Biology and Management of Navel Orangeworm (Lepidoptera: Pyralidae) in California

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Abstract

Navel orangeworm, *Amyelois transitella* (Walker), is a primary pest of almonds, pistachios, and walnuts in California. These specialty tree nut crops are widely planted across the state and account for a significant share of total agricultural revenue, with 1.7 million combined acres generating a total farm-gate value of \$8.9 billion. Larvae of *A. transitella* cause direct damage to the nut, burrowing into the kernel and contaminating it with frass and webbing, while adults are able to introduce fungi during oviposition that produce aflatoxin, a known human carcinogen that is heavily regulated both domestically and in key foreign markets. As such, there is little tolerance for *A. transitella* infestation, and most operations aim for <2% crop damage from this pest. Currently, integrated management of *A. transitella* involves a combination of orchard sanitation, well-timed insecticide sprays, timely harvest, and, most recently, mating disruption. Additional novel tools, such as sterile insect technique, are currently being explored. This species has a strong dispersal capacity, and given the extensive, and many times contiguous, acreage of tree nuts in California, long-term management will require the development of an effective areawide management strategy. Tools, tactics, and conditions are in an ongoing state of change, and therefore pest management for this economically important species is a work in progress. Here, we discuss the biology, seasonal phenology, monitoring, and management of *A. transitella* across almonds, pistachios, and walnuts.

Key words: navel orangeworm, Amyelois transitella, almond, walnut, pistachio

Distribution and Pest Status in California

The navel orangeworm, Amyelois transitella (Walker) (Lepidoptera: Pyralidae) is endemic to much of the lower latitudes in the Americas, and is not known to occur outside the Americas (Heinrich 1956, Solis 2006). Despite its common name, A. transitella is not actually a serious citrus pest. The common name comes from when it first came to the attention of economic entomologists in the southwestern United States by attacking split citrus in Arizona (Glick 1922, Mote 1922, Lockwood 1931). While this discovery quickly led to strict quarantine restrictions on movement of citrus into California (Mote 1922), the moth eventually made its way into the state. Adults were first trapped in southern California in 1942 and were reported in the 1940s on walnuts, dates, and dried figs (Keifer 1947, Stickney et al. 1950). Subsequent accounts documented A. transitella as a pest of walnuts in southern California (Ortega 1950) and of walnuts and almonds in northern California (Michelbacher and Ross 1955, 1957, Michelbacher 1956). At the time, walnuts had historically been the dominant tree nut in California and almond acreage had only recently expanded to a similar scale of production (CDFA 1950, USDA 1964). These early reports of *A. transitella* noted the difficulty of chemical controls due to the occluded nature of infestation within the nut shell, and thus emphasized the importance of cultural practices like early harvest and winter sanitation (Michelbacher and Davis 1960), which are still very relevant today. With the development of the pistachio industry in the 1970s, *A. transitella* was soon noted as a pest of this new crop as well (Rice 1978). For all of these crops, *A. transitella* is primarily considered an in-field pest, but it can also be a concern in postharvest situations as well. Today, *A. transitella* is considered a key pest of almonds, pistachios, and walnuts across California (Grant et al. 2020, Haviland et al. 2020a, b).

Nature of Injury

California has a total of approximately 9.3 million acres of cropland, 17% of which is dedicated to tree nuts (CDFA 2019a). California

tree nuts are dominated by almonds (1,090,000 bearing acres valued at \$5.5 billion per year), followed by walnuts (350,000 bearing acres valued at \$0.8 billion per year) and pistachios (264,000 bearing acres valued at \$2.6 billion per year). These are all important export crops, with 65%, 66%, and 78% of total walnut, almond, and pistachio production sold outside of the United States (CDFA 2019b). Given this strong export component, regulatory demands in key foreign markets (e.g., European Union, Korea) can place an additional burden on crop production decisions.

Adult A. transitella oviposit onto nuts and the feeding of larvae results in rasped and tunneled fruits and nut kernels, as well as contamination of the nut with frass and webbing (Fig. 1; Michelbacher and Davis 1960, Wade 1961). This not only reduces crop yield and quality, but also increases the difficulty of sorting and processing the crop after harvest, especially pistachios since so many are marketed as in-shell, making it difficult to identify infested nuts. Furthermore, adults are able to introduce spores of Aspergillus flavus Link (Eurotiales: Trichocomaceae) (Palumbo et al. 2014), and infestation of the nut by A. transitella larvae provides a suitable environment for A. flavus colonization. Presence of this fungus can lead to the development of aflatoxin, a known human carcinogen that is heavily regulated domestically and even more so in key export markets. Due to this association between A. transitella infestation and aflatoxin, growers, processors and exporters alike have an incredibly low tolerance for A. transitella damage in all nut crops, typically aiming for <2% infestation.

Description of Life Stages

Eggs

Eggs of *A. transitella* are small (0.5–1.0 mm), dorsoventrally flattened, reticulated, and oval in shape (Fig. 2). They are typically oviposited directly onto overripe, damaged, cracked, or mummified fruits/nuts. Though on occasion they may be found on adjacent leaves or stems. At oviposition eggs are creamy white but develop a reddish-orange hue as they mature (Wade 1961).

Larvae and Pupae

Larvae of *A. transitella* pass through five to six instars and will reach a length of 13–19 mm before pupation. Larvae enter the nut shortly after eclosion and will remain inside until they reach the adult stage. Typically found in association with their own frass and webbing, multiple larvae may be found in a single nut. Newly eclosed larvae are reddish-orange but become pinkish-orange or cream colored after the first molt (Fig. 3a). Body coloration is influenced by diet, for

instance, those fed on walnuts develop a pinkish orange hue, whereas those reared on almonds remain creamy white (Wade 1961). Larval head capsules are a solid dark red-brown, may exhibit some mottling, and do not change in color or pattern between instars (Fig. 3b). Larvae can be differentiated from other nut-boring lepidopterans in California by the presence of an enlarged crescent shaped sclerite on each side of the mesothorax (Fig. 3c). This crescent sclerite is typically found toward the dorsum, and may be completely closed in some specimens (Wade 1961). Amyelois transitella pupates either within the infested nut or outside of the shell. Pupae are dark brown in coloration, 7.25-12 mm long, and are typically encased within silk cocoons (Fig. 1; Wade 1961). The carob moth Ectomyelois ceratoniae (Zeller) (Lepidoptera: Pyralidae) is harder to distinguish from A. transitella, and in other parts of California and other Mediterranean climates E. ceratoniae has a niche and host range similar to A. transitella in California. In this case, the two species can be differentiated based on pupal characteristics—E. ceratoniae has a raised dark ridge toward the head and two short spines on each abdominal segment, whereas A. transitella does not (Haviland et al. 2020c).

Adults

Adult *A. transitella* are small and gray, measuring approximately 9–10 mm from head to the tip of the abdomen with a wingspan of 19–20 mm. The forewings of the species are predominantly silvergray, but are marked with irregular black patterning. These patterns show considerable variation between individual moths, but often take the form of irregular wavy black transverse lines and distal dots (Fig. 4). The hindwings of the species are a uniform white to dusky gray with some darkening one the wing edge and veins (Heinrich 1956, Wade 1961). There are lighter and darker forms, and adult size can vary considerably.

Biology

Reproduction

Adult *A. transitella* are nocturnal. Adults eclose from pupae in the early evening, followed by mating and oviposition within the next one to two nights (Andrews et al. 1980, Sanderson et al. 1989b). Females emit a pheromone to attract male moths (Coffelt et al. 1979a, Coffelt et al. 1979b, Leal et al. 2005, Kuenen et al. 2010, Kanno et al. 2010, Wang et al. 2010), who then proceed through a series of courtship behaviors before mating (Phelan and Baker 1990, Girling and Cardé 2006, Parra-Pedrazzoli and Leal 2006), after which they remain in copula for at least 2 hr (Wade 1961). Mating typically takes place in the final hours of the night just before dawn





Fig. 1. Feeding of *A. transitella* larvae results in rasped and tunneled kernels (a) and contaminates the nut with frass and webbing (a, b). Larvae pupate either within the infested nut or between the hull and shell of the nut, and are dark brown in coloration (a, b). Photos by Jack Kelly Clark, courtesy University of California Statewide IPM Program.

(Parra-Pedrazzoli and Leal 2006), although sexual activity starts earlier in the night when temperatures drop below 17°C (63°F) (Landolt and Curtis 1982). More detailed examinations determined that cooler nights led to earlier female calling and mating, as well as decreased the likelihood of successful mating on the first night after eclosion (Burks et al. 2011a). Females can be multiply mated (Wade 1961), although in the wild this is not very common and tends to correlate with increased moth abundance (Landolt and Curtis 1991). Gravid females can produce approximately 100–200 eggs each (Wade 1961, Burks 2014) and complete most oviposition on the first few nights after mating (Burks 2014), although this period too can be extended under cooler nighttime conditions (Andrews et al. 1980, Burks et al. 2011a).

Development

The lower developmental threshold of *A. transitella* is 12.8°C (55°F) (Engle and Barnes 1983a) and the upper threshold is 34.4°C (94°F) (Seaman and Barnes 1984). Eggs and pupae require 56 and 113 degree days (DD) to complete development, respectively (Engle and Barnes 1983a, Sanderson et al. 1989b). Development from egg to adult requires 424–427 DD on new crop almonds, but this rate varies with host quality. For instance, 623 DD are required for similar development on lower quality remnant 'mummy' almonds (Sanderson



Fig. 2. Eggs of *A. transitella* develop a reddish-orange hue as they mature. Photo by Jack Kelly Clark, courtesy University of California Statewide IPM Program.

et al. 1989b). Subsequent work has provided additional evidence of varied developmental rates across multiple crops as well as between varieties within a single crop, new and old nuts within a single variety, and multiple strains of *A. transitella* (Kuenen and Siegel 2010, Siegel et al. 2010). Under California conditions, *A. transitella* can have three to four generations per year, with more generations in the warmer southern San Joaquin Valley and fewer generations in the cooler northern Sacramento Valley.

Relationship With Aspergillus flavus

One of the primary drivers of low tolerance for A. transitella damage is its relationship with A. flavus (Palumbo et al. 2014), which when it infects tree nuts can lead to the production of aflatoxin, a known human carcinogen that is heavily regulated (Robens and Cardwell 2003). These moths are scavengers with a wide host range, and as such appear to have a strong ability to detoxify various mycotoxins, including aflatoxin (Lee and Campbell 2000, Niu et al. 2009). Furthermore, laboratory assays have demonstrated that larvae of A. transitella not only appear to prefer nuts that contain A. flavus, but seem to develop more rapidly when this compound is present (Ampt et al. 2016) and adult females appear to preferentially orient to and oviposit on substrates with A. flavus (Bush et al. 2017). This relationship is potentially supported by earlier field observations that A. transitella in some cases prefer to oviposit onto mummy nuts, which are more likely to contain A. flavus, but this may be difficult to disentangle from a preference to oviposit on previously infested nuts as well (Curtis and Barnes 1977, Andrews and Barnes 1982b). Regardless, it appears that there may be some types of mutualism between A. transitella and A. flavus. New crop nuts in the field that have not been infested by A. transitella are not known to contain A. flavus to any great degree, as such it seems that the fungus is brought to the nut via the moth and infestation provides the conditions for it to proliferate.

Movement and Dispersal

Movement of *A. transitella* between orchard blocks was first demonstrated by Meals and Caltagirone (1971), who found increased egg deposition on sentinel nuts in an uninfested orchard adjacent to a heavily infested orchard. Subsequent work documented upwind movement of adults as far as 375 m (Andrews et al. 1980) and increased damage in pistachio orchards adjacent to infested almond

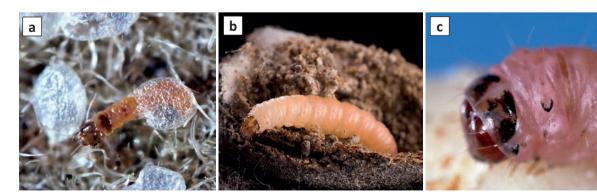


Fig. 3. Newly eclosed larvae are reddish-orange (a) but become pinkish-orange or cream colored after the first molt, depending on diet (b, c). Larvae can be differentiated from other nut-boring lepidopterans in California by the presence of an enlarged crescent shaped sclerite on each side of the mesothorax (c). Photos 3a and 3c by Jack Kelly Clark, courtesy University of California Statewide IPM Program, and 3b by Peggy Greb, courtesy of USDA Agricultural Research Service.

blocks (Andrews and Barnes 1982a). While originally noted as a weak disperser (Wade 1961) recent flight mill assays have shown that *A. transitella* can potentially disperse 7–15 km per night (Sappington and Burks 2014), and that mated females tend to fly further than unmated (Rovnyak et al. 2018). The range of flights observed in these flight mill studies were similar to the distances over which almonds were at significantly higher risk for *A. transitella* damage based on proximity to pistachio orchards (Higbee and Siegel 2009). Fatty acid profiles of adult moths have also been used to more definitively document movement between orchards (Bayes et al. 2014).

Seasonal Ecology

In California, A. transitella overwinter as larvae inside either unharvested tree nuts that have been left in the orchard (i.e., 'mummies' or 'mummy nuts'), or other vulnerable agricultural commodities such as apples, figs, and oranges (Michelbacher and Davis 1960, Wade 1961, Caltagirone et al. 1968, Rice 1978). There is evidence of a genetically determined and neurohormonally controlled dormancy at the end of the last larval instar occurring to a variable degree in some populations (Gal 1978, Legner 1983a, Tzanakakis et al. 1988), similar to dormancy in the same stage in stored product pest moths of the subfamily Phycitinae (Bell 1994). In physiological terms, this is diapause (Danks 1987) but, as noted from early on, all larval instars are found overwintering and the dormancy is of low intensity and duration, in contrast to the more intense and prolonged dormancy of orchard pests such as the codling moth Cydia pomonella (L.) (Lepidoptera: Tortricidae) (Neven 2012) or the walnut husk

fly *Rhagoletis completa* Cresson (Diptera: Tephritidae) (Emery and Mills 2019).

In the spring, larvae complete development, pupate and then adults begin to emerge from overwintering hosts as early as March (Wade 1961). Emergence is protracted and can extend through early June due to the wide range of larval instars that overwinter on a variety of variable quality hosts (Kuenen and Siegel 2010). This initial emergence is referred to as the 'overwintering' or 'first' flight (Fig. 5).

First flight adults primarily oviposit onto mummy nuts, since new crop nuts are not yet susceptible to attack. Susceptibility of tree nuts to *A. transitella* is contingent on integrity of the hull, since neonate *A. transitella* larvae are unable to bore through this protective layer. In almonds, hull split typically occurs in mid-June or early July, whereas pistachio and walnuts become vulnerable in approximately mid-August and mid-September, respectively. Exceptions to this include early splits in pistachio (Siegel and Kuenen 2011) and walnuts infested with *C. pomonella*, which facilitates entrance of *A. transitella* into the nut since *C. pomonella* is able to bore through intact walnut hulls (Michelbacher and Ross 1957).

Second flight adults typically begin to appear in early July (or late June, in the warmer southern San Joaquin Valley), at which point they can make use of new crop almonds following hull split (Curtis and Barnes 1977, Kuenen and Barnes 1981). From this point on, access to higher quality hosts and increased temperatures can rapidly accelerate population development (Fig. 5).

Broadly, third and fourth flight moths begin to appear in mid-August (or late July, in the southern San Joaquin Valley) and early

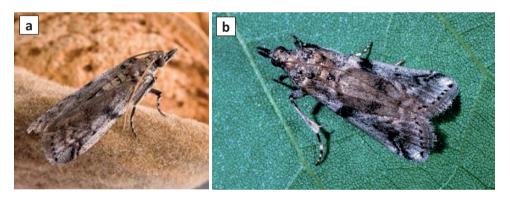


Fig. 4. Adult A. transitella are small and gray, the forewings are predominantly silver gray and marked with irregular black patterning. Photo 4a by Peggy Greb, courtesy of USDA Agricultural Research Service, and photo 4b by Jack Kelly Clark, courtesy University of California Statewide IPM Program.

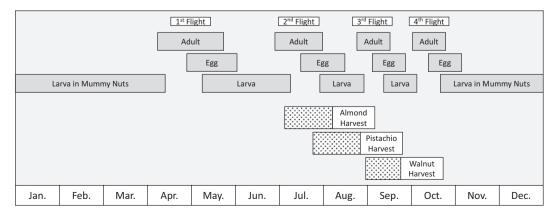


Fig. 5. General seasonal phenology of *A. transitella* and tree nut crops in California. The patterned boxes for each tree nut crop indicate the period of new crop nut vulnerability, followed by harvest.

September, respectively, although by this point flights may appear overlapping and discrete generations become less clear (Sanderson et al. 1989a, Kuenen and Siegel 2010). In the fall, declining nighttime temperatures lead to cessation of adult activity by November and larvae on remnant nuts form the basis of the overwintering population (Fig. 5).

Monitoring

Egg Traps

Egg traps can be used to monitor activity of gravid females (Rice 1976, Rice et al. 1976, Rice and Sadler 1977). These traps consist of a 9 x 4 cm black cylinder with a small mesh screen and rough edges (Sanderson and Barnes 1990) filled with an attractant, typically 50 g of almond meal with 10% crude almond oil by weight (Kuenen et al. 2008), although other baits have been evaluated (Curtis and Clarks 1979, Rice et al. 1979, van Steenwyk and Barnett 1985, Higbee and Burks 2011). Gravid female moths are attracted to the lure and oviposit on the surface of the cylinder, which can be used as an indicator of egg deposition timing in orchards. More recently, studies to refine the use of egg traps indicated that the proportion of egg traps with eggs, rather than total egg abundance, was a more reliable indicator of A. transitella phenology and abundance (Burks et al. 2011b, Higbee and Burks 2011). Egg traps are commercially available to growers and widely used.

Pheromone Traps

Synthetic pheromone lures can be used to monitor adult male activity in orchards (Higbee et al. 2014), and work best when used in a wing trap (Burks and Higbee 2015). These are commonly used by many tree nut growers to monitor *A. transitella* activity. Further efforts have been made to optimize use of these traps by determining the trap saturation point (Kuenen and Siegel 2016), ideal trap placement (Girling et al. 2013), effects of pheromone lure storage (Burks and Wilk 2017), and even how to more conveniently fold wing traps (Kuenen et al. 2005). Based on these efforts, the current recommendation is that growers place traps in the tree canopy at about 1 m height, replace liners weekly or biweekly, and avoid long-term storage of pheromone lures. In some parts of the state, widespread use of mating disruption for *A. transitella* reduces the usefulness or reliability of pheromone traps for *A. transitella*.

Bait Traps for Females

Wing traps can also be used in conjunction with a bait bag that contains almond and pistachio mummies to attract gravid females (Nay et al. 2012). In this way, activity of gravid females can be monitored similar to an egg trap. This is a relatively new tool that is now commercially available, and some growers are starting to find utility in this style of monitoring.

Phenyl Proprionate

Broad screening of novel compounds identified phenyl proprionate (PPO) as a potential attractant for *A. transitella* (Price et al. 1967), which was subsequently used for sampling adults in a single study in an almond orchard (Crane and Summers 1971). Interest in PPO lures was renewed as a potential substitute for pheromone lures, which were rendered ineffective in orchards under mating disruption (Burks et al. 2009). When combined with a pheromone lure, PPO can be used to effectively monitor adult *A. transitella* in orchards under mating disruption (Burks et al. 2016, 2020a, Burks 2017).

Commercially marketed PPO lures have recently become available and growers are starting to use them in orchards with mating disruption.

Host Plant Volatiles

Tree nut volatiles were initially explored for their utility as a synthetic lure in egg traps (Buttery et al. 1980), as an attracticide to increase efficacy of pesticides (Phelan and Baker 1987) or as a deterrent to reduce egg deposition (van Steenwyk and Barnett 1987, Cloonan et al. 2013). More recent work has focused on the use of these compounds as lures for monitoring, potentially under mating disruption conditions, but no commercial products have been generated yet (Beck et al. 2009, 2011, Roitman et al. 2011, Beck et al. 2012a,b, Beck et al. 2014a, b, c).

Combined Use of Traps for Estimating Phenological Events

No single trap type or lure provides perfect information to growers on the abundance or activity of *A. transitella* in their orchard, much less the ability to reliably predict crop infestation levels. As such, it is recommended that growers utilize a combination of approaches to track the timing and phenological development of *A. transitella* (Rosenheim et al. 2017b). In almonds and pistachios, this usually consists of egg traps with an almond meal lure (one trap per 10 acres or minimum four traps per orchard) paired with wing traps with a pheromone lure (one trap per 50 acres or minimum two traps per orchard) set out in mid-March (almonds) or early April (pistachios) (Haviland et al. 2020a, b). The bait bags mentioned above might be used in place of egg traps, and in areas where mating disruption potentially disrupts pheromone traps, PPO, or other alternative lures might be used in place of pheromone lures alone.

Traps should be hung in the canopy at about 1 m height and monitored once or twice per week in order to establish an accurate biofix. The biofix for A. transitella is based on egg trap data, and should be set on the first of two consecutive dates over which total egg numbers and number of traps with eggs consistently increase (Haviland et al. 2020a, b). The biofix effectively establishes the date on which A. transitella egg deposition is taking place in a given orchard. This date, when combined with knowledge on the minimum temperature thresholds for A. transitella development can be used to calculate DD accumulation in order to estimate the development of A. transitella life stages and timing of subsequent flights and egg deposition. When using these models, growers should continue trapping efforts in the orchard throughout the season to track A. transitella phenology and compare these observations with estimates based on the DD model. It is important to note that egg traps become less accurate later in the season as new crop nuts begin to appear, which effectively dilute the attractancy of egg traps to gravid

It should also be noted that the potential for crop damage by *A. transitella* involves interplay between the phenology of this pest and that of its host crops (see subsequent discussion of control with insecticides). Since walnuts often become susceptible to *A. transitella* later than other crops and often severe damage is associated with proximity to other nut crops, current research on monitoring in walnuts emphasizes informing husk-split treatments in late summer and early fall (Grant et al. 2020). In current practice, monitoring is used primarily to inform timing of insecticide treatments. It might be used to refine assessment for the need for insecticidal treatment, but often decisions about such need is based primarily on orchard factors such as recent history of damage and proximity to sources of abundance.

Further development of models based on combined trapping data is potentially valuable because it offers the potential for a confident assessment that insecticide can be forgone based on monitoring data (Rosenheim et al. 2017b). Development of automated remote monitoring (Lima et al. 2020) offers further promise of providing data with sufficient quality, intensity, and timeliness to support such an approach.

Cultural Control

Sanitation

The removal and destruction of remnant 'mummy' nuts in and around the orchard (i.e., winter sanitation) is the foundation of A. transitella management. Mummy nuts are those remnant nuts that remain in the orchard following harvest and can usually be found both in the tree canopy and on the orchard floor. Early reports note the importance of winter sanitation (Michelbacher and Davis 1960, Caltagirone et al. 1968). Not only does this remove overwintering larvae from the orchard, but it eliminates reproductive substrate for first flight adults in the spring, which in some studies seem to prefer to oviposit onto mummy nuts (Andrews and Barnes 1982b, Legner 1983b). Subsequently, field studies have demonstrated a negative correlation between sanitation levels and crop infestation rates in the following season (Engle and Barnes 1983b, Zalom et al. 1984). Removal of mummies from the tree canopy is critical, as survival of overwintering larvae tends to be higher in these remnant nuts over those on the orchard floor (Siegel et al. 2008).

Sanitation consists of mechanically shaking or hand poling trees after harvest to bring mummy nuts in the tree canopy or tree crotches to the ground, at which point they can be cleaned from the berms and aggregated into windrows in the row middles using a sweeper or blower. At this point, the mummies can then be mechanically destroyed with a flail mower or by tilling them into the soil (Haviland et al. 2020b). Sanitation should be completed by early March, and while thresholds have not been specifically developed for all tree nuts, in almonds it is recommended that growers have no more than two mummies per tree (Haviland et al. 2020b), although a recent study suggested 0.2 mummies per tree (i.e., one mummy across five trees) would be more appropriate (Higbee and Siegel 2009).

Sanitation efforts can be impeded by a variety of factors, such as weather conditions and the availability and costs of equipment and labor. Furthermore, due to their small size and the hard shells of pistachios, it is more difficult to remove them and destroy the larvae within their shells compared to almonds and walnuts. Increased abundance of *A. transitella* in pistachios has been attributed to poor sanitation (Burks et al. 2008), and in one study, almond infestation levels were positively correlated with orchard proximity to a neighboring pistachio orchard within 3 km (Higbee and Siegel 2009).

Early/Timely Harvest

Like winter sanitation, the importance of early harvest to reduce *A. transitella* infest has long been a key to the management of this pest (Michelbacher and Davis 1960), and has been demonstrated in walnuts (Olson et al. 1975) and almonds (Connell et al. 1989). Early or timely harvest can reduce crop damage by minimizing the amount of time new crop nuts are exposed to *A. transitella* populations late in the season. While pistachios and walnuts are both simultaneously harvested and removed from the orchard, almonds are typically shaken from trees and then allowed to dry for 4–10 d on the orchard floor before removal. Here, it is important to note that

A. transitella produce fewer viable eggs on grounded nuts at the time of Nonpareil harvest so that early harvest to reduce A. transitella damage in almonds can simply mean getting nuts out of the tree in a timely manner (Curtis et al. 1984). That said, increased time on the orchard floor can also result in increased crop damage from ants (Haviland et al. 2020b) and A. transitella will still oviposit onto them, albeit with less success.

Both almonds and pistachios are subject to multiple harvests, which can lead to differences in A. transitella infestation levels between the first and last harvest events. Almond orchards have multiple varieties (main crop and pollinizers) that have different phenological timings to maximize crop pollination during bloom. This phenological staggering also translates to differences in the timing of hull split, which can subsequently result in differences in A. transitella infestation depending on how well (or not) hull-split aligns with the flight of adult moths. At harvest, this means that certain varieties may be more or less infested with A. transitella than others. If the first variety to be harvested (usually 'Nonpareil') is highly infested, the mass removal of infested nuts may benefit the remaining varieties by reducing the intensity of subsequent A. transitella flights. In contrast, pistachio orchards comprised a single variety but still subject to multiple harvests due to incomplete removal of the nuts from trees during the first harvest. In many cases, a grower may return a second time to harvest the remaining nuts 2-3 wk after the initial harvest, which can result in higher A. transitella infestation due to the prolonged exposure of these new crop nuts in the field.

Variety Selection

While hull integrity determines crop vulnerability to A. transitella, in almonds, shell seal can also play an important role (Crane and Summers 1971). Although hard-shell varieties (e.g., 'Padre', 'Mission', and 'Carmel') are not immune to infestation, they do tend to be more resistant than soft-shell varieties (e.g., 'Nonpareil, 'Aldrich', and 'Wood Colony') (Soderstrom 1977). Granted, development of A. transitella can still take place on the almond hull alone, and in this way hard-shell varieties may still experience infestation but with little actual damage to the kernel itself. A more recent study also highlights that almond varieties with a later hull-split date and harder shell seal tend to have lower A. transitella infestation levels (Hamby et al. 2011), although these data implicitly suggest that weaker shell seal may be associated with earlier maturity in almonds. This trade-off in susceptibility is seen in the common practice of planting together 'Butte' and 'Padre', two relatively hard-shell varieties that sometimes mature at similar dates and that can be marketed co-mingled; thus, a lower price compared to 'Nonpareil' is offset by lower risk from A. transitella and some simplification of other management practices. While the use of hard-shell varieties may help reduce A. transitella infestation, this benefit may be offset or even negated by the increased force required to crack out the kernels, which can lead to unacceptable levels of mechanical damage to the nut meat.

Another recent study demonstrates that differences between levels of *A. transitella* infest between common almond varieties are small in comparison to variability by location and year within these varieties (Rosenheim et al. 2017a). This latter observation suggests that the relationship between population phenology of *A. transitella* and the phenology of almond maturation can also influence which varieties receive greater damage in a given year. Walnuts mature later than almonds (Fig. 5), and older earlier-maturing walnut varieties ('Ashley', 'Vina', and 'Serr') are generally more susceptible to lepidopteran pests (i.e., *C. pomonella*, as well as *A. transitella*) than the

more recently developed and later-maturing variety 'Chandler' that is now more widespread. The differences in susceptibility may be due in part to differences in shell seal, but the earlier varieties are also at peak susceptibility during the high abundance of the fourth flight, while 'Chandler' susceptibility is typically in October after peak A. transitella abundance has passed and cooling night temperatures reduce activity. Pistachio production has historically been dominated by a single variety ('Kerman'), although some new varieties are starting to see increased acreage (i.e., 'Golden Hills'). Degradation of hull integrity can, however, shift dramatically between years and the mechanisms for this are poorly understood.

Biological Control

Parasitoids

Early descriptions of A. transitella in California identified native natural enemies that included the larval parasitoids Parasierola (=Perisierola) breviceps (Krombein) (Hymenoptera: Bethylidae), Mesostenus gracilis Cresson (Hymenoptera: Ichneumonidae), and Microbracon hebetor (Say) (Hymenoptera: Braconidae) as well as a predaceous mite Blattisocius tarsalis (=tineivorus) Berlese (Oudemans) (Acari: Ascidae) and beetle Cymatodera ovipennis LeConte (Coleoptera: Cleridae) that feed on the eggs (Wade 1961). None of these were deemed suitable for adequate control, and so foreign exploration efforts were undertaken to identify better natural enemies.

Foreign exploration efforts were made in the early 1960s in Israel and Mexico (Caltagirone et al. 1964, Caltagirone 1966), which led to the introduction of *Copidosoma* (=*Pentalitomastix*) *plethorica* (Caltagirone) (Hymenoptera: Braconidae), a polyembryonic egglarval parasitoid that was originally recovered from another Pyralid, the carob moth *E. ceratoniae*.

Additional efforts were made in the 1970s to explore Texas, Uruguay, and Argentina, which led to the introduction of *Goniozus emigratus* (Rohwer) (Hymenoptera: Bethlyidae) and *G. legneri* Gordh, respectively (Gordh and Hawkins 1981, Gordh 1982, Legner et al. 1982, Legner and Silveira-Guido 1983). Biology and life tables of *G. legneri* were constructed on *A. transitella* and the pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae) (Gordh et al. 1983).

All three of these parasitoids have established in California, and likely contribute to some control of *A. transitella*, but do not alone reduce populations enough to keep infestation levels at <2% (Legner and Warkentin 1988, Legner and Gordh 1992). Some commercial insectaries do offer *Goniozus legneri* for purchase and release as part of a natural enemy augmentation program, but the efficacy of this practice has not been fully evaluated. Furthermore, *Goniozus* spp. exhibit brood-guarding behavior (Hardy and Blackburn 1991), which in situations of low host availability leads to restricted host searching, as the parasitoids spend more time guarding their eggs than seeking out additional hosts to attack (Sreenivas and Hardy 2015). In this way, *Goniozus legneri* may only be able to have a significant impact when *A. transitella* populations are high (Hardy et al. 2000, Wang et al. 2014), which most growers will not tolerate.

Predators

Predation of A. transitella eggs by Blattisocius keegani Fox (Acari: Ascidae) has been evaluated as well. While no commercial program exists, authors note the potential for an augmentative control program, especially given that these mites appear to be phoretic on adult moths (Thomas et al. 2011). In pistachios, Phytocoris relativus Knight (Hempitera: Miridae) and P. californicus Knight are both

known to attack *A. transitella* eggs as well (Rice and Jones 1988), although they can also attack pistachio nuts and so growers may be apt to control these small bugs. (Haviland et al. 2020a).

Nematodes

The use of entomopathogenic nematodes against *A. transitella* larvae was first evaluated as a spray solution that contained *Steinernema feltiae* (Filipjev, 1934) (=*Neoaplectana carpocapsae*) (Rhabditida: Steinernematidae) applied to in-season almonds (Lindegren et al. 1978, 1987). Later efforts focused on application of *Steinernema carpocapsae* (Weiser, 1955) (Rhabditida: Steinernematidae) onto overwintering mummy almonds (Agudelo-Silva et al. 1995) and pistachios (Siegel et al. 2004, 2006). Results of these efforts were unsatisfactory and so no commercial programs for control of *A. transitella* have been developed around the use of entomopathogenic nematodes.

Virus

A novel RNA stunt virus was isolated from *A. transitella* (Kellen and Hoffmann 1981) and subsequent lab assays demonstrated its ability to reduce development and increase mortality virus (Hillman et al. 1982, Hoffmann and Kellen 1982, Kellen and Hoffmann 1982, 1983a,b, Hoffmann and Hillman 1984), but no programs have ever been developed at scale. Later, a multiple nucleocapsid polyhedrosis virus isolated from celery looper, *Anagrapha falcifera* (Kirby) (Lepidoptera: Noctuidae) was shown to increase mortality of *A. transitella* as well (Cardenas et al. 1997), but again no further development of this technology took place.

Mating Disruption

Identification of Compounds and Product Development

The primary component of *A. transitella* pheromone is (Z,Z)11,13-hexadecadienal (Coffelt et al. 1979a, Leal et al. 2005, Kuenen et al. 2010, Wang et al. 2010) which is released by females to attract males (Coffelt et al. 1979b). Early on, this compound was shown to reduce mating of sentinel females under field conditions (Landolt et al. 1981), and additional work over the years demonstrated its ability to shut down traps baited with pheromone (Curtis et al. 1985, Shorey and Gerber 1996, Burks and Brandl 2004) and reduce crop damage (Higbee and Burks 2008, Haviland 2017).

Additional components of the *A. transitella* pheromone have been identified (Leal et al. 2005, Kuenen et al. 2010, Wang et al. 2010). Under field conditions, inclusion of these secondary compounds markedly increases capture of male moths in sticky traps (Kuenen et al. 2010). Data to date demonstrate that addition of secondary components increases effectiveness of suppression of mating (Higbee et al. 2017). Increased suppression of *A. transitella* damage has, however, not yet been demonstrated (Higbee et al. 2017). Differences in regulation between straight-chain lepidopteran pheromones like the primary component in the *A. transitella* sex pheromone and tricosapentaene, a longer hydrocarbon necessary for source contact in *A. transitella*, make development of a mating disruption product using the fuller blend more economically challenging (Higbee et al. 2017).

Multiple mating disruption products for *A. transitella* that utilize (Z,Z)11,13-hexadecadienal as the primary active ingredient became commercially available in the 2010s, and have been adopted on an estimated 500,000 acres of almonds, pistachios, and walnuts. Today, studies continue to refine the use of these products in order to reduce costs (Burks and Thomson 2019, Burks et al. 2020).

Implementation and Monitoring of Mating Disruption

Commercially available mating disruption products for A. transitella include aerosol dispensers (Pacific Biological Control, Vancouver, British Columbia; Semios, Quebec, Ontario; Suterra, Bend, OR), polymeric emitters (Trece Inc., Adair, OK), and flowable formulations (Suterra, Bend, OR). Depending on the manufacturer, aerosol dispensers are hung from the tree canopy in the spring at a rate of one to two dispensers per acre and can be programmed to emit a specified amount of synthetic pheromone at a given frequency. In some cases, the dispensers may be programmed to increase or decrease emissions at certain times of the season. Polymeric emitters are also hung from the tree canopy in the spring, but at a higher rate of approximately 20 emitters per acre. In this system, the polymeric tags will passively emit synthetic pheromone over the course of the season. Flowable pheromone has only recently been introduced. In this system growers are able to spray the microencapsulated synthetic pheromone onto the crop, and it will then persist in the orchard for some period of time (e.g., 4 wk). In this way, growers could potentially make targeted applications of pheromone to disrupt A. transitella mating during key phenological periods (i.e., adult flight periods) while avoiding the added labor of hanging pheromone dispensers/emitters in the tree canopy. While recent studies have documented the efficacy of aerosol dispenser and polymeric emitter mating disruption systems in almonds (Haviland 2017), data on the recently introduced flowable product are more limited, and no independent product comparisons have taken place in pistachios or walnuts.

Studies on the use of mating disruption in almonds (Higbee and Burks 2008, Haviland 2017) emphasize that the efficacy of this strategy is contingent on orchard block size and configuration, as well as background pest population levels. As mentioned, A. transitella has a high dispersal capacity (Sappington and Burks 2014) and large populations can spillover into neighboring orchards (Meals and Caltagirone 1971). As such, use of mating disruption in orchards less than 40 acres is not recommended, since in smaller blocks, the effects of reduced mating on local populations may be negated due to colonization by gravid females from neighboring orchards. Similarly, even in blocks larger than 40 acres, the perimeter to area ratio is critical. That is, a large orchard block that is long and narrow may see less benefit from mating disruption than a similar sized block that is more square and uniform. In the former, the increased amount of orchard edge relative to interior space allows more opportunities for gravid females to colonize the block. Also, mating disruption is generally considered not to work as well under conditions of very high population abundance. That said, mating disruption for A. transitella uses a noncompetitive or hybrid mechanism and is less density dependent compared to species using a competitive mechanism, such as C. pomonella (Burks and Thomson 2020). In general, mating disruption for A. transitella seems to provide the greatest return under conditions of moderate abundance, and benefits of mating disruption and insecticide treatments appear to be additive or possibly synergistic.

One drawback of mating disruption is that it does reduce the utility of pheromone lures to track male *A. transitella* populations (Burks et al. 2009). Still, it is important for growers to use these lures in order to verify that mating is indeed being disrupted. At the same time, the combined use of pheromone and PPO lures has been shown to effectively attract *A. transitella* males under mating disruption conditions (Burks et al. 2016, 2020, Burks 2017), and as such could be a useful tool to track local populations in these situations. Egg traps are not affected by mating disruption, and therefore should still be used to determine biofix and track *A. transitella* phenology, as previously described.

Control with Insecticides

Chemical control of *A. transitella* has always been impeded by limited coverage due to the protected nature of larvae residing inside of nuts. Early chemical controls included carbaryl and organophosphates (Summers and Price 1964) as well as pyrethroids (Sanderson and Barnes 1986, van Steenwyk et al. 1987). Use of these compounds has been linked to secondary pest outbreaks, primarily web-spinning spider mites *Tetranychus* spp. (Acari: Tetranychidae) (Bentley et al. 1987), but more recent work has shown that newer compounds like methoxyfenozide and chlorantraniliprole can be effectively used without inducing mite outbreaks (Haviland et al. 2011).

As such, the dominant chemistries currently recommended for control of *A. transitella* include pyrethroids (bifenthrin, permethrin, esfenvalerate, fenpropathrin, and lambda-cyhalothrin) along with a diacylhydrazine (methoxyfenozide), diamide (chlorantraniliprole), and spinosyn (spinetoram) (Holtz et al. 2008a, b, Haviland and Rill 2010, Haviland et al. 2011, Siegel et al. 2019a, b, Grant et al. 2020, Haviland et al. 2020a, b). Evaluation of Pesticide Use Reporting (PUR) data from the California Department of Pesticide Regulation over the past 11 years (2008–2018) shows decreased use of organophosphates in almonds, pistachios, and walnuts (Figs 6–8), whereas the use of pyrethroids and diacylhydrazines has notably increased in almonds and pistachios (Figs 6 and 7) and slightly increased in walnuts (Fig. 8). The use of diamides has also been slowly increasing, while the use of spinosyns and *Bacillus thuringiensis* remains minimal across all three crops (Figs 6–8).

Generally, insecticide applications should target periods of new crop vulnerability (Fig. 5) that is typically associated with hull split, hull slip, and husk split in almonds, pistachio, and walnuts, respectively-although there are some exceptions, such as early split pistachios. In almonds, growers are typically advised to make 1-2 insecticide applications around hull split in early July, as new crop nuts become vulnerable to ovipositing moths (Higbee and Siegel 2012). In pistachios, hull integrity is typically maintained later into the year, with hull slip occurring closer to third flight activity in late July or early August (Fig. 5). That said, early split pistachios can become infested earlier in the season, and a high proportion of early split nuts may merit control measures prior to the third flight. Finally, while walnut hull integrity is typically high throughout most of the season, damage to the hull from C. pomonella (which can bore through green walnut hulls) can facilitate access of A. transitella into new crop walnuts. Some growers may utilize an early season spray application as well, which in some instances has been shown to provide effective control in almonds (Hamby et al. 2015).

Trials with *Bacillus thuringiensis* have demonstrated some ability to control this pest (Summers and Price 1964, Pinnock and Milstead 1972, Connell et al. 1998), but this approach has not been widely adopted (Figs 6–8) outside of certified organic production, which currently accounts for <2% of total tree nut acreage (CDFA 2019a).

Recently, resistance of *A. transitella* to bifenthrin (a pyrethroid) was documented (Demkovich 2015b), and further investigation indicates that this may be due to a unique ability to detoxify certain compounds in the environment (Niu et al. 2011). Leveraging this knowledge, recent work has focused on the use of insecticide additives (e.g., piperonyl butoxide) to neutralize *A. transitella* ability to detoxify compounds in order to maintain or even enhance the efficacy of bifenthrin, as well as other active ingredients (Niu et al. 2012, Demkovich et al. 2015a, Bagchi et al. 2016). The commercial viability of this approach remains unclear.

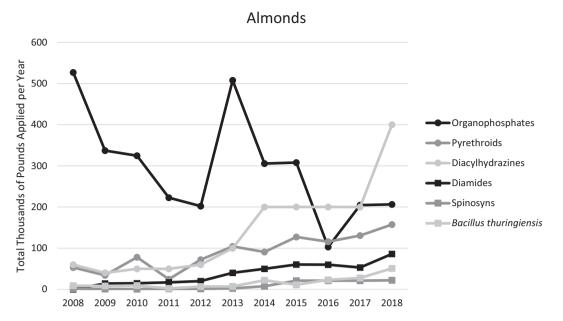


Fig. 6. Total annual use of key chemical subgroups for *A. transitella* control in California almond production. Trends indicate that use of organophosphates has declined over the past 10 yr while use of pyrethroids, diacylhydrazines, and diamides has steadily increased. While spinosyns and *Bacillus thuringiensis* can be used for control of *A. transitella*, overall use is relatively minimal.

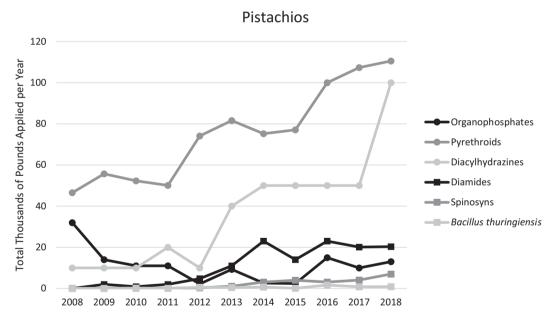


Fig. 7. Total annual use of key chemical subgroups for *A. transitella* control in California pistachio production. Overall use of organophosphates was initially low and has continued to decline over time while use of pyrethroids, diacylhydrazines, and diamides has steadily risen. While spinosyns and *Bacillus thuringiensis* can be used for control of *A. transitella*, overall use is relatively minimal.

Sterile Insect Technique

The potential use of sterile insect technique (SIT) for *A. transitella* was demonstrated in a series of experiments that documented radiotolerance of different life stages to gamma irradiation and conducted laboratory assays to evaluate wild:sterile overflooding ratios (Husseiny and Madsen 1964). Work in this area did not progress until recently, when the California pistachio and almond industries initiated a project to evaluate use of SIT for *A. transitella* control (Wilson and Burks 2019). At about the same time, others

have started to explore the use of x-ray irradiation for sterilization of *A. transitella* (Light et al. 2015, Haff et al. 2020). Research in this area is on-going and could potentially provide a new nonchemical tool for management of *A. transitella*.

Postharvest Control

Studies on postharvest control of *A. transitella* have demonstrated the utility of modified atmosphere (Storey and Soderstrom 1977,

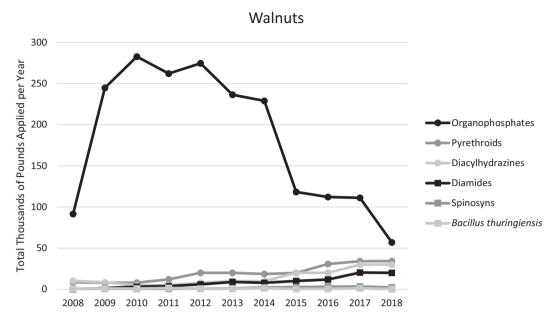


Fig. 8. Total annual use of key chemical subgroups for *A. transitella* control in California walnut production. Organophosphate use has dramatically declined in the past 5 yr, while use of pyrethroids, diacylhydrazines, and diamides has slightly risen. While spinosyns and *Bacillus thuringiensis* can be used for control of *A. transitella*, overall use is relatively minimal.

Soderstrom and Brandl 1982, Brandl et al. 1983, Zettler et al. 2002), low temperatures (Tebbets et al. 1978, Johnson 2007), high temperatures (Wang et al. 2013), low humidity (Johnson et al. 1996), methyl-bromide (Hartsell et al. 1986), and irradiation (Johnson and Vail 1988, 1989). Drawing this all together, efforts that combine low temperature, altered atmosphere, and application of granulovirus have produced good control as well (Johnson et al. 1998, Johnson et al. 2002). That said, prior to its regulation methyl bromide was the preferred postharvest treatment for almonds and pistachios (Aegerter and Folwell 2001). Currently, postharvest treatment primarily relies on phosphine (Hartsell et al. 1991, Hartsell et al. 2005). Sulfuryl fluoride can also be used (Leesch and Zettler 2000), sometimes in combination with propylene oxide as an antimicrobial. In California, many certified organic facilities utilize cold treatments.

Conclusion

In almonds, pistachios, and walnuts, winter sanitation is the foundation of *A. transitella* management, paired with close monitoring of crop and insect phenology in order to deliver well-timed insecticide sprays as new crop nuts become vulnerable to ovipositing moths, followed by timely harvest to minimize new crop exposure to late season *A. transitella* populations (Grant et al. 2020, Haviland et al. 2020a, b). Relatively new technologies like mating disruption are proving to be an effective means of further lowering crop damage (Higbee and Burks 2008, Haviland 2017, Higbee et al. 2017), and could readily be combined with existing control strategies. While significant adoption of mating disruption has occurred, in some cases, costs and/or minimum acreage requirements present a barrier to growers. Development of sterile insect technique for *A. transitella* is still quite nascent, and so the full utility of this strategy remains unclear.

The combined 1,704,000 acres of tree crops concentrated in California's Central Valley present a significant concentration of resources for the development of *A. transitella* populations. Paired

with a strong capacity for movement and dispersal, the need for area-wide management of this pest is clear. The challenge therein lies in determining how to best arrange economic, regulatory and social forces in a way that best promotes this type of coordinated, regional pest management strategy (Brewer and Goodell 2012). This is particularly relevant for certain tools like mating disruption, where minimum acreage barriers could be overcome by multiple small growers simultaneously adopting this technology across a contiguous region, or crop sanitation where the utility of this approach is also likely to be improved through increased adoption at the regional level. While insecticide controls have improved over the years, regulatory pressure paired with the development of resistance to bifenthrin may lead to the loss of this active ingredient. In this way, strategies using reduced insecticides will become increasingly important for future control of A. transitella. Rapid changes in pest management technologies, such as increased mating disruption, new attractants and technologies, and the potential for area-wide pest management provide both challenges and opportunities.

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