A Critical Evaluation of Augmentative Biological Control

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Abstract

The potential for using “augmentative” or “inundative” biological control for suppressing arthropod pests has been recognized for many years; however, augmentation is applied commercially in relatively few agricultural systems. To address why this should be the case, we reviewed the augmentative biological control literature to critically evaluate three questions. First, does augmentative biological control (or “augmentation”) effectively suppress agricultural pests? Second, is augmentation cost effective? Third, what ecological factors limit the effectiveness of augmentation? We evaluated effectiveness by assessing whether augmentative releases suppressed pest densities to target levels or thresholds, and by comparing the effectiveness of augmentation and conventional pesticide applications in studies that included both. We found that augmentation achieved target densities in about 20% of cases, and failed more than 50% of the time. Another 20% of cases were characterized by “mixed” efficacy, where releases achieved target densities in some situations but not others. In direct comparisons, augmentation was typically less effective than pesticide applications, but not always. In the evaluation of economics, augmentative releases were frequently more expensive than pesticides, though there were cases where augmentation was clearly cost effective. Finally, 12 ecological factors were implicated as potential limits on the efficacy of augmentation. Unfavorable environmental conditions, enemy dispersal, mutual interference and pest refuges from parasitism or predation were most often suggested as possible ecological limitations. We suggest that the burden of future research is to identify crop-pest systems in which augmentation can cost effectively control arthropod pests using rigorous field experiments that compare augmentation, pesticide application and control (no management) treatments.

Introduction

The potential for using “augmentative” or “inundative” biological control to suppress insect pests has been recognized for many years (Doutt and Hagen 1949, DeBach 1964, Ridgway and Vinson 1977, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992). Augmentative biological control (or “augmentation”) is simply the release of large numbers of insectary reared natural enemies with the goal of “augmenting” natural enemy populations or “inundating” pest populations with natural enemies. Such releases might be made, for example, if existing natural enemy populations fail to colonize fields or orchards, or colonize too late in the season to provide effective control of the pest (e.g., Obrycki *et al.* 1997).

To our knowledge, Doutt and Hagen (1949) were the first researchers to take this approach over 50 years ago. They released green lacewings to control out-breaking mealybug populations in pear orchards. Since Doutt and Hagen's pioneering study, augmentative biological control has been applied experimentally in a large number of pest systems (Ridgway and Vinson 1977, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992, this paper). Sales of natural enemies for augmentation have grown considerably in recent years (Cranshaw *et al.* 1996); however, the use of augmentation on a commercial basis is limited to a few systems (van Lenteren 1988, van Lenteren *et al.* 1997).

One of the major stimuli for investigating augmentative biological control has been the drive to reduce a historic reliance on broad-spectrum pesticides for pest control. The trend in both Europe and the U.S. has been to tighten regulation on pesticide use, with some pesticides having registrations withdrawn by governmental agencies. Augmentation might be used as a substitute for pesticide applications if the pest is sufficiently suppressed by the released natural enemies. van Lenteren (1988) argued that the first step in the successful implementation of augmentative biological control in greenhouses in the Netherlands has been to demonstrate to growers that augmentative releases are both effective and comparable in cost to pesticide treatments. In this paper, we address whether augmentation can provide effective pest suppression, and whether augmentation is cost-effective by conducting a literature review of published studies on augmentative biological control. We also reviewed the ecological factors that might limit the effectiveness of augmentation. On the basis on our review, we conclude by addressing whether augmentative releases are likely to replace broad-spectrum pesticides, and how further research might promote the implementation of augmentative biological control.

Methods

Using the AGRICOLA database, we identified over 140 published studies of augmentative biological control. We searched the key words “biological control” and either “augmentative,” “augmentation,” “inundative”, “inundation” or “releases.” Additional studies were identified in the literature sections of studies found in the AGRICOLA searches.

A number of studies were excluded from the review because they were judged to be lacking key information. All studies included in the analyses were required to use the following basic experimental design. In one set of experimental units (trees, plots, fields, etc.), natural enemies were released at one or more levels and/or frequencies. In another set of experimental units, no natural enemies were released (control plots). In some cases, both control plots and release plots were treated with one or more pesticides; however, as long as pesticide applications were the same in both types of plots, the effect of augmentation could be evaluated. Some appropriate studies included pesticide application(s) as a third, separate experimental treatment.

Studies were not considered further if they did not include experimental control plots or if control plots were clearly or systematically different from the treatment plots prior to-natural enemy releases. Studies that were unreplicated were also not considered. Third, we neglected studies that reported only percent parasitism or percent mortality as the sole measure of efficacy. Appropriate studies had to include a direct measure of pest suppression, either differences in pest densities, damage or reduced yields. Finally, we excluded laboratory and cage studies. Arguably, laboratory studies are unrealistic and cage-experiments restrict the dispersal of both pests and released natural enemies. Dispersal is a crucial factor determining the efficacy of augmentation under real-world conditions (see below).

Efficacy of augmentation

Identifying a reasonable and comparable measure of efficacy turns out to be a difficult problem. In many studies, effectiveness was equated with statistically significant differences between control plots and release plots. Unfortunately, a number of studies misused statistics by “pseudoreplicating”; that is they inappropriately used sampling units, e.g., leaves or plants, as experimental and statistical replicates instead of the truly independent experimental units, e.g., plots (Hurlbert 1984). Because of pseudoreplication and because statistical significance is not necessarily equivalent to *biological* significance, we did not use statistical significance as a criterion for evaluating efficacy.

Another frequent measure of effectiveness was the degree of suppression of pest numbers or damage in control plots versus release plots. Although this would seem to be a reasonable measure of efficacy, percent suppression *alone* provides little- to no-information about economic efficacy *per se*. A large percent suppression of a pest population achieved through augmentative releases may be accompanied by damagingly high pest densities and excessive economic loss.

In the end, we adopted two approaches for evaluating efficacy. We judged whether augmentation was “effective” on the basis of whether the author(s) indicated that pest densities or damage were suppressed below some specified target pest densities in release treatments but not in control treatments. These target densities may have been action or economic thresholds for pesticide application or post-harvest standards for damage. In other cases, authors simply stated that pest densities or damage were above economic targets without stating the value of the target density quantitatively. Our evaluation of efficacy is thus similar to an approach taken by Stiling (1993), who evaluated the efficacy of classical biological control based on authors’ assessments.

For each study that gave the appropriate information, we noted whether or not target densities were achieved. In studies in which multiple species of natural enemy were evaluated in separate experimental treatments, we counted each natural enemy species-pest species as a separate case. There were situations in which both control and release plots were below the threshold. In these cases, effectiveness of augmentation could not be judged (e.g., Hagley 1989, Poprawski *et al.* 1997, Lester *et al.* 1999, Michaud 2001).

Our second approach for evaluating efficacy applied only to a few studies that explicitly compared the efficacy of augmentative releases to conventional pesticide treatments. In each of these cases, the degree of pest suppression through augmentation could be directly compared to pest suppression using pesticides. Some of these studies also indicated whether pest densities were suppressed below the target level, which was also noted.

Implicit in our analysis is the fact that the benefits of augmentation are only represented by whether suppression was sufficient or not or how control though augmentation compared to control using pesticides. We did not consider other benefits, e.g., reduced environmental impacts, improved worker safety, and prevention or postponement of pesticide resistance (van Lenteren 1988). Nevertheless, our approaches provide two rigorous standards for evaluating efficacy. Our review represents a novel evaluation of augmentative biological control.

Economic costs of augmentation

Economic costs are crucial to the implementation of augmentative biological control. Whether or not augmentation can cost-effectively suppress pest populations has been debated since the first case studies (Flanders 1951, DeBach 1964, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992). For this part of the review, we included studies for which (a) efficacy could be judged as described above, and (b) the purchase price for the enemy species was available. We estimated current costs of augmentative releases using minimum prices for natural enemy species commercially available from Rincon-Vitova Insectaries. Prices were obtained online in November, 2002 (Table 1).

We had to make some assumptions to calculate the costs of *Trichogramma* releases. Prices were not available for all the *Trichogramma* species used in the studies that we identified. In addition, studies using *Trichogramma* typically presented information on the number of female parasitoids released rather than number of parasitized eggs used in releases. The latter is the unit of sale for *Trichogramma*. Consequently, we assumed that the *Trichogramma* species used in the studies cost the same as the species offered by Rincon-Vitova, and that, on average, about 0.5 female *Trichogramma* successfully emerged from each parasitized host egg, based on the results of Losey *et al.* (1995).

We had to make some additional assumptions to convert costs of augmentation per plant or per tree to costs per unit area (hectare), specifically for studies of augmentation in apples, corn, and hops. Some plant- or tree-density estimates were obtained from the USDA Crop Profiles Webpage-(http://pestdata.ncsu.edu/cropprofiles/) for the state in which the study was conducted or the nearest state for which data were-available. Tree densities for apples (670 trees/ha) were taken from Hagley (1989). Details about these assumptions are given in Table 2.

Our estimated costs of augmentation do not include all of the potential costs associated with augmentation. Because of a lack of information, we did not include costs of "scouting" or sampling pests prior to releases or application costs. Stevens *et al.* (2000) suggested that scouting and application costs for control of *Bemisia* on greenhouse poinsettias represented about 5% of the total cost of augmentation. By not considering the costs of sampling and application, we may therefore underestimate the true costs of augmentation in some cases.

We obtained the costs of crop production of the relevant commodities for the appropriate or closest state from the U.S.D.A. Crop Profiles-Web Page. Crop production costs include cultivation, pest management and harvest, and can be a useful benchmark for comparing costs of augmentation. Obtaining these values is much more straightforward than obtaining pesticide costs for the majority of crops, states and pest species. For augmentation to be cost-effective, costs of releases should be small compared to total crop production costs. If the cost of augmenting a natural enemy species against a specific pest exceeds total production costs for the crop, we can easily conclude that augmentation is not practical based on economic considerations. Finally, estimated costs of pesticide treatments and augmentative releases were explicitly given in some studies. We discuss these direct comparisons in addition to our own analysis.

Ecological Limits on Augmentation

To evaluate ecological factors that might limit the effectiveness of augmentation, we again took the approach of Stiling (1993), who tabulated explanations for the failure of classical biological control programs based on the authors' views. Although often anecdotal and potentially reflecting the biases of individual researchers, this type of information can be useful. Arguably, the researchers themselves are often in the best position to evaluate their own results. We tabulated and ranked ecological limits on the efficacy of augmentative releases in any study from our literature search that suggested one or more limit and satisfied our basic criteria for inclusion, i.e., replication, the presence of acceptable controls, etc... This larger collection of studies includes papers that did not evaluate whether augmentation achieved target pest densities.

Results

Is augmentation effective?

We begin with our evaluation of whether augmentation achieved target pest densities. Pest populations were suppressed below target densities in 7 out of 33 or a little more than 20% of the enemy-pest cases (Table 2). In 7 more cases, we designated pest suppression as “mixed” because pest suppression was adequate in some situations and not others. Losey *et al.* (1995), for example, found that releases of *Trichogramma nubilalis* suppressed European Corn Borer (ECB), *Ostrinia nubilalis*, damage sufficiently for processed corn market but not apparently for fresh market corn. In five cases, including three others involving ECB, “mixed” suppression reflected that suppression was only sufficient in some fields, some years or both. Such site-to-site and/or year-to-year variation is likely to be undesirable to growers, who are often risk averse (King *et al.* 1985, Carlson 1988).

In another scenario that we characterized as “mixed” efficacy, Trumble and Morse (1993) observed that augmentative releases of predacious mites, *Phytoselius persimilis*, in strawberries did not achieve economic threshold densities of two-spotted spider mite, *Tetranychus urticae*. However, a combination of augmentative releases and miticide applications, particularly abamectin, were very effective. In fact, better suppression in terms of both pest densities and fruit yields was achieved through a combination of miticide applications and predator releases than miticide alone (or releases alone). Trumble and Morse’s study illustrates that augmentation may more effectively suppress pests to sub-economic levels if used in combination with one or more pesticides, provided that these chemicals are not strongly detrimental to the released natural enemies.

Finally, pest populations were not suppressed below specified target or economic threshold densities in 19 of the 33 pest-enemy cases. Thus, by our “target-density” criterion, augmentation “failed” more than 50% of the time.

Seven studies allowed direct comparison of the efficacy of augmentation and conventional pesticide applications (Table 3), either on the basis of specified target densities or differences in percent suppression. Pesticide treatments usually achieved target densities, though not always. In both years of Udayagiri *et al.*’s (2000) study, for example, pesticide treatments resulted in *Lygus* nymph densities that were near but slightly above (ca 10-20%) the economic threshold. Likewise, insecticidal suppression of stinkbugs in Brazilian soybeans failed to achieve economic densities in Correa-Ferreira and Moscardi’s (1996) study.

Typically, augmentation was less effective than pesticide treatments. In 5 of 7 cases, pesticides achieved target pest densities where augmentation failed to achieve target densities. In the two studies where pesticides were ineffective, augmentation achieved sub-economic densities in one year but not the other (against *Lygus*; Udayagiri *et al.* (2000)) or failed to achieve target densities like the pesticide applications (against stinkbugs; Correa-Ferreira and Moscardi's (1996)). Overall, pest suppression through augmentation ranged from 3-85% compared to 35-100% for conventional pesticide applications.

What are the costs of augmentation?

A clear approach for evaluating the costs of augmentation is to directly compare the costs of releases with the costs of insecticidal control. A few studies included in our review explicitly made this comparison. For example, Moreno and Luck (1992) found that releases of *Aphytis melinus* in citrus were comparable if not less in cost to standard applications of organophosphate insecticides. Trumble and Morse (1993) showed that releases of *Phytoseilus persimilis* were cost effective in controlling two-spotted spider mite in strawberries. Although predator-release treatments were almost double in cost to abamectin treatments, the two treatments combined produced the greatest efficacy per dollar spent. Not surprisingly, releases of both *Aphytis melinus* in citrus and *Phytoseilus persimilis* in strawberries are commonly practiced commercially (UCIPM Webpage http://www.ipm.ucdavis.edu/).

In five other case studies, augmentation was more expensive than pesticide treatments. Wright *et al.* (2002) report that releases of *Trichogramma* were about half the cost of pesticide treatments, however, based on purchase prices for *Trichogramma* rather than the authors' laboratory rearing costs, releases would have been about 1.5 times the cost of insecticidal control. A number of studies suggested that augmentative releases were about 2-3 times the cost of pesticide applications; this was true for releases of a parasitoid (*Theocolax elegans*) to control a stored product pest (*Rhyzopertha dominica*)(Flinn-*et al.* 1996), releases of green lacewings, (*Chrysoperla carnea*) to control leafhoppers in grapes (Daane *et al.* 1996), and releases of *Trichogramma* to control cabbage feeding Lepidoptera (Lundgren *et al.* 2002). Finally, Hoddle *et al.* (1997) found that weekly releases of one *Encarsia formosa* per poinsettia plant could sufficiently control *Bemisia tabaci*, a whitefly pest. However, augmentative releases of *E. formosa* were found to be 9-11 times more expensive than pesticide treatments (Hoddle and van Driesch 1996, Stevens *et al.* 2000).

A second benchmark for evaluating the costs of augmentation is the cost of production of the commodity, which can be easily obtained (Table 2). Production costs include cultivation, pest management and harvest. In the two systems in which releases were shown to be efficacious and cost effective, (*Aphytis melinus* in citrus and *Phytoselius persimilis* in strawberries) augmentation costs were estimated to be less than 1% of the production costs for these crops (Table 2). In most cases, augmentation costs were less than about 10% of the production costs. However, in 5 of 20 cases, estimated costs of augmentation exceeded total production costs for the commodity. It can easily be concluded that augmentation was not cost effective in these cases.

In summary, we found that augmentative biological control was not cost effective in several cases. However, there were cases in which the costs of augmentation compared favorably to the costs of pesticide treatments or to overall production costs. As many authors reviewing augmentation have suggested before, analysis of cost is crucial to evaluating the potential for implementing augmentative biological control (DeBach 1964, Ridgway and Vinson 1977, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992). We have shown here that, at least for commercially available natural enemies, the estimated costs of augmentation can easily be compared to production costs for the commodity, and that this can yield insight into the implementation of augmentative biological control.

What are the ecological limits on augmentation?

Of the studies included in our review, one or more limitations were suggested in 20 studies for a total of 12 potential ecological limits (Table 4, 5). The potential limitations are discussed below in rank order based on the number of times each was cited.

(1) Environment Unfavorable for Enemy (4 cases). Environmental conditions at the time of release, particularly hot and/or dry conditions, may lead to high mortality of released natural enemies. This seemed to be true for predacious mites (Pickett and Gilstrap 1986, Lester *et al.* 2001), *Trichogramma nubilale* (Andow *et al.* 1995) and a ladybird beetle (Kehrli and Wyss 2001).

(2) Enemy Dispersal (3 cases). Dispersal of natural enemies away from the release site may limit the impact of augmentative releases. Potential examples include augmentation with: green lacewing, *Chrysoperla rufilabris*, in apples (Grasswitz and Burts 1995), a parasitoid of whitefly pests, *Eretmocerus eremicus*, in cotton (Minkenberg *et al.* 1994), and a parasitoid of *Lygus* bugs in strawberries, *Anaphes iole* (Norton and Welter 1996). In each case, the authors thought that these natural enemies left the experimental plots before having much of an impact on the pest population. The enemy-dispersal problem may, however, be largely an issue of experimental design – reflecting the relatively small spatial scales of experimental studies. In practice, natural enemy dispersal may be less important with augmentative releases on large spatial scales.

(3) Mutual Interference/Cannibalism (3 cases). Mutual interference occurs when increasing the density of natural enemy individuals actually reduces the efficiency of each natural enemy individual (e.g., Hassell 1976). This may occur if predators or parasitoids show aggressive behavior or if intraspecific contact reduces time available to encounter and kill pests. A consequence of mutual interference for augmentation is that high release rates may lead to less-effective pest suppression. Hoddle *et al.* (1997) suggested that higher release rates of *Encarsia formosa* used to control whiteflies in poinsettia were ineffective because of mutual interference; lower release rates were more effective. Wen *et al.* (1994) suggested a similar phenomenon in *Anisopteromalus calandrae*, a parasitoid released against the maize weevil in corn storages. Another potential mechanism of mutual interference in predators is cannibalism. Kehrli and Wyss (2001) suggested that cannibalism among juvenile ladybird beetles (*Adalia punctata*) limited the effectiveness of releases of this species. Cannibalism may, in fact, be common in generalist predators, and could limit the effectiveness of augmentative releases of some species.

(4) Refuge for the Pest (3 cases). A refuge for the pest can arise when a subset of the pest population is relatively invulnerable to attack by released natural enemies. In a clear example, Udayagiri *et al.* (2000) suggested that the egg parasitoid, *Anaphes iole*, could not reach *Lygus* bug eggs deposited within strawberry fruit achenes. Eggs deposited in other parts of the fruit or plant were parasitized with much higher frequency. A similar phenomenon might arise when the crop canopy is rapidly growing and pests escape predators by colonizing new growth (Strong and Croft 1995) or if predators or parasitoids cannot physically attack all pests in a “patch” (Correa-Ferreira and Moscardi 1996). Refuges from parasitism or predation may limit the ability of the released natural enemies to suppress pest populations (e.g., Murdoch 1992).

(5) Predation (3 cases). Natural enemies released in augmentative biological control programs may themselves be attacked by other predators and/or parasitoids. Cases in which one predator species is eaten by other predator species that also feed on the pest are specifically known as "intraguild predation", which may limit the effectiveness of natural enemies (Rosenheim *et al.* 1995). Heinz *et al.* (1999) and Ehler *et al.* (1997) implicated resident hemipterans as potential intraguild predators of augmentatively released juvenile *Delphastus catalinae* and *Chrysoperla carnea* respectively. Yu and Byers (1994) found evidence of predation on *Trichogramma*-parasitized host eggs released for control of ECB.

(6) Compensatory Mortality (2 cases). Releases of natural enemies that attack the young stages of the host may sometimes have little effect on later stages of the pest if there is "compensatory mortality", directly density dependent mortality factors on intervening stages. A consequence of compensatory mortality is that reduced density of young pests leads to higher *per capita* survival in later pest stages, and little ultimate reduction in pest damage. Cloutier and Bauduin (1995), for example, suggested that compensatory mortality followed considerable egg mortality of Colorado potato beetle (*Leptinotarsus decemlineata*) caused by predator releases. Suh *et al.* (2000) similarly suggested that releases of *Trichogramma exiguum* against *Heliothis* spp. in cotton were ineffective because of compensatory larval mortality. In another study with *Trichogramma*, however, Andow *et al.* (1995) tested and rejected the hypothesis that density dependent survival limited effectiveness of *Trichogramma nubilale* releases in corn.

(7) Enemy Quality (2 cases). Consistency in the quality of natural enemies used in augmentation has been a concern for many years (Stinner 1977, Parella *et al.* 1992). Clearly, natural enemies of "poor quality" may have a limited impact on pest populations. Winglessness and small size has been occasionally noted in mass-produced *Trichogramma*, although this explanation for failure of *Trichogramma exiguum* releases in cotton was rejected by Suh *et al.* (2000). Two studies, however, implicated enemy quality. Ehler *et al.* (1997) noted a reduced ability in insectary reared lacewings (*Chrysoperla carnea*) to attack bean aphid (*Aphis fabae*) relative to wild-caught lacewings. Norton and Welter (1996) also suggested that failure of *Anaphes iole* to control *Lygus* bug may have reflected poor quality of mass-reared *Anaphes*.

(8) Pest-Enemy Incompatibility (2 cases). Failure of augmentative releases may simply reflect that the natural enemy is not compatible with the pest in some way. Lundgren *et al.* (2002), for example, questioned whether the strain or species of *Trichogramma* they augmentatively released (*T. brassicae*) was appropriate for suppressing *Pieris rapae* and *Trichoplusia ni*; parasitism and pest suppression was poor following augmentative releases. In another case, released lacewings (*Chrysoperla rufilabris*) appeared to have insufficiently fed on the pest, *Aphis pomi*, and starved (Grasswitz and Burts 1995). Ineffectiveness of *C. rufilabris* may thus have reflected a poor match between the pest and the enemy species.

(9) Pest Immigration (2 cases). Massive influx of pests into release plots may overwhelm released natural enemies' ability to control them. Minkenberg *et al.* (1996) suggested that pest immigration, coupled with natural enemy emigration, prevented *Eretmocerus eremicus* from having any impact on whiteflies in experimental cotton plots. Similarly, immigration of Colorado potato beetle adults may have limited efficacy of releases of a combination of *Podisus maculiventris* and *Edovum puttleri* (Tipping et al. 1999). As with enemy dispersal, the relative small scale of experimental plots may contribute to this phenomenon.

(10) Timing of Releases (2 cases). The timing of releases during the growing season may be crucial to the effectiveness of augmentation. Two studies suggested that improper timing may have prevented sufficient suppression of the pest through augmentation. In one study, the authors suggested that *Chrysoperla carnea* were released at the wrong time to control leafhoppers in grapes (Daane *et al.* 1996). In a second case, improperly timed releases of a predacious coccinelid (*Stethorus picipes*) were thought to have prevented adequate control of avocado brown mite (*Oligonychus punicae*; McMurtry *et al.* 1969). Two studies that explicitly varied the timing of releases showed that suppression did indeed depend on release date. Trouve *et al.* (1997) found that early releases of the coccinelid *Harmonia axyridis* could suppress damson-hop aphid, *Phorodon humulus*, below an economic threshold density of 80 aphids per leaf, whereas augmentative releases two- or four-weeks later could not. Cambell and Lilley (1999) similarly found that a single early season release of predacious mites (*Phytoseilus persimilis*) was more effective than a later release at the same rate against two-spotted spider mite on hops.

(11) Fungicide (1 case). Application of pesticides may cause mortality of released natural enemies and thereby limit the effectiveness of augmentative releases. For this reason, pesticide applications are often not compatible with augmentation and are therefore avoided. Lester *et al.* (2001) suggested that fungicides applied to peaches may have limited the effectiveness of *Neoseiulus* (=*Amblyseius*) *fallacis* against two phytophagous mite pests.

(12) Release Method (1 case). Augmentation requires that mass-reared natural enemies be handled during release into the field. Release methods may lead to poor efficacy if handling leads to high natural enemy mortality. Daane *et al.* (1996) suggested that the effectiveness of augmentative releases of *Chrysoperla carnea* in vineyards was limited by mortality imposed by handling the eggs.

In summary, our review suggested that a number of different ecological mechanisms may limit the effectiveness of augmentative biological control. Clearly, some of the above limitations might be ameliorated or counter-acted in future augmentative biological control reasearch or implementation. Release timing, release methods, enemy quality and incompatibility of the enemy and the pest can all be improved. The remaining limits on augmentation may initially seem beyond human control. For example, in one of the case studies that explored the use of *Anaphes iole* to control *Lygus* in strawberries, a refuge from parasitism appeared to limit the effectiveness of augmentative releases (Udayagiri *et al.* 2000). A refuge from parasitism would be difficult to alter *per se*. Udayagiri *et al.* suggested, however, that effective control might be achieved by using releases of a second natural enemy species or application of a selective pesticide in combination with *Anaphes*. Pesticides and/or complementary releases of a second enemy species might be used to counteract a number of the other potential ecological limitations on augmentation: compensatory mortality, intraguild predation, adverse environmental conditions, fungicides, etc. In general, integrating augmentative releases with other pest management practices may be instrumental in overcoming the ecological limitations on the effectiveness of augmentative biological control.

Conclusions

Our goal was to critically evaluate three questions related to augmentative biological control using a literature survey. Does augmentation effectively suppress agricultural arthropod pests? Is augmentation cost effective? What ecological factors limit the effectiveness of augmentation? We found first that augmentative releases were usually less effective than conventional pesticide applications. Second, augmentation achieved target pest densities in less than a quarter of cases and failed in more than 50% of cases. Third, augmentative releases were often more expensive than overall production costs and pesticide application costs. Fourth, a number of different ecological factors may explain why augmentation is sometimes ineffective; these factors may be overcome by altering practical aspects of augmentative releases, such as number and identity of species released, timing of releases and/or integration with other management practices.

It could be argued that our approach for evaluating efficacy of augmentation is unduly conservative. Comparing augmentation to pesticide applications and/or specific target pest densities, which are undoubtedly set by a standard of insecticidal control, may not be fair. van Lenteren (1988) argued that low pest densities are easily achieved using relatively inexpensive and highly effective pesticides; however, such low densities may be difficult to achieve through augmentative releases (van Lenteren 1988). Undoubtedly, augmentation would have been effective more frequently in our review if greater damage had been acceptable. There may also have been cases that were "effective" by some measure, but were not included in the review because target pest thresholds had not yet been determined and/or were difficult to determine (e.g., Schweizer et al. 2002).

We argue first that there are likely to be situations in which economic thresholds are not particularly flexible and greater damage is not acceptable. This should be true when damage levels are set by consumer preferences or the ability of plants to compensate for insect feeding (e.g., Trumble *et al.* 1993). In these cases, suppression to specific target pest densities would be required for efficacy. Second, we would argue that studies of augmentation *must* incorporate some standard for judging effectiveness besides percent suppression of pest populations or pest-induced damage. Percent suppression cannot suggest whether augmentation can effectively replace pesticide applications without some standard associated with pesticide efficacy. We agree with van Lenteren (1988) that implementation of augmentative biological control requires research that demonstrates augmentative releases are effective and comparable in costs to pesticide treatments. We argue that the key objective of research on augmentation ought to be to determine whether augmentation can achieve economic pest densities. Better yet, studies of augmentation should compare augmentative releases and pesticide treatments to untreated controls, as did a number of the best studies we reviewed (Trumble and Morse 1993, Andow *et al.* 1995, Correa Ferreira and Moscardi 1996, Olson *et al.* 1996, Suh *et al.* 2000, Udayagiri *et al.* 2000, Lundgren *et al.* 2002)

Based on our review, we argue that augmentative biological control is not likely to be a *panacea* for all agricultural production, and is unlikely to replace pesticides on its own in pest management in the near future. We emphasize, however, that there were clear cases where augmentation *was* effective both in terms of suppression relative to target densities or pesticides, and economic considerations. These successes may reflect that a considerable amount of research had already been conducted, and that much was known about these systems, e.g., *Aphytis melinus-Aonidiella aurantii* in citrus (DeBach *et al.* 1950, DeBach and White 1960), *Encarsia formosa* and whiteflies in greenhouses (van Lenteren and Woets 1988, Hoddle *et al.* 1998), and *Tetranychus urticae* and *Phytoseilus persimilis* on strawberries (Oatman *et al.* 1967, Oatman *et al.* 1968). Parenthetically, the same should be true of *Trichogramma*, which performed disappointingly in the studies in our review (Table 3). Further research may lead to successes in pest-crop combinations for which augmentation had previously “failed” or produced mixed effectiveness, through releases of different enemy species or combinations of enemies, or through the integration of releases with other management practices, e.g., selective, “low-risk” pesticides. Augmentative biological control can and does work in some systems. Future research on augmentative biological control must identify the systems in which augmentative releases can work in a cost-effective manner, using rigorous, well-designed field experiments.

Literature Cited

Andress, E.R. and Cambell, J.B. 1994. Inundative releases of pteromalid parasitoids (Hymenoptera: Pteromalidae) for the control of stable flies, *Stomoxys calicitrans* (L.) (Diptera: Muscidae) at confined cattle installations in west central Nebraska. *Journal of Economic Entomology* **87**: 714-722.

Andow, D.A., Klacan, G.C., Bach, D., and Leahy, T.C. 1995. Limitations of *Trichogramma nubilale* (Hymenoptera: Trichogrammatidae) as an inundative biological control of *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Environmental Entomology* **24**: 1352-1357.

Cambell, C.A.M., and Lilley, R. 1999. The timing and rates of release of *Phytoseilus persimilis* against two-spotted spider mite *Tetranychus urticae* on dwarf hops. *Biocontrol Science and Technology* **9**: 453-465.

Carlson, G.A. 1988. Economics of biological control. *American Journal of Alternative Agriculture* **3**: 110-116.

Cloutier, C., and Bauduin, F. 1995. Biological control of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) in Quebec by augmentative releases of the two-spotted stinkbug *Perillus bioculatus* (Hemiptera: Pentatomidae). *Canadian Entomologist* **127**:195-212.

Correa Ferreira, B.S., and Moscardi, F. 1996. Biological control of soybean stink bugs by inoculative releases of *Trissolcus basalis*. *Entomologia Experimentalis et Applicata* **79:**1-7.

Cossentine, J.E., and Jensen, L.B.M. 2000. Releases of *Trichogramma platneri* (Hymenoptera; Trichogrammatidae) in apple orchards under a sterile codling moth release program. *Biological Control* **18**: 179-186.

Daane, K.M., Yokota, G.Y., Zheng, Y., and Hagen, K.S. 1996 Inundative release of common green lacewings (Neuroptera: Chrysopidae) to suppress *Erythroneura variabilis* and *E. elegantula* (Homoptera: Cicadellidae) in vineyards. *Environmental Entomology* **25**:1224-1234.

DeBach, P. 1964. *Biological Control of Insect Pests and Weeds*. Chapman and Hall, London.

DeBach, P., Dietrick, E.J., Fleshner, C.A., and Fisher, T.W. 1950. Periodic colonization of *Aphytis* for control of the California red scale. Preliminary tests, 1949. *Journal of Economic Entomology* **43**: 783-802.

DeBach, P. and White, E.B. 1960. Commercial mass culture of California red scale parasite *Aphytis lingnanensis*. *California Agricultural Experiment Station Bulletin* **770**.

Doutt, R.L. and Hagen, K.S. 1949. Periodic colonization of *Chrysoperla californica* as a possible control of mealybugs. *Journal of Economic Entomology* **42**: 560-561.

Ehler, L.E., Long, R.F., Kinsey, M.G., and Kelley, S.K. 1997. Potential for augmentative biological control of black bean aphid in California sugarbeet. *Entomophaga* **42**: 241-256.

Flinn, P.W., and Hagstrum, D.W. 2001. Augmentative release of parasitoid wasps in stored wheat reduces insect fragments in flour. *Journal of Stored Product Research* **37**: 179-186.

Flinn, P.W., Hagstrum, D.W., and McGaughey, W.H. 1996. Suppression of beetles in stored wheat by augmentative releases of parasitic wasps. *Environmental Entomology* **25**: 505-511.

Grafton-Cardwell, E.E., and Ouyang, Y. 1995. Augmentation of *Eusieus tularensis* (Acari: Phytoseiidae) in Citrus. *Environmental Entomology* **24**: 738-747.

Grasswitz, T.R., and Burts, E.C. 1996. Effect of native natural enemies and augmentative releases of *Chrysoperla rufilabris* Burmeister and *Aphidoletes aphidimyza* (Rondani) on the population dynamics of the green apple aphid, *Aphis pomi* De Geer. *International Journal of Pest Management* **41**:176-183.

Hagley, E.A.C. 1989. Release of *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) for control of the green apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae). *The Canadian Entomologist* **121**: 309-314.

Hassell, M.P. 1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, Princeton, N.J.

Hoddle, M.S., and Van Driesche, R.G. 1999. Evaluation of inundative releases of *Eretmocerus eremicus* and *Encarsia formosa* Beltsville strain in commercial greenhouses for control of *Bemisia argentifolii* (Hemiptera: Aleyrodidae) on poinsettia stock plants. *Journal of Economic Entomology* **92**: 811-824.

Hoddle, M., Van Driesche, R., and Sanderson, J. 1997. Biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on Poinsettia with inundative releases of *Encarsia formosa* (Hymenoptera: Aphelinidae): are higher release rates necessarily better? *Biological Control* **10**: 166-179.

Hoddle, M.S., Van Driesche, R.G., and Sanderson, J.P. 1998. Biology and use of the whitefly parasitoid *Encarsia formosa*. Annual Review of Entomology **43**: 645-669.

Hoddle, M.S., Van Driesche, R.G., Sanderson, J.P., and Minkenberg, O.P.M.J. 1998. Biological control of *Bemisia argentifolii* (Hemiptera: Aleyrodidae) on pointsettia with inundative releases of *Eretmocerus eremicus* ((Hymenoptera: Aphelinidae): do release rates affect parasitism? *Bulletin of Entomological Research* **88**: 47-58.

Heinz, K.M., Brazzle, J.R., Parella, M.P., and Pickett, C.H. 1999. Field evaluations of augmentative releases of *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae) for suppression of *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) infesting corn. *Biological Control* **16**:241-251.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological experiments. *Ecological Mongraphs* **54**: 187-211.

Kehrli, P., and Wyss, E. 2001. Effects of augmentative releases of the coccinellid, *Adalia bipunctata*, and of insecticide treatments in autumn on the spring population of aphids of the genus *Dysaphis* in apple orchards. *Entomologia Experimentalis et Applicata* **99**:245-252.

King, E.G., Hopper, K.R., and Powell, J.E. 1985. Analysis of systems for biological control of crop arthropod pests in the U.S. by augmentation of predators and parasites. pp. 201-227. *In*: Hoy, M.A., and Herzog, D.C. (eds.) *Biological Control in Agricultural IPM Systems*. Academic Press, London.

Losey, J.E., Fleischer, S.J., Calvin, D.D., Harkness, W.L., and Leahy, T. 1995. Evaluation of *Trichogramma nubilalis* and *Bacillus thuringiensis* in management of *Ostrinia nubilalis* (Lepidoptera: Pyralidae) in sweet corn. *Environmental Entomology* **24**: 436-445.

van Lenteren, J. C. 1988. Implementation of biological control. *American Journal of Alternative Agriculture* **3**: 102-109.

van Lenteren, J. C., Roskam, M.M., and Timmer, R. 1997. Commercial mass production and pricing of organisms for biological control of pests in Europe. *Biological Control* **10**: 143-149.

van Lenteren, J. C., and Woets, J. 1988. Biological control and intergrated pest control in greenhouses. *Annual Review of Entomology* **33**: 239-269.

Lester, P.J., Thistlewood, H.M.A., Marshall, D.B., and Harmsen, R. 1999. Assessment of *Amblyseius fallacis* (Acari: Phytoseiidae) for biological control of tetranychid mites in an Ontario peach orchard. *Experimental and Applied Acarology* **23**: 995-1009.

Lundgren, J.C., Heimpel, G.E., and Bomgren, S.A. 2002. Comparison of *Trichogramma brassicae* (Hymenoptera; Trichogrammatidae) augmentation with organic and synthetic pesticides for control of cruciferous Lepidoptera. *Environmental Entomology* **31(6)**: 1231-1239.

McMurtry, J.A., Johnson, H.G., and Scriven, G.T. 1969. Experiments to determine effects of mass releases of *Stethorus picipes* on the level of infestation of the avocado brown mite. *Journal of Economic Entomology* **62(5)**: 1216-1221.

Mertz, B.P., Fleisher, S.J., Calvin, D.D., and Ridgway, R.L. 1995. Field assessment of *Trichogramma brassicae* (Hymenoptera; Trichogrammatidae) and *Bacillus thruingiensis* for control of *Ostrinia nubilalis* (Lepidoptera; Pyralidae) in sweet corn. *Journal of Economic Entomology* **88(6)**: 1616-1625.

Michaud, J.P. 2001. Evaluation of green lacewings, *Chrysoperla ploribunda* (Fitch)(Neurop., Chrysopidae), for augmentative release against *Toxoptera citricida* (Hom., Aphididae) in citrus. *Journal of Applied Entomology* **125**: 383-388.

Minkenberg, O., Simmons, G.S., Malloy, R., Kaltenbach, J., and Leonard, C. 1994. Biological control of whiteflies on cotton: a reality check. *Proceedings of the Beltwide Cotton Conferences* **3**: 887-890.

Moreno, D.S., and Luck, R.F. 1992. Augmentative releases of *Aphytis melinus* (Hymenoptera: Aphelinidae) to suppress California redscale (Homoptera: Diaspididae) in southern California lemon orchards. *Journal of Economic Entomology* **85**: 1112-1119.

Murdoch, W.W. 1992. Ecological theory and biological control. pp. 197-221. *In*: Jain, S.K., and Botsford, L.W. (eds), *Applied Population Biology*. Kluwer Academic Publishers, The Netherlands.

Norton, A.P., Welter, S.C. 1996. Augmentation of the egg parasitoid *Anaphes iole* (Hymenoptera: Mymaridae) for *Lygus hesperus* (Heteroptera: Miridae) management in strawberries. *Environmental Entomology* **25**:1406-1414.

Oatman, E.R., McMurty, J.A., Shorey, H.H., and Voth, V. 1967. Studies integrating *Phytoseiulus persimilis* releases, chemical applications, cultural manipulations, and natural predation for control of the two-spotted spider mite on strawberry in Southern California. *Journal of Economic Entomology* **60**: 1344-1351.

Oatman, E.R., McMurty, J.A., and Voth, V. 1968. Suppression of the two-spotted spider mite on strawberry with mass releases of *Phytoseiulus persimilis*. *Journal of Economic Entomology* **61(6)**: 1517-1521.

Obrycki, J.J., Lewis, L.C. and Orr, D.B. 1997. Augmentative releases of entomophagous species in annual cropping systems. *Biological Control* **10**: 30-36.

Olson, D.L., Nechols, J.R., and Schurle, BW. 1996. Comparative evaluation of population effect and economic potential of biological suppression tactics versus chemical control for squash bug (Heteroptera: Coreidae) management on pumpkins. *Journal of Economic Entomology* **89(3)**: 631-639.

Parella, M.P., Heinz, K.M. and Nunney, L. 1992. Biological control through augmentative releases of natural enemies: a strategy whose time has come. *American Entomologist* **38**: 172-179.

Pickett, C.H., and Gilstrap, F.E. 1986. Inoculative releases of Phytoseiids (Acari) for the biological control of spider mites (Acari: Tetranychidae) in corn. *Environmental Entomology* **15(4)**: 790-794.

Poprawski, T.J., Carruthers, R.I., Speese, J., Vacek, D.C., and Wendel, L.E. 1997. Early-season applications of the fungus *Beauveria bassiana* and introduction of the hemipteran predator *Perillus bioculatus* for control of Colorado potato beetle. *Biological Control* **10**: 48-57.

Prokrym, D.R., Andow, D.W., Ciborowski, J.A., and Sreenivasam, D.D. 1992. Suppression of *Ostrinia nubilalis* by *Trichogramma nubilale* in sweet corn. *Entomologia Experimentalis et Applicata* **64**: 73-85.

Ridgway, R.L., and Vinson, S.B. 1977. *Biological Control by Augmentation of Natural Enemies*. Plenum Press, New York. 480 pp.

Schweizer, H., Morse, J.G., Luck, R.F., and Forster, L.D. 2002. Augmentative releases of a parasitoid (*Metaphycus* sp. nr. *flavus*) against citricola scale (*Coccus pseudomagnoliarum*) on oranges in the San Joaquin Valley of California. *Biological Control* **24**: 153-166.

Stevens, T.J. III, Kilmer, R.L., and Glenn, S.J. 2000. An economic comparison of biological and conventional control strategies for whiteflies (Homoptera: Aleyrodidae) in greenhouse pointsettias. *Journal of Economic Entomology* **93**: 623-629.

Stiling, P. 1993. Why do natural enemies fail in classical biological control programs? *American Entomologist* **39**:31-37.

Stinner, R.E. 1977. Efficacy of inundative releases. *Annual Review of Entomology* **22**: 515-31.

Strong, W.B., and Croft, B.A. 1995. Inoculative release of Phytoseiid mites (Acarina: Phytoseiidae) into the rapidly expanding canopy of hops for control of *Tetranychus urticae* (Acarina: Tetranychidae). *Environmental Entomology* **24**: 446-453.

Strong, W.B., and Croft, B.A. 1996. Release strategies and cultural modifications for biological control of twospotted spider mite by *Neoseilulus fallacis* (Acari: Tetranychidae, Phytoseiidae) on Hops. *Environmental Entomology* **25**: 529-535.

Suh, C.P.C., Orr, D.B., Van Duyn, J.W. and Borchert, D.M. 2000. *Trichogramma exiguum* (Hymenoptera: Trichogrammatidae) releases in North Carolina cotton: evaluation of heliothine pest suppression. *Journal of Economic Entomology*: **93**: 1127-1136.

Tipping, P.W., Holko, C.A., Abdul-Baki, A.A., and Aldrich, J.R. 1999. Evaluating *Edovum puttleri* Grissell and *Podiscus maculiventris* (Say) for augmentative biological control of Colorado potato beetle in tomatoes. *Biological Control* **16**: 35-42.

Trouve, C., Ledee, C., Ferran, A. and Brun, J. 1997. Biological control of the damson-hop aphid, *Phorodon humuli* (Hom.: Aphididae), using the ladybeetle *Harmonia axyridis* (Col.: Coccinelidae). *Entomophaga* **42**: 57-62.

Trumble, J.T. and Morse, J.P. 1993. Economics of integrating the predaceous mite *Phytoseiulus persimilis* (Acari: Phytoseiidae) with pesticides in strawberries. *Journal of Economic Entomology* **86**: 879-885.

Trumble, J.T., Kolodny-Hirsch, D.M., and Ting, I.P. 1993. Plant compensation for arthropod herbivory. *Annual Review of Entomology* **38**: 93-119.

Udayagiri, S., Welter, S.C., and Norton, A.P. 2000. Biological control of *Lygus hesperus* with inundative releases of *Anaphes iole* in a high cash value crop. *Southwest Entomologist Supplement* **23**:27 39.

Wen, B., and Brower, J.H. 1994. Suppression of maize weevil, *Sitophilus zeamais* (Coleoptera: Curculionidae), populations in drums of corn by single and multiple releases of the parasitoid *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae). *Journal of the Kansas Entomological Society* **67(4)**: 331-339.

Wright, M.G., Kuhar, T.P., Hoffmann, M.P., and Chenus, S.A. 2002. Effect of inoculative releases of *Trichogramma ostriniae* on populations of *Ostrinia nubilalis* abd damage to sweet corn and field corn. *Biological Control* **23**: 149-155.

Yu, D.S., and Byers, J.R. 1994. Inundative release of *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) for control of European corn borer in sweet corn. *Canadian Entomologist* 126 (2): 291 301.

Table 1. Minimum purchase prices used in economic cost assessment as given by Rincon-Vitova Insectaries (www.rinconvitova.com). Price is for adults unless otherwise shown. Recording Date: October 2003.

Natural Enemy (Authority)	Cost per 1000
Anaphes iole	$9.50
Aphidoletes aphidimyza (Rondani)	$10.00
Aphytis melinus	$2.05
Chrysoperla carnea (larvae)	$11.40
Chrysoperla rufilabris (larvae)	$11.40
Harmonia axyridis (Pallas)	$200.00
Amblysieus californicus	$10.60
Amblysieus (=*Neoseiulus*) *fallacis* (Garman)	$9.12
Phytoseilus persimilis	$7.15
“*Trichogramma* spp.” (adult female)	$0.216

Table 2. Summary of analysis of the efficacy and economics of augmentative biological control in published studies. Efficacy was assessed based on author evaluation of whether pest densities exceeded specified target levels. “No. Released” is the minimum release rate that was effective in cases where releases were effective. In cases that gave mixed or insufficient suppression, “No. Released” is the full range of release rates. Costs are based on Table 1. Production costs for the commodity are based on U.S. Crop Profile data; see text.

Pest Species Authority	Commodity/ Country	Natural Enemy Species	No. Released	Below Threshold?	Est. Costs of Release	Crop Prod. Costs	Ref. No
Aonidiella aurantii (Maskell)	citrus / U.S.	*Aphytis melinus*	50,000/ha	yes	$102/ha	$24,750-98,800/ha[a]	1
Aphis pomi	apples / U.S.	*Aphidoletes aphidimyza*	2,800/tree	no	$18,760/ha[b]	$14,330-16,300/ha[c]	2
Aphis pomi	apples / U.S.	*Chrysoperla rufilabris*	1,200/tree	no	$9,166/ha[b]	$14,330-16,300/ha[c]	2
Bemisia argentifolii Bellows and Perring	cotton / U.S.	*Delphastus catalinae*	3.5-5.5 /plant	no	estimate not possible	--[d]	3
Bemisia argentifolii	cotton / U.S.	*Eretmocerus eremicus*	not given	no	estimate not possible	--[d]	4
Cydia pomonella (L.)	apples/ Canada	*Trichogramma platneri* Nagarkatti	6,000-9,000/ha[e]	no	$1.30-1.94/ha	$14,330-16,300/ha[c]	5
Dysaphis spp.[f]	apples/ Switzerland	*Adalia bipunctata*	20-100 /tree	no	estimate not possible	--[d]	6
Erythroneura[g] *spp.*	grapes/ / U.S.	*Chrysoperla carnea*	22,200-37,000/ha	no	$253-421/ha	$3,000-17,000/ha[a]	7
Leptinotarsa decemlineata	tomato / U.S.	*P.maculiventris /E. puttleri*[h]	not given	no	estimate not possible	--[d]	8

Table 2. (continued). Summary of analysis of the efficacy and economics of augmentative biological control

Pest Species Authority	Commodity/ Country	Natural Enemy Species	No. Released	Below Threshold?	Est. Costs of Release	Crop Prod. Costs	Ref. No
Lygus hesperus	strawberries / U.S.	*Anaphes iole*	296,000/ha	no	$2,812/ha	$61,750-74,100/ha[a]	9
Lygus hesperus	strawberries / U.S.	*Anaphes iole*	175,000-545,000/ha	mixed[i]	$1,662-5,178/ha	$61,750-74,100/ha[a]	10
Ostrinia nubialis	corn / U.S.	*Trichogramma brassicae*	300,000/ha[e]	no[j]	$64.80 /ha	$860/ha[k]	11
Ostrinia nubialis	corn / U.S.	*Trichogramma ostriniae*	75,000/ha[e]	mixed[l]	$16.20 /ha	$860/ha[k]	12
Ostrinia nubialis	corn / U.S.	*Trichogramma nubilale*	511,000-3,311,000/ha[e]	mixed[m]	$110-715/ha	$860/ha[k]	13
Ostrinia nubialis	corn / U.S.	*Trichogramma nubilale*	22,000-30,000/ha[e]	mixed[n]	$4.75-6.48/ha	$860/ha[k]	14
Ostrinia nubialis	corn / U.S.	*Trichogramma nubilale*	67,000-2,113,000/ha[e]	no[j]	$14.47-456/ha	$860/ha[k]	15
various Pentatomids[o]	soybeans / Brazil	*Trissolcus basalis* (Wollaston)	15,000/ha	no	estimate not possible	--[d]	16
Phorodon humuli (Schrank)	hops / France	*Harmonia axyridis*	50/plant	mixed[i]	$22,000 /ha[p]	$8,650-10,370/ha[q]	17
Pieris rapae / Trichoplusia ni	cabbage / U.S.	*Trichogramma brassicae*	6,517,00-7,200,000/ha[r]	no	$70.38-778/ha	$1235 /ha[s]	18
Rhizopertha dominica	stored wheat / U.S.	*Choetospila elegans*	0.2 /kg	mixed[i]	estimate not possible	--[d]	19

Table 2. (continued). Summary of analysis of the efficacy and economics of augmentative biological control

Pest Species (Authority)	Commodity/ Country	Natural Enemy Species	No. Released	Below Threshold?	Est. Costs of Release	Crop Prod. Costs	Ref. No
Scirtothrips citri (Moulton)	citrus / U.S.	*Euseius tularensis* Congdon	500-2000 /tree	no	\$430-1,730/ha[t]	\$24,750-98,880/ha[a]	20
Tetranychus mcdanieli McGregor	apples / U.S.	*Metaseiulus* (=*Typhlodromus*) *occidentalis* (Nesbitt)	128 /tree	yes	estimate not possible	--[d]	21
Tetranychus urticae	hops / U.S.	*Amblysieus* (=*Neoseiulus*) *fallacis*	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*Metaseiulus occidentalis*	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*A. fallacis/ M. occidentalis*	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*T. pyri/ A. andersoni*[u]	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*Amblysieus fallacis*	20-120 /plant	no	\$401-\$2,408/ha[p]	\$8,650-10,370/ha[q]	23
Tetranychus urticae	hops / U.K.	*Phytoseilus persimilis*	10/plant	yes	\$157/ha[p]	\$8,650-10,370/ha[q]	24
Tetranychus urticae	corn / U.S.	*Phytoseilus persimilis*	5/plant	yes	\$3,710/ha[v]	\$860/ha[k]	25
Tetranychus urticae	corn / U.S.	*Amblysieus californicus*	5/plant	yes	\$2,500/ha[v]	\$860/ha[k]	25
Tetranychus urticae	strawberries / U.S.	*Phytoseilus persimilis*	12,150 /ha	no[w]	\$87/ha	\$61,750-74,100/ha[a]	26

Table 2. (continued). Summary of analysis of the efficacy and economics of augmentative biological control

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Notes: a. production costs for California; b. assuming 670 trees/ha (after Hagley 1989); c. production costs for WA; d. estimate or comparison not possible; e. adult females; f. *Dysaphis plantaginea* Passerini, *D. anthrisci* Börner, *D. chaerophylli* Börner, and *D. radicola* Mordvilko; g. *Erythroneura variabilis* Beamer and *E. elegantula* Osborn; h. combination of *Podisus maculiventris* and *Edovuum puttleri*; i. augmentation treatment below economic threshold in one year, above threshold in the next year; j. based on acceptable damage level of 5% (Wright *et al.* 2001); l. damage above acceptable levels in some fields, below in other fields; k. production costs for WI; m. augmentation less effective at higher release rates; n. augmentation treatment suppressed damage sufficiently for processed corn but not fresh market corn; o. *Nezara viridula* (L.), *Piezodorus guildiniii* (Westwood) and *Eustichus heros* (F.); p. assuming 2,200 hop plants per hectare (est. from crop profile for WA); q. average production costs for OR and WA; r. parasitized eggs; s. production costs for NC; t. based on costs in original paper, not current costs; u. combination of *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* Chant; v. assuming 70,000 corn plants per hectare, est. from crop profile for KS; w. augmentation was effective in combination with pesticide but not without.

References: 1. Moreno and Luck 1992; 2. Grasswitz and Burts 1996; 3. Heinz *et al.* 1999; 4. Minkenberg *et al.* 1995; 5. Cossentine and Jensen 2000; 6. Kehrli and Wyss 2001; 7. Daane *et al.* 1996; 8. Tipping *et al.* 1999; 9. Norton and Welter 1996; 10. Udayagiri *et al.* 2000; 11. Mertz *et al.* 1995; 12. Wright *et al.* 2002; 13. Prokrym *et al.* 1992; 14. Losey *et al.* 1995; 15. Andow *et al.* 1995; 16. Correa-Ferreira and Moscardi 1996; 17. Trouve *et al.* 1997; 18. Lundgren *et al.* 2002; 19. Flinn *et al.* 1996; 20. Grafton-Cardwell and Ouyang 1995; 21. Croft and McMurtry 1972; 22. Strong and Croft 1995; 23. Strong and Croft 1996; 24. Campbell and Lilley 1999; 25. Pickett and Gilstrap 1986; 26. Trumble and Morse 1993.

Table 3. Comparison of the efficacy of augmentation and "conventional" insecticide applications in studies that explicitly included both types of control measures in field experiments. Shown is the range of pest suppression in treatment plots relative to control plots, and whether suppression in either treatment acheived specified "target" or economic threshold pest densities.

		Augmentation			Conventional			
Pest Species	Commodity/ Country	Natural Enemy Species	% Pest Suppress.	Below Threshold?	Insect- icide	% Pest Suppress.	Below Threshold?	Ref. No
Anasa tristis	pumpkins / U.S.	*G. pennsyl- vanicum*[a]	43-85%[b]	--[c]	esfen- valerate	85-95%[b]	--[c]	1
Heliothine spp.[d]	cotton / U.S.	*Trichogramma exiguum*	15-33%[e]	--[c]	lambda- cyhalothrin	96-100%[e]	--[c]	2
Lygus hesperus	strawberries / U.S.	*Anaphes iole*	51-64%[f]	mixed[g]	various[h]	45-59%[f]	marg.[i]	3
Ostrinia nubialis	corn / U.S.	*Trichogramma nubilale*	3-72%[j]	no	various[k]	63-89%[j]	yes	4
various Pentatomids[l]	soybeans / Brazil	*Trissolcus basalis*	48%[m]	no[n]	endo- sulfan	35%[m]	no[n]	5
Pieris rapae/ *Trichoplusia ni*/	cabbage / U.S.	*Trichogramma brassicae*	3%[o]	no	methomyl	63%[o]	yes	6
Tetranychus urticae	strawberries / U.S.	*Phytoseilus persimilis*	15-25%[p]	no[q]	abamectin[r]	45-100%[p]	yes	7

Table 3. (continued).

Notes: a. *Gryon pennsylvanicum*; b. density of nymphs and adults, which varied by year and cultivar; c. “target” threshold not given; d. *Heliothis virescens* (F.) and *Heliocoverpa zea* (Boddie); e. density of late instar larvae, which varied by year; f. 2nd instar nymphs, which varied by year; g. augmentation below economic threshold in one year, above threshold in the next year; h. naled, malathion or fenpropathrin; i. near or slightly above a threshold of 0.1 nymphs/plant; j. number of larvae per 100 plants, which varied by year and cultivar; k. Capture, MVP-G or Pounce; l. *Nezara viridula*, *Piezodorus guildiniii* and *Eustichus heros*; m. number of stinkbugs per square meter; n. insufficient suppression in both treatments; o. damage rating; p. % plants infested with pest mites, which varied by year; q. augmentation was effective in combination with insecticide but not without; r. best of three pesticides.

References: 1. Olson *et al.* 1996; 2. Suh *et al.* 2000; 3. Udayagiri *et al.* 2000; 4. Andow *et al.* 1995; 5. Correa Ferreira and Moscardi 1996; 6. Lundgren *et al.* 2002; 7. Trumble and Morse 1993.

Table 4. Ecological limits on augmentative biological control in published studies. Assessment of ecological limits was based on authors' evaluations.

Pest Species	Commodity/ Country	Natural Enemy Species	Below Threshold?	Ecological Limit	Ref. No
Aphis fabae	sugarbeets / U.S.	*Chrysoperla spp.*[a]	--[b]	enemy quality/ predation	1
Aphis pomi	apples / U.S.	*Chrysoperla rufilabris*	no	enemy dispersal	2
Aphis pomi	apples / U.S.	*Aphidoletes aphidomyza*	no	pest-enemy incompatibility	2
Bemisia argentifolii	cotton / U.S.	*Delphastus catalinae*	no	predation	3
Bemisia argentifolii	cotton / U.S.	*Eretmocerus eremicus*	no	enemy dispersal/ pest immigration	4
Dysaphis spp.[c]	apples / Switzerland	*Adalia bipunctata*	no	cannibalism/ unfav. env.	5
Erythroneura spp.[d]	grapes / U.S.	*Chrysoperla carnea*	no	timing/release method	6
Heliothine spp.[e]	cotton / U.S.	*Trichogramma exiguum*	no	compensatory mortality	7
Leptinotarsa decemlineata	tomato / U.S.	*P.maculiventris /E. puttleri*[f]	no	pest immigration	8
Leptinotarsa decemlineata	potato / Canada	*Perillus bioculatus*	--[b]	compensatory mortality	9

Table 4. (continued). Summary of analysis of the ecological limits on augmentative biological control

Pest Species	Commodity/ Country	Natural Enemy Species	Below Threshold?	Ecological Limit	Ref. No
Lygus hesperus	strawberries / U.S.	*Anaphes iole*	no	enemy quality/ enemy dispersal	10
Lygus hesperus	strawberries / U.S.	*Anaphes iole*	mixed[g]	refuge for pest	11
Oligonychus punicae (Hirst)	avocados / U.S.	*Stethorus picipes*	--[b]	timing of release	12
Ostrinia nubialis	corn / U.S.	*Trichogramma nubilale*	no[h]	unfavor. environment	13
Ostrinia nubialis	corn / U.S.	*Trichogramma nubilale*	mixed[i]	compensatory mortality	14
Ostrinia nubialis	corn / Canada	*Trichogramma nubilale*	--[b]	predation	15
various Pentatomids[j]	soybeans / Brazil	*Trissolcus basalis*	no	refuge for pest	16
Pieris rapae / *Trichoplusia ni*	cabbage / U.S.	*Trichogramma brassicae*	no	pest-enemy incompatibility	17
Sitophilus zeamais Motschulsky	stored corn / U.S.	*Anisopteromalus calandrae*	--[b]	mutual interference	18

Table 4. (continued). Summary of analysis of the ecological limits on augmentative biological control

Pest Species	Commodity/ Country	Natural Enemy Species	Below Threshold?	Ecological Limit	Ref. No
Tetranychids[k]	peaches / U.S.	*Amblyseius* (= *Neoseiulus*) *fallacis*	--[l]	unfavor. env./ fungicides	19
Tetranychus urticae	Hops / U.S.	various[m]	no	refuge for pest	20
Tetranychus urticae	corn / U.S.	*P. persimilis/ A. californicus*[n]	yes	unfavor. environment	21

Notes: a. *Chrysoperla carnea* or *C. rufilabris*; b. no specified target or economic threshold density given; c. *Dysaphis plantaginea*, *D. anthrisci*, *D. chaerophylli*, and *D. radicola*; d. *Erythroneura variabilis* and *E. elegantula*; e. *Heliothis virescens* and *Heliocoverpa zea*; f. combination of *Podisus maculiventris* and *Edovuum puttleri*; g. below threshold in one year and above threshold in the next year; h. based on acceptable damage level of 5% (Wright *et al.* 2001); i. augmentation treatment suppressed damage sufficiently for processed corn but not fresh market corn; j. *Nezara viridula*, *Piezodorus guildiniii* and *Eustichus heros*; k. *Panonychus ulmi* and *Tetranychus urticae*; l. both control and release plots below threshold in year of release; m. *Neoseiulus fallacis*, *Metaseiulus occidentalis*, *Typhlodromus pyri*, *Amblyseius andersoni* or combination; n. *Phytoseilus persimilis* and *Amblyseius californicus*.

References: 1. Ehler *et al.* 1997; 2. Grasswitz and Burts 1996; 3. Heinz *et al.* 1999; 4. Minkenberg *et al.* 1994; 5. Kehrli and Wyss 2001; 6. Daane *et al.* 1996; 7. Suh *et al.* 2000; 8. Tipping *et al.* 1999; 9. Cloutier and Bauduin 1995; 10. Norton and Welter 1996; 11. Udayagiri *et al.* 2000; 12. McMurtry *et al.* 1969; 13. Andow *et al.* 1995; 14. Losey *et al.* 1995; 15. Yu and Byers 1994; 16. Correa Ferreira and Moscardi 1996; 17. Lundgren *et al.* 2002; 18. Wen and Brower 1994; 19. Lester *et al.* 1999; 20. Strong and Croft 1995; 21. Pickett and Gilstrap 1986.