INTRODUCTION

The success of classical biological control in orchard crops might suggest that orchards would be equally suitable environments for the development of effective biological control augmentation programs. In contrast to row crops, orchards represent a more permanent habitat with high architectural complexity within the crop itself and often with added diversification provided by a herbaceous or graminaceous ground cover. Thus orchards provide a variety of factors that may be limiting for natural enemies in other agricultural environments, including variation in microclimate, honeydew from sap-sucking insects, flowering plants in the ground cover, and even alternative hosts or prey.

It is perhaps surprising then, that there are so few examples of success in biological control augmentation from orchard crops in the United States (Elzen and King, 1999). The most successful program is the periodic release of *Aphytis melinus* DeBach for control of California red scale (*Aonidiella aurantii* [Maskell]) in the San Joaquin Valley of California (Hoffman et al., 1998). Although several other studies have demonstrated some potential for success (Elzen and King, 1999), none have led to commercial implementation. The most promising cases of natural enemy augmentation in orchards (Elzen and King, 1999) are frequently based on the use of more specialized natural enemies, such as *A. melinus*. This suggests that the degree of specialization and ecology of the natural enemies used in augmentative releases may be of greater importance than previously thought in determining their performance in the field.

The codling moth, *Cydia pomonella* (L.), is a notorious pest of pome fruit and walnuts, and in California we have investigated the potential for suppressing codling moth damage through inundative release of *Trichogramma* egg parasitoids. Inundative releases of commercially produced *Trichogramma platneri* Nagarkatti, an arboreal species indigenous to the western United States, consistently reduce fruit and nut damage by codling moth by about 60%, particularly in pear and walnut orchards (Mills et al., 2000). The efficacy of *Trichogramma* inundation, however, is dependent upon correct handling of the parasitoids and a thorough understanding of the factors that can limit their performance under field conditions. Here I discuss the importance of specialization, dispersal, and survivorship in the context of enhancing the efficacy of *Trichogramma* inundation for codling moth in California.

FACTORS LIMITING FIELD PERFORMANCE

The Influence of Specialization

Although most *Trichogramma* species are generalist parasitoids of lepidopteran eggs, they are often habitat specialists (trees or herbaceous plants) and can be greatly influenced by both plant structure (leaf surface and shape) and climate (humidity and temperature). Thus the few *Trichogramma* species that have been selected for commercial production may not be equally suitable for use against all target lepidopteran pests.

In a field trial in 1997, the field performance of four commercially produced *Trichogramma* species (*T. brassicae* [Bezdenko], *T. minutum* Riley, *T. platneri* and *T. pretiosum* Riley) was tested in a replicated block design in a commercial walnut orchard (Gustine cultivar, 120 trees per ha, tree height 8 m) in the Sacramento Valley of California. *Trichogramma brassicae* attacks hosts on low
Growing plants and is indigenous to the Palearctic region; *T. minutum* is an arboreal species occurring east of the Rocky Mountain chain in North America; *T. platneri* is also arboreal but is restricted to the western United States; and *T. pretiosum* occurs on low growing plants throughout the Nearctic region (Pinto, 1998). A 5 ha section of the orchard was partitioned into five replicated blocks each containing five 0.2 ha plots, one for release of each of the four *Trichogramma* species and a no-release control. Each *Trichogramma* species was released at a rate of 500,000 parasitized eggs per ha (see Mills et al., 2000). A series of four releases were made at weekly intervals (10 day intervals during the first generation) during the oviposition period of each of the three codling moth generations, starting around 100 degree days after the start of the flight period for each generation as determined by pheromone trap catches.

The activity of the *Trichogramma* parasitoids in these orchards was verified by monitoring sentinel codling moth eggs exposed to parasitism on PVC poles running through the canopy of individual trees in each plot. Sentinel eggs were rarely parasitized in the no-release control plots, indicating an absence of wild populations of parasitoids in this orchard, but were consistently parasitized in the release plots, suggesting that any reduction in fruit damage in the experimental plots was due to the action of the released parasitoids. *Trichogramma* performance was assessed from the extent of nut damage at harvest, which was estimated by sampling 750 nuts from each plot. Nut damage from codling moth averaged 3.7%, and although nut damage showed significant variation between *Trichogramma* species (*H* = 11.2, *P* = 0.02), only the *T. platneri* release plots showed a significant reduction in comparison with the no-release control plots (Fig. 1).

![Figure 1](image_url)

**Figure 1.** The efficacy of *Trichogramma* species in suppressing nut damage from codling moth in a walnut orchard. Bars headed by different letters are significantly different at *P* < 0.05.

The two poorest performers of the four *Trichogramma* species tested, *T. brassicae* and *T. pretiosum*, are specialized on low-growing plants rather than on trees. *Trichogramma minutum*, although an arboreal species, is indigenous to the eastern United States and its performance may have been compromised by the much drier climate of California. Thus the indigenous *T. platneri* outperformed the other commercially available *Trichogramma* species, suggesting that both habitat and climatic specialization can be important criteria limiting the success of inundative releases of *Trichogramma* in biological control.
The Influence of Limited Dispersal

Although *Trichogramma* parasitoids have been shown to disperse some distance in row crops (e.g., Wright et al., 2001), observations on dispersal of *T. platneri* in apple orchards in California indicate that movement from point sources is limited to about 15 m (McDougall and Mills, 1997a). The limited powers of dispersal of *T. platneri* in an orchard environment highlight the importance of an even distribution of release points. To illustrate the consequences of release distribution, we set up a replicated field trail in two pear orchards (Bartlett variety, 500 trees per ha, tree height 5 m) in the Sacramento delta of California in 1995. A 3.2 ha section of each orchard was partitioned into four replicate blocks of four 0.2 ha plots. A constant release rate of 500,000 parasitized eggs per ha was used, but the release treatments were 0 (no-release control), 25, 50, or 100 release points (trees) in a plot. Bartlett pears are harvested in July and thus experience damage from codling moth during its first two generations only. Six *Trichogramma* releases were made at weekly intervals during the first generation of codling moth and four weekly releases in the second generation. Fruit damage at harvest was recorded from 1,000 fruit in each plot.

The number of release points in a plot had a significant influence on the efficacy of suppression of codling moth damage in the pear orchards (Fig. 2, $F = 6.38$, $df = 3,24$, $P = 0.002$). The two orchards also differed significantly in the overall level of damage reduction achieved by the *Trichogramma* releases (Fig. 2, $F = 24.70$, $df = 1,24$, $P < 0.001$). In contrast to the second orchard, the first orchard had not been treated with insecticides the previous season, suggesting that management practices may have contributed to the difference in *Trichogramma* performance. These results clearly demonstrate, however, that the more evenly the *Trichogramma* are released, the better the reduction in codling moth damage. Thus the limited dispersal of *T. platneri* through the orchard environment must be taken into consideration in developing an effective augmentation program, and these results suggest that a method of broadcast release of parasitized eggs is needed for orchard canopies. Initial studies using aerial application of loose parasitized eggs, coated with a sticker to adhere them to the canopy of walnuts, have shown considerable promise for improving the efficacy of *Trichogramma* inundation in orchards (Mills et al., 2000).

![Figure 2. The influence of number of release points in a plot on suppression of fruit damage by codling moth from inundative releases of *T. platneri* in two pear orchards.](image)
The Influence of Limited Survivorship

Although it is well known from laboratory studies that the longevity of *Trichogramma* adults is temperature dependent (McDougall and Mills, 1997b; Mansfield and Mills, 2002; and references therein), how well these relationships apply to mass-reared individuals released under field conditions is questionable. It has proven difficult to accurately estimate the survivorship of *Trichogramma* in the field, and in all cases survivorship has been inferred indirectly from the duration of parasitism of sentinel eggs (e.g., Bourchier and Smith, 1996). The problem with this approach is that survivorship tends to be overestimated because the extended survival of a single individual is sufficient to generate parasitism of sentinel eggs and give the impression of more general survivorship of the parasitoid population.

By using cellulose-based dialysis tubing as small sleeve cages, we have been able to monitor directly the survivorship of cohorts of female *T. platneri* in a walnut orchard in California (Mansfield and Mills, 2002). The tubing is both translucent, facilitating direct observation of small parasitoid individuals, and porous, preventing the buildup of condensation and the occurrence of large temperature gradients. By monitoring the median survivorship of cohorts of *T. platneri* in the field at a series of intervals over the season and using data loggers to record temperatures in the walnut canopy, we have been able to obtain direct field estimates of the survivorship of *T. platneri*. Using a threshold temperature derived from laboratory observations (McDougall and Mills, 1997b), there was a very close relationship between median survivorship and cumulative degree-days (Fig. 3). This relationship indicates that survivorship of the mass-reared *T. platneri* did not extend beyond 70°C D, which corresponds to just less than three days for a typical daily thermal accumulation of 25°C D—a shorter survivorship than expected from laboratory observations.

In California, codling moth has an oviposition period that spans about one month. For fruit or nuts to be protected from hatching larvae during this period it is essential to know the duration of activity of the female parasitoids that emerge from the parasitized eggs released into the orchard. Initial estimates indicate that adult parasitoids emerge from parasitized eggs over a period of two to three days in the field and with a survivorship of just less than three days, each release probably provides active coverage of the orchard for about five days. Thus our general approach of weekly
releases of parasitized eggs through the oviposition period of each codling moth generation may not have been sufficient to provide continuous *Trichogramma* activity during these periods of the season. This suggests that either more frequent releases, or an extended period of emergence of adult parasitoids from each release, could increase the efficacy of *Trichogramma* inundation and further suppress codling moth damage.

**DISCUSSION**

Inundative release of a sufficient number of *T. platneri* can lead to substantial reduction in fruit and nut damage by codling moth, particularly in walnut and pear orchards (Mills *et al.*, 2000). These releases are not as effective as conventional insecticide sprays, as they appear not to be able to reduce damage by more than 60%, but have proved to be consistent in their impact both in the presence or absence of pheromone-based mating disruption. However, we have been able to identify three key factors that can limit the efficacy of *Trichogramma* inundation as a means to suppress codling moth damage in orchards in California. Firstly, the indigenous and locally adapted *T. platneri* provides significantly greater suppression of codling moth damage than other commercially available *Trichogramma* species. Secondly, an even broadcast release is necessary to overcome the limited dispersal of *T. platneri* in orchard environments. Then thirdly, more frequent releases or extending the period of emergence from parasitized eggs would help to overcome the limited survivorship of mass-produced *T. platneri* under field conditions.

Although augmentative biological control has proved commercially viable in glasshouse crops, success in the open field has been elusive (Elzen and King, 1999; van Lenteren, 2000). In many cases, field augmentation programs have been initiated without sufficient knowledge of how well suited the control agent is for the target pest. Although many mass-produced natural enemies have a broad host range, this does not mean that they are well suited for augmentation against a broad range of potential pests. For augmentation to be effective, it must be based on a sound scientific basis, with sufficient understanding of the ecological factors limiting the field performance of the selected control agent in attacking a specific pest in a particular crop. We have used this approach to improve the efficacy of *Trichogramma* augmentation against codling moth in fruit and nut orchards in California, and our experiences provide an interesting case study and valuable insights for augmentation programs in orchards in the future.

**REFERENCES**


