

Pest Management

Winter Cover Crops Reduce Spring Emergence and Egg Deposition of Overwintering Navel Orangeworm (Lepidoptera: Pyralidae) in Almonds

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Abstract

Habitat diversification has been shown to positively influence a variety of ecosystem services to agriculture, including biological control of arthropod pests. The impact of increased biodiversity tends to be species specific though, and practices therefore need to be developed on a case-by-case basis for each cropping system. In perennial systems, numerous studies have demonstrated that cover crops can have positive impacts on soil quality and other ecosystem services, such as pollination and pest management. However, few studies have focused on the use of cover crops to enhance pest control in almond orchards, especially winter cover crops. The primary pest of almonds in North America is navel orangeworm, *Amyelois transitella* Walker, which overwinter as larva or pupa on remnant nuts, many of which remain on the orchard soil surface. In the spring, first flight adults subsequently use these remnant nuts as reproductive substrate. An experiment was conducted to evaluate the influence of two distinct winter cover crop mixtures on overwintering mortality and spring egg deposition of *A. transitella*. Remnant nuts placed into cover crop plots produced fewer adult *A. transitella* in the spring, suggesting increased overwintering mortality. Additionally, spring egg deposition was reduced on remnant nuts in the cover crops, possibly due to the ground covers interfering with host location and access. In this way, winter cover crops appear to contribute to the reduction of *A. transitella* populations in the orchard by altering abiotic and physical conditions, although studies to document specific mechanisms are still needed.

Key words: cover crop, habitat diversification, navel orangeworm, almond, orchard

California is the leading agricultural state in the United States, with approximately 24.3 million acres of crop and rangeland that generate an annual farm-gate value of \$50.1 billion (CDFA 2021). Within this agricultural matrix, tree nuts are planted on approximately 2.2 million acres, which represents 31% of the total 9.3 million acres of cultivated farmland in the state (USDA 2020) and their annual value of \$9.2 billion accounts for 18% of total agricultural value (CDFA 2021). Almond, *Prunus dulcis* (Mill.) D. A. Webb (Rosales: Rosaceae) is the most dominant tree nut, with orchards planted over 1.5 million acres that span the entirety of California's Central Valley and generate \$6.1 billion in annual sales (CDFA 2021). The primary insect pest of almonds is the navel orangeworm,

Amyelois transitella Walker (Lepidoptera: Pyralidae), which directly attacks tree nuts leading to reduced crop yield and quality (Wilson et al. 2020). Infestation of almonds by *A. transitella* is also associated with the presence of *Aspergillus flavus* Link (Eurotiales: Trichocomaceae) (Palumbo et al. 2014), which produces aflatoxin, a known human carcinogen that is heavily regulated in key domestic and export markets. As such, growers and processors have a low tolerance for *A. transitella* populations and typically strive for <2% crop infestation.

Amyelois transitella overwinter as larvae or pupae in remnant 'mummy' nuts that remain in the orchard after harvest (Wade 1961). As temperature and photoperiod increase in the spring,

adults emerge from the remnant nuts, typically in April. In the absence of new crop nuts, these first flight moths make use of these same remnant nuts as a reproductive substrate. The second flight typically occurs in late June, at which point new crop almonds are available. The ability of *A. transitella* to infest these new crop nuts is mediated by hull integrity. In almonds, hull split of new crop nuts typically occurs in early July, which approximately coincides with the emergence of this second flight *A. transitella* in the early summer. The development of new crop nuts represents an exponential increase in both the quantity and quality of host material for *A. transitella*, which can develop much more rapidly on the higher quality new crop nuts relative to the lower quality remnant nuts (Siegel and Kuenen 2011). This subsequently leads to a significant increase in population size during the third and fourth flights in August and September, respectively, which coincides with almond maturation and harvest (Wilson et al. 2020).

Biological control of *A. transitella* is fairly limited due to the ecology and behavioral traits of its key natural enemies. The primary parasitoids of *A. transitella* include *Copidosoma* (= *Pentalitomastix*) *plethoricum* (Caltagirone) (Hymenoptera: Encyrtidae) and *Goniozus legneri* Gordh (Hymenoptera: Bethyridae). The former is a polyembryonic egg-larval parasitoid imported from northern Mexico in the 1960s that was originally recovered from the carob moth, *Ectomyelois ceratoniae* (Zeller) (Hymenoptera: Pyralidae) (Caltagirone et al. 1964, Caltagirone 1966), while the latter is a larval parasitoid that was recovered from parasitized *A. transitella* collected in Uruguay in the 1970s (Legner et al. 1982, Gordh et al. 1983). While these parasitoids have established in California, their ability to adequately regulate *A. transitella* populations on their own has been quite limited. Since *C. plethoricum* is polyembryonic, it does not necessarily need a large quantity of host material to successfully increase population, and due to this does not typically parasitize a large number of *A. transitella*. Furthermore, in the absence of *A. transitella* eggs, local populations can rapidly decrease. The other parasitoid, *G. legneri*, exhibits a unique brood guarding behavior (Hardy and Blackburn 1991), which can limit host searching in the presence of low *A. transitella* densities, since they spend more time protecting their eggs rather than seeking out additional hosts (Sreenivas and Hardy 2015). While *G. legneri* could maybe have a significant impact when *A. transitella* populations are higher (Hardy et al. 2000, Wang et al. 2014), most growers have an extremely low tolerance for this pest due to concerns about aflatoxin, and as such will take additional action to control *A. transitella* before they ever reach such abundance.

Predators of *A. transitella* include the predaceous mites *Blattisocius keegani* (Fox) (Acari: Ascidae) and *B. tarsalis* Berlese (Oudemans), a predaceous beetle *Cymantodera ovipennis* LeConte (Coleoptera: Cleridae) and the small bugs *Phytocoris relativus* Knight (Hemiptera: Miridae) and *P. californicus* Knight (Wade 1961, Rice and Jones 1988, Thomas et al. 2011). All of these are known to attack the eggs of *A. transitella*, but none are considered effective enough for reliable control.

Given the limits of biological control and the extremely low tolerance for infestation, successful management of *A. transitella* in almonds requires the combined use of multiple cultural and chemical strategies. Given their reliance on remnant nuts to successfully overwinter, crop sanitation by removing and destroying remnant nuts during the winter period is fundamental to control *A. transitella* (Zalom et al. 1984). This is complemented by the use of mating disruption (Haviland et al. 2021), well-timed application of chemical controls and timely harvest (Haviland et al. 2022, Wilson et al. 2020).

More recently, almond growers have expressed interest in the use of winter cover crops to improve orchard sustainability (Wauters

et al. 2021). In agroecosystems, the use of cover crops has been shown to influence soil quality (Roberson et al. 1991, Rodrigues et al. 2013, Zheng et al. 2018), soil microbiome (Castellano-Hinojosa and Strauss 2020) and macrobiome (Kelly et al. 2021), pest control (Stephens et al. 1998, Aguilar-Fenollosa et al. 2011), water conservation (Cao et al. 2021, Novara et al. 2021), and weed suppression (Linares et al. 2008). In almonds in particular, ground covers have similarly been shown to increase soil quality (Ramos et al. 2010, Repullo-Ruiberriz de Torres et al. 2021), enhance arbuscular mycorrhizal fungi (Vasilikiotis et al. 2020), and support wild pollinators (Saunders et al. 2013, Alomar et al. 2018). While habitat diversification has generally been shown to enhance a variety of ecosystem services to agriculture, including suppression of some arthropod pests, specific practices must be uniquely tailored to the target crop and pest complex (Landis et al. 2000, Kremen and Miles 2012). For instance, while one study demonstrated that winter vegetative cover was associated with increased abundance of *Goniozus* spp. (Hymenoptera: Bethyridae) and *C. plethoricum*, key parasitoids of *A. transitella*, no changes in *A. transitella* infestation levels were observed (Eilers and Klein 2009).

The use of cover crops in integrated pest management has typically focused on their ability to either increase biological control by supporting natural enemies (Letourneau 1987, Landis et al. 2000) or lower pest densities by reducing host-plant colonization (Andow 1991, Segoli and Rosenheim 2012), acting as a trap crop (Tillman et al. 2015, Gordon et al. 2017) or inducing changes in host-plant quality that make the crop less suitable for pest development (Daane and Costello 1998, Wilson et al. 2017). With the exception of some natural enemies that are active in the winter, these processes are largely irrelevant to *A. transitella* overwintering in remnant nuts. Instead, it may be that the addition of a winter cover crop influences *A. transitella* populations by affecting overwintering mortality in remnant nuts and/or by limiting oviposition access of first flight adults in the spring.

The addition of winter ground covers could lead to changes in abiotic conditions or natural enemy populations that, either alone or in combination, increase mortality of overwintering *A. transitella* in remnant nuts on the ground (Siegel et al. 2008), as well as deter egg deposition by first flight adults onto ground remnant nuts in the spring. Here, an experiment was conducted to measure the impacts of two winter cover crop mixtures on overwintering mortality and spring egg deposition of *A. transitella*. While the cover crop treatments were selected for their ability to restore soil health and enhance pollinator populations (Wauters et al. 2021), this project aimed to characterize an additional potential ecosystem service in order to help provide a better estimate of the net benefits of this diversification practice.

Materials and Methods

Field Site and Experimental Treatments

The experimental cover crop mixtures included a 'pollinator mix' and a 'soil builder mix' (Kamprath Seed Co., Manteca, CA). The pollinator mix was composed of 15% bracco white mustard, *Sinapsis alba* L. (Brassicales: Brassicaceae), 20% daikon radish, *Raphanus sativus* (L.) Domin. (Brassicales: Brassicaceae), 15% nemfix yellow mustard, *Brassica juncea* (L.) Czern. (Brassicales: Brassicaceae), 15% common yellow mustard, *S. alba* L. (Brassicales: Brassicaceae), and 35% canola, *B. napus* L. (Brassicales: Brassicaceae), while the soil builder mix was composed of 10% bracco white mustard (*S. alba*), 10% daikon radish (*R. sativus*), 30% Merced ryegrass, *Lolium* spp. (Poales: Poaceae), 20% PK berseem clover, *Trifolium alexandrinum*

L. (Fabales: Fabaceae), and 30% hairy vetch, *Vicia villosa* Roth. (Fabales: Fabaceae). These cover crop treatments were compared to bare soil control plots, which over the winter period developed a small amount of resident weedy vegetation, which was consistently comprised of hare barley, *Hordeum murinum* L. ssp. leporinum (Link) Arcang. (Poales: Poaceae).

As mentioned, these specific cover crop blends were initially selected for their ability to enhance soil quality (i.e., soil builder mix) or support pollinators (i.e., pollinator mix), rather than control *A. transitella*. As such, the mixes contain somewhat different densities of seed and sowing rates, and were not necessarily intended to specifically modify conditions or optimally support natural enemies that might lead to an increase in *A. transitella* overwintering mortality. That said, both seed mixes would likely produce a healthy stand of ground cover that merits investigation for impacts on *A. transitella*, especially given the importance of measuring the full range of additional ecosystem services that may be generated by these ground covers.

This 2-year study was carried out over two successive winter/spring periods. In the fall of each year, replicated plots with the pollinator mix, soil builder mix, and bare soil control were established in a five-acre almond orchard at the University of California Westside Research and Extension Center (Five Points, CA). The almond trees were 11 y old and each tree row consisted of three alternating varieties, with Nonpareil, NePlus Ultra and Carmel each planted every third tree. Each experimental plot consisted of the two row middles contained within three tree rows (5 × 6.5 m tree × row spacing). A randomized complete block design was used with five replicates of each treatment in each year of the study. Each replicate block consisted of six row middles (i.e., three pairs of two adjacent middles), and each pair of two middles was randomly assigned to one of the three experimental ground cover treatments (Fig. 1). These plots were kept consistent in Year 1 and Year 2 of the study.

Prior to planting, all plots were mowed and tilled to remove any resident weedy vegetation. Cover crop species were directly sown using a no-till seed drill (T. G. Schmeiser Co., Fresno, CA) on 26 November and 26 October in Year 1 and Year 2, respectively. The pollinator mix was sown at 8.9 kg per ha (8 lbs per acre) and the

soil builder mix at 56 kg per ha (50 lbs per acre). To ensure a healthy experimental treatment, the stands of cover crop were provided with supplemental sprinkler irrigation the stands each month (Year 1, 16.8 cm precipitation and 14.6 cm irrigation total; Year 2, 15.0 precipitation and 15.2 cm irrigation total). In each year of the study, the cover crop stand was allowed to grow through the spring, with termination occurring in late May when all ground covers were mown and incorporated into the soil.

Cover Crop Biomass and Height

During each monthly visit to the experimental orchard, the biomass and vegetation stand height was measured in the cover crop and control plots. Biomass was measured using a 25 cm² quadrat. On each sample date, samples were collected from three randomly selected locations in the row middle of each plot. For each sample, all vegetation within the 25 cm² quadrat was removed, dried for 72 h at 50°C, and then weighed. Prior to removing the vegetation, the height of the stand was measured and recorded.

Inoculation of Plots with Remnant Mummy Nuts

Over the study period, the almond orchard was not treated for *A. transitella* and went unharvested. A reservoir of heavily infested remnant nuts was created each fall by shaking two rows of trees (outside of the experimental area) at the end of the season. These remnant nuts remained on bare soil until they were introduced into the various experimental plots each month. In Year 1, plots were inoculated with remnant nuts once (13 December) and in Year 2 plots were inoculated four different times (17 November, 15 December, 25 January, and February 15). On each inoculation date, cohorts of remnant nuts (50 nuts per cohort) were placed into three randomly selected areas within the row middles of each replicate plot (150 nuts per inoculation event per plot). Each cohort of 50 nuts was confined to a 50 cm² area in the row middle.

While the initial experimental design included a singular inoculation event in each year immediately after sowing the cover crops, it

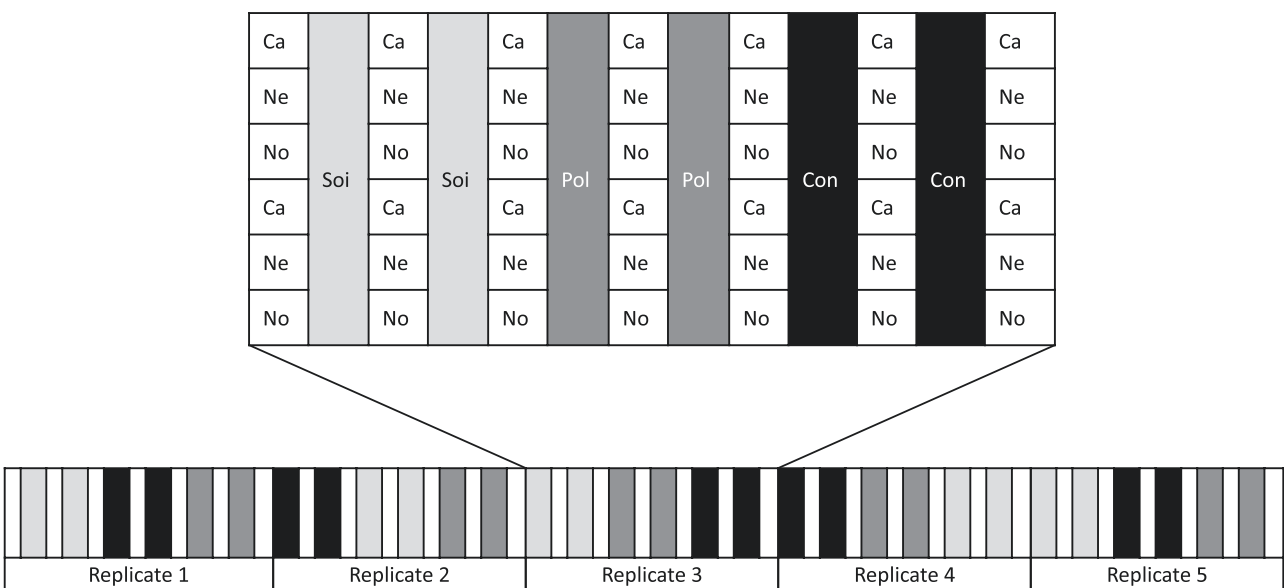


Fig. 1. Diagram of the experimental plot layout, which utilized a replicated complete block design. Each tree row consisted of 30 trees comprised of alternating varieties Nonpareil (No), Carmel (Ca), and NePlus Ultra (Ne). Experimental treatments included a Soil Builder (Soi) and Pollinator (Pol) cover crop mix compared with a resident weedy vegetation control plot (Con).

was decided that multiple inoculations in Year 2 could provide some insight on the temporal effects of ground covers on overwintering mortality. That is, to determine whether *A. transitella* overwintering mortality increased as remnant nuts spent longer amounts of time in the ground covers. As such, Year 2 included four total inoculation events rather than just one.

In early March of each year (Year 1, March 15; Year 2, March 1), the cohorts of remnant nuts were removed from the plots and *A. transitella* adults were reared out in the greenhouse over 12 wk using summer photoperiod (14:10 L:D) and climate conditions ($23.6 \pm 0.1^\circ\text{C}$, $54.7 \pm 0.3\%$ RH). Each cohort of nuts was placed into a ventilated plastic box ($30 \times 15 \times 10$ cm), which was checked daily for any emerged *A. transitella* adults. All emerged moths were counted, sexed, and removed from the emergence chamber.

Spring Egg Deposition

In the absence of new crop nuts, the first flight of adult *A. transitella* in the spring make use of remnant nuts as a reproductive substrate. In order to measure this spring egg deposition, egg traps loaded with an ovipositional bait were used to emulate remnant nuts. When the cohorts of remnant nuts were removed in March, egg traps were placed out into the plots. Each egg trap (Pherocon IV, Trece Inc., Adair, OK) contained 50 g of an almond/pistachio oviposition bait that consisted of ground up remnant nuts (Peterson Trap Co., Visalia, CA). All baits were replaced weekly. Eight traps were placed in each plot, with four at ground level within the row middles (approximately 15 cm above the soil surface) and four in the tree canopy (approximately 1.5 m height), since remnant nuts can be found in both locations in the spring. The total number of *A. transitella* eggs on each egg trap was recorded weekly over the spring period in each year (Year 1, 4 March–15 May; Year 2, 18 March–3 June).

Abiotic Conditions on the Orchard Floor

In Year 2 of the study, data were collected on temperature ($^\circ\text{C}$) and relative humidity (%) on the orchard ground in the row middles within the control and cover crop treatment plots. Data loggers (HOBO U12, Onset Co., Bourne, MA) were suspended beneath a small shelter (Pherocon 1C, Trece Inc., Adair, OK) approximately 15 cm above the soil surface. Data were recorded hourly between 17 November and 1 March in Year 2.

Statistical Analysis

All data were analyzed using linear mixed-effects models ('lmer' function in the 'lme4' package) with the R Statistical Program (<http://www.r-project.org/>). Individual fixed effects were evaluated with likelihood ratio tests using the 'drop1' function, which generated the χ^2 and *P*-values reported here. When a fixed effect with more than two levels was significant, means were separated using Tukey's post hoc test ('glht' function in the 'multcomp' package). Data for Year 1 and Year 2 were analyzed separately since the cohorts were exposed for different amounts of time in each year. For some variables that were measured repeatedly (i.e., cover crop biomass and height, temperature, and relative humidity), data from each month in each year were analyzed separately.

Models to evaluate monthly cover crop biomass and height included the fixed effect 'cover crop treatment' with 'replicate' as random effect. Monthly measurements of abiotic conditions (temperature, relative humidity) in Year 2 were evaluated with a model that included 'cover crop treatment' as a fixed effect and 'replicate' as a random effect. Adult *A. transitella* emergence from the cohorts of mummy almonds was analyzed using a model that included 'cover crop treatment' as a fixed effect and 'replicate' as a random effect. Spring egg deposition included 'cover crop treatment' as a fixed effect and 'replicate' nested within 'sample week' as a random effect. With the exception of temperature and relative humidity, all data were $\log(x+1)$ transformed prior to analysis since residuals did not meet the assumptions of normal distribution.

Results

Cover Crop Height and Biomass

In both years of the study, the two cover crop treatments had greater height (Table 1) and biomass (Table 2) than the control plots. While height was similar within the cover crop treatments, the soil builder mix tended to produce more biomass.

Emergence of Overwintering Adults

Spring emergence of adult *A. transitella* from the various cohorts of remnant nuts was reduced by the presence of one or both cover crop treatments in Year 1 (December–March, $\chi^2 = 8.8$, $n = 60$, $P = 0.01$) and in most months of Year 2 (November–March,

Table 1. Summary (mean \pm SEM) and analysis of monthly cover crop height (cm; $n = 45$)

Year	Month	Control	Pollinator	Soil builder	χ^2
Year 1	Nov.	—	—	—	—
	Dec.	0.4 \pm 0.4 A	5.7 \pm 0.3 B	10.4 \pm 1.2 C	83.8***
	Jan.	0.5 \pm 0.5 A	9.1 \pm 0.8 B	12.2 \pm 0.9 B	90.3***
	Feb.	6.3 \pm 1.3 A	19.1 \pm 3.0 B	19.5 \pm 1.1 B	20.5***
	Mar.	21.3 \pm 2.2 A	49.4 \pm 4.3 B	60.8 \pm 4.3 B	51.1***
	Apr.	—	—	—	—
Year 2	May	38.6 \pm 2.5 A	91.6 \pm 7.4 B	86.2 \pm 3.5 B	55.3***
	Nov.	0.0 \pm 0.0 A	7.5 \pm 0.5 B	7.2 \pm 0.8 B	131.1***
	Dec.	1.7 \pm 0.4 A	7.5 \pm 0.4 B	10.2 \pm 0.4 C	74.5***
	Jan.	3.0 \pm 1.2 A	20.1 \pm 1.2 B	26.7 \pm 0.8 B	72.7***
	Feb.	6.8 \pm 2.5 A	36.2 \pm 2.0 B	45.7 \pm 2.8 B	58.6***
	Mar.	25.4 \pm 3.4 A	89.7 \pm 4.4 B	78.7 \pm 3.4 B	80.5***
	Apr.	71.5 \pm 8.6 A	116.0 \pm 4.8 B	119.2 \pm 4.9 B	27.7***
May	84.3 \pm 11.5 A	134.5 \pm 8.1 B	135.0 \pm 4.0 B	17.9***	

Letters represent differences between the three treatments within a given month.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2. Summary (mean \pm SEM) and analysis of monthly cover crop biomass (kg/cm²; $n = 45$)

Year	Month	Control	Pollinator	Soil builder	χ^2
Year 1	Nov.	—	—	—	—
	Dec.	0.0 \pm 0.0 A	0.5 \pm 0.0 A	1.6 \pm 0.3 B	35.1***
	Jan.	0.1 \pm 0.0 A	4.1 \pm 0.8 B	4.0 \pm 0.4 B	32.2***
	Feb.	1.2 \pm 0.3 A	12.3 \pm 2.6 B	10.9 \pm 1.0 B	25.4***
	Mar.	4.2 \pm 0.9 A	16.2 \pm 2.5 B	30.2 \pm 3.3 C	40.6***
	Apr.	—	—	—	—
Year 2	May	7.8 \pm 1.4 A	22.6 \pm 3.1 B	80.0 \pm 6.6 C	74.2***
	Nov.	0.0 \pm 0.0 A	0.4 \pm 0.1 B	1.1 \pm 0.1 C	62.6***
	Dec.	0.3 \pm 0.1 A	1.3 \pm 0.2 B	5.6 \pm 0.5 C	71.0***
	Jan.	—	—	—	—
	Feb.	1.0 \pm 0.5 A	21.2 \pm 1.5 B	31.5 \pm 2.2 C	82.1***
	Mar.	9.0 \pm 1.6 A	61.9 \pm 6.5 B	60.8 \pm 4.6 B	52.5***
	Apr.	59.9 \pm 10.3 A	115.2 \pm 11.0 B	114.3 \pm 10.3 B	19.8***
	May	50.2 \pm 9.8 A	114.3 \pm 12.6 B	98.9 \pm 10.5 B	17.5***

Letters represent differences between the three treatments within a given month.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

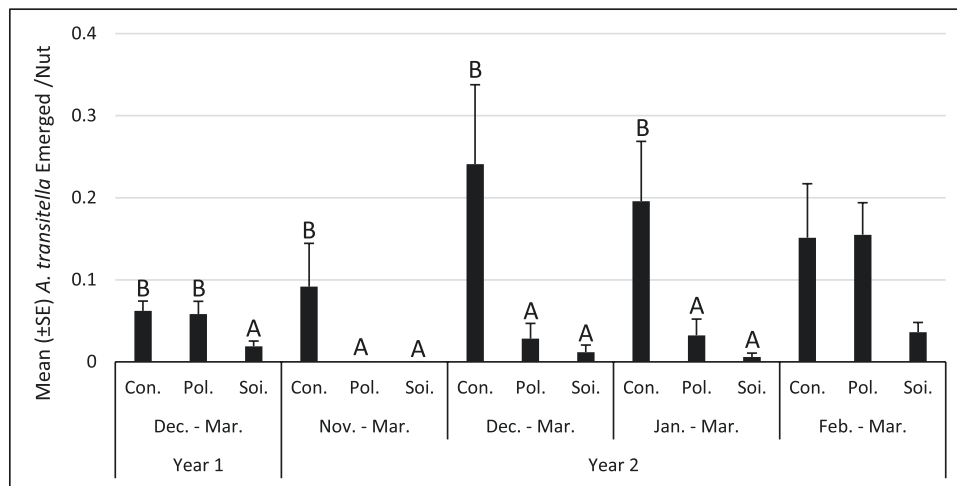


Fig. 2. Emergence of adult *A. transitella* from the different ground cover treatments. Data are grouped by the date range in each study year during which the different cohorts of nuts resided in the various ground cover plots. Within each time period, bars that do not share letters are statistically different.

$\chi^2 = 6.4$, $n = 44$, $P = 0.04$; December–March $\chi^2 = 12.0$, $n = 42$, $P < 0.01$; January–March $\chi^2 = 12.3$, $n = 44$, $P < 0.01$) with the exception of the February–March period ($\chi^2 = 5.7$, $n = 43$, $P = 0.06$; Fig. 2).

Spring Egg Deposition

Egg deposition was generally higher in the tree canopy than on the orchard ground (Year 1, $\chi^2 = 136.0$, $P < 0.001$; Year 2, $\chi^2 = 731.2$, $P < 0.001$; Fig. 3). While ground cover treatment led to reduced egg deposition on the orchard floor in Year 2 (Year 1 $\chi^2 = 2.1$, $P = 0.36$; Year 2, $\chi^2 = 11.5$, $P < 0.01$; Fig. 3A), there were no differences observed in the tree canopy in both years (Year 1 $\chi^2 = 4.8$, $P = 0.10$; Year 2, $\chi^2 = 0.1$, $P = 0.95$; Fig. 3B).

Abiotic Conditions in the Cover Crops

Over the winter period (November–February) in Year 2, plots with the soil builder mix tended to have lower mean temperature, while plots with either the soil builder or pollinator mix had higher relative humidity compared with the control plots (Table 3).

Discussion

The addition of winter ground covers in an almond orchard tended to result in reduced emergence of *A. transitella* adults in the spring from remnant nuts. Siegel et al. (2008) found no differences in mortality of overwintering *A. transitella* between remnant pistachios located in the undisturbed vegetated row middles and the bare soil berms; however, in that study, the row middles contained dense resident vegetation that was closely mowed rather than winter cover crops. While both winter cover crop treatments evaluated here produced greater biomass than the resident weedy vegetation in the control plots, the soil builder mix in particular produced the most biomass and contained a wider functional diversity of plant types, which may have been responsible for the lower temperature and higher relative humidity observed in these stands compared with the pollinator mix. These differences may have further exacerbated the effect of the soil builder mix on winter mortality of *A. transitella*, which was at times greater in plots with this specific cover crop blend.

In Year 2 of the study, data from the monthly inoculations suggest that mortality was positively correlated with total amount of time spent in the ground covers, with the most and least mortality

occurring in nuts that were placed into cover crop plots in November and February, respectively (Fig. 2). As such, it may be that prolonged exposure to the cooler and moister microclimate within the cover crop stands led to enhanced decomposition of remnant nuts, in effect a degradation of host quality for overwintering *A. transitella*. Alternatively, it may be that biotic factors such as the microbial community or natural enemy activity varied between the winter cover crops and the sparse resident weedy vegetation in control plots. Previous studies have documented distinct microbial (Bulgarelli et al. 2013) and natural enemy (Lawton 1983, Langellotto and Denno 2004) communities associated with different annual plants, which could then have impacts on mortality of arthropods. The addition of cover crops can potentially enhance natural enemy populations and activity through the provision of floral nectar, pollen, shelter, and/or alternate prey (Landis et al. 2000). Here, cover crops did not

reach the flowering stage prior to removal of the remnant nuts in the spring, although they could have benefitted key parasitoids of *A. transitella* in other ways, since they can be active during the winter period. Although changes in the microbial and natural enemy community were not measured in the current study, they may be important mechanisms for future experiments to evaluate.

When egg deposition was high, as seen in Year 2, both winter cover crop treatments seemed to equally impede egg deposition by first flight *A. transitella* adults in the spring. The lack of a significant effect in Year 1 is likely due to the lower overall abundance of egg deposition, which was nonsignificant but still numerically lower in the cover crop plots. In this experiment, the winter cover crops were allowed to persist through the spring flight period, and this led to reduced egg deposition on egg traps close to the orchard floor, which served as an analog for remnant nuts on the ground. While the attractancy of egg traps baited with an ovibait lure comprised of remnant pistachios and almonds has not been directly compared to actual remnant nuts in an orchard setting, egg deposition on the individual traps was likely higher than for individual remnant nuts due to the larger size of the egg trap itself, which may have made it more apparent to *A. transitella* females. Regardless, not all almond growers may benefit from this reduced egg deposition effect, since many terminate their winter cover crops in the late winter to minimize the risk of frost during almond bloom (Wauters et al. 2021). That said, some growers do leave full or partial stands of cover crops in place into the early spring flight period. Additional research to measure the effect of different spring mowing programs could be useful to better understand how much vegetation is necessary to impede egg deposition.

Regardless of cover crops, spring egg deposition by *A. transitella* tended to generally be higher in the tree canopy (Fig. 3B), where nuts are likely easier for *A. transitella* to locate and provide better abiotic conditions for development. While remnant nuts in the tree canopy may be of higher value to *A. transitella*, the overall abundance of remnant nuts tends to be greater on the orchard floor (Burks et al. 2008) and infestation rates can vary between these two locations (Burks et al. 2008, Siegel et al. 2008). As such, the importance of reduced spring egg deposition onto remnant nuts on the orchard floor remains unclear but could potentially lead to lower populations later in the season.

Despite their known benefits to soil quality enhancement, adoption of cover crops has been limited in specialty crops (LaRose and Myers 2019). This includes almonds, where the practice has sometimes been difficult to economically justify relative to the known agronomic benefits (DeVincents et al. 2020). As such, generating new knowledge of additional benefits of winter cover crops could improve

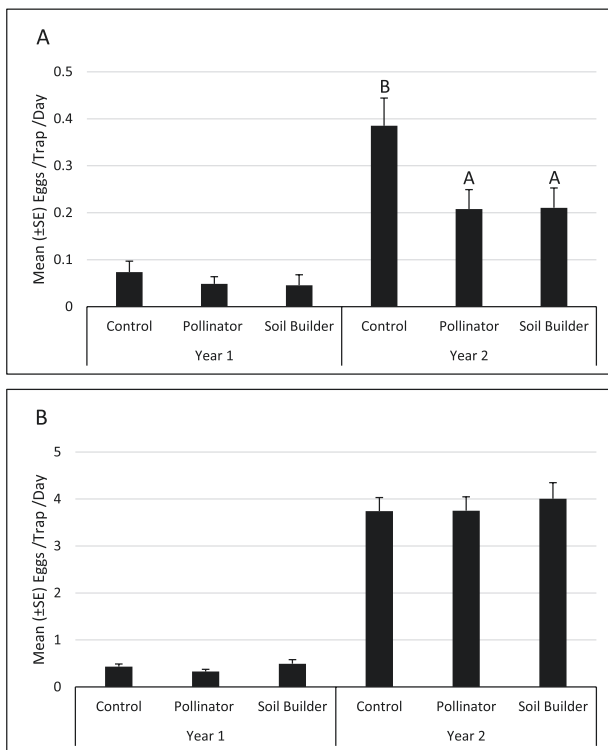


Fig. 3. Spring egg deposition in the different ground cover treatment plots by first flight *A. transitella* at ground level (3A) and in the tree canopy (3B). Bars that do not share letters are statistically different within years.

Table 3. Summary (mean ± SEM) and analysis of monthly temperature (Temp.) and relative humidity (RH) measurements from the orchard ground in Year 2

Variable	Month	Control	Pollinator	Soil builder	χ^2	<i>n</i>
Temp. (°C)	Nov.	9.6 ± 0.2	9.3 ± 0.2	9.2 ± 0.2	2.4	2,898
	Dec.	7.7 ± 0.1 AB	7.7 ± 0.1 B	7.4 ± 0.1 A	7.5*	6,696
	Jan.	8.8 ± 0.1 B	8.7 ± 0.1 B	8.1 ± 0.1 A	27.1***	6,667
	Feb.	10.8 ± 0.1 B	10.7 ± 0.2 B	9.8 ± 0.1 A	36.2***	5,371
RH (%)	Nov.	64.6 ± 0.6 A	68.8 ± 0.5 B	69.7 ± 0.5 B	51.8***	2,898
	Dec.	73.5 ± 0.4 A	76.3 ± 0.4 B	77.7 ± 0.4 C	63.0***	6,696
	Jan.	74.3 ± 0.4 A	77.7 ± 0.4 B	83.0 ± 0.3 C	282.0***	6,667
	Feb.	65.2 ± 0.5 A	66.8 ± 0.6 A	76.6 ± 0.3 B	410.6***	5,371

Letters represent differences between the three treatments within a given month.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

return on investment that may lead to increased adoption (Fiedler et al. 2008, Robertson et al. 2014). Furthermore, increased biodiversity can lead to simultaneous changes to multiple agroecosystem processes which can generate a range of both ecosystem services and dis-services to crop production (Zhang et al. 2007). For this reason, it is critical that researchers quantify the full range of impacts, both positive and negative, associated with the addition of on-farm habitat. Data presented here on the contribution of a winter cover crop to control of *A. transitella* provides evidence of another ecosystem service that can accrue from a winter cover crop in addition to soil quality and pollinator benefits. Future studies should focus on the specific mechanisms driving the increased mortality observed here, including changes to the microbial community, remnant nut decomposition rate, and natural enemy activity as a function of cover crops species and traits.

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