Journal of Insect Physiology 59 (2013) 1199–1211

Contents lists available at ScienceDirect

Journal of Insect Physiology

journal homepage: www.elsevier.com/locate/jinsphys

Thermal biology, population fluctuations and implications of temperature extremes for the management of two globally significant insect pests

Casper Nyamukondiwa [a,1], Christopher W. Weldon [b,c], Steven L. Chown [d], Peter C. le Roux [b,e,2], John S. Terblanche [a,*]

[a] Centre for Invasion Biology, Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[b] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[c] Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa
[d] School of Biological Sciences, Monash University, Victoria 3800, Australia
[e] Department of Geosciences and Geography, University of Helsinki, P.O. Box 64, FI-00014, Finland

ARTICLE INFO

Article history:
Received 31 July 2013
Received in revised form 16 September 2013
Accepted 18 September 2013
Available online 28 September 2013

Keywords:
Thermal biology
Phenotypic plasticity
Population dynamics
Pest management

ABSTRACT

The link between environmental temperature, physiological processes and population fluctuations is a significant aspect of insect pest management. Here, we explore how thermal biology affects the population abundance of two globally significant pest fruit fly species, *Ceratitis capitata* (medfly) and *C. rosa* (Natal fruit fly), including irradiated individuals and those expressing a temperature sensitive lethal (*tsl*) mutation that are used in the sterile insect technique. Results show that upper and lower lethal temperatures are seldom encountered at the field sites, while critical minimum temperatures for activity and lower developmental thresholds are crossed more frequently. Estimates of abundance revealed that *C. capitata* are active year-round, but abundance declines markedly during winter. Temporal autocorrelation of average fortnightly trap captures and of development time, estimated from an integrated model to calculate available degree days, show similar seasonal lags suggesting that population increases in early spring occur after sufficient degree-days have accumulated. By contrast, population collapses coincide tightly with increasing frequency of low temperature events that fall below critical minimum temperatures for activity. Individuals of *C. capitata* expressing the *tsl* mutation show greater critical thermal maxima and greater longevity under field conditions than reference individuals. Taken together, this evidence suggests that low temperatures limit populations in the Western Cape, South Africa and likely do so elsewhere. Increasing temperature extremes and warming climates generally may extend the season over which these species are active, and could increase abundance. The sterile insect technique may prove profitable as climates change given that laboratory-reared *tsl* flies have an advantage under warmer conditions.

1. Introduction

Knowledge of thermal biology has proven especially useful for understanding insect demography, population fluctuations and in forecasting pest outbreaks (e.g. Kingsolver, 1989; Bale, 2010). Low temperatures associated with winter generally suppress insect population growth rates, through reductions in development, suppression of activity, indirect chilling injury, and/or direct chilling mortality (Chown and Nicolson, 2004; Bale, 2010). Insects may cope with winter conditions by either behavioural or physiological compensation, arrested development (e.g. diapause) or some combination thereof (Denlinger and Lee, 2010). Physiologically, insects can adjust thermal tolerance over either the short-term (hardening) or longer-term (acclimatization in the field and acclimation under controlled laboratory conditions). A common example of acclimatization is the suite of physiological changes occurring at the onset of winter, typically providing improved low temperature tolerance (Hoffmann et al., 2003). Knowledge of overwintering biology, including physiological responses, is therefore often critical for assessments of pest insect population dynamics (Bale, 2010). For many economically significant pest insects, seasonal variation in physiology or overwintering biology is poorly

* Corresponding author. Tel.: +27 21 808 9225; fax: +27 21 808 2356.
E-mail address: jst@sun.ac.za (J.S. Terblanche).
[1] Present address: Department of Earth and Environmental Sciences, Botswana International University of Science and Technology (BIUST), Private Bag BO 041 Bontleng, Gaborone, Botswana.
[2] Present address: Department of Plant Sciences, University of Pretoria, Private Bag X20, Hatfield 0083, South Africa.

0022-1910/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jinsphys.2013.09.004

elucidated. Improving this situation is important not only for pest management over the short term, but is also significant in the context of rapidly changing climates globally (Bale and Hayward, 2010).

This is true for two of the most significant pests of commercially-grown fruit crops: the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) and the Natal fruit fly, *C. rosa* Karsch. Both are multivoltine, polyphagous tephritid flies that result in millions of dollars of losses annually (Malacrida et al., 2007; De Meyer et al., 2008). Demographic analyses of the two species suggest a very high net reproduction rate while young and a lack of diapause (Carey, 1984; Manrakhan and Addison, 2007). *Ceratitis capitata* probably originated from sub-Saharan East Africa and has become widely distributed in most continents with tropical and temperate climates (Malacrida et al., 2007). By contrast, *C. rosa* has a restricted African distribution (De Meyer et al., 2008; De Villiers et al., 2012), but is considered a significant biosecurity threat. In consequence, both species represent a burden to agriculture and act as barriers to economic transformation of rural communities through direct crop losses, the costs of control practices, and reduced market access. Comparatively little is known however about the relationships between their demography, abundance and thermal biology, and this is not a typical consideration in their management.

In addition to chemical control (pesticides including malathion), the Sterile Insect Technique (SIT) is one of the main methods used to control *C. capitata* (Klassen and Curtis, 2005). SIT involves releasing many males that have been rendered reproductively sterile by radiation, with the intent that they will mate with wild females and reduce the number of viable offspring (Knipling, 1959). Strains of *C. capitata* currently used in SIT campaigns possess a 'temperature sensitive lethal' (*tsl*) mutation that makes females homozygous for the *tsl* gene more susceptible to high temperature mortality (Franz, 2005). Application of a heat stress to eggs kills female embryos and permits large-scale, male-only releases. The release of a male-only strain improves the efficacy of SIT because only wild females will be present in the target area (Caceres, 2002). Females homozygous for the *tsl* gene remain sensitive to high temperatures throughout their lifetime such that sustained temperatures of over 28 °C lead to significant adult mortality within only a few days (Franz, 2005). It remains unknown however, whether the *tsl* mutation or irradiation affects the thermal tolerance of released male *tsl C. capitata* under field conditions. Such data have direct implications for ongoing SIT control programmes in South Africa and other parts of the world where *C. capitata* is considered a major pest. By contrast, control of *C. rosa* does not yet involve the release of sterile males, but the future of large-scale SIT campaigns could benefit from knowledge of radiation effects on the thermal tolerance of this species.

The overall aim of this work is therefore to determine aspects of the thermal environment that influence the population fluctuations of these two key horticultural pests to inform management and control practice. Specifically, to understand the influence of *tsl* and climate on demography or population fluctuations more generally, especially given expectations of future warming climates around the globe (Archer and Rahmstorf, 2010), we examined the extent to which thermal physiology accounts for population variability in both species. We determined the key thermobiological traits, including plastic responses in the field, across both species and in irradiated/unirradiated and untreated vs. *tsl* strains of *C. capitata*, and complemented these investigations with assessments of longevity of adults in the field. These data were then used in conjunction with microclimate information to estimate which physiological parameters, including developmental rates and limits, estimated from other studies, might be most significant in affecting population fluctuations, how SIT treatments might affect them, and what a warmer future might mean for the management of these species.

2. Materials and methods

We focused on traits likely to modify the impact of temperature on population growth. Our primary focus here was to understand factors influencing the field population abundances of wild flies and for this reason these traits were scored on untreated flies which were assumed to be representative of wild flies. These included upper and lower lethal temperature (ULT, LLT), supercooling point (SCP), functional activity limits (or critical thermal limits) recorded as critical thermal minima (CT_{min}) and maxima (CT_{max}), and, where possible, variation among key life-stages (see Nyamukondiwa et al., 2010). Using previously established low temperature thresholds for development (LDT) and the accumulation of development time above these thresholds (sum of effective temperatures, SET) (Duyck and Quilici, 2002; Grout and Stoltz, 2007), combined with microclimate data gathered in four major fruit production areas, we then reviewed variation in population abundance to consider potential explanatory traits. A secondary aim of this work was to inform current management practises and better understand how extrinsic (e.g. season) and intrinsic factors (e.g. irradiation, *tsl* mutation) or species differences might influence the outcomes of this work and we therefore also sought to compare these factors, particularly under field conditions. To this end, we used a combination of species and strains. Each experiment is outlined below with additional details given in Electronic Supplementary Material (ESM).

2.1. Origin of study animals

Unless otherwise indicated, *C. capitata* and *C. rosa* used in all experiments came from a large outbred culture, maintained in high numbers under buffered, variable temperatures (25 ± 4 °C), and has been in the laboratory for *c*. 200 generations. The culture is regularly supplemented with wild flies caught during summer, by mating wild-caught males to cultured females, to minimise inbreeding effects. Relative humidity is not strictly controlled throughout rearing, but is typically ~65–75% in culture containers.

2.2. Supercooling points and lower lethal temperatures

The supercooling point of three stages was examined for each *Ceratitis* species: third instar larvae, pharate (pink eye stage) pupae, and adults of mixed sex that were ~5–6 days old. Mixed-sex cohorts were tested because no sex effect could be detected in pilot trials. To determine supercooling points (SCPs), sixteen individuals of each species in each stage were individually loaded into 0.65 ml microcentrifuge tubes. Each insect was placed in contact with the tip of a type-T copper-constantan thermocouple (36-AWG; Omega, Laval, Canada), inserted through the tube's lid and both the insect and thermocouple held in place using cotton wool. Each tube was placed into a plastic bag and then into ethanol that was regulated at experimental temperatures by a circulating programmable refrigeration bath (Huber CC410WL, Offenburg, Germany). Thermocouples were connected to one of two 8-channel Picotech TC-08 (Pico Technology, Cambridge, UK) thermocouple interfaces and temperature recorded at 1 Hz using PicoLog software. Experiments began at 10 °C, at which flies were held for 10 min to allow equilibration, before the ethanol in the bath was cooled at 0.5 °C min^{-1} (and see ESM). Variation in cooling rate was not however, a major factor influencing SCP (Table S1). SCP for each individual was determined as the lowest temperature recorded prior to a spike in temperature associated with the latent heat of crystallisation.