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Biology and Management of the Spotted Lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae), in the United States

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Abstract

Spotted lanternfly, *Lycorma delicatula* (White), invaded the eastern United States in 2014 and has since caused economic and ecological disruption. In particular, spotted lanternfly has shown itself to be a significant pest of vineyards and ornamental plants and is likely to continue to spread to new areas. Factors that have contributed to its success as an invader include its wide host range and high mobility, which allow it to infest a wide range of habitats, including agricultural, urban, suburban, and managed and natural forested areas. Management is dependent on chemical use, although no single currently available control measure alone will be sufficient.

1. INTRODUCTION

Spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae), is a phloem-feeding planthopper that is highly polyphagous (5). Its voracious feeding across a wide range of hosts, including grapes and other specialty crops, as well as plants and trees in nonagricultural habitats including urban, suburban, and managed and natural forested areas, makes it a serious invasive threat. Local spotted lanternfly populations can be extremely high (thousands of insects on a single tree), and in urban and suburban areas, it is a nuisance pest to residents. Because it feeds on plant sap, its sugary excrement or honeydew accumulates on understory plants and any other substrate beneath the insects. Sooty mold grows upon honeydew and blackens these substrates; honeydew also attracts other insects, often including stinging Hymenoptera. Spotted lanternfly is a known introduced pest in South Korea, where damage to apple, grape, and stone fruit has been reported (23, 57). It was first detected in the United States in Berks County, Pennsylvania on September 22, 2014. Spotted lanternfly is suspected to have entered the United States in the egg mass stage, with an unknown number of eggs laid on a shipment of landscaping stone (59). Since 2014, the range of spotted lanternfly within the United States has expanded considerably, with established populations in Pennsylvania and all contiguous states, as well as Virginia and Indiana (**Figure 1**). Spotted lanternfly has been detected but not established in eight additional states (53). The history of the initial spread in the United States and initial responses to this pest have been summarized elsewhere (66). In this review, we examine the potential for spread, hosts important to the success of this species, recent research on its biology and management, and future directions of research that are needed to further mitigate the impacts of spotted lanternfly. A review of the biology and management of spotted lanternfly, focusing on literature associated with this insect in South

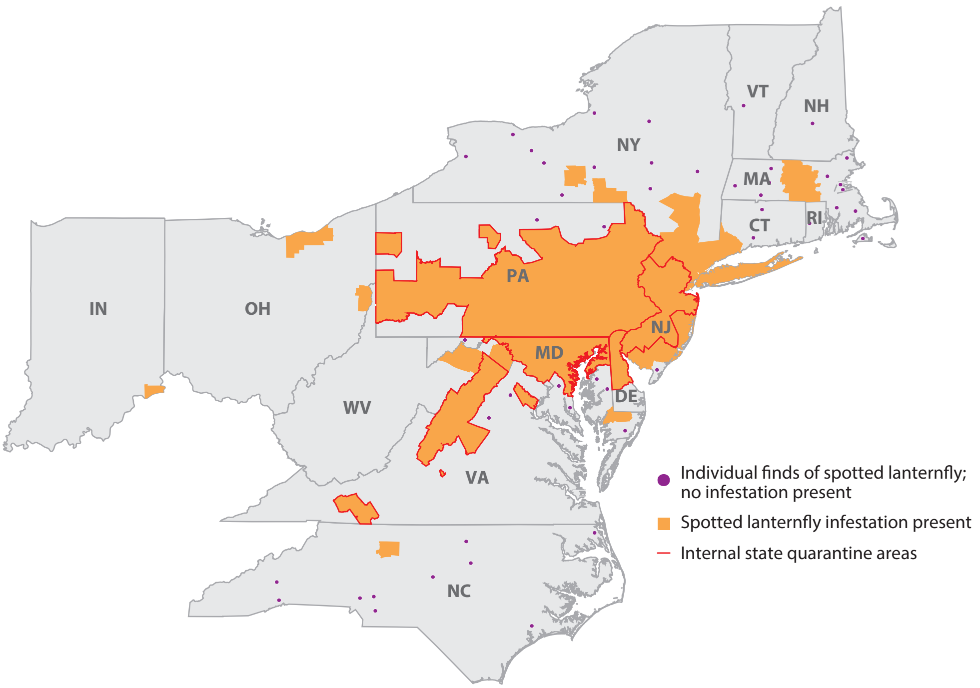

Figure 1

Map of spotted lanternfly known distribution. Adapted from NYS IPM, Cornell University, updated July 14, 2022.

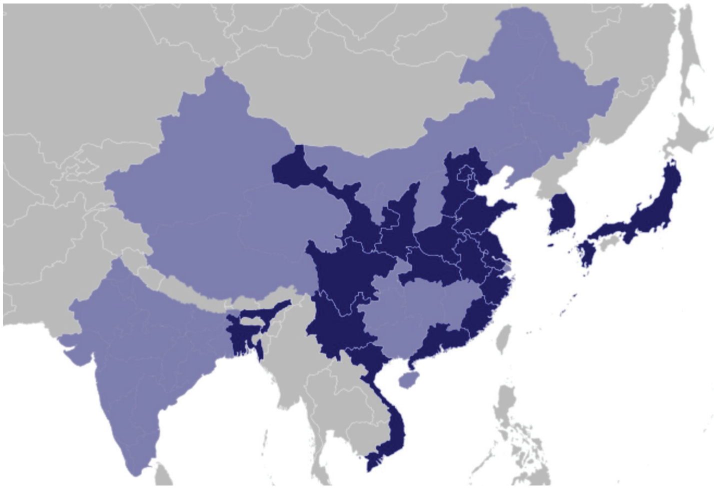

Figure 2

Native range of spotted lanternfly. Areas of dark purple denote accurate records, according to Bourgoin (7; adapted with permission from **https://flow.hemiptera-databases.org**). Light purple areas denote available records with less geographic specificity (e.g., presence in country).

Korea, has been published (42). The current review summarizes work conducted since that review was written on spotted lanternfly and its biology and management, primarily in the United States.

2. NATURAL HISTORY

Spotted lanternfly is native to China, Japan, and Vietnam (7, 18). A map based on available records (7) (**Figure 2**) showing disjunct distribution in some areas suggests that the extent of its native range is not fully known. Furthermore, some records are highly doubtful, such as its presence in India (20). Two subspecies are currently recognized (7), although no research has been conducted to validate or delimit these putative taxa.

In South Korea and in the United States, spotted lanternfly is univoltine. In Pennsylvania, spotted lanternfly overwinters in the egg stage, and nymphs hatch in May–June. They develop through three additional instars and emerge as adults in late July (**Figure 3**). First through third instars feed on the tender plant tissue of a broad range of host plant species. Fourth instars feed through woody plant tissues, as do adults. The host range appears to narrow somewhat in later life stages, with the preferred hosts being *Ailanthus altissima* (tree of heaven), grapes (*Vitis* spp.), black walnut (*Juglans nigra*), silver maple (*Acer saccharinum*), red maple (*Acer rubrum*), and willow (*Salix* spp.). Mating has been observed in September–November, and egg laying has been observed in this same time interval. Also at this time, spotted lanternfly seem to feed voraciously, as evidenced by observations of high levels of honeydew deposition and significant weight gain (J.M. Urban, unpublished data). Adults are noticeably more active at this time and fly in high numbers onto trees or plants in previously uninfested or less infested areas (65). Eggs are laid on a wide variety of substrates, including on natural and manufactured items, which contributes to the potential for spread on cargo or conveyances (40).

3. DEVELOPMENT AND HOST PLANT PHENOLOGY

3.1. Degree Day Requirements

Multiple studies have focused on degree day (DD) requirements of various spotted lanternfly life stages. Smyers et al. (61) collected spotted lanternfly eggs in Pennsylvania in 2018 and 2019 and

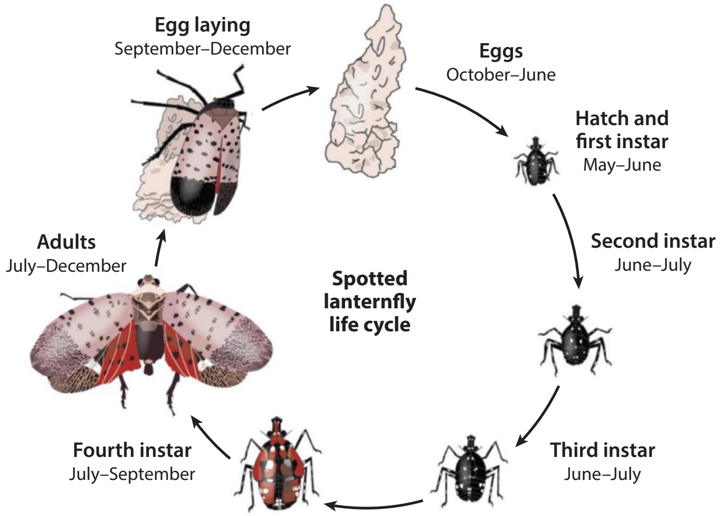

Figure 3

Spotted lanternfly life cycle recorded in Pennsylvania (adapted with permission from Penn State Extension; see 40).

measured hatch rate and survival at 19.9°C, 24.2°C, 25.1°C, 26.7°C, and 30°C. Average temperature and hatch rate were combined with data from South Korean studies (11, 58) and validated against observed spotted lanternfly hatch in Pennsylvania in 2017 and in Virginia in 2019. The resulting model estimated the lower temperature threshold to be 10.4°C, and 50% egg hatch was predicted to occur at 310 DDs. Percentage of eggs hatched decreased with increasing temperatures, with observed values of 88.3% at 19.9°, 49.0% at 24.2°, 56.7% at 25°, and 28.8% at 27°C. Keena & Nielsen (28) collected fresh egg masses and exposed them either to constant temperatures (10°C, 15°C, or 20°C) for the duration of the study or to a combination of chill plus incubation at higher temperatures. Eggs exposed to variable temperatures were chilled either at 5° for 7, 28, 56, 84, 112 or 140 days or at 10° for 7, 28, 56, or 84, 216, or 250 days. After the chill period, eggs were held at 20° for 7 days, then incubated at 25°. For eggs held at constant temperatures, percentage hatch was significantly higher at 15°C (65.9%) than at 10°C (13.1%) or 20°C (13.9%). The lower threshold for egg development was estimated to be 7.39°C, and eggs held at 5°C, 10°C, and 15°C required 635, 715, and 849 DDs, respectively, to hatch. Exposure to chill at 5°C or 10°C for up to 100 days increased the percentage and synchrony of hatch within an egg mass compared to eggs kept at a constant temperature. Eggs exposed to chill for more than 100 days showed lower percentages of hatch. Eggs entered diapause after exposure to either 5°C or 10°C chill for 7 days, but this duration did not allow for completion of diapause, as these eggs were not able to hatch when moved to 25°C. Interestingly, because eggs held at constant temperature did hatch, albeit at lower rates, we can assume that diapause is not required for spotted lanternfly eggs.

Kreitman et al. (32) reared first- through fourth-instar nymphs on potted tree of heaven at constant temperatures of 5°C, 10°C, 15°C, 20°C, 25°C, 30°C, 35°C, and 40°C. All first instars died at 5°C, 10°C, and 40°C without molting, and survival for all instars was poor at 35°C, suggesting that southern expansion of spotted lanternfly populations might be limited by higher temperatures. Lower developmental thresholds and degree day requirements to reach each developmental stage varied across instars. Development of first instars to second instars required 166.6 DD (base threshold: 13.00°C), development of second instars to third instars required

Table 1 CDD estimates for the onset of spotted lanternfly life stages observed in the field

Publication	Year(s)	First instar onset and range	Second instar onset and range	Third instar onset and range	Fourth instar onset and range	Adult onset and range	Egg mass and range	Location
Liu (45)	2016–2017	153 153–652	340 340–881	567 567–1,020	738 738–1,227	942 942–1,795	NR	Berks County, PA
Liu (46)	2019	270 228–321	465 356–639	645 575–743	825 758–936	1,112 954–1,170	1,825 1,656–1,956	Berks County and Chester County, PA
Dechaine et al. (19)	2019	135 NR	300 NR	413 NR	649 NR	835 NR	1,673.5 NR	Winchester, VA
Dechaine et al. (19)	2020	111.5 NR	129 NR	304 NR	566 NR	887 NR	1,611.5 NR	Winchester, VA

All studies used a base threshold of 10°C.
Abbreviations: CDD, cumulative degree day; NR, not reported.

208.8 DD (base: 12.43°C), development of third instars to fourth instars required 410.5 DD (base: 8.48°C), and development of fourth instars to adults required 620.1 DD (base: 6.29°C). Challenges in rearing spotted lanternfly in captivity (resource depletion, humidity differences between temperatures, host plant choosiness of insects) were identified, as was the need to combine laboratory with field data to develop more accurate models of spotted lanternfly development.

Cumulative degree day (CDD) estimates were generated for the onset of each active life stage of spotted lanternfly based on field observations performed in Pennsylvania (45, 46) and Virginia (19), all using the base threshold of 10°C and showing that the timing of development varies across years and sites, likely in relation to variation in weather patterns (see **Table 1**). The range of CDDs among each life stage was used to estimate the range of calendar dates at which each life stage was observed, and a similar trend was found across these studies. That is, the data show a large overlap of life stages, with spotted lanternfly at two to three different life stages co-occurring throughout their active seasons. This may be due to localized temperature variation or timing of initial egg mass deposition or be associated with the differential availability of nutrient resources.

3.2. Host Plant Use and Requirements

The most recently updated list of host plant associations for spotted lanternfly, which is based on observations and records of actual feeding behavior, indicates that, worldwide, spotted lanternfly feeding is associated with 103 plant taxa, 56 of which are North American host plants (5). Given these polyphagous feeding habits, it is difficult to characterize spotted lanternfly host plant feeding trends across the life cycle, preferences, and feeding requirements. Several field studies documenting spotted lanternfly host plant associations have been described for early years of infestation in a given area (19, 45, 46, 51). Beginning with field observations in 2016 and 2017 in eastern Pennsylvania, Liu (45) found that tree of heaven, flowering dogwood, multiflora rose, Oriental bittersweet, summer grape, and black walnut were important hosts and observed that the range of host plants used narrowed as spotted lanternfly moved into adult stages. Subsequent field observations conducted in 2019 allowed Liu (46) to conclude that additional hosts preferred by early nymphal instars included tree of heaven, American beech, black birch, and multiflora rose. Adults were found on tree of heaven as well as black birch and red maple. In Virginia, Dechaine et al. (19) observed first-instar nymphs on 33 different plant species, whereas later instars were found on 25 plant species. Spotted lanternfly was most commonly found on tree of heaven, *Vitis* spp. (grape), and *Tetradium daniellii* (the invasive bee bee tree); these preferences were particularly pronounced for fourth instars and adults. Murman et al. (51) used glue traps to identify species more favored by spotted lanternfly and estimate host suitability using spotted lanternfly that were confined to insect sleeves on 26 host plant species. Capture rates on tree bands found that more spotted lanternfly were captured on tree of heaven than on other species; however, the spotted lanternfly on tree of heaven only comprised 45% of the total number of insects captured, and the remaining insects were captured on 34 other plant species. Sleeve-rearing trials indicated that eight species were able to support spotted lanternfly development from first instars to adults: tree of heaven, black walnut, chinaberry, Oriental bittersweet, hops, sawtooth oak, butternut, and tulip tree.

Given spotted lanternfly's wide host range and the finding that tree of heaven tends to be a preferred host, several studies have been conducted to attempt to determine the developmental requirements of spotted lanternfly when raised in captive settings and the degree to which spotted lanternfly may require tree of heaven for its development. Uyi et al. (68) established large enclosures in which weeping willow (*Salix babylonica*) and silver maple (*A. saccharinum*) were planted with either tree of heaven or river birch (*Betula nigra*), and spotted lanternfly was introduced into enclosures as first-instar nymphs. Spotted lanternfly was able to survive and develop to the adult stage with and without access to tree of heaven; however, survival was 10% higher for those with access to tree of heaven. Females laid eggs in both treatments, with 46 egg masses laid with access to tree of heaven and 6 egg masses laid without access. The proportion of successful hatch did not vary across conditions. A similar study (67) was conducted introducing spotted lanternfly to cages with and without tree of heaven in enclosures containing two-year-old trees. Spotted lanternfly was able to complete development from first instars to adults without access to tree of heaven. Spotted lanternfly with access to tree of heaven showed higher survival and faster development time and produced more egg masses than those reared without tree of heaven. In a study rearing spotted lanternfly on potted plants of various species, Nixon et al. (54) assessed two-week survivorship of spotted lanternfly early instars, late instars, and adults on single-host diets. When given only a single host, early instars had higher survivorship than later life stages across a range of hosts for up to 12 days in these trials. Significantly higher survivorship of early and late instars was found on tree of heaven and black walnut than on other hosts; adult survivorship was highest on tree of heaven. This study also tested spotted lanternfly development from hatching to adulthood on single-host diets of tree of heaven, black walnut, grapevine, apple, and peach, as well as on mixed diets with multiple hosts. Of the single-host diets, only tree of heaven and black walnut allowed for development of spotted lanternfly to the adult stage, with survivorship being greater on tree of heaven than on black walnut. All mixed diets tested allowed for adult development, and the development rate was 12% faster on mixed diets compared to a single-host diet of tree of heaven. Dissections of available surviving females showed that some reproductive maturation was occurring in females fed on tree of heaven alone, tree of heaven + apple, and tree of heaven + black walnut. However only one female was postvitellogenic (it had fed on a diet of tree of heaven + black walnut), with five visible eggs present.

Variation in the results of these laboratory, semifield, and field studies is likely due to the size and quality of the host trees upon which spotted lanternfly fed, how many insects were exposed to a given host, and the degree to which movement or host choice was constrained. Appropriate interpretation of these results requires recognizing the inherent trade-offs among study types, i.e., having full knowledge of the content of spotted lanternfly diet in highly controlled laboratory studies versus allowing spotted lanternfly the full range of host choice (host species and host plant quality) available to free-ranging spotted lanternfly. As such, these studies could likely benefit from including some assessment of benchmarks of spotted lanternfly fitness (nutritional status or reproductive development; 54) that allows for comparison to fitness of wild populations of spotted lanternfly. Nixon et al. (54) found that only one examined female had any mature eggs, with substantially fewer eggs than what is typical of spotted lanternfly females in wild populations (i.e., 5 eggs versus 30–50 observed in egg masses; see 45).

Several studies have investigated patterns of egg mass deposition on hosts. Spotted lanternfly egg deposition occurred across both host and nonhost species, although eggs were most often found on common hosts such as tree of heaven and black walnut (47). Counting of egg masses on trees after felling found that the majority of egg masses were laid at heights above 3 meters (29, 47).

4. DISPERSAL BEHAVIOR

To better understand the distances that nymphs and adults may travel to host plants, Nixon et al. (56) performed a series of mobility assays. Second-instar nymphs climbed the longest vertical distances in 15 min (approximately two-thirds m), followed by third instars (approximately one-half m), with late-season adults moving significantly shorter distances than other stages. Early season adults performed significantly longer single jumps (approximately one-fifth–one-fourth m) than did late-season adults and any nymphal instar. In a mark-recapture study in which spotted lanternfly were released on tree of heaven, more than 90% of nymphs were found within 10 m of the site of release after 2 weeks (16). In a contiguous forest in which tree of heaven was largely absent, Keller et al. (30) found greater nymphal dispersal: Third-instar nymphs moved farthest (approximately 17 m by 7 days after release), although all instars moved similar distances. The maximum distance was 65 m over 10 days. Many insects remained near the release site, but the percentage that did so ranged from approximately 33% to 67% across instars.

Studies of adults have shown that, in a single bout, spotted lanternfly can only fly short distances (<40 m) (4, 52, 70). A study collected spotted lanternfly adult females on four days (September 20, September 26, October 3, and October 11, 2018) and found that females that were mated and heavier than unmated females only flew approximately 4 m when thrown into the air in a flight assay, compared to unmated, lighter females, which flew more than 20 m (70). However, Leach & Leach (33, 34) showed that spotted lanternfly continued to move into vineyards from surrounding areas from early September through the end of October, while insecticide applications were being conducted. This means that new spotted lanternfly were continuing to move into these vineyards throughout these two months with no single source of incoming spotted lanternfly observed nearby. Similarly, Mason et al. (50) recorded numbers of spotted lanternfly moving onto red maples (*A. rubrum*) at five suburban sites from August to November. Because spotted lanternfly egg laying is reported to occur from mid-September to early November in Pennsylvania (45, 46), it seems unlikely that spotted lanternfly reproductive maturation tightly restricts their dispersal into new areas. The dispersal of spotted lanternfly across all active life stages remains unknown, and determining it will likely require the development of novel methodological approaches, such as the use of long-term marking with isotopes (60) or molecular gut content analysis (2).

5. MODELING POTENTIAL FOR ESTABLISHMENT AND SPREAD

An initial estimate of areas unsuitable for spotted lanternfly establishment in the United States (59) was based on mortality of eggs collected from three different regions in South Korea with different minimum winter temperatures (43). From these data, a minimum January temperature below −13.9°C was used to define unsuitability, and unsuitable regions were found to occur in the northern United States, including states such as Maine, Wisconsin, and North and South Dakota and higher-elevation sites in the Adirondack and Rocky Mountains. Jung et al. (27) applied CLIMEX modeling using the known distribution of spotted lanternfly eggs within South Korea to predict the relative favorability of locations around the world for spotted lanternfly establishment. From their results, they estimated that the eastern United States is favorable for establishment and predicted higher climatic suitability for more coastal and southern areas from eastern Texas to Maryland and lower suitability in the western United States. Wakie et al. (69), who applied the MaxEnt niche modeling approach, made different predictions, concluding that temperate regions were more suitable for spotted lanternfly, with the highest suitability in the United States occurring in the northeastern, mid-Atlantic, and midwestern states, as well as in fruit-growing regions in the western United States.

Reconciling these contradictory findings is challenging in light of the limitations of any given study. Jung et al. (27) used spotted lanternfly samples only from South Korea, which may not have a sufficient range of climate data to extrapolate to global distributions. Although Wakie et al. (69) sampled spotted lanternfly distributions from broader regions, relatively few occurrence points were sampled from within spotted lanternfly's native range in China, and the samples may not have sufficiently included sites from spotted lanternfly's currently unknown southern range. Huron et al. (26) used establishment potential from existing populations in both Asia and North America, as well as the presence of one of spotted lanternfly's preferred hosts, tree of heaven, and found that grape-growing regions of the western United States are at risk of invasion.

While these studies have largely focused on establishment potential based on climate suitability, Cook et al. (15) quantified the rate of actual spread of spotted lanternfly from 2014 to 2019 using field survey data, thus including human-associated spread. They estimated the radial rate of spread at 40 km/yr and median jump distances ranging from 55 to 92 km/yr. These data were used to model drivers of further spread, which allowed Cook et al. to identify a positive correlation between rates of spread and human population numbers.

6. DAMAGE AND ECONOMIC IMPACTS

Spotted lanternfly can cause damage and potential economic impact via feeding (damage to plant host), indirect feeding (deposition of honeydew), or its mere presence (unsightly due to high infestations and honeydew on plants, quarantine regulations), and its impacts vary greatly by industry. In grapevines, Leach & Leach (33) found a significant correlation between higher numbers of adult spotted lanternflies observed weekly on vines and lower yields of those same vines in the following year. In a study to evaluate the physiological response of grapevines to spotted lanternfly feeding, increasing spotted lanternfly numbers led to reductions in phloem transport and increased bud sensitivity to cold temperatures (M. Centinari, unpublished manuscript). Reduced growth potential of grapevines as a result of spotted lanternfly has been reported in South Korean vineyards (62). While the colonization of sooty mold resulting from spotted lanternfly feeding has been suggested to cause significant fruit contamination (see 42), this has not been observed in the US wine grape industry (34); however it could be of greater concern in table grape production. There are currently no data to support the idea that spotted lanternfly is a plant pathogen vector (65). Spotted lanternfly was unable to vector *Verticillium nonalfalfae* to tree of heaven in a laboratory setting (9). Research has not established thresholds for feeding damage on grapevines. Increases in insecticide costs have been noted; nearly 3× the amount of product has been applied in response to spotted lanternfly compared to normal insecticide inputs prior to spotted lanternfly (65). In modeling economic loss caused by spotted lanternfly, Harper et al. (24) used a worst-case scenario of 50% damage to grapevines to estimate $7.9 million loss in grape revenue in Pennsylvania alone (24). It is expected that spotted lanternfly will establish in other regions, particularly in important wine-producing areas such as France and Italy (26), which has the potential to cause serious monetary losses. However, because spotted lanternfly cause indirect damage to a plant (e.g., sap flow reduction), and many other causes of plant stress are possible, it is not clear that spotted lanternfly alone is responsible for these observed losses in plant health. A deeper understanding of the physiological response to plant feeding is necessary to more accurately predict losses due to spotted lanternfly.

There have been few studies of spotted lanternfly damage in other crops. In semifield trials where increasing numbers of spotted lanternfly nymphs and adults were introduced to cucumber plants, there was a correlative decrease in yield (37). Similar trials were carried out on hops, hemp, peach, and raspberry, with low or no levels of damage reported (37). Further work is required to confirm these findings and evaluate other crops. When spotted lanternfly first arrived in the United States, significant population levels were observed on apple (66); however, this appears to have been a localized event, with no subsequent events or crop damage reported. Nixon et al. (54) found that spotted lanternfly could not survive past the first instar on peach alone or past the second instar on apple alone. Spotted lanternfly feeding on tree fruit appears to be incidental, occurring when adults are highly mobile and transient.

Feeding damage to ornamental and woody plants, both commercial and naturalized, requires further study. Spotted lanternfly is highly mobile and can lay eggs nearly anywhere, and its economic burden is apparent in the landscape nursery, timber, and Christmas tree industries through quarantine and inspection requirements. Signs of feeding damage (wilting, oozing, dieback) are occasionally reported but thought to be limited to areas with large populations of insects (39). The population levels of spotted lanternfly reported in the invaded Asian regions appear to be substantially lower than what has been observed in the United States. Therefore, in the United States, spotted lanternfly may exert greater pressure on plants and have greater spillover to other plant hosts, potentially increasing the economic impact. It is unknown, however, whether these populations will remain large as spotted lanternfly spreads into new regions. Spotted lanternfly is present in wooded landscapes and forests, although the impact in these systems has yet to be studied. In edge habitats where high spotted lanternfly populations have been observed, large depositions of honeydew and subsequent sooty mold have been reported (65). This could result in the localized death of understory plants and requires further evaluation.

Spotted lanternfly damage has been reported from the tourism, business, and residential sectors, where it is a significant nuisance pest (e.g., insects present in high numbers at wedding venues, tasting rooms, etc. are disruptive and unattractive to guests and customers) (66). These types of impacts are difficult to quantify in terms of their economic value; however, they have received substantial media attention (see 65, 66). Many residents and businesses have taken action against spotted lanternfly, spending money on pesticides, traps, or tree removal. Quantifying the cost of these mitigation actions is challenging as it depends not only on the action taken, but also on the size and type of property (e.g., woodlot, parking lot) where such actions are taken. Taken together, the economic damage of spotted lanternfly is difficult to estimate, in large part due to the large host range and indirect feeding damage caused by this insect across diverse habitat types.

7. MONITORING

Monitoring for spotted lanternfly in the United States began with the use of glue traps wrapped around the trunks of trees; use of these traps has also been considered as a potential control method (40, 59). This type of trap relies on the negative geotaxis of spotted lanternfly (56) and their attraction to tall silhouettes such as tree trunks (3). However, due to the high frequency of bycatch of other species, including birds and mammals, and trap saturation in areas with high spotted lanternfly density, this trap is problematic. Research on modified traps has shown that a cone trap, funneling upward moving spotted lanternfly on the trunks of trees, is comparable to the glue traps while reducing bycatch dramatically (22, 55). These traps rely on the passive movement of spotted lanternfly, which can be effective in heavily populated areas during the nymphal and adult stages but not in the winter or in areas where spotted lanternfly may exist in low populations. Placement of these traps for both monitoring and management is suggested on common hosts, such as tree of heaven, maples, or black walnut. However, in areas with low population densities, where detection is most critical, spotted lanternfly tend to have a more random, rather than aggregated, dispersion pattern (10), making optimized trap placement challenging. Moreover, trap deployment is not possible on some critical hosts, such as wild grape, due to their small trunk size. To increase trap efficacy, research has focused on developing attractants to improve detection probability. Methyl salicylate, a common plant volatile, was found to be attractive to all life stages of spotted lanternfly in a laboratory setting, and (Z)-3-hexenol and (E,E)-α-farnesene were attractive to older life stages (17). When the methyl salicylate was used in combination with traps in field assays, however, there was no difference in capture compared with unbaited traps for either nymphal or adult spotted lanternfly (55). To date, no sex or aggregation pheromone has been found for spotted lanternfly. Monitoring continues to be a challenge to early detection and evaluation of control programs, with a large sample size needed to accurately estimate populations (10).

Additional methods for monitoring for spotted lanternfly are being tested. Environmental DNA (eDNA) has been used to detect this insect without the need for visual observations, a significant advantage given the high mobility of this pest (1). This method collects honeydew from vegetation (collected by washing leaf surfaces) or tree branches and trunks (collected by a roller applied to the substrate) and uses quantitative polymerase chain reaction to test for the presence of spotted lanternfly DNA (shed with its honeydew excretions). Detection probability using eDNA was over twice that using visual surveys (1). This eDNA approach has been used for early detection in vineyards and by state regulatory agencies in locations where spotted lanternfly is not yet thought to be present. However, eDNA will only last in an environment for approximately 1 week without rain and requires a laboratory to run samples. Canines have been used to detect spotted lanternfly by smell, particularly in human travel corridors such as shipping ports and rail lines (21). Trained canines have the ability to detect both new and 1-year-old egg masses with an accuracy of at least 90%. Moreover, spotted lanternfly is visible in the infrared spectrum, being warmer than its surrounding habitat (48). This phenomenon is poorly understood but may result from the metabolic activity of spotted lanternfly. Detection using thermal cameras has never exceeded 50% and works best in the early morning (H. Leach, unpublished data). Current monitoring efforts are dependent on either passive movement of spotted lanternfly (using funnel traps), which can be unreliable, or active searching for spotted lanternfly (visual surveys, eDNA, etc.), which is time consuming. There is no standard approach to delimiting a spotted lanternfly population within a given area.

8. CULTURAL CONTROL

Mechanical removal of spotted lanternfly, particularly in the egg mass stage, has been suggested for areas with small populations or residential areas as a nonchemical method of management (40). This method is likely impractical, as most egg masses are deposited in hidden places or are more than 3 m high in tree canopies (29). Likewise, the use of traps, such as the glue trap or funnel trap, has been suggested for local management of spotted lanternfly. This method has never been evaluated for its ability to reduce populations or host damage, although it is expected that it may reduce pressure on a single tree, such as in a backyard (40). Eliminating preferred host plants for spotted lanternfly has been suggested as a control tactic, predominantly focused on tree of heaven (59). However, whether this approach reduces local populations of spotted lanternfly or instead increases pressure on other plant hosts in the area has not been determined. More work is needed to substantiate tree of heaven removal as a control method.

Spotted lanternfly adults are attracted to tall vertical structures (3), which has provided an opportunity for the development of targeted trap and kill devices using tall structures coupled with insecticides, particularly along habitat edges. Leach & Leach (34) found that spotted lanternfly populations within vineyards are strongly spatially aggregated at the edge, providing a focus point for management such as flight-intercept walls or targeted applications of insecticides. Exclusion netting has been investigated as a way to reduce spotted lanternfly populations on grapevines in lieu of chemical applications, with reductions of spotted lanternfly on vines up to 99.8% (38). Additional focus on cultural control methods to manage spotted lanternfly is needed, particularly on potential behavioral control, such as the use of attractants, repellents, or disruption of insect communication.

9. BIOLOGICAL CONTROL

Various predators, including insects, birds, mammals, and fish, have been documented consuming spotted lanternfly within the United States. Spotted lanternfly is thought to sequester toxins from plant hosts, and it is suspected that this sequestration limits the natural control of spotted lanternfly (18). Despite these potential chemical defenses, citizen science reports confirm that general predators, predominantly birds and other insects, feed on or attempt to feed on spotted lanternfly (6, 25). At least one parasitoid, *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), not endemic to the United States, has been found to parasitize spotted lanternfly eggs at rates of 2.2% (49), although this is not expected to offer appreciable control of spotted lanternfly populations (63). At least four entomopathogenic fungus species have been observed to attack spotted lanternfly in the United States. (12, 13). In 2018, *Batkoa major* and *Beauveria bassiana* were found to cause reduction in spotted lanternfly populations, although only within a <0.5 ha area within Pennsylvania (12). Given that *B. bassiana* has been developed as a commercialized biopesticide for use against other insect pests, these observations fueled further research on its use as a control method in the United States (see Section 10). Upon later investigation of the same field sites in Pennsylvania, two additional fungal pathogens, *Metarhizium pemphigi* and *Ophiocordyceps delicatula*, were also discovered (13). Of these pathogens, *B. major* is thought to have caused the most significant local population decline (12), although it is not known how widely *B. major* or the other three pathogens are distributed among US spotted lanternfly populations.

In the endemic range, two parasitoid species have been discovered attacking spotted lanternfly. An egg parasitoid, *Anastatus orientalis* Yang & Choi (Hymenoptera: Eupelmidae), was discovered in 2012 (31) with parasitism rates of up to 15% (71). A nymphal parasitoid, *Dryinus sinicus* Olmi (Hymenoptera: Dryinidae), was later discovered with reported parasitism rates of up to 30% (71). Both parasitoid species are currently being evaluated within quarantine containment. The most extensive work has focused on the egg parasitoid, *A. orientalis*, which is suspected to have contributed to population decline of spotted lanternfly in South Korea (72); however, studies to evaluate this claim are lacking (8). The attraction of *A. orientalis* to spotted lanternfly egg masses and successful rearing of these parasitoids (8) make it a promising biological control agent. The nymphal parasitoid, *D. sinicus*, in contrast, has been less studied as a potential classical biological control agent, in part due to the difficultly of rearing this species (H. Broadley, personal communication). Both of these parasitoids are promising biological control agents for release in the United States; however, more information on their nontarget effects is still being pursued.

10. CHEMICAL CONTROL

To date, use of chemicals has been the predominant method of reducing spotted lanternfly populations in the United States. Significant effort has focused on the evaluation of commercially available products. Nymphal and adult spotted lanternfly have been found to be susceptible to a variety of chemical classes available in the United States, consistent with insecticide evaluations carried out in its Asian range (43). For agricultural use, predominantly in vineyards, products like bifenthrin, beta-cyfluthrin, and dinotefuran are highly efficacious on both nymphs and adults

(35, 41). Pyrethroids, in particular, including bifenthrin, beta-cyfluthrin, and fenpropathrin, have exceptional residual activity when foliarly applied in vineyards of up to 21 days of control against adult spotted lanternfly in field assays. Some less toxic compounds, such as neem oil or essential oil products, have shown contact efficacy against spotted lanternfly (36). The shorter residual chemicals require repeated applications due to the high repopulation of spotted lanternfly (33, 34). Unfortunately, more selective chemical groups, which are considered less toxic (anthranilic diamides, growth regulators, buccal pump inhibitors), have not been found to be effective against spotted lanternfly (36, 40). However, these studies lack data beyond 48 h of spotted lanternfly exposure and focus on adult mortality. Spotted lanternfly ovicides are less reliable than treating for nymphs or adults, with only chlorpyrifos (now banned in the United States) offering appreciable control of egg masses (36). Oils, such as paraffinic oil and soybean oil, have variable efficacy against spotted lanternfly egg masses, with less than 45% and 8% mortality, respectively, reported.

For management of spotted lanternfly on trees, two neonicotinoid insecticides have been relied on: dinotefuran and imidacloprid. Both of these insecticides are systemically active and can be applied in a variety of ways (drench, injection, bark spray), although dinotefuran is more reliable and has greater longevity (44). Dinotefuran has been the chemical principally used by government regulatory agencies to manage spotted lanternfly populations on tree of heaven (59, 66). The majority of tree of heaven in an area are killed using herbicide, and the remaining trees are treated with insecticide and considered to be baited trap trees. Large numbers of dead spotted lanternfly (>10,000 from a single tree) have been observed due to these single-tree treatments (65). However, this is unlikely to cause spotted lanternfly populations to decline due to the insect's high dispersal capacity and large host range. As a result, recent focus has been on biological pesticides with reduced nontarget effects for use in area-wide control programs. *Beauveria bassiana*, a commercially available biopesticide, has been evaluated in an area-wide application for reduction of spotted lanternfly nymph and adult populations. Semifield assays of these biopesticides, including BoteGHA®, Aprehend®, and PFR-97™, all show significant mortality (>90%) of spotted lanternfly 9 days after being directly sprayed with these products (14). When BoteGHA was applied to a landscape setting to evaluate an area-wide approach, populations of fourth-instar nymphs were 48% lower in sprayed versus unsprayed plots, and populations of adults were 43% lower (14). Importantly, this study recorded minimal impacts to nontarget arthropods. However, subsequent evaluations of *B. bassiana* have suggested more variable results in mortality of spotted lanternfly when applied over large areas, possibly due to the dispersal of spotted lanternfly, microclimate factors, or the need for high sample size in evaluating spotted lanternfly population response (10), and *B. bassiana* is not currently recommended for practical control. Nontarget impacts of spotted lanternfly management practices are not well understood but are potentially large given the variety of stakeholders and host plants that are affected by spotted lanternfly. Underwood et al. (64) found that honeybees fed on honeydew excreted from spotted lanternfly that contained dinotefuran. However, no dinotefuran above detectable levels was subsequently found in hives or honey products from these bees. Moreover, the prophylactic use of broad-spectrum insecticides can often flare secondary pests in agroecosystems, and recent reports from growers suggest that this may already be occurring in vineyards.

11. CHALLENGES

The increase in research on spotted lanternfly has improved our understanding of this invasive species and how best to manage it. Nevertheless, spotted lanternfly still poses many challenges that hinder our ability to understand its impacts fully, including its wide and unpredictable host range, its erratic movement, its feeding habits and damage to plants, and the difficulty of rearing it. Examinations of host plant use patterns and feeding requirements need to ground truth results from controlled laboratory and semifield studies against wild populations; the development of fitness benchmark measurements is needed for such comparisons. Similar challenges exist in estimating the natural dispersal capacity of spotted lanternfly across its life cycle, which is critically important to improve monitoring and detection. New methodologies such as the use of stable isotopes or other signatures of spotted lanternfly (e.g., thermal imagery, eDNA, plant damage indices) or spotted lanternfly movement (e.g., molecular gut content analysis) may provide additional insights. Thermal requirements and limits of spotted lanternfly biology are not fully known, and as such, it is not clear whether spotted lanternfly populations will continue to expand south and perhaps increase (as warmer areas provide a longer duration for feeding and egg laying), or whether higher temperatures will limit spotted lanternfly's southern spread.

Current management is highly dependent on chemical control. Pesticide restrictions in other countries where spotted lanternfly is expected to spread (26), pesticide resistance (which has not yet been investigated for spotted lanternfly), and potential nontarget environmental impacts make this a problematic approach. Thresholds for spotted lanternfly, particularly in grape, are needed to better inform growers on when to take management actions and reduce potential economic damage. However, this type of data is contingent on understanding the impact of spotted lanternfly short-term and long-term feeding. Moreover, we lack the ability to evaluate control programs in natural habitats and need continued research into attractive or repellent stimuli for spotted lanternfly, chemical, physical, or otherwise, to increase the efficiency and accuracy of monitoring programs.

SUMMARY POINTS

1. Spotted lanternfly was first discovered in the eastern United States in 2014; subsequently, populations have expanded, causing potential damage to numerous plant hosts. The wide host range and mobility of spotted lanternfly contribute to its success as an invader, and both rate and distance of spread are likely to increase in association with higher human populations.
2. Spotted lanternfly poses a serious threat to grape production; however, quantifying this threat has proved challenging. The economic burden from spotted lanternfly has been felt in the landscape, nursery, and Christmas tree industries due to costs associated with quarantine requirements. Spotted lanternfly is a nuisance pest; although its impacts have been reported in the tourism and residential sectors, these impacts have not been quantified. The impacts of spotted lanternfly feeding on other crops and of sooty mold deposition, particularly in forested areas, require further study.
3. Management of spotted lanternfly remains dependent on chemical use, although there are promising biological control agents, including entomopathogenic fungi and parasitoids. Identification of additional natural enemies would benefit from further study of lanternfly in its native range, including validation and delimitation of the two subspecies of *L. delicatula* that are currently recognized. No single control measure alone will allow for sufficient management of spotted lanternfly. An area-wide approach with a variety of tools is necessary. However, limitations to our current understanding of patterns of host plant use and associated movement across habitat types hinder the development and evaluation of an integrated approach.
4. The eradication program in response to spotted lanternfly in the eastern United States was not sufficient to prevent its spread because we lacked basic information on this

pest when it was first detected. While we have seen population explosions of spotted lanternfly in the eastern United States, this may not occur in other areas, as new research continues to be conducted.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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