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Temperature, development and establishment potential of *Thrips palmi* (Thysanoptera: Thripidae) in the United Kingdom

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Abstract. In order to manage the risks posed to domestic crop production by quarantine pests such as *Thrips palmi*, their potential to establish in a new environment must be assessed. The thermal requirements for development of *T. palmi* were determined and compared with UK temperatures, to estimate its potential for development under UK conditions. Temperature and rate of development of *T. palmi* from egg to adult were linearly related between 15 and 30°C, allowing calculation of an overall threshold of 10.1°C, and a sum of effective temperatures of 194 degree-days. In the UK, development of *T. palmi* would be possible outdoors during the summer when a maximum of up to four or five generations could occur. Comparison of these data with those of the recently established and biologically similar pest, *Frankliniella occidentalis*, shows that establishment of *T. palmi* in the UK is unlikely to be limited by an inability to complete the life cycle during the favourable season.

INTRODUCTION

Many insect crop pests are dispersed globally by means of their association with international trade in plant produce or growing plants (Baker et al., 1993; Vierbergen, 1995). In order to manage the risks posed by non-indigenous insects dispersing in this way, it is necessary to determine their potential for establishment in the area to which they may be introduced. Through a variety of direct and indirect mechanisms, temperature is a fundamental determinant of the viability of insect populations in different locations. At a fundamental level, in order to establish in a seasonal or temperate climate, an insect's thermal requirements for development must enable completion of the life cycle during the favourable season, and/or development to a stage with a level of cold tolerance that is sufficient to enable overwintering. Furthermore, interaction of the thermal requirements for development and temperatures may affect and/or reflect the capacity of non-diapausing species to exploit intermittent periods of favourable winter temperatures in order to feed, repair low-temperature injury, and/or to develop and reproduce.

The melon thrips (*Thrips palmi* Karny, Thysanoptera: Thripidae) is a polyphagous, quarantine pest that feeds by bursting the cells of its host plants and imbibing the cell sap (Kirk, 1997). This feeding behaviour gives tissues a silver or bronze sheen where damaged cells coalesce and can lead to stunting, distortion and scarring of plants and produce, with marketability and yield being significantly reduced (Kawai, 1990; Tsai et al., 1995). In addition to direct feeding damage, *Thrips palmi* can transmit a number of plant tospoviruses, including groundnut bud necrosis tospovirus and watermelon silvery mottle tospovirus (Ullman et al., 1997). The thrips/virus complex can thus cause significant economic losses in countries where it has established.

International dispersal of this insect is possible in association with movement of crops typically grown in protected cultivation, and this trade may facilitate introduction to glasshouses in importing nations. Thus, although *T. palmi* is a species of tropical and sub-tropical origin, its establishment at higher latitudes may be facilitated by the availability of suitable host plants grown in protected cultivation (i.e. glasshouses).

In this study, the thermal requirements for development of *T. palmi* were determined and related to UK weather records to assess whether the species could complete its life cycle under winter and summer field conditions in the UK. The developmental capacity of *T. palmi* was also compared with that of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), the western flower thrips, a biologically similar and recently established pest of UK crops (Baker et al., 1993; McDonald et al., 1998).

MATERIAL AND METHODS

Insect stock culture

A stock culture of *T. palmi* was reared at 25°C, 18L : 6D photoperiod in electrical switch boxes (15 × 15 × 15 cm) with clear, "screw-down" lids sealed by means of rubber O-rings. The boxes were ventilated by a constant flow of compressed air that vented through a sintered glass outlet set into the wall of the box. A combination of pollen, bean pods and germinated bean seeds was used as a food source, and provided oviposition sites. These substrates were replaced as they desiccated, after about two weeks. Tissue paper was placed in the bottom of the cage to provide pupation sites.

Determination of thermal budget for development

Experimental insects were reared on sections of bean pod maintained on 4 ml of non-nutrient agar in glass vials (diameter

20 mm, height 30 mm) that were ventilated through 65 µm nylon mesh attached over a hole punched in the snap-on lid (as detailed in McDonald et al., 1997). To allow oviposition, four females from the stock culture were placed in each of sixty vials, and these were left at 25°C (18L : 6D) for 24 h. Upon removal of adults, ten vials were placed in each of six controlled environment cabinets set at 10, 15, 21, 23, 30 and 35°C (photoperiod 18L : 6D). Temperatures inside each cabinet were recorded at 16 min intervals using dataloggers. Bean sections were checked daily for emergence of first instar larvae.

Each newly emerged larva was placed in an individual rearing vial and returned to the experimental regime. The date of emergence of first instar larvae, propupae, pupae and adults was determined by daily observation (second instar larvae could not be accurately determined, as exuviae were not visible). Bean sections and agar were changed regularly in order to avoid deterioration in food quality and to prevent contamination with fungi or bacteria.

Within an "intermediate" range of temperatures (typically between 10 and 30°C), the relationship between developmental rate of insects and temperature is broadly linear (Wagner et al., 1984; Lamb, 1992). Although beyond this range the pattern becomes curvilinear (Cambell et al., 1974; Wagner et al., 1984; Lamb, 1992; Phelps et al., 1993; van Rijn et al., 1995; McDonald et al., 1998), this was not evident at the temperatures used in this study. Accordingly, linear regression was used to estimate a lower thermal threshold and corresponding sum of effective temperatures (i.e. number of degree-days above the threshold) for completion of different developmental events (egg, larval stages, propupa, pupa and total pre-imaginal development). Rate was estimated as 1/days to completion of the developmental event, and temperature was calculated as the mean of daily mean temperatures experienced by each individual insect during this period.

Average air temperatures in the field were calculated for each day between January 1988 and December 1997, using daily maxima and minima recorded at an automated recording station at the University of Birmingham. These data were related to the thermal requirements of *T. palmi* in order to estimate its developmental potential under outdoor conditions in the Midlands area of the UK.

RESULTS

At 10°C, only one larva emerged (after 45 days), but it died soon after. At 35°C, larvae emerged between two and four days after oviposition but none survived to the propupal stage. As such, these data were omitted from subsequent analyses.

The time taken for development of each developmental stage is shown in Table 1. The relationship of developmental rate (1/days) and temperature is linear between 15 and 30°C (R^2 0.96, Fig 1, Table 2). Thus, for development from egg to adult, *T. palmi* required 194 degree-days (i.e. 1/0.00515) above a lower thermal threshold of 10.1°C (i.e. 0.0519/0.00515). The corresponding estimates for different developmental stages are provided in Table 2. The larval stages have the highest threshold temperature for development, 11.5°C while the propupa has the lowest, 7.2°C.

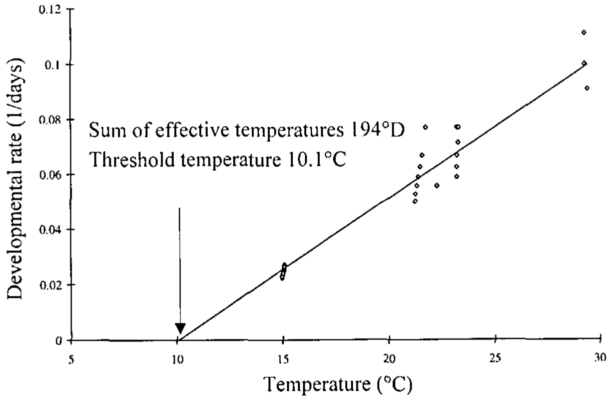

Fig. 1. The rate of development of *Thrips palmi* from egg to adult, at a range of constant rearing temperatures. Linear regression: Rate of development = 0.005 (temperature) – 0.05, R^2 0.96, F = 5868, df 1, 217, $p < 0.0001$.

Between 1988 and 1997 annual outdoor development of *T. palmi* would have been largely confined to the period between April and November, with little potential for development during winter months. Nevertheless, the thermal environment prevalent over the last ten years would have been sufficient to enable development of *T. palmi* through between 3 and 5 generations annually, in the Midlands area of the UK (Table 3). As this analysis is based on extrapolation from laboratory studies, these estimates reflect a maximum potential voltinism, rather than being a definitive prediction.

Although *T. palmi* has a higher rate of development than *F. occidentalis* (gradients of the regression lines for each species are 0.00515 (*T. palmi*) and 0.0037 (*F. occidentalis*), giving estimates of 194 and 268°D respectively), its higher threshold temperature (10.1 vs 7.9°C) limits development to a shorter period of the year than *F. occidentalis*, resulting in a comparable maximum potential voltinism for both species (Table 3).

DISCUSSION

The relationship between developmental rate and temperature is linear from 15 to 30°C, and while at temperatures beyond this range the pattern is likely to be curvilinear, this dataset does not justify the use of a non-linear model (Wagner et al., 1984; Lamb, 1992; Phelps et al., 1993). Furthermore, when considering brief events such as development at high temperatures, or of individual immature stages (e.g. propupa, Tables 1, 2), the reso-

TABLE 1. Mean (± S.E.) duration (days) of developmental stages of *Thrips palmi* reared at different temperatures.

Temperature (°C)	Egg	n	Larval stages	n	Propupa	n	Pupa	n	Total	n
15	16.1 (±0.17)	103	12.2 (±0.14)	83	3.37 (±0.11)	60	9.07 (±0.26)	28	40.2 (±0.43)	28
21	5.97 (±0.07)	117	5.18 (±0.10)	72	1.58 (±0.07)	59	4.08 (±0.10)	51	16.6 (±0.15)	51
23	6.09 (±0.07)	126	4.63 (±0.07)	80	1.50 (±0.08)	72	3.01 (±0.06)	69	15.2 (±0.09)	69
30	4.11 (±0.05)	105	2.90 (±0.05)	86	1.06 (±0.03)	81	2.18 (±0.05)	71	10.1 (±0.05)	71

TABLE 2. Thermal requirements for development, and results of linear regression relating developmental rate (y) of immature stages of *Thrips palmi* to temperature (x).

	Egg	Larval stages	Propupa	Pupa
Threshold (°C)	9.43	11.5	7.21	10.1
Degree-Days	81.2	50.3	21.3	38.9
Equation y =	0.012 x – 0.116	0.020 x – 0.228	0.047 x – 0.338	0.026 x – 0.261
n	450	307	271	218
R^2	0.87	0.83	0.55	0.64

lution of such datasets may not always support accurate use of a multi-parameter non-linear approach (van Rijn et al., 1995).

The failure of larvae to emerge at 10°C, within experimental time limits, indicates that a lower thermal threshold for development of 10.1°C is realistic, and this finding is supported by an egg-specific threshold of 9.4°C. The failure of larvae to develop at 35°C is consistent with an upper threshold in the region of 33–35°C, similar to that of *F. occidentalis* (Jarošík et al., 1997; McDonald et al., 1998).

Previous work on *T. palmi* estimated general developmental thresholds of 11.6°C on cucumber (Kawai, 1985) and 8.1°C on vegetable marrow (Jiajiao et al., 1995). The disparity of these estimates may arise both from the use of different host plants and a different range of rearing temperatures (Kawai, 1990; Tsai et al., 1995). However, the results on cucumber (a significant glasshouse crop in Britain, and a potential host of *T. palmi*) are similar to those presented here, particularly as the lower degree-day requirement estimated on cucumber (189°D) compensates for the higher threshold (11.6 vs 10.1°C, Kawai, 1985; Lamb, 1992).

Estimates of thermal requirements for individual instars should be treated with some caution because of the inherently lower resolution of the data when brief events are being considered (McDonald et al., 1998). Nevertheless, individual developmental stages may have thresholds that differ from the generalised model. Thus, individual stages may be capable of development during winter when the overall model predicts no development. This effect, as with the use of non-linear models of development rate, would be most significant when considering development of populations at temperatures fluctuating around the generalised developmental threshold (Phelps et al., 1993), or when planning the precise timing of control measures, for example in order to target susceptible instars.

Regional- and micro-climate, food quality, solar inputs, the effects of fluctuating and low temperatures and other abiotic and biotic factors may all modify the actual voltinism of field populations relative to laboratory-derived estimates (Kawai, 1990; Honěk, 1991, 1994; Leather et al., 1993; Gaum et al., 1994; Soria & Mollema, 1995), but it is unlikely that completion of at least one generation per year will be precluded. Furthermore, whilst in other species the incidence of hibernal or aestival diapause may complicate estimation of voltinism (Obrycki & Tauber, 1981), *T. palmi* is not known to enter diapause and is therefore unlikely to be prone to this potential source of error.

The exploitation of microhabitats by insects is fundamental in determining their survival during periods of abiotic stress, such as winter or arid summers. Relative to other stages of the life cycle, the eggs of many insects are tolerant of low temperature and desiccation (Hinton, 1981; Tauber et al., 1986; Tenow & Bylund, 1989; Leather et al., 1993). While in the tubuliferan thrips *Haplothrips faurei* (Putman, 1965) and *Aleurodothrips fasciapennis* (Watson et al., 1998), the egg is known to be sensitive to desiccation, no information is available on the effects of low temperature on these or other thrips eggs. In contrast to the Tubulifera, in which eggs are largely exposed to the air, those of *T. palmi* and other Terebrantia are inserted into plant tissues (Terry, 1997). However, as the desiccation and cold tolerance of the egg is unknown, it is difficult to determine if this microhabitat compensates for any inherent susceptibility to stress. Thus, to establish the role of the egg and its microhabitat in facilitating survival of *T. palmi* during periods of abiotic stress such as winter, a study of the effects of both desiccation and low temperature on egg development and survival is required.

Temperatures experienced in the thermally-buffered sites that are likely to be exploited by thrips in a winter

TABLE 3. The number of degree-days available to *Thrips palmi* (i.e. above 10.1°C) and *Frankliniella occidentalis* (i.e. above 7.9°C) in the midlands area of the UK and the estimated maximum potential voltinism of both species (1988–1995 *F. occidentalis* data reproduced from McDonald et al., 1998).

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
°Days										
T. palmi	589	876	864	750	746	597	737	954	717	841
F. occidentalis	1,043	1,333	1,371	1,181	1,200	1,023	1,229	1,416	1,123	1,297
Generations										
T. palmi	3.0	4.5	4.5	3.9	3.9	3.1	3.8	4.9	3.7	4.3
F. occidentalis	3.9	5.0	5.1	4.4	4.5	3.8	4.6	5.3	4.2	4.8

field situation are generally lower than the threshold estimates provided for each developmental stage of *T. palmi* (McDonald et al., 1997). Thus, *T. palmi* may be less capable of exploiting intermittent periods of favourable temperatures for feeding, repair of low-temperature-induced damage or for development and reproduction, such as occurs in other non-diapausing insects that have lower developmental thresholds.

In the UK, the glasshouses to which *T. palmi* may be introduced via international trade, offer thermally-buffered conditions that are suitable for population maintenance for most of the year (McDonald et al., 1997). A generalised developmental threshold of 10.1°C (Table 2) effectively confines development of *T. palmi* to protected cultivation during winter. However, during the summer months, there is sufficient thermal input in an open field site (depending on the time of introduction) to drive development of several generations (Table 3). Thus, it is reasonable to expect that *T. palmi* could survive and develop outdoors during summer, and potentially be a source of re-infestation, if phytosanitary measures were to be deployed mainly within a glasshouse environment. It is possible that such a characteristic added to the non-sustainability of the phytosanitary campaign adopted against *F. occidentalis* (Baker et al., 1993; McDonald et al., 1998).

F. occidentalis, a recently established pest of UK crops, has a lower threshold for development than *T. palmi* (7.9 vs 10.1°C, McDonald et al., 1998) and has been recorded outdoors during summer. Whilst the higher developmental threshold of *T. palmi* prevents development as early in the year as *F. occidentalis*, its faster rate of development would result in a comparable number of generations for both species. On the basis of this comparison, it is reasonable to conclude that *T. palmi* would be as capable of developmental success in the field under UK summer conditions as *F. occidentalis*.

In summary, the establishment potential of *Thrips palmi* in the UK is unlikely to be limited by inadequate thermal inputs for completion of the life cycle, in either open field sites during summer or in glasshouses. Thus, it is likely that if *T. palmi* were introduced, it would be capable of persisting outdoors during summer, a pattern which could potentially complicate phytosanitary campaigns directed at glasshouse populations.

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