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Effect of temperature on development of the Western Flower Thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae)

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Abstract. The development of the Western Flower Thrips (*Frankliniella occidentalis* Pergande; Thysanoptera: Thripidae) was studied at six temperatures between 10 and 35°C. Developmental rate increased linearly as rearing temperature increased. It was estimated that 268 degree-days, above a threshold temperature of 7.9°C, were required to complete development from egg to adult. These data were related to records of field temperatures in the West Midlands region of the UK, to estimate the potential number of generations per year that could complete development in outdoor conditions. Using this data, a maximum of between three and five generations could have developed annually between 1986 and 1995, (in the absence of factors impairing continuous development). The application and relevance of this data as an indicator of the potential range of *F. occidentalis* is discussed.

Introduction

The geographical range of an insect will be determined, in part, by its response to temperature. For a species to establish in a new environment, the thermal conditions must allow reproduction and development to occur, and a significant proportion of the population to survive through periods of unfavourable conditions, such as winter.

The Western Flower Thrips (*Frankliniella occidentalis* Pergande) is a polyphagous thrips species that acts as a vector for tomato spotted wilt virus (Baker et al., 1993). This complex can cause significant damage to a diverse range of crops in the UK, mainland Europe, North and Central America. The species is difficult to control because of its small size, rapid reproduction (parthenogenetic or sexual), widespread resistance to pesticides and its preference for secluded habitats (Baker et al., 1993). *F. occidentalis* was first recorded in Britain in 1986 and has since become a widespread glasshouse pest (Baker et al., 1993). In the UK, overwintering of *F. occidentalis* is likely to occur within or around commercial glasshouses (McDonald et al., 1997a, b, c), but the ability of the species to develop outdoors has not been assessed.

The relationship between temperature and the developmental rate of insects can be described using linear or non-linear techniques (Eckenrode & Chapman, 1972; Campbell et al., 1974; Wagner et al., 1984a, b, 1985; Higley et al., 1986; Lamb, 1992; Phelps et al., 1993; van Rijn et al., 1995). These methods define the thermal input necessary for development, and as such can be used to estimate the number of generations that can develop per unit time.

This study investigates the relationship between temperature and development of *F. occidentalis*, and determines the basic thermal requirements for development. These data are related to temperature records for the Midlands area of the UK, and used to estimate the maximum number of generations per year that could potentially complete development in this region and in Southern Britain.

Methods

A stock culture of *F. occidentalis* was maintained on chrysanthemum flowers at 20°C (photoperiod 18L : 6D). Experimental individuals were reared in glass vials containing 4 ml non-nutrient agar and a leaf disc of chrysanthemum as detailed in McDonald et al. (1997a). To ensure sufficient oviposition, 120 vials each containing four adult females were placed at 20°C (photoperiod 18L : 6D) for 24 h. Adults were removed and 20 vials placed in each of six incubators set at 10, 15, 20, 25, 30 and 35°C (photoperiod 18L ; 6D). Temperatures inside each cabinet were recorded at 15 min intervals using a Grant Squirrel SQ32-16u datalogger. Vials were checked daily for emergence of first instar larvae. Newly hatched insects were individually placed in rearing vials and returned to the experimental regime. The date of emergence of first instar larvae, propupae, pupae and adults were noted. Emergence of second instar larvae was not recorded due to difficulty in discriminating late first and early second instar when exuviae were not visible. Leaf discs were changed regularly where necessary (after no more than seven days) in order to avoid deterioration in food quality and to prevent fungal or bacterial growth.

Linear regression of the mean temperatures experienced by individual insects and their developmental rate (1/days) was carried out, to estimate the threshold temperature and the number of degree-days necessary for development between stages and to adulthood.

In the absence of a more complete temperature dataset, records of daily maximum (T_{max}) and minimum air temperature (T_{min}) between 1986–1995 were used to calculate the number of degree-days above the threshold for development, that were available in the field between January and December each year. The number of degree-days available each day was calculated using the equation:

$$\text{Degree-days} = [(T_{max} + T_{min}) / 2] - \text{threshold for development}$$

Other work has shown that exposure to cold-stress inducing temperatures (e.g. –5°C) can reduce the developmental rate of *F. occidentalis*, leading to an extension of immature stages totalling two days at 20°C (McDonald et al., 1997c). Whilst this effect may be important at particular times of year (e.g. when temperatures fluctuate between developmental threshold and cold stress induction), the impact in terms of potential annual voltinism is likely to be minimal.

Results

The time taken to complete development of each stage decreases as the rearing temperature increases (Table 1). At 35°C, there was 96% larval mortality and only four individuals survived to adulthood; these data were therefore included only in analysis of egg development.

TABLE 1. Mean (± S.E.) duration (days) of developmental stages of *Frankliniella occidentalis* reared at different temperatures. N/A denotes a sample size of less than 10 individuals.

Temperature	Egg	n	Larval stages	n	Propupa	n	Pupa	n	Total	n
10°C	31.3 ± 0.2	150	59 ± 1.5	36	9.4 ± 0.4	31	22.1 ± 6.8	22	118.6 ± 1.8	22
15°C	9.2 ± 0.1	103	17 ± 0.7	40	3.9 ± 0.2	37	7.8 ± 0.1	33	37.1 ± 0.7	33
20°C	6.7 ± 0.1	132	9.4 ± 0.2	89	1.6 ± 0.1	87	3.8 ± 0.1	85	21.6 ± 0.2	85
25°C	4.1 ± 0.1	72	7.8 ± 0.3	33	1.3 ± 0.1	32	2.8 ± 0.1	30	15.9 ± 0.4	30
30°C	3.1 ± 0.1	109	6.3 ± 0.2	60	1.1 ± 0.1	55	1.9 ± 0.1	45	11.8 ± 0.2	45
35°C	2.5 ± 0.1	160	N/A		N/A		N/A		N/A	

The relationship between developmental rate (egg to adult) and mean rearing temperature is described by the equation $y = 0.0037x - 0.029$ ($R^2 = 0.946$, ANOVA $F = 3701$, df 1,213, $p < 0.001$, Fig. 1). Thus, development from egg to adult required 268 degree-days (i.e., 1/0.0037) above a threshold of 7.9°C (i.e., 0.029/0.0037). Threshold temperatures and degree-day requirements of immature stages are shown in Table 2.

The number of degree-days derived from an automatic weather station at the University of Birmingham, UK between 1986 and 1995, and the corresponding estimate of the number of generations that could complete development in each year (between January and December), are summarised in Table 3. On the

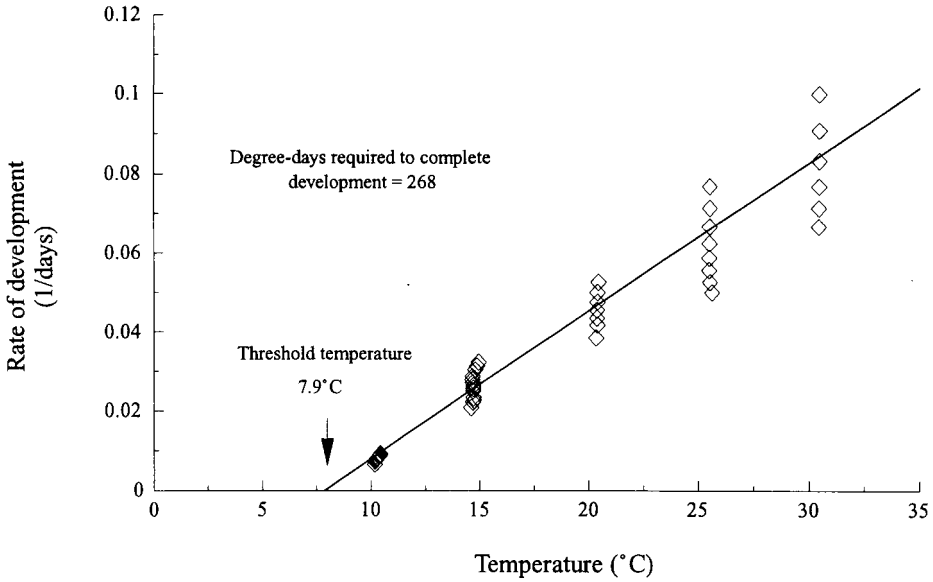

Fig. 1. Rate of development, from egg to adult (1/days), of *Frankliniella occidentalis* as a function of mean daily temperature experienced (°C). Linear regression: Rate of development = 0.0037 (temperature) – 0.029, ANOVA F = 3701, d.f. 1,213, $p < 0.001$, $R^2 = 0.946$.

basis of temperature data alone, a maximum of between three and five generations could complete development annually under field conditions. It should be remembered, however that these estimates are based on extrapolation from laboratory experiments and so should be treated as an estimate of maximum potential voltinism. Particular care should be taken when applying a similar approach to insects that may have a diapause stage in one or more generations of their life cycle (Obrycki & Tauber, 1981), though this is not the case with *F. occidentalis* (Brødsgaard, 1993; McDonald et al., 1997b).

TABLE 2. Thermal requirements for development and results of linear regression relating developmental rate of immature stages of *Frankliniella occidentalis* to temperature.

	Egg	Larval stages	Propupa	Pupa
Equation	y = 0.017x – 0.168	y = 0.007x – 0.043	y = 0.041x – 0.214	y = 0.026x – 0.239
R^2	0.866	0.809	0.638	0.692
p	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Threshold	9.9°C	6.1°C	5.2°C	9.2°C
Degree-days	59.0	143	24	38
Observations	726	265	248	219

TABLE 3. The number of degree-days (above 7.9°C) available, and the estimated maximum number of generations that could complete development in the field, for each year between 1986 and 1995 (January to December, inclusive), assuming no impediment to continuous development. (Based on temperature records collected at Birmingham, West Midlands, UK, and considered representative of this area.)

	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
Degree-days	951	1030	1043	1333	1371	1181	1200	1023	1229	1416
Generations	3.5	3.8	3.9	5.0	5.1	4.4	4.5	3.8	4.6	5.3

Discussion

The rate of development of *F. occidentalis* from egg to adult is linearly related to temperature over the range of temperatures studied ($R^2 = 0.946$). The linear model estimates a threshold temperature of 7.9°C, and a requirement of 268 degree-days for full development (Fig. 1). Use of non-linear models to estimate developmental rate was considered unnecessary, because although at the low and high sections of the developmental rate versus temperature curve, the relationship is often non-linear, this was not apparent in this study, over the range of temperatures used (Wagner et al., 1984a; Lamb, 1992; van Rijn et al., 1995).

Van Rijn et al. (1995) used multi-parameter non-linear models to describe the effect of temperature on the development of the egg and first instar of *F. occidentalis*, and (using a narrower range of temperatures) employed linear regression to estimate a threshold temperature for development. Whilst direct comparison with the work of van Rijn et al. (1995) is difficult because the present study involves observations of all stages of the life cycle, it is interesting to note that the threshold temperature for the egg, 10.8°C (calculated using the data and methods of van Rijn et al. (1995) is comparable to that given for the egg in this paper, 9.9°C, particularly in light of the fact that fewer degree-days (42.5 as opposed to 59) would be required above the higher threshold in order to complete egg development. Furthermore, high larval mortality at about 35°C, is consistent with estimates of an optimal temperature for development of larvae of around 31°C (Gaum et al., 1994a; van Rijn et al., 1995).

Clearly, in order to accurately resolve the relationship of temperature and developmental rate, the frequency of observation should be maximised, particularly in the study of brief events such as development of individual instars and when using sensitive multi-parameter models. Even when using a relatively basic method of analysis R^2 values associated with individual stages are lower than for the entire life cycle (Table 2). Although the use of mean developmental rates (Lowry et al., 1992; Gaum et al., 1994a; van Rijn et al., 1995) or rates calculated as 1/mean developmental time instead of values for individual insects results in increased R^2 values, this gives the impression of increased accuracy which is not necessarily true across a population. Stage-specific descriptions or estimates of developmental requirements should, therefore, be treated with caution. Furthermore, when such data is extrapolated to estimate the required thermal budget per generation and hence potential voltinism, it is highly desirable that the thermal requirements of all stages of the life cycle are studied. However, as in this study the egg has the highest threshold (9.9°C, Table 2), the minimum temperature necessary for complete development of a generation may be higher than 7.9°C.

Previous estimates of the developmental requirements of *F. occidentalis* have used linear extrapolation from as few as two or three temperatures which were markedly higher than the calculated thresholds [Lowry et al., 1992, in which data from Bryan & Smith (1956) and Lublinkhof & Foster (1977) are also analysed]. The potential error associated with this procedure has been addressed in this work by studying development at six temperatures, the lowest of which was 10°C. The temperatures used may account for the difference between the egg to adult threshold calculated here (7.9°C) and that determined by Gaum et al. (1994a) of 9.4°C, in which 15°C was the lowest of the six temperatures studied. Differences in the published developmental parameters for *F. occidentalis* may also be attributable to food quality (Gaum et al., 1994b; Soria & Mollema, 1995), variation between populations, and different experimental photoperiods (Brødsgaard, 1994).

In the absence of field data (against which to validate predictions) and information on environmental factors, the use of more complex, non-linear models of developmental rate (Wagner et al., 1984a; van Rijn et al., 1995) to predict general patterns across a wide geographical area is unlikely to offer a significant improvement over the linear model used here. Particularly where developmental rate data are linear, and when field temperatures also fall within the linear range.

Based on UK outdoor temperatures, a maximum of between three and five generations could complete development annually on chrysanthemum, in the absence of factors impairing development. Whilst in other insects diapause may complicate such an approach (Obrycki & Tauber, 1981), *F. occidentalis* overwinters in an active state, feeding and developing as temperatures and food availability allow (McDonald et al., 1997b). Incorporation of data on reproduction will affect estimates of voltinism, but is unlikely to reduce them to a level at which local extinction appears probable. Insufficient thermal inputs for development are therefore unlikely to prevent persistence of *F. occidentalis* in the field. The lack of permanent

open field populations at high latitudes (Brødsgaard, 1993) may therefore be attributable (at least partially) to limited tolerance of winter conditions (McDonald et al., 1997a, b, c).

The ability of *F. occidentalis* to develop outdoors may help to explain the non-sustainability of some glasshouse eradication procedures (Baker et al., 1993). Although glasshouse populations are likely to be severely reduced by these control measures, external populations may re-colonise and, together with individuals introduced through trade in contaminated plant material, facilitate re-infestation of glasshouses.

This study assesses a fundamental aspect of the potential viability of an insect in a specific location. Applying a similar experimental approach, or extrapolating this data to a number of different locations, may be a useful initial guide to the potential geographical range of this and other non-diapausing insects.

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