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# Habitat and plant specificity of *Trichogramma* egg parasitoids—underlying mechanisms and implications

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## Summary

Egg parasitoids of the genus *Trichogramma* are among the most important and best-studied natural enemies worldwide. Parasitism levels by *Trichogramma* vary greatly among different habitats, plants or plant structures on which the host eggs are located. Here we summarise the published evidence on mechanisms that may underlie the observed variation in parasitism rates. These mechanisms include plant spacing, plant structure, plant surface structure and chemistry, plant volatiles and plant colour. In addition, plants can affect parasitoid behaviour and activity by providing carbohydrate food sources such as nectar to the adult wasps, and by affecting the nutritional quality of the host eggs for progeny development. Knowledge of plant and habitat factors that affect *Trichogramma* spp. efficacy has important implications for biological control, and for assessing the risks that mass-released *Trichogramma* spp. may pose to non-target insects.

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## Zusammenfassung

Eiparasitoide der Gattung *Trichogramma* gehören weltweit zu den wichtigsten und am besten bekannten Nützlingen. Parasitierungsraten von *Trichogramma* variieren deutlich zwischen verschiedenen Habitaten, Wirtspflanzen bzw. Teilen einer Pflanze, auf denen sich die Wirtseier befinden. In der vorliegenden Arbeit fassen wir zusammen, was hinsichtlich der Mechanismen bekannt ist, die für die beobachteten

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Unterschiede in der Parasitierungsleistung verantwortlich sein können. Diese Mechanismen umfassen Faktoren wie den Abstand zwischen den Pflanzen, die Pflanzenstruktur, die strukturelle und chemische Beschaffenheit der Pflanzenoberfläche, pflanzliche Duftstoffe sowie die Farbe der Pflanze. Hinzu kommt, dass Pflanzen das Verhalten bzw. die Aktivität der adulten Parasitoide beeinflussen können indem sie zuckerhaltige Nahrung z.B. in Form von Nektar zur Verfügung stellen. Außerdem haben die Pflanzen einen Einfluss auf die chemische Zusammensetzung der Wirtseier, was sich wiederum auf die Eiparasitoide auswirken kann. Ein gutes Verständnis der Habitat- und Pflanzen-Faktoren, welche die Eiparasitoide beeinflussen, ist wichtig um den Einsatz von *Trichogramma* spp. in der biologischen Schädlingsbekämpfung zu fördern und auch um die möglichen Umweltauswirkungen von im Pflanzenschutz eingesetzten *Trichogramma* spp. zu erfassen.

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## Introduction

There is a large and expanding body of evidence that habitat and plant characters have a strong impact on the parasitism efficacy of parasitic wasps in natural systems as well as in biological control (Kester & Barbosa, 1991; Bottrell, Barbosa, & Gould, 1998; Rutledge & Wiedenmann, 1999; Hare, 2002; Lill, Marquis, & Ricklefs, 2002). Egg parasitoids belonging to the genus *Trichogramma* (Hymenoptera: Trichogrammatidae) are important natural enemies of a wide range of pests and are successfully used in inundative and inoculative biological control programmes worldwide (Li, 1994; Smith, 1996; van Lenteren, 2000). Most species are regarded as generalists, even though the better-known species show a specialisation at the level of the insect order of Lepidoptera (Pinto & Stouthamer, 1994). *Trichogramma* species differ distinctly from most other parasitic wasps due to their minute size, ranging from 0.2 to 1.5 mm (Pinto & Stouthamer, 1994). As a consequence, they are for instance more affected by plant surface structures and have a low capacity for active flights.

*Trichogramma* spp. are thought to be more habitat- than host-specific (Salt, 1935; Flanders, 1937; Curl & Burbutis, 1978). Habitat and plant factors can directly or indirectly affect various steps in the host selection process of a female *Trichogramma* spp. A thorough understanding of the searching and parasitisation behaviour of these parasitoids and their habitat and plant preferences can be key to the optimisation of biological control programmes (van Steenburgh, 1934; Flanders & Quednau, 1960) as well as to the assessment of possible non-target effects in mass-release programmes. Here, we summarise the available information on the interactions between *Trichogramma* spp. and the habitat or food plants of its hosts. Literature on *Trichogrammatoidea* spp.

(Hymenoptera: Trichogrammatidae) is not included in this review, but many of the findings for *Trichogramma* spp. are likely to be similarly valid for *Trichogrammatoidea* spp. and other small-bodied egg parasitoids such as Mymaridae and Scionidae. Since the taxonomy of the *Trichogramma* genus is still much debated (Pinto & Stouthamer, 1994; Pinto, 1999), we use the species names as they have been used in the original studies throughout this review.

## Habitat specificity

Evidence is accumulating that *Trichogramma* spp. are more prevalent in certain habitats or on specific plants (Salt, 1935; Flanders, 1937; Pinto & Oatman, 1988; Hirose, 1994; Pinto, 1999). Due to the habitat and plant specificity of different *Trichogramma* species, the spectrum of species reared from a certain host can vary with the food plant from which the eggs were collected (Lopez, Jones, & House, 1982; Pinto & Oatman, 1988; Monje, Romeis, Zebitz, & Shanower, 1998). Also, parasitism levels on a specific host species can vary widely, depending on the plant on which the eggs are found (Martin, Lingren, Greene, & Ridgway, 1976; Martin, Lingren, Greene, & Grissell, 1981; Nordlund, Chalfant, & Lewis, 1984; Keller, Lewis, & Stinner, 1985; Romeis & Shanower, 1996; Stuart & Polavarapu, 2000; Gingras, Dutilleul, & Boivin, 2003; Kuhar, Barlow, Hoffmann, Fleischer, Groden et al., 2004).

In addition to habitat effects, parasitisation by *Trichogramma* spp. may also vary with the plant structure or region of the plant on which the host eggs are located. Studies on cotton (*Gossypium hirsutum*) (Orphanides & Gonzalez, 1970) and maize (*Zea mays*) (Phillips & Barber, 1933) have shown that egg parasitism levels can differ between upper and lower leaf surface. Other

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