Western flower thrips feeding on pollen, and its implications for control

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Abstract: The development time, fecundity, longevity and the resulting intrinsic growth rate (r_m) of the western flower thrips Frankliniella occidentalis encaged on a cucumber (Cucumis sativus) leaf and supplied with seven food sources, i.e. six pollen species and a mixture of milk powder and yeast, were compared. All food sources, except the mixture of milk powder and yeast, offered a nutritional benefit for thrips. The addition of pollen increased the fecundity and reduced the development time, mainly during the larval stage. Additionally, *Betula pubescens* and *Corylus avellana* pollen increased the adult longevity. The r_m of F. occidentalis on the mere cucumber leaf increased from 0.163 to 0.240 when Pinus sylvestris pollen was supplied to the leaf. The fecundity was the life history component that was mostly affected by the addition of pollen. Increase in fecundity by the addition of B. pubescens and P. sylvestris pollen explained a minimum of 68 % and a maximum of 90% of the total change of the r_m, when compared to the r_m obtained for thrips feeding on mere cucumber leaf. Therefore, the fecundity is considered as a good indicator for the nutritional benefit thrips can obtain from feeding on pollen. On poinsettia (Euphorbia pulcherrima), F. occidentalis was able to reproduce in the presence of pine pollen but not in the absence of pollen. Thrips reproduction in the presence of pollen, on plants that otherwise do not support thrips reproduction, might cause unexpected thrips problems. Therefore, it may be worthwhile to reduce the chances of such plants becoming contaminated by, for example, air-born pollen, and to increase the awareness of the consequences of the presence of such pollen.

Key words: Frankliniella occidentalis, Cucumis sativus, alternative food, pollen, Euphorbia pulcherrima

Introduction

The success of the preventative introduction and the subsequent augmentation of omnivore thrips predators (e.g. *Neoseiulus cucumeris, Ipheseius degenerans, Orius* spp.) seems to depend on the crop. The difference in their persistence in sweet pepper and greenhouse cucumber may be explained by the presence of pollen as an alternative food source for these predators (van den Meiracker & Ramakers, 1991 & Chambers et al., 1993, Van de Veire & Degheele, 1993), suggesting that adding alternative food to non pollen producing crops (e.g. modern cucumber varieties) might support the preventative introduction of some thrips control agents.

Not only predators, but also thrips might benefit from pollen. The effect depends on the thrips species (generalist or specialist, leaf or flower thrips), as well as the species and characteristics of the pollen (nutritional value, size, adhesiveness, presence of a feeding stimulant) (Murai & Ishii, 1982; Kirk, 1985; Teulon & Penman, 1991). Different pollen species are known to enhance the growth and fecundity of *F. occidentalis* (Trichillio & Leigh, 1988; Van Rijn & Sabelis 1993; de Jager & Butôt, 1993), and an influx of pollen speeded up the population growth of this thrips on pot roses (Hulshof, pers. obs.). Therefore, it is important that food sources used for the preventative introduction of predators offer no or only little benefit to thrips, to avoid the risk of giving the pest a reproductive advantage that might result in its population built-up beyond the predators' control capacity.

Knowledge about the relative impact of pollen on the different life history components of thrips (e.g. development time, fecundity, longevity) could indicate how the addition of pollen might hamper thrips control. However, a comparison of food sources in respect to their relative impact on the different life history components of *F. occidentalis* does not exist. We studied the effect of seven food sources supplied on a cucumber leaf on the development time, fecundity and longevity of *F. occidentalis*. Life tables were used to calculate the r_m and to determine which life history component was mostly affected by the addition of these food sources. This component could be used for screening the nutritional benefit thrips can obtain from feeding on pollen. Subsequently, we looked at the effect of pollen on thrips fecundity when added to poinsettia, a less suitable host plant.

Materials & methods

Additional food sources

The additional food sources were five pollen species and a milk powder/yeast mixture, a potential artificial diet for Anthocoridae (Bronnimann, 1964). Cucumber leaf (cv. Jessica) served as the control. Pollen of birch (Betula pubescens), common cattail (Typha latifolia), hazel (Corylus avellana) and pine (Pinus sylvestris), all collected by hand, were used as alternative food of plant origin. Both hand and bee collected pollen of fireweed (Epilobium angustifolium) were included to test whether the collection of pollen by bees, a way of easily obtaining large amounts of pollen, affects its suitability for thrips. The bee-collected pollen was offered as small clumps. Immediately after collection, pollen was stored in glass vials at -20°C until use, with the exception of hazel pollen, this being dried for two days at 37°C (van Rijn & Tanigoshi, 1999).

Development time from larva to adult

Thrips larvae (0-4h old) were confined individually on pieces of cucumber leaf (cv. 'Jessica') in mini-cages (Hulshof & Vänninen, 1999). The additional food sources were offered on the leaf. Every third day the thrips were transferred to a fresh leaf to maintain the food source fresh. Upon replacing the leaf, additional food was added in portions of 9 mg per cage. The cages were kept in a growth chamber at 25°C (\pm 1°C), 80 % RH and L16:D8 photoperiod. The thrips were observed every 12h and the stage transitions were recorded until adult eclosion. Upon adulthood the sex of the thrips was determined.

Adult female longevity and fecundity

Using the mini-cage method, batches of even aged larvae were raised to the pupal stage on their respective diets. Upon adult eclosion, chambers with males were discarded. The longevity of unmated females was determined by checking them once a day until they died. The age related fecundity rate was determined based on the number of larvae that hatched from the cucumber leaves within seven days after their replacement.

Life history parameters

The r_m of the thrips that had been fed different food sources was calculated with the following formula: (Sexp $(-r_m x)l_x m_x = 1$), where l_x and m_x denote the age-specific survival and age-specific fecundity, respectively. The l is calculated as the juvenile survival (=0.95) * the estimated adult survival function. The juvenile survival was assumed to equal 95% for all food sources (observed range 90-100%, variation probably due to handling the thrips rather than due to the food source). The m_i is calculated as the observed median fecundity rate * sex ratio * correction factor. This factor corrects for the difference between the estimated and observed fecundity. It was obtained for every food source by dividing the estimated total fecundity at the median longevity by the observed total fecundity at the median longevity. The sex ratio of 0.65 was used for the calculations (Trichilo & Leigh, 1988; van Rijn et al., 1995). Further, the net reproduction rate (R_0) $= \sum l_x * m_y$ and the cohort generation time (T_c = $(\sum_{x} 1_{x} * m_{x} * x)/R_{0})$ were calculated (Birch, 1948). The extent to which the additional food sources changed the r_m in comparison to the r_m obtained on mere cucumber leaf was calculated separately for the three life history components (development time, l and m) and the six food sources as follows: r_m (thrips feeding on cucumber plus a given food source affecting either development time, l_x or m_x) - 0.163 (r_m on mere cucumber leaf).

Thrips fecundity on Poinsettia

Female adult thrips mass reared on cucumber were individually confined in mini-cages and randomly assigned to one of the following treatments: leaves of five poinsettia (*Euphorbia pulcherrima*) cultivars (i.e. Marlene, Peter Star, Regina, Steffi and Cortez), a poinsettia leaf (cv. Cortez) with additional pine pollen, or just a cucumber leaf (cv. Jessica). After 2 days the thrips were transferred to a new cage with the same treatment. The fecundity rate of the 2 successive periods of 2 days was determined as described above.

Statistical analyses

The proportional hazards regression model, which is widely used in the analysis of timeto-event data, was used for the analyses of the effect of the food sources on the development time from larva to adult and on the adult female longevity (Cox, 1972). The analysis of the effect of the food sources on fecundity, measured as the total number of hatched larvae, was based on the generalized linear mixed model (SAS Institute Inc., 2000). The detailed statistical analyses are given in Hulshof et al. (2002).

Results

Development time from larva to adult The addition of food sources accelerated development, as compared to cucumber leaf alone, by approximately half a day (Table 1). This reduction occurred mainly during the larval stage, but also during the non-feeding prepupal and pupal stages (Hulshof et al, 2002). In addition, there was strong evidence that males developed faster than females (Wald $\chi^2 = 17.59$, df = 3, p < 0.001).

Adult female longevity

The addition of food sources to a cucumber leaf had a significant effect on the longevity of unmated adult female thrips ($\chi^2(7)=27.28$, p<0.001). Thrips offered birch and hazel pollen lived respectively 13 and 16 days longer, and those offered the milk powder/yeast mix lived 7 days shorter than those on cucumber leaf alone (Table 1).

Fecundity

All pollen species had a positive effect on total fecundity. Based on their effect on fecundity, the food sources could be divided into three groups: 1) cucumber leaf plus milk powder/yeast mix, 2) pine pollen, and 3) other pollen species (table 1). The shape of the fecundity rate was similar for all food sources: 6 to 9 days after adult eclosion there was a peak, which was followed by a steady decline (data not shown). Further we observed that thrips supplied with pollen reproduced until they died, in contrast to thrips on cucumber leaf alone that did not reproduce during the last three days of their life.

Life history parameters

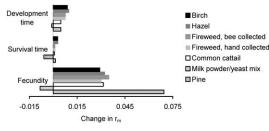
For all tested food sources, except for the milk powder/yeast mix, net reproduction and r_m increased beyond that obtained on cucumber leaf alone. These r_m values should be considered as crude values only, because they are based on estimates with wide confidence intervals. The differences in the r_m values mainly reflected

	Development time from	Adult female	Total fecundity
Food source	larva to adult	longevity	(larva /
	(days) ^{a)}	(days) ^{a)}	(female)
Cucumber leaf	8.9	21	59a
Birch	8.4**	34*	165b
Hazel	8.4**	37*	168b
Fireweed, bee collected	8.6*	24	133b
Fireweed, hand collected	8.5*	24	127b
Common cattail	8.4**	23	113b
Milk powder/yeast mix	9.0	14*	37a
Pine	8.4**	24	250c
^{a)} * p<0.01, ** p<0.01, Cox proportion	nal hazard model.		
^{b)} Treatment with a different letter dif	fer significantly $(p < 0.0)$	5, generalized linear	mixed model).

Table 1. The estimated median development time, median adult female longevity and median fecundity of *F. occidentalis* offered additional food sources on a cucumber leaf. (cv. Jessica) at 25°C, 16L:8D.

	Net reproduction	Mean generation time	Intrinsic growth rate
Food source	R_0 (female ⁻¹)	T_{c} (days)	$r_m(day^{-1})$
Cucumber leaf	32	23	0.163
Birch	91	28	0.206
Hazel	98	29	0.211
Fireweed, bee collected	73	24	0.207
Fireweed, hand collected	77	25	0.204
Common cattail	66	25	0.201
Milk powder/yeast mix	21	20	0.157
Pine	141	24	0.240

Table 2. Life history parameters of *F. occidentalis* offered additional food sources on a cucumber leaf. (cv. Jessica) at 25°C, 16L: 8D.



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Figure 1. The change in r_m of *F. occidentalis* in case the additional food source affects either the development time, survival time or fecundity (see text for details).

differences in the effect of the different food sources on fecundity. This implies that the contributions of the development time and adult longevity to each r_m value were minor compared to the contribution of fecundity (Figure 1).

Thrips fecundity on Poinsettia

The median fecundity rate of thrips encaged on leaves of poinsettia cultivars Marlene and Cortez was zero. On three other cultivars (Peter Star, Steffi, and Regina), the median fecundity rate was one larva per 2 days during the first two days and zero during the third and fourth day. The addition of pine pollen to the cultivar Cortez induced thrips reproduction, the fecundity rate being 6.5 and 10.5 larvae per female per day on poinsettia and cucumber, respectively, and on cucumber leaf alone it was 2.8. The effect of pine pollen on thrips reproduction on cultivar Cortez occurred during the first 2 days of the experiment but strengthened during the following 2 days (Figure 2).

Figure 2. The median fecundity rate (+/- 25% quartile) of *F. occidentalis* encaged on a poinsettia leaf cv. Cortez (with and without pine pollen) or a cucumber leaf cv. Jessica during 2 successive periods of 2 days at 25° C, 16L:8D.

Discussion

Fecundity was the life history component most affected by the addition of pollen. It explained 68 - 90% of the total increase of the r_m . Therefore, the effect of pollen on fecundity can be considered as an indicator for the potential nutritional benefit thrips can obtain from feeding on introduced pollen on plants that otherwise lack pollen. Pollen boosting the fecundity of generalist thrips seems to be a general phenomenon (Murai & Ishii, 1982; Kirk, 1985; Trichilo & Leigh, 1988; Teulon & Penmann, 1991; de Jager & Butôt, 1993). However, its relative importance compared to the impact of pollen on the development or survival time was not established before. Thrips fecundity can be used as an indicator of the potential nutritional benefit for more host specific thrips species, because their host specificity is reflected in their fecundity (Kirk, 1985).

The reduction in development time from larva to adult occurred mainly during the larval stages, but also during the non-feeding prepupal and pupal stages. Although the effect on development time is not as pronounced as on fecundity, the consequences could be important. The larval diet is a key nutritional factor that affects not only development time, but also body size (Gerin et al., 1999; de Kogel et al., 1999). Faster developing, larger thrips larvae might be less vulnerable to their natural enemies. It has been shown that the success of the predators N. cucumeris and N. barkeri and the parasitoid Ceranisus menes reduces with increasing size and strength of the thrips larvae (van de Hoeven & van Rijn, 1990; Loomans et al., 1993).

The addition of pollen to a cucumber leaf resulted in an increase of the r_m of *F. occidentalis*. At maximum, this increase was 47% when pine pollen served as the additional food. For the other five pollen species, the increase in r_m ranged from 23% to 29% for common cattail and hazel pollen. Among those five it was not possible to differentiate one or more that would offer the smallest benefit for the thrips. Chemical analyses showed that the pollen species differed in their nutritional content (Brodbeck et al., 2002). However, specific effects of particular nutrients still merit further investigation. The negative effect of the milk powder/yeast mix on thrips probably only occurs in an encaged situation where thrips cannot escape from the unfavorable conditions created by the presence of this food source. It seems likely that on a plant thrips would avoid this food source. Furthermore the mix did not support the development of O. laevigatus (Hulshof, unpubl. data). The suitability of the bee-collected fireweed pollen for thrips seemed not to differ from that of the hand collected pollen. Additional experiments should reveal whether this phenomenon can be generalized when comparing hand and bee collected pollen of other plant species. The pollen tested here differed significantly in their suitability for N. cucumeris and I. degenerans (van Rijn & Tanigoshi, 1999). Therefore, it seems a better strategy to first determine the suitability of additional food sources for the predators and subsequently, the effect of only the suitable food sources on thrips fecundity.

The relative impact of pine pollen on thrips fecundity on poinsettia was considerable. The induction of reproduction following the addition of pollen is not limited to poinsettia, but has been observed when pollen was added to a resistant cotton cultivar (Trichilo & Leigh, 1988). To avoid thrips problems in the presence of pollen on host plants that usually are not suitable for thrips reproduction, it is advisable to reduce the availability of pollen by, for example, removing flowering weeds in the greenhouse. During monitoring the pest situation in glasshouses one should also pay attention to pollen influx from outdoors, especially during times when windpollinated crops shed their pollen. The awareness of the presence of pollen on plants, being conducive or non-conducive for thrips reproduction in the absence of pollen, facilitates anticipation of increased thrips population growth in the crop.

Pollen affects not only the life history parameters but also the behavior of thrips and their predators (e.g. van Rijn & Tanigoshi, 1999). Cotton pollen decreased the migration rate of thrips larvae (Trichillo & Leigh, 1988), and adult thrips concentrated on cucumber leaves with pine pollen (Hulshof, unpubl. data). Furthermore, the presence of pollen affects the predation rate of natural enemies. In the presence of pollen, the predation rate of O. laevigatus increased, whereas it decreased for N. cucumeris (van Rijn, 2002; Hulshof & Linnamäki, 2002; Bennison pers. comm.). However, even a decreased predation rate might, if it is accompanied by a higher fecundity rate induced by pollen feeding of the predator, result in a higher predator density and, subsequently, in an increase of the total number of prey attacked (McMurtry & Scriven, 1966; Fouly, 1997).

In conclusion, additional pollen has a big impact on *F. occidentalis*, especially on their fecundity. The presence of pollen could even induce reproduction on a plant that, in the absence of pollen, does not support thrips reproduction. Therefore, it seems to be worth reducing the availability of pollen on plants and increasing the awareness of consequences of pollen that enter the crop, e.g. from outdoors. The extent to which thrips are able to exploit the potential benefit of pollen, introduced as alternative food to sustain omnivore predators, depends on the interaction between thrips, the pollen and the predator. Such interactions determine eventually whether additional pollen is suitable for the preventative introduction and augmentation of predators, without stimulating the pest's reproduction beyond the control capacity of the predator.

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