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Flowers to selectively enhance the fitness of a host-feeding parasitoid: Adult feeding by *Tuta absoluta* and its parasitoid *Necremnus artynes*

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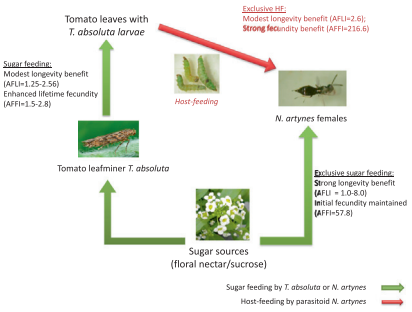
HIGHLIGHTS

- Effect of nectar and host-feeding (HF) on *T. absoluta* and *N. artynes* is studied.
- Floral nectar enhanced lifetime fecundity in *T. absoluta* and *N. artynes* longevity.
- Only HF increased fecundity in *N. artynes*.
- Flowers had different effects on lifetable parameters of both pest and parasitoid.

GRAPHICAL ABSTRACT



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ABSTRACT

Several parasitoids require both host and non-host resources, such as nectar, for maintenance, survival and egg maturation. However, the impact of sugar feeding has primarily been studied in parasitoid species that do not engage in host-feeding, and the importance of non-host resources for host-feeding parasitoids has so far received little attention. The Palaearctic parasitoid *Necremnus artynes* has been shown to attack the exotic invasive *Tuta absoluta* in the field, but its parasitism is generally low. Understanding the use of host and non-host resources by this parasitoid could reveal whether there is potential for enhancing the biocontrol of *T. absoluta* through provision of targeted food supplements. Cage experiments were conducted to investigate the influence of selected non-host resources on the longevity and fecundity of both the pest and its parasitoid. The parasitoid was also provided with the opportunity to feed on larvae of the pest. Sweet Alyssum, *Lobularia maritima*, had the most pronounced effect on the fecundity and longevity of *T. absoluta*, while buckwheat *Fagopyrum esculentum* had the strongest effect on parasitoid longevity. Fecundity of *T. absoluta* was shown to be a function of the age of the adults and food sources provided. Sugar resources did not influence the egg load of *N. artynes*, whilst host-feeding was relatively ineffective at enhancing parasitoid longevity. Host-feeding had a strong positive effect on egg load. The impact of non-host resources on host-parasitoid interactions and the potential for using selective food resources in conservation biological control of the exotic pest *T. absoluta* are explored.

1. Introduction

Predators and parasitoids often require non-host resources, such as pollen, nectar or honeydew, which can strongly prolong longevity and/or enhance fecundity of these species (Wäckers and van Rijn, 2005, 2012). Conservation biological control (CBC) practices entail targeted management of the environment in order

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to selectively enhance natural enemy efficacy (Landis et al., 2000). The use of CBC practices in managing alien pests has recently been reviewed, with results indicating that targeted habitat management practices can enhance natural enemy populations and/or parasitism and predation rates. Nevertheless, the effects on (invasive) pest species has been varied (Jonsson et al., 2010). Indeed, pollen and sugar resources have also been observed to increase fitness of several herbivorous pests (Baggen et al., 1999; Baggen and Gurr, 1998; Romeis and Wackers, 2002; Lavandero et al., 2006; Wäckers et al., 2007; Winkler et al., 2010). This underlines the need for empirical studies investigating nutrient requirements and resource-utilisation of both pest species and their natural enemies to optimise CBC.

The leaf miner *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) is a devastating pest of tomato *Solanum lycopersicum* L. and originates from South America. In Europe this pest was first introduced in eastern Spain in 2006 and has since spread to several European, Middle Eastern and North African countries (Desneux et al., 2010), where it has caused considerable yield losses. The most common control strategy against *T. absoluta* has so far been based on chemical control, with calendar-based applications in large-scale open field systems of tomato normally grown for the processing industry (Balzan and Moonen, 2012). In South America this strategy has already been shown to increase the risk of developing insecticide resistance (Salazar and Araya, 1997, 2001; Siqueira et al., 2000a,b, 2001). Moreover, the frequent application of pesticides is likely to have negative effects on natural enemies of *T. absoluta* and other tomato pests (Balzan and Moonen, 2012). Integrated pest management (IPM) strategies in tomato crops has already been shown to be more efficient in reducing the number of pests, and increase the abundance of several natural enemies as compared to conventional calendar-based treatments (Picanço et al., 2007). Since the introduction of *T. absoluta* in the Mediterranean region several native natural enemies have been identified as biological control agents of this pest (Desneux et al., 2010; Urbaneja et al., 2012), some of which have already been employed in IPM strategies (Calvo et al., 2012; Mollá et al., 2011). Invading herbivores can be attacked by native parasitoids soon after being introduced to a new environment (Godfray et al., 1995; Vercher et al., 2005), and such new parasitoid-pest associations have also been documented for *T. absoluta* in the Mediterranean region (Zappalà et al., 2012). Given the fact that parasitoids in annual cropping systems are often limited by the lack of nectar sources (Heimpel and Jervis, 2005), there is scope to enhance the biological control of this invasive pest of tomato crops through selective use of floral resources.

The parasitoid *Necremnus artynes* Walker (Hymenoptera: Eulophidae), an idiobiont ectoparasitoid of *T. absoluta* larvae, has been recorded in several studies carried out in Spain and Italy (Desneux et al., 2010; Gabarra and Arnó, 2010; Zappalà et al., 2012). This parasitoid is a Palearctic species and its primary hosts within its native region include *Cosmopterix pulchrimella* Chambers and *Vulcaniella pomposella* Zeller (Lepidoptera: Cosmopterigidae) (Noyes, 2012). The life-history of *N. artynes* is characterised by a short preimaginal development time, while synovigenic females of this species destructively host feed on second and third instar stages of *T. absoluta* larvae (Soriano et al., 2011).

Adults of synovigenic parasitoids are typically born with a limited number of mature eggs. Their reproductive success is therefore strongly dependent on the number of further eggs females can produce during their adult life (Jervis et al., 2001; Jervis and Ferns, 2011). Synovigenic females have a relatively longer lifespan, during which they actively feed on nectar, honeydew and host haemolymph, which are used to fuel somatic functions and ovigenesis (Briggs et al., 1995; Ellers and Jervis, 2003; Jervis et al., 2007, 2008; Jervis and Kidd, 1986). Feeding on host haemolymph by adult females, termed as host-feeding, is often destructive to the host. Consequently, parasitoids face a trade-off between the long-term benefits of host-feeding and the immediate cost of forgoing oviposition. Nutrients obtained through host-feeding are primarily used to mature eggs, and in some cases host-feeding supplies all the nutrients necessary for egg maturation (Giron et al., 2002; Heimpel and Collier, 1996; Jervis and Kidd, 1986). Feeding on sugar sources, such as floral nectar, primarily provides metabolic energy supporting parasitoid survival (Wäckers, 2001). While this nutritional dichotomy holds in general, there is variation among species and there are certainly exceptions to this general principle: while generally host-feeding tends to be an inefficient energy source, in some species it has been shown to simultaneously increase egg production and longevity, whilst other parasitoids are able to mature eggs while feeding exclusively on a sugar source (Wackers, 1998; Rivero and Casas, 1999; Burger et al., 2004; Pelosse et al., 2011). Although, the parasitoid *N. artynes*, similar to other *Necremnus* sp. (Bernardo and Viggiani, 2002), is known to host-feed empirical data about resource-allocation to egg production and metabolic energy remains unavailable.

Fitness of several herbivorous species may be enhanced when provided with sugar resources (Wäckers et al., 2007). The influence of nectar feeding on adult life-span and egg production has been shown to be a function of the egg-maturation strategy in Lepidoptera as well (Jervis and Boggs, 2005; Jervis et al., 2007). *T. absoluta* adults fed on honey solution have been observed to benefit in terms of lifespan, the number of matings, number of ovipositions and eggs laid, and extension of their oviposition period (Imenes et al., 1990). Nevertheless, we know little about the specificity of resource-utilisation between adults of *T. absoluta*, and its larval parasitoid *N. artynes*. Only on the basis of this information will it be possible to identify "selective food sources" that benefit the biological control agent, without benefiting the pest (Wäckers et al., 2007). Classical and augmentative biological control practices, involving the introduction of natural enemies in order to enhance the level of biological control, have often given little attention to the needs of the biological control agent, which has likely limited success rate of biocontrol programs (Bale et al., 2008; Lavandero et al., 2006). A better understanding of the role of floral resources in enhancing the fitness and efficacy of natural enemies can improve this situation (Landis et al., 2000; Wäckers, 2003). Moreover, conservation biological control studies providing resources for natural enemies also need to consider the possible influence these might have on herbivore populations (Begum et al., 2006; Lavandero et al., 2006; Wäckers et al., 2007).

The present study aims at investigating (1) the affect of floral resources on longevity and fecundity of both the exotic invasive *T. absoluta* and its parasitoid *N. artynes*, and (2) the allocation of resource-income from host and non-host feeding in *N. artynes*, both of which may have important implications on the use of CBC practices for the control of the pest *T. absoluta*.

2. Materials and methods

2.1. Insects and plants

The experiment was conducted in two greenhouse fine insect screen cages (3 × 4 m and 2 m high) at Biobest N.V., Westerlo, Belgium. The average recorded temperature was 23.8 ± 3.9 °C and the mean relative humidity was 53.7 ± 8.5%. Tomato plants utilised in the experiment were sown individually in pots (11 cm diameter) under the above conditions. No fertiliser or chemical crop protection products were applied. Similarly, plants of alyssum *Lobularia martima* L., bishop's flower *Ammi majus* L., buckwheat *Fagopyrum esculentum* Moench, and coriander *Coriandrum sativum* L., all of