (Thangavel et al., 2022; Xing et al., 2016). Additionally, PM_{2.5} has been shown to induce inflammatory and endothelial dysfunction in the hearts of mice (J. Zhang et al., 2021; Y. Zhang et al., 2016). Therefore, the particulate matter could potentially enter the thoracic spiracles of insects, leading to stimulation of internal organs and subsequently affecting their flight performance.

In addition, In insects, air exchange occurs through diffusion directly through tracheoles into surrounding tissues, bypassing specialized respiratory systems. Consequently, certain smoke chemicals like nitrogen oxides (NO_x) and sulfur dioxide (SO₂) may stimulate the insect's body and potentially influence their physiological responses (Tan et al., 2018).

Therefore, while the presence of particulates on butterfly antennae is one aspect to consider, the impact on flight performance may involve a more complex interplay of factors, including the direct stimulation of the insect's body by specific smoke chemicals.

5.6 Summary

The study in this chapter finds that butterflies increase their flight speed in stable smoke conditions that are relatively realistic in terms of $\text{PM}_{2.5}$ concentration and the natural world, although the range of increase in flight speed decreases as the smoke concentrations rise. It is also - to our knowledge - the first time that *Vanessa cardui* have been put on TFMs for a long period to quantify their flight behavior, which helps us to further understand the flight performance of *Vanessa cardui* flying in a realistic environment for extended periods of time (e.g. as they might during migration). In addition, this study is the first to further understand whether gaseous emissions or particulate emissions from smoke affect the flight performance of butterflies, we suggest that particles may be the main reason that stimulates butterflies to change their flight performance.

In the natural environment, the effects of smoke on butterflies may be more complex, not only in terms of flight speed and flight duration but also in possible changes in migration routes. Additional studies would be valuable for example to understand the effect of smoke on the changes in the flight direction of butterflies. Under the joint pressure of climate change and human activities, the global landscape fire pattern may continue to change, and the ecological impact may be more serious. Thus, more studies are needed to further understand how landscape fire smoke affects the local ecosystem.

Chapter 6

Conclusion and Future Work

This chapter provides conclusions and implications related to the Aims and Objectives of this thesis, as outlined in Chapter 2. Furthermore, this chapter also outlines recommendations for future research to understand the drivers and real-world effects of smoke on insects.

6.1 Summary of Thesis Achievements

This thesis focused on investigating the potential impacts of smoke pollution from landscape fires on the flight behaviour of migratory insects. Chapter 2 first summarised the evidence on this topic from studies conducted between the 1930s and 2021 using systematic mapping methods. There were forty-two studies related to this topic, with forty insect species discussed in terms of their reactions to smoke exposure from landscape fires. The systematic mapping method provided an unbiased database of studies relating to smoke impacts on insects which highlighted that so far the majority of studies have been focused on behaviour, whilst fewer studies looked at development and mortality. However, there were few studies exploring the effects of smoke exposure on the flight behaviour of migratory insects. Therefore, two experiments were designed to investigate these effects.

Before investigating the impacts of smoke exposure on insects, it was important to measure emissions from landscape fires and determine a suitable smoke source (Chapter 3). To do this, emissions were measured from fuels commonly burned as part of agricultural residue burning. Experiments were undertaken in laboratory conditions, but additional measurements were also made on real-world agricultural fires. A series of instruments have been used to measure the mixing ratios of CO₂, CO, CH₄, and mass concentrations of PM_{2.5} from agricultural residues burning, including rice, wheat, millet, soybean, and corn straw with different moisture contents, packing densities, and combustion types in the laboratory. We have reported weighted averaged emission factors (EFs) of trace gases and particles measured in the smoke for different combustion phases from thirteen fires. The results showed that EFs of CO₂, CO and CH₄ were similar between different types of straw burning under completely dry conditions, while EFs of PM_{2.5} from wheat straw are much higher than those from burning other types of straw. In addition, we found that an increase in moisture contents and packing densities of straw led to a decrease in Modified Combustion Efficiency (MCE), accompanied by a gradual decrease of EFs of CO₂ and a gradual increase of CO and CH₄. We further developed a method to estimate the EFs from actual agricultural fires by comparing the emission ratios (ERs) of CO and CO₂ collected from laboratory work and *in situ* measurements. Moreover, as the PM_{2.5} concentrations created by agricultural residue burning were extremely high and unstable, incense stick burning as an alternative source to create smoke conditions was able to produce a steady supply of fresh smoke in a sustained way. We measured the emissions from incense burning and the evidence indicated that the EFs of CO₂, CO and CH₄ from incense burning were reasonably similar to those from agricultural burning.

After finding a suitable smoke source - incense sticks, an experiment was designed to help determine whether smoke exposure affects migratory insects (Chapter 4). *Vanessa cardui* L. (painted lady butterfly) as one of the migratory insects has been chosen as a research target because of their wide distribution, their sensitivity to environmental change and, more importantly, their famous annual migratory move-

ments. A tethered flight mill (TFM) system was identified as a suitable tool to quantitatively explore the effects of smoke exposure on the flight behaviour of *V. cardui*. The TFM could measure flight distance, speed, and duration of the flight, whilst the insects were subjected to three different concentrations of combustion-generated PM_{2.5}. Incense sticks were used to generate different smoke conditions with peak PM_{2.5} concentrations at 500 $\mu\text{g}\cdot\text{m}^{-3}$, 1500 $\mu\text{g}\cdot\text{m}^{-3}$, and 4000 $\mu\text{g}\cdot\text{m}^{-3}$ within 20 minutes. *V. cardui* were exposed to the clean-air conditions for the first 10 minutes and then smoke conditions for another twenty minutes. Compared to the flight behaviour of butterflies in clean-air environments for thirty minutes, butterflies in smoke conditions showed a significantly negative linear relationship between flight speed and PM_{2.5} concentrations. Additionally, flight distance and duration also showed a significant decrease in these smoke conditions.

As smoke concentrations in Chapter 4 were very dense, and the experiment time was far lower than what *V. cardui* could normally be expected to fly during their migration (around 8 hours per day; Abbott 1951, Stefanescu et al. 2013), a further follow-up experiment was designed in Chapter 5. After proving a link between flight and PM_{2.5} concentration (Chapter 4), this second experiment is to investigate the impacts of more realistic smoke conditions on the flight behaviour of *V. cardui* for a longer period of 6 hours (determined by the pilot experiment showing that *V. cardui* would not normally fly for longer than this on the TFM within a 24 hour period). Thus, *V. cardui* were exposed to three stable smoke conditions created by incense coils with PM_{2.5} at low (mean of 120 $\mu\text{g}\cdot\text{m}^{-3}$), medium (mean of 371 $\mu\text{g}\cdot\text{m}^{-3}$), and high (mean of 832 $\mu\text{g}\cdot\text{m}^{-3}$) smoke conditions for six hours respectively, which are more comparable to the smoke conditions from actual landscape fires. Compared with those in clean-air conditions, the results showed that *V. cardui* increased their flight speed by 52%, 44%, and 36% in LS, MS, and HS respectively. The flight distance increased by 26%, 27% and 23% in LS, MS, and HS respectively, despite varying decreases in the flight duration. To further explore whether particles may affect flight behaviour, *V. cardui* were exposed to HS and Gas conditions (similar to HS but with particulates filtered out) for six hours and the results showed that

V. cardui were nearly twice as fast in HS as in Gas conditions, which indicated the particulate matter was likely to be the main cause of butterfly acceleration. Furthermore, scanning electron microscopy (SEM) was applied to help understand if particulates were physically covering their bodies after exposure to smoke. We found that the particles were unevenly distributed in the antennae and abdomen, but not elsewhere and they were not present in high concentrations.

6.2 Future Work

The results presented in this thesis add to our knowledge of the impacts of air pollution on insect migration. However, our understanding is far from complete, so we have outlined below some gaps in our knowledge that remain to be filled and suggested some ways of furthering the work we have presented.

6.2.1 Effects of the light smoke environment on the flight behaviour of the butterfly

Following up with chapter 5, an aspect of future work that needs to be examined is investigating the impact of lower smoke concentrations (less than $120 \mu\text{g}\cdot\text{m}^{-3}$) on the flight behaviour of butterflies to find a threshold at which butterflies start to change their flight behaviour. This will help us comprehensively understand the sensitivity and tolerance of *V. cardui* to air pollution with different $\text{PM}_{2.5}$ concentrations. As flight behaviour can impact the dispersal ability, which then determines, and ultimately affects the local ecological balance (Cormont et al., 2011; Talavera and Vila, 2017). If we can understand the smoke concentrations that start to make butterflies change their behaviour, this could also help us to better predict butterfly flight behaviour in the context of real smoke pollution.

6.2.2 Effects of the smoke components on the flight behaviour of the butterfly

Although we have confirmed that particles have a significant impact on the flight behavior of *V. cardui* in Chapter 5, we do not know the effect of the chemical composition of particle exposure on *V. cardui*, for example, carbonaceous aerosol. *V. cardui* may be sensitive to some specific compounds present in particles that drive the behavioral response. In addition to particulate matter, smoke emissions contain a variety of gases, including CO₂, CO, CH₄, NO_x and other trace gases. *V. cardui* should be exposed to separate gaseous components of smoke emissions from landscape fires and are compared with them in clean-air conditions to further understand what other smoke components may impact the flight behavior of *V. cardui* and how these components may impact. In the natural environment, the effects of smoke exposure on insects can be direct and indirect, for instance, the population density of herbivore insects increased in a polluted area because their predators showed a decreased trend (Zvereva and Kozlov, 2010). The smoke compositions should therefore be precisely controlled to allow quantitative analysis of the mechanisms by which smoke affects insects and thus more accurately predict insect behavior.

6.2.3 Effects of the smoke emissions on the flight direction of migratory insects

This thesis focussed on exploring the effect of smoke exposure on the flight distance, speed and duration of *V. cardui*, but the effect on flight direction also needs to be studied. To explore the effect of smoke exposure on butterfly flight direction, a computerized flight simulator can be used to obtain the average flight direction of *V. cardui* exposed to different smoke conditions. However, the butterfly must also be tethered to this apparatus, which may interfere with the butterfly's flight. To avoid disturbance, another possible approach is to place *V. cardui* in transparent enclosures where they can move freely under different smoke conditions. High-speed cameras could be installed to track the movements of *V. cardui*, helping us understand how the smoke affects the flight direction of butterflies during their

migration. However, with all these possibilities, it is hard to replicate in the real world where a butterfly may be able to fly in a constant direction, for example, may be navigated by sun and wind.

6.2.4 Effects of the smoke emissions on the actual insect migration

We are currently only exploring the effects of smoke on the flight behaviour of *V. cardui* from a controlled laboratory environment, but do not know the effects of smoke on the *V. cardui* during their migration. One option would be to collect the actual migration flight data by using vertical-looking radar to analyse the trajectory of *V. cardui* migration. This could be combined with measurements of atmospheric PM_{2.5}, however, there are still practical limitations that would restrict the size of the area that could be measured at any time. Modelled PM fields might be a solution to this. Furthermore, exploration of the smoke spread path from landscape fires in areas covered by migration would be beneficial. This would help understand the types of smoke-polluted air that the butterflies may encounter during migration (e.g. isolated plumes from small local fires to large areas of well-mixed smoke). This work would assist in comprehensively understanding the impacts of smoke exposure on butterfly migration, facilitate greater scrutiny and assessment of the butterfly migration, predict where the butterfly breed, and have a systematic plan for butterfly conservation.

6.2.5 Effects of the landscape fire smoke on the other insects

Another work is to investigate the smoke emissions on insects that mainly occur in the areas where agricultural residue burning takes place. TFM can be applied to various insect species to quantify their flight performance. This work will help the community to build a prediction system to know insect response to environmental changes, effectively manage the impacts of smoke from landscape fires, protect the abundance of natural resources and comprehensively understand the impacts of smoke pollution from agricultural fires on local ecosystems.

6.2.6 Effects of the landscape fire on migratory insects

In addition to our previous work, it is essential to explore the broader implications of how fire can affect a wide range of migratory insects. The impact of fire on migratory insects can be far-reaching, as it might disrupt established migration routes by altering the plant community composition (Bowd et al., 2018). This disturbance might force migratory insects to adjust their migratory paths, resulting in the time and directions of their movements.

Furthermore, fires might have detrimental effects on habitats that migratory insects depend on for breeding, feeding, and resting. The fragmentation of these habitats might significantly reduce the availability and diversity of crucial plant species (Honnay et al., 2005). For instance, Stefanescu et al. (2017) found that *V. cardui* track specific plant resources during their autumn migration, such as false yellowhead, golden crownbeard, and alfalfa. Once these host plants are destroyed by fires, it can influence the migratory behavior of *V. cardui*. Understanding the underlying mechanisms behind these shifts in behavior can provide insights into how other migratory insects might alter their movement patterns in fire-affected areas.

Additionally, the changes in habitat availability and vegetation composition induced by fires can affect the quality and connectivity of stopover sites along migration routes, potentially leading to changes in the distribution and population dynamics of migratory insects. During a long-distance migration, migratory insects always take stopovers at specific locations to rest, feed and refuel their energy reserves. If the availability of suitable stopover sites is reduced due to habitat loss, it can negatively impact the survival of migratory insects.

In summary, investigating how fire influences a wider range of migratory insects is crucial. The effects of fire extend beyond behavioral changes of migratory insects and can impact habitat availability, vegetation composition, and the dynamics of migratory populations.

References

- Abbott, C. H. (1951). A quantitative study of the migration of the painted lady butterfly, *vanessa cardui* l. *Ecology*, *32*(2), 155–171.
- Akagi, S., Yokelson, R. J., Wiedinmyer, C., Alvarado, M., Reid, J., Karl, T., Crouse, J., & Wennberg, P. (2011). Emission factors for open and domestic biomass burning for use in atmospheric models. *Atmospheric Chemistry and Physics*, *11*(9), 4039–4072.
- Alerstam, T., Chapman, J. W., Bäckman, J., Smith, A. D., Karlsson, H., Nilsson, C., Reynolds, D. R., Klaassen, R. H., & Hill, J. K. (2011). Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1721), 3074–3080.
- Andreae, M. O. (2019). Emission of trace gases and aerosols from biomass burning - an updated assessment. *Atmospheric Chemistry and Physics*, *19*(13), 8523–8546.
- Andreae, M. O., & Merlet, P. (2001). Emission of trace gases and aerosols from biomass burning. *Global biogeochemical cycles*, *15*(4), 955–966.
- Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G., Jeffcoate, S., et al. (2001). *The millennium atlas of butterflies in Britain and Ireland*. Oxford University Press.
- Attisano, A., Murphy, J. T., Vickers, A., & Moore, P. J. (2015). A simple flight mill for the study of tethered flight in insects. *JoVE (Journal of Visualized Experiments)*, (106), e53377.

- Barroso, F. G., de Haro, C., Sánchez-Muros, M.-J., Venegas, E., Martínez-Sánchez, A., & Pérez-Bañón, C. (2014). The potential of various insect species for use as food for fish. *Aquaculture*, *422*, 193–201.
- Bartomeus, I., Potts, S. G., Steffan-Dewenter, I., Vaissiere, B. E., Woyciechowski, M., Krewenka, K. M., Tscheulin, T., Roberts, S. P., Szentgyörgyi, H., Westphal, C., et al. (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ*, *2*, e328.
- Bates, A. J., Sadler, J. P., Everett, G., Grundy, D., Lowe, N., Davis, G., Baker, D., Bridge, M., Clifton, J., Freestone, R., et al. (2013). Assessing the value of the garden moth scheme citizen science dataset: How does light trap type affect catch? *Entomologia Experimentalis et Applicata*, *146*(3), 386–397.
- Becciu, P., Menz, M. H., Aurbach, A., Cabrera-Cruz, S. A., Wainwright, C. E., Scacco, M., Ciach, M., Pettersson, L. B., Maggini, I., Arroyo, G. M., et al. (2019). Environmental effects on flying migrants revealed by radar. *Ecography*, *42*(5), 942–955.
- Belovsky, G., & Slade, J. (2000). Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences*, *97*(26), 14412–14417.
- Bhuvaneshwari, S., Hettiarachchi, H., & Meegoda, J. N. (2019). Crop residue burning in india: Policy challenges and potential solutions. *International journal of environmental research and public health*, *16*(5), 832.
- Bowd, E. J., Lindenmayer, D. B., Banks, S. C., & Blair, D. P. (2018). Logging and fire regimes alter plant communities. *Ecological Applications*, *28*(3), 826–841.
- Brown, L. M., & Crone, E. E. (2016). Individual variation changes dispersal distance and area requirements of a checkerspot butterfly. *Ecology*, *97*(1), 106–115.
- Cao, G., Zhang, X., Gong, S., & Zheng, F. (2008). Investigation on emission factors of particulate matter and gaseous pollutants from crop residue burning. *Journal of Environmental Sciences*, *20*(1), 50–55.
- Carlson, J., Whalon, M., Landis, D., & Gage, S. (1992). Springtime weather patterns coincident with long-distance migration of potato leafhopper into michigan. *Agricultural and Forest Meteorology*, *59*(3-4), 183–206.

- Cascio, W. E. (2018). Wildland fire smoke and human health. *Science of the total environment*, *624*, 586–595.
- Celorio-Mancera, M. d. I. P., Wheat, C. W., Huss, M., Vezzi, F., Neethiraj, R., Reimegård, J., Nylin, S., & Janz, N. (2016). Evolutionary history of host use, rather than plant phylogeny, determines gene expression in a generalist butterfly. *BMC Evolutionary Biology*, *16*(1), 1–10.
- Chapman, J. W., Nesbit, R. L., Burgin, L. E., Reynolds, D. R., Smith, A. D., Middleton, D. R., & Hill, J. K. (2010). Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science*, *327*(5966), 682–685.
- Chapman, J. W., Reynolds, D. R., Mouritsen, H., Hill, J. K., Riley, J. R., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008). Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology*, *18*(7), 514–518.
- Chapman, J. W., Reynolds, D. R., & Smith, A. D. (2003). Vertical-looking radar: A new tool for monitoring high-altitude insect migration. *Bioscience*, *53*(5), 503–511.
- Chapman, J. W., Reynolds, D. R., & Wilson, K. (2015). Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology letters*, *18*(3), 287–302.
- Chapman, J., Smith, A., Woiwod, I., Reynolds, D., & Riley, J. (2002). Development of vertical-looking radar technology for monitoring insect migration. *Computers and Electronics in Agriculture*, *35*(2-3), 95–110.
- Chen, G., Wang, Z.-W., Qin, Y., & Sun, W.-B. (2017). Seed dispersal by hornets: An unusual insect-plant mutualism. *Journal of integrative plant biology*, *59*(11), 792–796.
- Chen, J., Li, C., Ristovski, Z., Milic, A., Gu, Y., Islam, M. S., Wang, S., Hao, J., Zhang, H., He, C., et al. (2017). A review of biomass burning: Emissions and impacts on air quality, health and climate in china. *Science of the Total Environment*, *579*, 1000–1034.

- Chen, L.-W., Verburg, P., Shackelford, A., Zhu, D., Susfalk, R., Chow, J., & Watson, J. (2010). Moisture effects on carbon and nitrogen emission from burning of wildland biomass. *Atmospheric Chemistry and Physics*, *10*(14), 6617–6625.
- Chen, R.-L., Bao, X.-Z., Drake, V., Farrow, R., Wang, S.-Y., Sun, Y.-J., & Zhai, B.-P. (1989). Radar observations of the spring migration into northeastern china of the oriental armyworm moth, *mythimna separata*, and other insects. *Ecological Entomology*, *14*(2), 149–162.
- Cheng, W.-H., Lai, C.-H., Tzeng, W.-J., Her, C., & Hsu, Y.-H. (2015). Gaseous products of incense coil combustion extracted by passive solid phase microextraction samplers. *Atmosphere*, *6*(6), 822–833.
- Cheng, Z., Wang, S., Fu, X., Watson, J. G., Jiang, J., Fu, Q., Chen, C., Xu, B., Yu, J., Chow, J. C., et al. (2014). Impact of biomass burning on haze pollution in the yangtze river delta, china: A case study in summer 2011. *Atmospheric Chemistry and Physics*, *14*(9), 4573–4585.
- Chowdhury, S., Fuller, R. A., Dingle, H., Chapman, J. W., & Zalucki, M. P. (2021). Migration in butterflies: A global overview. *Biological Reviews*, *96*(4), 1462–1483.
- Chowdhury, S., Zalucki, M. P., Amano, T., Woodworth, B. K., Venegas-Li, R., & Fuller, R. A. (2021). Seasonal spatial dynamics of butterfly migration. *Ecology Letters*, *24*(9), 1814–1823.
- Chuvieco, E., Lizundia-Loiola, J., Pettinari, M. L., Ramo, R., Padilla, M., Tansey, K., Mouillot, F., Laurent, P., Storm, T., Heil, A., et al. (2018). Generation and analysis of a new global burned area product based on modis 250 m reflectance bands and thermal anomalies. *Earth System Science Data*, *10*(4), 2015–2031.
- Cleary, D. F., & Grill, A. (2004). Butterfly response to severe enso-induced forest fires in borneo. *Ecological Entomology*, *29*(6), 666–676.
- Clem, C. S., Hobson, K. A., & Harmon-Threatt, A. N. (2022). Do nearctic hover flies (diptera: Syrphidae) engage in long-distance migration? an assessment of evidence and mechanisms. *Ecological Monographs*, *92*(4), e1542.

- Comay, O., Ben Yehuda, O., Benyamini, D., Schwartz-Tzachor, R., Pe'er, I., Melech, T., & Pe'er, G. (2020). Analysis of monitoring data where butterflies fly year-round. *Ecological Applications*, *30*(8), e02196.
- Cook, J. M., & Rasplus, J.-Y. (2003). Mutualists with attitude: Coevolving fig wasps and figs. *Trends in Ecology & Evolution*, *18*(5), 241–248.
- Cormont, A., Malinowska, A. H., Kostenko, O., Radchuk, V., Hemerik, L., Wallis-DeVries, M. F., & Verboom, J. (2011). Effect of local weather on butterfly flight behaviour, movement, and colonization: Significance for dispersal under climate change. *Biodiversity and Conservation*, *20*(3), 483–503.
- Cuadrado, M. (2017). The year-round phenology of the migratory red admiral vanessa atalanta (lepidoptera: Nymphalidae) in a mediterranean area in southern Spain. *European Journal of Entomology*, *114*, 517–525.
- Delmas, R., Lacaux, J., & Brocard, D. (1995). Determination of biomass burning emission factors: Methods and results. *Environmental monitoring and assessment*, *38*(2), 181–204.
- Denno, R. F., Douglas, L. W., & Jacobs, D. (1985). Crowding and host plant nutrition: Environmental determinants of wing-form in *prokelisia marginata*. *Ecology*, *66*(5), 1588–1596.
- Denno, R. F., Gratton, C., & Langellotto, G. A. (2001). Significance of habitat persistence and dimensionality in the evolution of insect migration strategies. *Insect movement: mechanisms and consequences. Proceedings of the Royal Entomological Society's 20th Symposium, London, UK, September 1999*, 235–259.
- de Vega, C., Arista, M., Ortiz, P. L., Herrera, C. M., & Talavera, S. (2011). Endozoochory by beetles: A novel seed dispersal mechanism. *Annals of Botany*, *107*(4), 629–637.
- Díaz, S., Purvis, A., Cornelissen, J. H., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P., & Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and evolution*, *3*(9), 2958–2975.

- Dingle, H. (2006). Animal migration: Is there a common migratory syndrome? *Journal of Ornithology*, *147*, 212–220.
- Dingle, H. (2014). *Migration: The biology of life on the move*. Oxford University Press, USA.
- Dingle, H., & Drake, V. A. (2007). What is migration? *Bioscience*, *57*(2), 113–121.
- Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual review of Environment and Resources*, *28*(1), 137–167.
- Dong, T. T., Stock, W. D., Callan, A. C., Strandberg, B., & Hinwood, A. L. (2020). Emission factors and composition of pm_{2.5} from laboratory combustion of five western australian vegetation types. *Science of the Total Environment*, *703*, 134796.
- Donley, G., Sun, Y., Pass, G., Adler, P. H., Beard, C. E., Owens, J., & Kornev, K. G. (2022). Insect antennae: Coupling blood pressure with cuticle deformation to control movement. *Acta Biomaterialia*.
- Donley, G. J. (2022). Insect antennae as bioinspirational superstrong fiber-based microfluidics.
- Drake, V. A., & Reynolds, D. R. (2012). *Radar entomology: Observing insect flight and migration*. Cabi.
- Dreyer, D., Frost, B., Mouritsen, H., Lefèvre, A., Menz, M., & Warrant, E. (2021). A guide for using flight simulators to study the sensory basis of long-distance migration in insects. *Frontiers in Behavioral Neuroscience*, *15*, 678936.
- Du, H., Kong, L., Cheng, T., Chen, J., Du, J., Li, L., Xia, X., Leng, C., & Huang, G. (2011). Insights into summertime haze pollution events over shanghai based on online water-soluble ionic composition of aerosols. *Atmospheric Environment*, *45*(29), 5131–5137.
- Dupuy, J.-l., Fargeon, H., Martin-StPaul, N., Pimont, F., Ruffault, J., Guijarro, M., Hernando, C., Madrigal, J., & Fernandes, P. (2020). Climate change impact on future wildfire danger and activity in southern europe: A review. *Annals of Forest Science*, *77*(2), 1–24.
- Duthie, C., Gibbs, G., & Burns, K. (2006). Seed dispersal by weta. *Science*, *311*(5767), 1575–1575.

- Dwivedi, M., Shadab, M. H., & Santosh, V. (2020). Insect pest detection, migration and monitoring using radar and lidar systems. In *Innovative pest management approaches for the 21st century* (pp. 61–76). Springer.
- Ecuador, G. I. (1992). World distribution of the vanessa cardui group (nymphalidae). *Journal of the Lepidopterists' Society*, *46*(3), 235–238.
- Espírito-Santo, M. M., & Fernandes, G. W. (2007). How many species of gall-inducing insects are there on earth, and where are they? *Annals of the Entomological Society of America*, *100*(2), 95–99.
- Fachinger, F., Drewnick, F., Gieré, R., & Borrmann, S. (2017). How the user can influence particulate emissions from residential wood and pellet stoves: Emission factors for different fuels and burning conditions. *Atmospheric environment*, *158*, 216–226.
- Fahrner, S. J., Lelito, J. P., Blaedow, K., Heimpel, G. E., & Aukema, B. H. (2014). Factors affecting the flight capacity of tetrastichus planipennisi (hymenoptera: Eulophidae), a classical biological control agent of agrilus planipennis (coleoptera: Buprestidae). *Environmental entomology*, *43*(6), 1603–1612.
- Farrow, R. (1984). Detection of transoceanic migration of insects to a remote island in the coral sea, willis island. *Australian Journal of Ecology*, *9*(3), 253–272.
- Feng, H., Wu, K., Cheng, D., & Guo, Y. (2004). Spring migration and summer dispersal of loxostege sticticalis (lepidoptera: Pyralidae) and other insects observed with radar in northern china. *Environmental Entomology*, *33*(5), 1253–1265.
- Feng, H.-Q., Zhang, Y.-H., Wu, K.-M., Cheng, D.-F., & Guo, Y.-Y. (2007). Nocturnal windborne migration of ground beetles, particularly pseudoophonus griseus (coleoptera: Carabidae), in china. *Agricultural and Forest Entomology*, *9*(2), 103–113.
- Feng, H.-Q., Wu, K.-M., Cheng, D.-F., & Guo, Y.-Y. (2003). Radar observations of the autumn migration of the beet armyworm spodoptera exigua (lepidoptera: Noctuidae) and other moths in northern china. *Bulletin of Entomological Research*, *93*(2), 115–124.

- Fernandez-Gomez, I., De Castro, A., Guijarro, M., Madrigal, J., Aranda, J., Diez, C., Hernando, C., & Lopez, F. (2011). Characterization of forest fuels in a mass loss calorimeter by short open-path ftir spectroscopy. *Journal of Quantitative Spectroscopy and Radiative Transfer*, *112*(3), 519–530.
- Finney, M. A., et al. (1999). Mechanistic modeling of landscape fire patterns. *Spatial Modeling of Forest Landscapes: Approaches and Applications*. Cambridge University Press, Cambridge, 186–209.
- Finney, M. A. (2004). Landscape fire simulation and fuel treatment optimization. *Methods for integrating modeling of landscape change: Interior Northwest Landscape Analysis System. Gen. Tech. Rep. PNW-GTR-610*. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 117–131.
- Flockhart, D. T., Wassenaar, L. I., Martin, T. G., Hobson, K. A., Wunder, M. B., & Norris, D. R. (2013). Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern north america. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1768), 20131087.
- Flores, G. B., & Lazzari, C. R. (1996). The role of the antennae in triatoma infestans: Orientation towards thermal sources. *Journal of insect physiology*, *42*(5), 433–440.
- Fornacca, D., Ren, G., & Xiao, W. (2017). Performance of three modis fire products (mcd45a1, mcd64a1, mcd14ml), and esa fire_cci in a mountainous area of northwest yunnan, china, characterized by frequent small fires. *Remote Sensing*, *9*(11), 1131.
- França, D. d. A., Longo, K. M., Neto, T. G. S., Santos, J. C., Freitas, S. R., Rudorff, B. F., Cortez, E. V., Anselmo, E., & Carvalho Jr, J. A. (2012). Pre-harvest sugarcane burning: Determination of emission factors through laboratory measurements. *Atmosphere*, *3*(1), 164–180.
- Frick, W. F., Stepanian, P. M., Kelly, J. F., Howard, K. W., Kuster, C. M., Kunz, T. H., & Chilson, P. B. (2012). Climate and weather impact timing of emergence of bats.

- Gadde, B., Bonnet, S., Menke, C., & Garivait, S. (2009). Air pollutant emissions from rice straw open field burning in india, thailand and the philippines. *Environmental Pollution*, *157*(5), 1554–1558.
- Gage, S. L., Ahumada, F., Rivera, A., Graham, H., & DeGrandi-Hoffman, G. (2018). Smoke conditions affect the release of the venom droplet accompanying sting extension in honey bees (hymenoptera: Apidae). *Journal of insect science*, *18*(4), 7.
- Galante, E., & Marcos-Garcia, M. A. (2008). Decomposer insects. *Encyclopedia of Entomology*, 1158–1169.
- Gauthreaux Jr, S. A., Livingston, J. W., & Belser, C. G. (2008). Detection and discrimination of fauna in the aerosphere using doppler weather surveillance radar. *Integrative and Comparative Biology*, *48*(1), 12–23.
- Gewecke, M. (1970). Antennae: Another wind-sensitive receptor in locusts. *Nature*, *225*(5239), 1263–1264.
- Ghannem, S., Touaylia, S., & Boumaiza, M. (2018). Beetles (insecta: Coleoptera) as bioindicators of the assessment of environmental pollution. *Human and Ecological Risk Assessment: An International Journal*, *24*(2), 456–464.
- Giglio, L., Randerson, J., Van der Werf, G., Kasibhatla, P., Collatz, G., Morton, D., & DeFries, R. (2010). Assessing variability and long-term trends in burned area by merging multiple satellite fire products. *Biogeosciences*, *7*(3), 1171–1186.
- Giglio, L., Boschetti, L., Roy, D. P., Humber, M. L., & Justice, C. O. (2018). The collection 6 modis burned area mapping algorithm and product. *Remote sensing of environment*, *217*, 72–85.
- Guérette, E.-A., Paton-Walsh, C., Desservettaz, M., Smith, T. E., Volkova, L., Weston, C. J., & Meyer, C. P. (2018). Emissions of trace gases from australian temperate forest fires: Emission factors and dependence on modified combustion efficiency. *Atmospheric Chemistry and Physics*, *18*(5), 3717–3735.
- Guo, J., Fu, X., Zhao, S., Shen, X., Wyckhuys, K. A., & Wu, K. (2020). Long-term shifts in abundance of (migratory) crop-feeding and beneficial insect species in northeastern asia. *Journal of Pest Science*, *93*(2), 583–594.

- Hallworth, M. T., Marra, P. P., McFarland, K. P., Zahendra, S., & Studds, C. E. (2018). Tracking dragons: Stable isotopes reveal the annual cycle of a long-distance migratory insect. *Biology Letters*, *14*(12), 20180741.
- Hanusz, Z., & Tarasińska, J. (2015). Normalization of the kolmogorov–smirnov and shapiro–wilk tests of normality. *Biometrical Letters*, *52*(2), 85–93.
- Hao, Y.-N., Miao, J., Wu, Y.-Q., Gong, Z.-J., Jiang, Y.-L., Duan, Y., Li, T., Cheng, W.-N., & Cui, J.-X. (2013). Flight performance of the orange wheat blossom midge (diptera: Cecidomyiidae). *Journal of Economic Entomology*, *106*(5), 2043–2047.
- Harvey, J. A., Biere, A., Fortuna, T., Vet, L. E., Engelkes, T., Morriën, E., Gols, R., Verhoeven, K., Vogel, H., Macel, M., et al. (2010). Ecological fits, mis-fits and lotteries involving insect herbivores on the invasive plant, bunias orientalis. *Biological Invasions*, *12*(9), 3045–3059.
- Hawkins, B. A., & Porter, E. E. (2003). Does herbivore diversity depend on plant diversity? the case of california butterflies. *The American Naturalist*, *161*(1), 40–49.
- He, M., Zheng, J., Yin, S., & Zhang, Y. (2011). Trends, temporal and spatial characteristics, and uncertainties in biomass burning emissions in the pearl river delta, china. *Atmospheric Environment*, *45*(24), 4051–4059.
- Hegedüs, R., Åkesson, S., & Horváth, G. (2007). Anomalous celestial polarization caused by forest fire smoke: Why do some insects become visually disoriented under smoky skies? *Applied Optics*, *46*(14), 2717–2726.
- Henderson, S. B., Brauer, M., MacNab, Y. C., & Kennedy, S. M. (2011). Three measures of forest fire smoke exposure and their associations with respiratory and cardiovascular health outcomes in a population-based cohort. *Environmental health perspectives*, *119*(9), 1266–1271.
- Henderson, S. B., & Johnston, F. H. (2012). Measures of forest fire smoke exposure and their associations with respiratory health outcomes. *Current opinion in allergy and clinical immunology*, *12*(3), 221–227.

- Hirowatari, T., Makihara, H., & Sugiarto. (2007). Effects of fires on butterfly assemblages in lowland dipterocarp forest in east kalimantan. *Entomological Science*, *10*(2), 113–127.
- Hobson, K. A., Jinguji, H., Ichikawa, Y., Kusack, J. W., & Anderson, R. C. (2021). Long-distance migration of the globe skimmer dragonfly to japan revealed using stable hydrogen (δ 2h) isotopes. *Environmental Entomology*, *50*(1), 247–255.
- Hocking, B., et al. (1953). The intrinsic range and speed of flight of insects. *Transactions of the Royal Entomological Society of London*, *104*(Pt. 8), 223–345.
- Hoddle, M., Hoddle, C., Faleiro, J., El-Shafie, H., Jeske, D., & Sallam, A. (2015). How far can the red palm weevil (coleoptera: Curculionidae) fly?: Computerized flight mill studies with field-captured weevils. *Journal of Economic Entomology*, *108*(6), 2599–2609.
- Holland, R. A., Wikelski, M., & Wilcove, D. S. (2006). How and why do insects migrate? *Science*, *313*(5788), 794–796.
- Honnay, O., Jacquemyn, H., Bossuyt, B., & Hermy, M. (2005). Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist*, *166*(3), 723–736.
- Howard, E., & Davis, A. K. (2009). The fall migration flyways of monarch butterflies in eastern north america revealed by citizen scientists. *Journal of Insect Conservation*, *13*(3), 279–286.
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual review of ecology and systematics*, *13*, 201–228.
- Hu, G., Lim, K. S., Reynolds, D. R., Reynolds, A. M., & Chapman, J. W. (2016). Wind-related orientation patterns in diurnal, crepuscular and nocturnal high-altitude insect migrants. *Frontiers in Behavioral Neuroscience*, *10*, 32.
- Hu, G., Stefanescu, C., Oliver, T. H., Roy, D. B., Brereton, T., Van Swaay, C., Reynolds, D. R., & Chapman, J. W. (2021). Environmental drivers of annual population fluctuations in a trans-saharan insect migrant. *Proceedings of the National Academy of Sciences*, *118*(26), e2102762118.

- Huang, X., Li, M., Li, J., & Song, Y. (2012). A high-resolution emission inventory of crop burning in fields in china based on modis thermal anomalies/fire products. *Atmospheric Environment*, *50*, 9–15.
- James, C. D., Hoffman, M. T., Lightfoot, D. C., Forbes, G. S., & Whitford, W. G. (1994). Fruit abortion in yucca elata and its implications for the mutualistic association with yucca moths. *Oikos*, 207–216.
- Jankielsohn, A. (2018). The importance of insects in agricultural ecosystems. *Advances in Entomology*, *6*(2), 62–73.
- Jetter, J. J., Guo, Z., McBrian, J. A., & Flynn, M. R. (2002). Characterization of emissions from burning incense. *Science of the Total Environment*, *295*(1-3), 51–67.
- Jiang, B., Xingfuand Cai, Luo, L., Cao, Y., & Liu, Y. (2003). Influences of temperature and humidity synthesize on flight capacity in the moth s of oriental armyworm, mythimna separata (walker). *Acta Ecologica Sinica*, *23*(4), 738–743.
- Jiang, D., Zhuang, D., Fu, J., Huang, Y., & Wen, K. (2012). Bioenergy potential from crop residues in china: Availability and distribution. *Renewable and sustainable energy reviews*, *16*(3), 1377–1382.
- Jiang, R., & Bell, M. L. (2008). A comparison of particulate matter from biomass-burning rural and non-biomass-burning urban households in northeastern china. *Environmental health perspectives*, *116*(7), 907–914.
- Jiang, X., Luo, L., Zhang, L., Sappington, T. W., & Hu, Y. (2011). Regulation of migration in mythimna separata (walker) in china: A review integrating environmental, physiological, hormonal, genetic, and molecular factors. *Environmental Entomology*, *40*(3), 516–533.
- Johnson, D., Naylor, D., & Scudder, G. (2005). Red sky in day, bugs go astray. *Annual Meeting of the Canadian Association of Geographers, Western Division, Lethbridge, Alberta, Canada, 12 March 2005*, 45.
- Johnston, F. H., Henderson, S. B., Chen, Y., Randerson, J. T., Marlier, M., DeFries, R. S., Kinney, P., Bowman, D. M., & Brauer, M. (2012). Estimated global

- mortality attributable to smoke from landscape fires. *Environmental health perspectives*, 120(5), 695–701.
- Jones, H. B., Lim, K. S., Bell, J. R., Hill, J. K., & Chapman, J. W. (2016). Quantifying interspecific variation in dispersal ability of noctuid moths using an advanced tethered flight technique. *Ecology and Evolution*, 6(1), 181–190.
- Jones, M. W., Abatzoglou, J. T., Veraverbeke, S., Andela, N., Lasslop, G., Forkel, M., Smith, A. J., Burton, C., Betts, R. A., van der Werf, G. R., et al. (2022). Global and regional trends and drivers of fire under climate change. *Reviews of Geophysics*, e2020RG000726.
- Kawakita, A., & Kato, M. (2006). Assessment of the diversity and species specificity of the mutualistic association between epicephala moths and glochidion trees. *Molecular Ecology*, 15(12), 3567–3581.
- Keane, R. E., & Finney, M. A. (2003). The simulation of landscape fire, climate, and ecosystem dynamics. In *Fire and climatic change in temperate ecosystems of the western americas* (pp. 32–68). Springer.
- Keshtkar, H., & Ashbaugh, L. L. (2007). Size distribution of polycyclic aromatic hydrocarbon particulate emission factors from agricultural burning. *Atmospheric Environment*, 41(13), 2729–2739.
- Khalifa, S. A., Elshafiey, E. H., Shetaia, A. A., El-Wahed, A. A. A., Algethami, A. F., Musharraf, S. G., AlAjmi, M. F., Zhao, C., Masry, S. H., Abdel-Daim, M. M., et al. (2021). Overview of bee pollination and its economic value for crop production. *Insects*, 12(8), 688.
- Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the royal society B: biological sciences*, 274(1608), 303–313.
- Knight, S. M., Pitman, G. M., Flockhart, D. T., & Norris, D. R. (2019). Radio-tracking reveals how wind and temperature influence the pace of daytime insect migration. *Biology letters*, 15(7), 20190327.
- Korontzi, S., Ward, D. E., Susott, R. A., Yokelson, R. J., Justice, C., Hobbs, P. V., Smithwick, E., & Hao, W. M. (2003). Seasonal variation and ecosystem de-

- pendence of emission factors for selected trace gases and pm_{2.5} for southern african savanna fires. *Journal of Geophysical Research: Atmospheres*, 108(D24).
- Koss, A. R., Sekimoto, K., Gilman, J. B., Selimovic, V., Coggon, M. M., Zarzana, K. J., Yuan, B., Lerner, B. M., Brown, S. S., Jimenez, J. L., et al. (2018). Non-methane organic gas emissions from biomass burning: Identification, quantification, and emission factors from ptr-tof during the firex 2016 laboratory experiment. *Atmospheric Chemistry and Physics*, 18(5), 3299–3319.
- Krell, R. K., Wilson, T. A., Pedigo, L. P., & Rice, M. E. (2003). Characterization of bean leaf beetle (coleoptera: Chrysomelidae) flight capacity. *Journal of the Kansas Entomological Society*, 406–416.
- Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., et al. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology letters*, 10(4), 299–314.
- Krogh, A., & Weis-Fogh, T. (1952). A roundabout for studying sustained flight of locusts. *Journal of Experimental Biology*, 29(2), 211–219.
- Lebeau, J., Wesselingh, R. A., & Van Dyck, H. (2016). Nectar resource limitation affects butterfly flight performance and metabolism differently in intensive and extensive agricultural landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 283(1830), 20160455.
- Lee, J., Brumley, J., Ryckley, M., Smith, C., Lemaster, J., Ricci, C., Meier, A. J., & McPhail, B. (2016). Pitcher plant moths (exyra) fly from pitchers in response to smoke. *The Journal of the Lepidopterists' Society*, 70(4), 268–270.
- Lee, S.-C., & Wang, B. (2004). Characteristics of emissions of air pollutants from burning of incense in a large environmental chamber. *Atmospheric Environment*, 38(7), 941–951.
- Leff, B., Ramankutty, N., & Foley, J. A. (2004). Geographic distribution of major crops across the world. *Global biogeochemical cycles*, 18(1).

- Lemoine, N. P. (2015). Climate change may alter breeding ground distributions of eastern migratory monarchs (*Danaus plexippus*) via range expansion of *Asclepias* host plants. *PloS one*, *10*(2), e0118614.
- Leskinen, M., Markkula, I., Koistinen, J., Pylkkö, P., Ooperi, S., Siljamo, P., Ojanen, H., Raiskio, S., & Tiilikkala, K. (2011). Pest insect immigration warning by an atmospheric dispersion model, weather radars and traps. *Journal of Applied Entomology*, *135*(1-2), 55–67.
- Li, W., Shao, L., & Buseck, P. (2010). Haze types in Beijing and the influence of agricultural biomass burning. *Atmospheric Chemistry and Physics*, *10*(17), 8119–8130.
- Li, X., Wang, S., Duan, L., Hao, J., Li, C., Chen, Y., & Yang, L. (2007). Particulate and trace gas emissions from open burning of wheat straw and corn stover in China. *Environmental Science & Technology*, *41*(17), 6052–6058.
- Liu, Y., Francis, R. A., Wooster, M. J., Grosvenor, M. J., Yan, S., & Roberts, G. (2022). Systematic mapping and review of landscape fire smoke (LFS) exposure impacts on insects. *Environmental Entomology*, *51*(5), 871–884.
- Liu, Y., Wooster, M. J., Grosvenor, M. J., Lim, K. S., & Francis, R. A. (2021). Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.) *Ecological Entomology*, *46*(2), 195–208.
- Liu, Z., McNeil, J. N., & Wu, K. (2011). Flight mill performance of the lacewing *Chrysoperla sinica* (Neuroptera: Chrysopidae) as a function of age, temperature, and relative humidity. *Journal of Economic Entomology*, *104*(1), 94–100.
- Lobert, J. M., Scharffe, D. H., Weimin, H., Kuhlbusch, T. A., Seuwen, R., Warneck, P., & Crutzen, P. J. (1991). Experimental evaluation of biomass burning emissions: Nitrogen and carbon containing compounds. In *Global biomass burning. atmospheric, climatic, and biospheric implications*.
- Long, T., Hu, C., Wang, R., Zhang, T., Kong, S., Li, W., Cai, J., Tian, W., & Zeng, T. (2020). Entomological radar overview: System and signal processing. *IEEE Aerospace and Electronic Systems Magazine*, *35*(1), 20–32.

- Lopez, V. M., McClanahan, M. N., Graham, L., & Hoddle, M. S. (2014). Assessing the flight capabilities of the goldspotted oak borer (coleoptera: Buprestidae) with computerized flight mills. *Journal of Economic Entomology*, *107*(3), 1127–1135.
- Lui, K., Bandowe, B. A. M., Ho, S. S. H., Chuang, H.-C., Cao, J.-J., Chuang, K.-J., Lee, S., Hu, D., & Ho, K. (2016). Characterization of chemical components and bioreactivity of fine particulate matter (pm_{2.5}) during incense burning. *Environmental pollution*, *213*, 524–532.
- Lukach, M., Dally, T., Evans, W., Hassall, C., Duncan, E. J., Bennett, L., Addison, F. I., Kunin, W. E., Chapman, J. W., & Neely III, R. R. (2022). The development of an unsupervised hierarchical clustering analysis of dual-polarization weather surveillance radar observations to assess nocturnal insect abundance and diversity. *Remote Sensing in Ecology and Conservation*.
- Lukowski, A., Popek, R., Jagiełło, R., Maderek, E., & Karolewski, P. (2018). Particulate matter on two prunus spp. decreases survival and performance of the folivorous beetle gonioctena quinquepunctata. *Environmental Science and Pollution Research*, *25*(17), 16629–16639.
- Lundmark, C. (2010). Long-distance insect migration. *BioScience*, *60*(5), 400–400.
- Lung, S.-C. C., & Hu, S.-C. (2003). Generation rates and emission factors of particulate matter and particle-bound polycyclic aromatic hydrocarbons of incense sticks. *Chemosphere*, *50*(5), 673–679.
- Maelzer, D., Zalucki, M., & Laughlin, R. (1996). Analysis and interpretation of long term light trap data for helioverpa punctigera (lepidoptera; noctuidae) in australia: Population changes and forecasting pest pressure. *Bulletin of Entomological Research*, *86*(5), 547–557.
- Magnone, E., Park, S.-K., & Park, J. H. (2016). Effects of moisture contents in the common oak on carbonaceous aerosols generated from combustion processes in an indoor wood stove. *Combustion Science and Technology*, *188*(6), 982–996.

- Martí-Campoy, A., Ávalos, J. A., Soto, A., Rodríguez-Ballester, F., Martínez-Blay, V., & Malumbres, M. P. (2016). Design of a computerised flight mill device to measure the flight potential of different insects. *Sensors*, *16*(4), 485.
- May, R. M. (1988). How many species are there on earth? *Science*, *241*(4872), 1441–1449.
- McCarty, J. L., Korontzi, S., Justice, C. O., & Loboda, T. (2009). The spatial and temporal distribution of crop residue burning in the contiguous united states. *Science of the Total Environment*, *407*(21), 5701–5712.
- McCracken, G. F., Gillam, E. H., Westbrook, J. K., Lee, Y.-F., Jensen, M. L., & Balsley, B. B. (2008). Brazilian free-tailed bats (*tadarida brasiliensis*: Molossidae, chiroptera) at high altitude: Links to migratory insect populations. *Integrative and Comparative Biology*, *48*(1), 107–118.
- McGregor, S. E. (1976). *Insect pollination of cultivated crop plants*. Agricultural Research Service, US Department of Agriculture.
- Menchetti, M., Guéguen, M., & Talavera, G. (2019). Spatio-temporal ecological niche modelling of multigenerational insect migrations. *Proceedings of the Royal Society B*, *286*(1910), 20191583.
- Merlin, C., Gegear, R. J., & Reppert, S. M. (2009). Antennal circadian clocks coordinate sun compass orientation in migratory monarch butterflies. *Science*, *325*(5948), 1700–1704.
- Miller, N. G., Wassenaar, L. I., Hobson, K. A., & Norris, D. R. (2011). Monarch butterflies cross the appalachians from the west to recolonize the east coast of north america. *Biology Letters*, *7*(1), 43–46.
- Mills, S. C., Oliver, T. H., Bradbury, R. B., Gregory, R. D., Brereton, T., Kühn, E., Kuussaari, M., Musche, M., Roy, D. B., Schmucki, R., et al. (2017). European butterfly populations vary in sensitivity to weather across their geographical ranges. *Global Ecology and Biogeography*, *26*(12), 1374–1385.
- Minter, M., Pearson, A., Lim, K. S., Wilson, K., Chapman, J. W., & Jones, C. M. (2018). The tethered flight technique as a tool for studying life-history strategies associated with migration in insects. *Ecological entomology*, *43*(4), 397–411.

- Moore, T. T. (2011). Climate change and animal migration. *Envtl. L.*, 41, 393.
- Moritz, M. A., Parisien, M.-A., Batllori, E., Krawchuk, M. A., Van Dorn, J., Ganz, D. J., & Hayhoe, K. (2012). Climate change and disruptions to global fire activity. *Ecosphere*, 3(6), 1–22.
- Mouritsen, H., & Frost, B. J. (2002). Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proceedings of the National Academy of Sciences*, 99(15), 10162–10166.
- Naranjo, S. E. (2019). Assessing insect flight behavior in the laboratory: A primer on flight mill methodology and what can be learned. *Annals of the Entomological Society of America*, 112(3), 182–199.
- Nesbit, R., Hill, J., Woiwod, I., Sivell, D., Bensusan, K., & Chapman, J. (2009). Seasonally adaptive migratory headings mediated by a sun compass in the painted lady butterfly, *vanessa cardui*. *Animal Behaviour*, 78(5), 1119–1125.
- New, T. R., et al. (1992). *Insects as predators*. New South Wales University Press in association with Australian Institute of . . .
- New, T. (1997). Are lepidoptera an effective ‘umbrella group’ for biodiversity conservation? *Journal of insect conservation*, 1(1), 5–12.
- Nguyen, P. D., Martinussen, N., Mallach, G., Ebrahimi, G., Jones, K., Zimmerman, N., & Henderson, S. B. (2021). Using low-cost sensors to assess fine particulate matter infiltration (pm_{2.5}) during a wildfire smoke episode at a large inpatient healthcare facility. *International Journal of Environmental Research and Public Health*, 18(18), 9811.
- O’Dell, K., Bilsback, K., Ford, B., Martenies, S. E., Magzamen, S., Fischer, E. V., & Pierce, J. R. (2021). Estimated mortality and morbidity attributable to smoke plumes in the united states: Not just a western us problem. *GeoHealth*, 5(9), e2021GH000457.
- Okada, R., Pham, D. L., Ito, Y., Yamasaki, M., & Ikeno, H. (2018). Measuring the flight ability of the ambrosia beetle, *platypus quercivorus* (murayama), using a low-cost, small, and easily constructed flight mill. *JoVE (Journal of Visualized Experiments)*, (138), e57468.

- O'Neal, B. J., Stafford, J. D., & Larkin, R. P. (2015). Migrating ducks in inland north america ignore major rivers as leading lines. *Ibis*, *157*(1), 154–161.
- Pan, H., Yang, X., Bidne, K., Hellmich, R. L., Siegfried, B. D., & Zhou, X. (2015). Selection of reference genes for rt-qpcr analysis in the monarch butterfly, *danaus plexippus* (l.), a migrating bio-indicator. *PloS one*, *10*(6), e0129482.
- Pardo, A., & Borges, P. A. (2020). Worldwide importance of insect pollination in apple orchards: A review. *Agriculture, Ecosystems & Environment*, *293*, 106839.
- Parikh, G., Rawtani, D., & Khatri, N. (2021). Insects as an indicator for environmental pollution. *Environmental Claims Journal*, *33*(2), 161–181.
- Parmesan, C. (2019). Butterflies as bioindicators for climate change effects. In *Butterflies* (pp. 541–560). University of Chicago Press.
- Pausas, J. G., & Keeley, J. E. (2021). Wildfires and global change. *Frontiers in Ecology and the Environment*, *19*(7), 387–395.
- Piazzalunga, A., Belis, C., Bernardoni, V., Cazzuli, O., Fermo, P., Valli, G., & Vecchi, R. (2011). Estimates of wood burning contribution to pm by the macro-tracer method using tailored emission factors. *Atmospheric Environment*, *45*(37), 6642–6649.
- Pollard, E. (1998). Increased abundance of the red admiral butterfly *vanessa atalanta* in britain: The roles of immigration, overwintering and breeding within the country. *Ecol Lett*, *1*, 77–81.
- Possell, M., & Bell, T. L. (2012). The influence of fuel moisture content on the combustion of eucalyptus foliage. *International journal of wildland fire*, *22*(3), 343–352.
- Price-Allison, A., Lea-Langton, A., Mitchell, E., Gudka, B., Jones, J., Mason, P., & Williams, A. (2019). Emissions performance of high moisture wood fuels burned in a residential stove. *Fuel*, *239*, 1038–1045.
- Price-Allison, A., Mason, P. E., Jones, J. M., Barimah, E. K., Jose, G., Brown, A. E., Ross, A. B., & Williams, A. (2021). The impact of fuelwood moisture content on the emission of gaseous and particulate pollutants from a wood stove. *Combustion Science and Technology*, *195*(1), 133–152.

- Qi, G.-J., Ma, J., Wan, J., Ren, Y.-L., McKirdy, S., Hu, G., & Zhang, Z.-F. (2021). Source regions of the first immigration of fall armyworm, *spodoptera frugiperda* (lepidoptera: Noctuidae) invading australia. *Insects*, *12*(12), 1104.
- Randerson, J., Chen, Y., Van Der Werf, G., Rogers, B., & Morton, D. (2012). Global burned area and biomass burning emissions from small fires. *Journal of Geophysical Research: Biogeosciences*, *117*(G4).
- Rau, J. A. (1989). Composition and size distribution of residential wood smoke particles. *Aerosol Science and Technology*, *10*(1), 181–192.
- Reinhardt, T. E., Ottmar, R. D., & Castilla, C. (2001). Smoke impacts from agricultural burning in a rural brazilian town. *Journal of the Air & Waste Management Association*, *51*(3), 443–450.
- Reisen, F., Meyer, C., Weston, C., & Volkova, L. (2018). Ground-based field measurements of pm_{2.5} emission factors from flaming and smoldering combustion in eucalypt forests. *Journal of Geophysical Research: Atmospheres*, *123*(15), 8301–8314.
- Rennie, S. J. (2014). Common orientation and layering of migrating insects in south-eastern a ustralia observed with a d oppler weather radar. *Meteorological Applications*, *21*(2), 218–229.
- Reppert, S. M., & de Roode, J. C. (2018). Demystifying monarch butterfly migration. *Current Biology*, *28*(17), R1009–R1022.
- Reynolds, D. R., Chapman, J. W., & Drake, V. A. (2017). Riders on the wind: The aeroecology of insect migrants. In *Aeroecology* (pp. 145–178). Springer.
- Reynolds, D., Chapman, J., & Harrington, R. (2006). The migration of insect vectors of plant and animal viruses. *Advances in virus research*, *67*, 453–517.
- Reynolds, D., Riley, J., et al. (1997). *Flight behaviour and migration of insect pests. radar studies in developing countries*. Natural Resources Institute (NRI).
- Riley, J. R., Reynolds, D., Mukhopadhyay, S., Ghosh, M., & Sarkar, T. (1995). Long-distance migration of aphids and other small insects in northeast india. *European Journal of Entomology*, *92*(4), 639–653.

- Riley, J., Downham, M., & Cooter, R. (1997). Comparison of the performance of cicadulina leafhoppers on flight mills with that to be expected in free flight. *Entomologia Experimentalis et Applicata*, 83(3), 317–322.
- Riley, J., XIA-NIAN, C., XIAO-XI, Z., Reynolds, D., GUO-MIN, X., Smith, A., JI-YI, C., AI-DONG, B., & BAO-PING, Z. (1991). The long-distance migration of nilaparvata lugens (stål)(delphacidae) in china: Radar observations of mass return flight in the autumn. *Ecological Entomology*, 16(4), 471–489.
- Riley, K. L., Williams, A. P., Urbanski, S. P., Calkin, D. E., Short, K. C., & O'Connor, C. D. (2019). Will landscape fire increase in the future? a systems approach to climate, fire, fuel, and human drivers. *Current Pollution Reports*, 5(2), 9–24.
- Roberts, G., & Wooster, M. (2021). Global impact of landscape fire emissions on surface level pm2.5 concentrations, air quality exposure and population mortality. *Atmospheric Environment*, 252, 118210.
- Rytkönen, S., Vesterinen, E. J., Westerduin, C., Leviäkangas, T., Votka, E., Mutanen, M., Välimäki, P., Hukkanen, M., Suokas, M., & Orell, M. (2019). From feces to data: A metabarcoding method for analyzing consumed and available prey in a bird-insect food web. *Ecology and evolution*, 9(1), 631–639.
- Sabrosky, C. W. (1953). How many insects are there? *Systematic Zoology*, 2(1), 31–36.
- Sahai, S., Sharma, C., Singh, D., Dixit, C., Singh, N., Sharma, P., Singh, K., Bhatt, S., Ghude, S., Gupta, V., et al. (2007). A study for development of emission factors for trace gases and carbonaceous particulate species from in situ burning of wheat straw in agricultural fields in india. *Atmospheric Environment*, 41(39), 9173–9186.
- Sánchez-Muros, M.-J., Barroso, F. G., & Manzano-Agugliaro, F. (2014). Insect meal as renewable source of food for animal feeding: A review. *Journal of Cleaner Production*, 65, 16–27.
- Sanchis, E., Ferrer, M., Calvet, S., Coscollà, C., Yusà, V., & Cambra-López, M. (2014). Gaseous and particulate emission profiles during controlled rice straw burning. *Atmospheric Environment*, 98, 25–31.

- Sane, S. P. (2016). Neurobiology and biomechanics of flight in miniature insects. *Current opinion in neurobiology*, *41*, 158–166.
- Sane, S. P., Dieudonné, A., Willis, M. A., & Daniel, T. L. (2007). Antennal mechanosensors mediate flight control in moths. *science*, *315*(5813), 863–866.
- Satterfield, D. A., Sillett, T. S., Chapman, J. W., Altizer, S., & Marra, P. P. (2020). Seasonal insect migrations: Massive, influential, and overlooked. *Frontiers in Ecology and the Environment*, *18*(6), 335–344.
- Satyendra, T., Singh, R., & Shaishav, S. (2013). Emissions from crop/biomass residue burning risk to atmospheric quality. *Int Res J Earth Sci*, *1*(1), 1–5.
- Schaefer, G. (1969). Radar studies of locust, moth and butterfly migration in the sahara. *Proc Royal Entomol Soc Lond C*, *34*(33), 39–40.
- Schmid-Hempel, P. (1998). *Parasites in social insects* (Vol. 60). Princeton University Press.
- Schowalter, T. (2012). Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry*, *31*(6), 518–536.
- Schütz, S., Weissbecker, B., Hummel, H. E., Apel, K.-H., Schmitz, H., & Bleckmann, H. (1999). Insect antenna as a smoke detector. *Nature*, *398*(6725), 298–299.
- Shafie, M. S., Wong, A. B., Harun, S., & Fikri, A. H. (2017). The use of aquatic insects as bio-indicator to monitor freshwater stream health of liwagu river, sabah, malaysia. *Journal of Entomology and Zoology Studies*, *5*(4), 1662–1666.
- Shapiro, A. (2019). *Field guide to butterflies of the san francisco bay and sacramento valley regions*. University of California Press.
- Shi, T., Liu, Y., Zhang, L., Hao, L., & Gao, Z. (2014). Burning in agricultural landscapes: An emerging natural and human issue in china. *Landscape Ecology*, *29*(10), 1785–1798.
- Smith, A., Riley, J., & Gregory, R. (1993). A method for routine monitoring of the aerial migration of insects by using a vertical-looking radar. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *340*(1294), 393–404.

- Smithers, C. (1983). Migration records in australia, 4. pieridae (lepidoptera) other than 'anaphaeis java teutonia'(f.) *The Australian Entomologist*, 10(4), 47–54.
- Sparks, T. H., Dennis, R. L., Croxton, P. J., Cade, M., et al. (2007). Increased migration of lepidoptera linked to climate change. *European Journal of Entomology*, 104(1), 139–143.
- Stefanescu, C. (2001). The nature of migration in the red admiral butterfly *vanessa atalanta*: Evidence from the population ecology in its southern range. *Ecological Entomology*, 26(5), 525–536.
- Stefanescu, C. (2011). Moroccan source areas of the painted lady butterfly *vanessa cardui* (nymphalidae: Nymphalinae) migrating into europe in spring. *The Journal of the Lepidopterists' Society*, 65(1), 15–26.
- Stefanescu, C., PUIG-MONTSERRAT, X., Samraoui, B., Izquierdo, R., Ubach, A., & Arrizabalaga, A. (2017). Back to africa: Autumn migration of the painted lady butterfly *vanessa cardui* is timed to coincide with an increase in resource availability. *Ecological Entomology*, 42(6), 737–747.
- Stefanescu, C., Alarcón, M., & Àvila, A. (2007). Migration of the painted lady butterfly, *vanessa cardui*, to north-eastern spain is aided by african wind currents. *Journal of Animal Ecology*, 888–898.
- Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T., Carnicer, J., Cassar, L. F., Fox, R., Heliölä, J., et al. (2013). Multi-generational long-distance migration of insects: Studying the painted lady butterfly in the western palaeartic. *Ecography*, 36(4), 474–486.
- Stefanescu, C., Soto, D. X., Talavera, G., Vila, R., & Hobson, K. A. (2016). Long-distance autumn migration across the sahara by painted lady butterflies: Exploiting resource pulses in the tropical savannah. *Biology letters*, 12(10), 20160561.
- Stepanian, P. M., Horton, K. G., Melnikov, V. M., Zrnić, D. S., & Gauthreaux Jr, S. A. (2016). Dual-polarization radar products for biological applications. *Ecosphere*, 7(11), e01539.
- Stockwell, C., Yokelson, R., Kreidenweis, S., Robinson, A., DeMott, P., Sullivan, R., Reardon, J., Ryan, K., Griffith, D., & Stevens, L. (2014). Trace gas emissions

- from combustion of peat, crop residue, domestic biofuels, grasses, and other fuels: Configuration and fourier transform infrared (ftir) component of the fourth fire lab at missoula experiment (flame-4). *Atmospheric chemistry and physics*, *14*(18), 9727–9754.
- Talavera, G., Bataille, C., Benyamini, D., Gascoigne-Pees, M., & Vila, R. (2018). Round-trip across the sahara: Afrotropical painted lady butterflies recolonize the mediterranean in early spring. *Biology letters*, *14*(6), 20180274.
- Talavera, G., García-Berro, A., Talla, V. N., Ng'iru, I., Bahleman, F., Kébé, K., Nzala, K. M., Plasencia, D., Marafi, M. A., Kassie, A., et al. (2023). The afrotropical breeding grounds of the palearctic-african migratory painted lady butterflies (*vanessa cardui*). *Proceedings of the National Academy of Sciences*, *120*(16), e2218280120.
- Talavera, G., & Vila, R. (2017). Discovery of mass migration and breeding of the painted lady butterfly *vanessa cardui* in the sub-sahara: The europe–africa migration revisited. *Biological Journal of the Linnean Society*, *120*(2), 274–285.
- Tan, Y. Q., Dion, E., & Monteiro, A. (2018). Haze smoke impacts survival and development of butterflies. *Scientific reports*, *8*(1), 1–10.
- Tang, H., Liu, G., Zhu, J., Han, Y., & Kobayashi, K. (2013). Seasonal variations in surface ozone as influenced by asian summer monsoon and biomass burning in agricultural fields of the northern yangtze river delta. *Atmospheric research*, *122*, 67–76.
- Tao, M., Chen, L., Wang, Z., Tao, J., & Su, L. (2013). Satellite observation of abnormal yellow haze clouds over east china during summer agricultural burning season. *Atmospheric environment*, *79*, 632–640.
- Taylor, G. K. (2001). Mechanics and aerodynamics of insect flight control. *Biological Reviews*, *76*(4), 449–471.
- Taylor, R. A., Bauer, L. S., Poland, T. M., & Windell, K. N. (2010). Flight performance of *agrilus planipennis* (coleoptera: Buprestidae) on a flight mill and in free flight. *Journal of Insect Behavior*, *23*, 128–148.

- Thangavel, P., Park, D., & Lee, Y.-C. (2022). Recent insights into particulate matter (pm_{2.5})-mediated toxicity in humans: An overview. *International journal of environmental research and public health*, *19*(12), 7511.
- Throop, H. L., & Lerdau, M. T. (2004). Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes.
- Tihay-Felicelli, V., Santoni, P., Gerandi, G., & Barboni, T. (2017). Smoke emissions due to burning of green waste in the mediterranean area: Influence of fuel moisture content and fuel mass. *Atmospheric Environment*, *159*, 92–106.
- Topp, E. N., Tschardtke, T., & Loos, J. (2022). Fire and landscape context shape plant and butterfly diversity in a south african shrubland. *Diversity and Distributions*, *28*(3), 357–371.
- Tribe, G., Tautz, J., Sternberg, K., & Cullinan, J. (2017). Firewalls in bee nests—survival value of propolis walls of wild cape honeybee (*apis mellifera capensis*). *The Science of Nature*, *104*(3), 1–4.
- Tutt, J. (1902). The migration dispersal of insects. *The Migration of Butterflies*.
- Van der Werf, G. R., Randerson, J. T., Giglio, L., Collatz, G., Mu, M., Kasibhatla, P. S., Morton, D. C., DeFries, R., Jin, Y. v., & van Leeuwen, T. T. (2010). Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009). *Atmospheric chemistry and physics*, *10*(23), 11707–11735.
- Van Doren, B. M., Horton, K. G., Stepanian, P. M., Mizrahi, D. S., & Farnsworth, A. (2016). Wind drift explains the reoriented morning flights of songbirds. *Behavioral Ecology*, *27*(4), 1122–1131.
- Venkataraman, C., Habib, G., Kadamba, D., Shrivastava, M., Leon, J.-F., Crouzille, B., Boucher, O., & Streets, D. (2006). Emissions from open biomass burning in india: Integrating the inventory approach with high-resolution moderate resolution imaging spectroradiometer (modis) active-fire and land cover data. *Global biogeochemical cycles*, *20*(2).
- Vernooij, R., Winiger, P., Wooster, M., Strydom, T., Poulain, L., Dusek, U., Grosvenor, M., Roberts, G. J., Schutgens, N., & Van Der Werf, G. R. (2022). A quad-copter unmanned aerial system (uas)-based methodology for measuring biomass

- burning emission factors. *Atmospheric Measurement Techniques*, 15(14), 4271–4294.
- Visscher, P. K., Vetter, R. S., & Robinson, G. E. (1995). Alarm pheromone perception in honey bees is decreased by smoke (hymenoptera: Apidae). *Journal of Insect Behavior*, 8(1), 11–18.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389–395.
- Wang, Q., Wang, L., Li, X., Xin, J., Liu, Z., Sun, Y., Liu, J., Zhang, Y., Du, W., Jin, X., et al. (2020). Emission characteristics of size distribution, chemical composition and light absorption of particles from field-scale crop residue burning in northeast china. *Science of the Total Environment*, 710, 136304.
- Wang, X.-G., Johnson, M. W., Daane, K. M., & Opp, S. (2009). Combined effects of heat stress and food supply on flight performance of olive fruit fly (diptera: Tephritidae). *Annals of the Entomological Society of America*, 102(4), 727–734.
- Ward, D., Hao, W., Susott, R., Babbitt, R., Shea, R., Kauffman, J., & Justice, C. (1996). Effect of fuel composition on combustion efficiency and emission factors for african savanna ecosystems. *Journal of Geophysical Research: Atmospheres*, 101(D19), 23569–23576.
- Ward, D., Susott, R., Kauffman, J., Babbitt, R., Cummings, D., Dias, B., Holben, B., Kaufman, Y., Rasmussen, R., & Setzer, A. (1992). Smoke and fire characteristics for cerrado and deforestation burns in brazil: Base-b experiment. *Journal of Geophysical Research: Atmospheres*, 97(D13), 14601–14619.
- Watanabe, M. E. (1994). Pollination worries rise as honey bees decline. *Science*, 265(5176), 1170–1170.
- Westbrook, J., Fleischer, S., Jairam, S., Meagher, R., & Nagoshi, R. (2019). Multi-generational migration of fall armyworm, a pest insect. *Ecosphere*, 10(11), e02919.

- Westbrook, J., & Eyster, R. (2017). Doppler weather radar detects emigratory flights of noctuids during a major pest outbreak. *Remote Sensing Applications: Society and Environment*, 8, 64–70.
- Westbrook, J., Eyster, R., & Wolf, W. (2014). Wsr-88d doppler radar detection of corn earworm moth migration. *international Journal of Biometeorology*, 58(5), 931–940.
- Westbrook, J. K. (2008). Noctuid migration in texas within the nocturnal aeroecological boundary layer. *Integrative and Comparative biology*, 48(1), 99–106.
- Wiens, J. J., Lapoint, R. T., & Whiteman, N. K. (2015). Herbivory increases diversification across insect clades. *Nature communications*, 6(1), 1–7.
- Williams, C. B., et al. (1930). The migration of butterflies. *The Migration of Butterflies*.
- Williams, C. (1957). Insect migration. *Annual review of entomology*, 2(1), 163–180.
- Wood, C. R., Reynolds, D., Wells, P., Barlow, J. F., Woiwod, I., & Chapman, J. (2009). Flight periodicity and the vertical distribution of high-altitude moth migration over southern britain. *Bulletin of entomological research*, 99(5), 525–535.
- Wooster, M. J., Gaveau, D. L., Salim, M. A., Zhang, T., Xu, W., C. Green, D., Huijnen, V., Murdiyarto, D., Gunawan, D., Borchard, N., et al. (2018). New tropical peatland gas and particulate emissions factors indicate 2015 indonesian fires released far more particulate matter (but less methane) than current inventories imply. *Remote Sensing*, 10(4), 495.
- Wooster, M. J., Roberts, G., Smith, A. M., Johnston, J., Freeborn, P., Amici, S., & Hudak, A. T. (2013). Thermal remote sensing of active vegetation fires and biomass burning events. *Thermal Infrared Remote Sensing: Sensors, Methods, Applications*, 347–390.
- Wooster, M., Freeborn, P., Archibald, S., Oppenheimer, C., Roberts, G., Smith, T., Govender, N., Burton, M., & Palumbo, I. (2011). Field determination of biomass burning emission ratios and factors via open-path ftir spectroscopy and fire radiative power assessment: Headfire, backfire and residual smoul-

- dering combustion in african savannahs. *Atmospheric Chemistry and Physics*, *11*(22), 11591–11615.
- Wotton, K. R., Gao, B., Menz, M. H., Morris, R. K., Ball, S. G., Lim, K. S., Reynolds, D. R., Hu, G., & Chapman, J. W. (2019). Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. *Current Biology*, *29*(13), 2167–2173.
- Xia, X., Zong, X., & Sun, L. (2013). Exceptionally active agricultural fire season in mid-eastern china in june 2012 and its impact on the atmospheric environment. *Journal of Geophysical Research: Atmospheres*, *118*(17), 9889–9900.
- Xing, Y.-F., Xu, Y.-H., Shi, M.-H., & Lian, Y.-X. (2016). The impact of pm_{2.5} on the human respiratory system. *Journal of thoracic disease*, *8*(1), E69.
- Yan, X., Ohara, T., & Akimoto, H. (2006). Bottom-up estimate of biomass burning in mainland china. *Atmospheric Environment*, *40*(27), 5262–5273.
- Yela, J. L., & Holyoak, M. (1997). Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (lepidoptera: Noctuidae). *Environmental Entomology*, *26*(6), 1283–1290.
- Yevich, R., & Logan, J. A. (2003). An assessment of biofuel use and burning of agricultural waste in the developing world. *Global biogeochemical cycles*, *17*(4).
- Yokelson, R. J., Goode, J. G., Ward, D. E., Susott, R. A., Babbitt, R. E., Wade, D. D., Bertschi, I., Griffith, D. W., & Hao, W. M. (1999). Emissions of formaldehyde, acetic acid, methanol, and other trace gases from biomass fires in north carolina measured by airborne fourier transform infrared spectroscopy. *Journal of Geophysical Research: Atmospheres*, *104*(D23), 30109–30125.
- Yokelson, R. J., Griffith, D. W., & Ward, D. E. (1996). Open-path fourier transform infrared studies of large-scale laboratory biomass fires. *Journal of Geophysical Research: Atmospheres*, *101*(D15), 21067–21080.
- Yousuf, M., Khaliq, A., & Najam, M. (1998). Population and feeding capacity of dragonflies on insect pests of rice in pakistan (anisoptera: Libellulidae). *Notulae odonatologicae*, *5*(2), 17–19.

- Zada, N., Farid, A., Ahmed Zia, M. S., Masaud, S., Khan, A. K., Khan, I. A., & Fazlullah, T. B. (2016). Damselflies (odonata: Zygoptera) fauna of district buner, khyber pakhtunkhwa, pakistan. *J Entomol Zool Stud*, *4*, 49–495.
- Zeng, J., Liu, Y., Zhang, H., Liu, J., Jiang, Y., Wyckhuys, K. A., & Wu, K. (2020). Global warming modifies long-distance migration of an agricultural insect pest. *Journal of Pest Science*, *93*, 569–581.
- Zhan, S., Merlin, C., Boore, J. L., & Reppert, S. M. (2011). The monarch butterfly genome yields insights into long-distance migration. *Cell*, *147*(5), 1171–1185.
- Zhang, H., Hu, J., Qi, Y., Li, C., Chen, J., Wang, X., He, J., Wang, S., Hao, J., Zhang, L., et al. (2017). Emission characterization, environmental impact, and control measure of pm2. 5 emitted from agricultural crop residue burning in china. *Journal of Cleaner Production*, *149*, 629–635.
- Zhang, H., Ye, X., Cheng, T., Chen, J., Yang, X., Wang, L., & Zhang, R. (2008). A laboratory study of agricultural crop residue combustion in china: Emission factors and emission inventory. *Atmospheric Environment*, *42*(36), 8432–8441.
- Zhang, J., Cheng, H., Wang, D., Zhu, Y., Yang, C., Shen, Y., Yu, J., Li, Y., Xu, S., Zhang, S., et al. (2021). Chronic exposure to pm2. 5 nitrate, sulfate, and ammonium causes respiratory system impairments in mice. *Environmental Science & Technology*, *55*(5), 3081–3090.
- Zhang, L., Liu, Y., & Hao, L. (2016). Contributions of open crop straw burning emissions to pm2. 5 concentrations in china. *Environmental Research Letters*, *11*(1), 014014.
- Zhang, T., Wooster, M. J., De Jong, M. C., & Xu, W. (2018). How well does the ‘small fire boost’ methodology used within the gfed4. 1s fire emissions database represent the timing, location and magnitude of agricultural burning? *Remote Sensing*, *10*(6), 823.
- Zhang, T., Wooster, M. J., Green, D. C., & Main, B. (2015). New field-based agricultural biomass burning trace gas, pm2. 5, and black carbon emission ratios and factors measured in situ at crop residue fires in eastern china. *Atmospheric Environment*, *121*, 22–34.

- Zhang, Y., Ji, X., Ku, T., & Sang, N. (2016). Inflammatory response and endothelial dysfunction in the hearts of mice co-exposed to so₂, no₂, and pm 2.5. *Environmental toxicology*, *31*(12), 1996–2005.
- Zhang, Y., Shao, M., Lin, Y., Luan, S., Mao, N., Chen, W., & Wang, M. (2013). Emission inventory of carbonaceous pollutants from biomass burning in the pearl river delta region, china. *Atmospheric environment*, *76*, 189–199.
- Zvereva, E. L., & Kozlov, M. V. (2010). Responses of terrestrial arthropods to air pollution: A meta-analysis. *Environmental Science and Pollution Research*, *17*, 297–311.