Environmental Entomology, 48(6), 2019, 1452–1468
doi: 10.1093/ee/nvz123
Advance Access Publication Date: 25 October 2019
Research

Plant-Insect Interactions

Oviposition Substrate Selection, Egg Mass Characteristics, Host Preference, and Life History of the Spotted Lanternfly (Hemiptera: Fulgoridae) in North America

Houping Liu[1]

Pennsylvania Department of Conservation and Natural Resources, 400 Market Street, Harrisburg, PA

[1]Corresponding author, e-mail: hliu@pa.gov

Subject Editor: Gregory Sword

Received 20 June 2019; Editorial decision 20 September 2019

Abstract

Oviposition substrate selection, egg mass characteristics, host preference, and life history of *Lycorma delicatula* (White) (Hemiptera: Fulgoridae) were studied in Pennsylvania between 2016 and 2017. Twenty-four substrate types (trees, shrubs, and nonliving materials) were selected by females for oviposition. Tree-of-heaven, black cherry, black birch, and sweet cherry were favored at 62.5% of the types and accounted for 68.5% of the egg masses based on survey results 200 cm above ground. Egg mass density ranged between 0.2 and 75.2 egg masses/m^2 with no significant difference among substrate types. Egg mass size ranged between 0 and 192 eggs/egg mass, with 91.8% containing <50 eggs. Significantly larger egg masses were found on sweet and black cherry compared with tree-of-heaven, with significantly higher hatch success on black locust. Eggs hatched between May 2 and June 5 and peaked on 18 May 2017. Tree-of-heaven and summer grape were preferred by nymphs and adults, while multiflora rose and black walnut were favored by the first, second, and the fourth instar nymphs, respectively. The first, second, third, fourth instars and adults lasted for 62 (2 May–3 July), 42 (8 June–20 July), 35 (26 June—31 July), 39 (10 July—18 Aug.), and 114 (24 July—15 Nov.) days, with peaks on 25 May, 22 June, 6 July, 31 July, and 22 Aug., respectively. Adult feed for 2 months before laying eggs in early October. Cumulative degree-days were 0–325, 153–652, 340–881, 567–1,020, 738–1,227, and 942–1,795 for the egg, first, second, third, fourth instar, and adult stage, respectively. Oviposition strategies and development patterns were discussed.

Key words: *Lycorma delicatula,* oviposition substrate selection, egg mass characteristics, host preference, life history.

The spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae), an exotic pest of tree-of-heaven, *Ailanthus altissima* (Mill.) Swingle (Sapindales: Simaroubaceae) from China, Taiwan, and Vietnam (White 1845, Liu 1939, Zhou 1992), was first discovered near Boyertown (40.33366N, 75.63744W) in Berks County, Pennsylvania in 2014 (Barringer et al. 2015, Dara et al. 2015, Lee et al. 2019). It was previously introduced to South Korea in 2004 (Han et al. 2008, Kim and Kim 2005), and Japan in 2009 (Tomisawa et al. 2013). Significant damage to cultivated grapes was reported in South Korea (Lee et al. 2009). Infestation in North American is now found in Pennsylvania (14 counties), New Jersey (3 counties), Virginia (1 county), Delaware (1 county), and Maryland (1 county), with a few regulation incidences (insects found but no infestation) in New York, Connecticut, and Massachusetts (NYS IPM 2019). Feeding by its nymphs and adults in host phloem tissues causes oozing wounds on trunks and branches. Heavy infestation results in large amounts of honeydew deposition on host trees and understory species, which promotes growth of sooty mold that hinders plant photosynthesis and contaminates agricultural and forest crops (Han et al. 2008, Barringer et al. 2015). Mold-contaminated crops are deemed unmarketable. It is a direct threat to the $18 billion fruit, nursery and landscape, and hardwood industries, as well as the livelihoods of local producers and businesses, and the quality of life of the residents in Pennsylvania (PDA 2018). The Pennsylvania Department of Agriculture and the United States Department of Agriculture have moved rapidly to eradicate and contain pest populations through cultural (host tree removal), mechanical (egg scraping and tree banding), and chemical (foliar spray of contact insecticides and trunk treatment with systemic insecticides) control since 2015 (Cooperband et al. 2018, Leach et al. 2018).

According to Zhou (1992), *L. delicatula* completes one generation a year and overwinters as eggs on tree trunks in its native range of China. Egg hatch starts in mid-April and peaks in early May. Nymphs pass through four instars to become adults between mid-June and early July. Adults mate and lay eggs in mid-August. Eggs are usually laid in masses and covered by a layer of gray wax. They are arranged in a single layer of 5–10 rows, with 10–30 eggs/row. Adults live up to 4 mo and continue feeding until October. Similar life cycles are also reported in South Korea and Japan, except adults do not appear until early July to early August, and eggs are not observed until mid- to late September (Park et al. 2009, Lee et al. 2011, Tomisawa et al. 2013).

In Asia, *L. delicatula* egg masses have been reported from the bark surface of 24 species of trees in 14 families (Table 1). Host list for nymphs and adults includes 73 species of trees, woody plants, vines, and weeds in 32 families (Table 2). In North America, egg masses have been observed from tree-of-heaven, red maple (*Acer rubrum* L. [Sapindales: Sapindaceae]), American beech (*Fagus grandifolia* Ehrh. [Fagales: Fagaceae]), chestnut oak (*Quercus montana* Willd. [Fagales: Fagaceae]), tulip tree (*Liriodendron tulipifera* L. [Magnoliales: Magnoliaceae]), American sycamore (*Platanus occidentalis* L. [Proteales: Platanaceae]), and black cherry (*Prunus serotina* Ehrh. [Rosales: Rosaceae]) (Dara et al. 2015). Feeding damage by nymphs and adults in the field has been observed on northern red oak (*Q. rubra* L. [Fagales: Fagaceae]), black walnut (*Juglans nigra* L. [Fagales: Juglandaceae]), silver maple (*A. saccharinum* L. [Sapindales: Sapindaceae]), and bigtooth aspen (*Populus grandidentata* Michaux [Malpighiales: Salicaceae]) in Pennsylvania (Liu 2019). Initial research efforts to understand and control the pest population of *L. delicatula* in PA have included mechanical control of egg masses through chipping (Cooperband et al. 2018), structure and possible function of antennal and mouthpart sensilla (Hao et al. 2016, Wang et al. 2018), adult flight behavior (Domingue and Baker 2019, Myrick and Baker 2019), kairomone identification (Cooperband et al. 2019), defense sequestration (Song et al. 2018), chemical control (Leach et al. 2019), predators (Barringer and Smyers 2016), egg parasitoids (Liu 2019, Liu and Mottern 2017), and fungal pathogens (Clifton et al. 2019).

Table 1. *Lycorma delicatula* oviposition substrate types reported from Asia

Family / Species	Common name	China	South Korea	Japan	Ref.
Betulaceae					
Betula platyphylla Sukaczev	Siberian silver birch		Yes		1,5
Ebenaceae					
Diospyros kaki L.	Persimmon	Yes			7
Fabaceae					
Robinia pseudoacacia L.	Black locust			Yes	3
Styphnolobium japonicum (L.) Schott	Pagoda tree	Yes			4
Fagaceae					
Castanea crenata Siebold & Zucc.	Korean chestnut		Yes		6
Quercus acutissima Carruth	Sawtooth oak			Yes	3
Lythraceae					
Punica granatum L.	Pomegranate	Yes			8
Meliaceae					
Melia azedarach L.	Chinaberry	Yes			2
Toona sinensis (A. Juss.) M. Roem.	Chinese mahogany		Yes		5
Oleaceae					
Syringa vulgaris L.	Common lilac		Yes		5,6
Rosaceae					
Pyrus sp.	Pear	Yes			12
Prunus armeniaca L.	Armenia plum	Yes			9
Prunus serrulata Lindl.	Oriental cherry		Yes		1,5
Prunus × yedoensis Matsum.	Yoshino cherry		Yes		1,5
Rutaceae					
Tetradium daniellii (Benn.) T.G. Hartley	Bee-bee tree		Yes		5,6
Zanthoxylum bungeanum Maxim.	Chinese pepper	Yes			10
Salicaceae					
Populus alba L.	White poplar		Yes		1,5
Populus tomentiglandulosa T. Lee			Yes		6
Salix sp.	Willow	Yes	Yes		5
Sapindaceae					
Acer palmatum Thunb.	Japanese maple		Yes		1,5
Simaroubaceae					
Ailanthus altissima (Mill.) Swingle	Tree-of-heaven	Yes	Yes	Yes	1–6, 9, 11
Ulmaceae					
Ulmus spp.	Elms	Yes			4
Zelkova serrata (Thunb.) Makino	Japanese zelkova		Yes		1,5
Vitaceae					
Vitis vinifera L.	Common grape vine	Yes	Yes		6,11

1. Kim et al. (2011), 2. Chu (1930), 3. Tomisawa et al. (2013), 4. Zhou (1992), 5. Dara et al. (2015), 6. Lee et al. (2011), 7. Zu (1992), 8. Hou (2013), 9. Chou et al. (1985), 10. Gao (1993), 11. Chou (1946), 12. Yang et al. (2015).

Table 2. Host list of *Lycorma delicatula* nymphs and adults in Asia

Family Species	Common name	China	South Korea	Japan	Ref.
Actinidiaceae					
Actinidia chinensis Planch	Kiwifruit	Yes	Yes		2,3,12
Apiaceae					
Angelica dahurica (Fisch. ex Hoffm.) Benth. et Hook.	Dahurian angelica		Yes		2,3
Anacardiaceae					
Rhus chinensis Mill.	Chinese sumac		Yes		2.3
Toxicodendron vernicifluum (Stokes) F. Barkley	Chinese lacquer		Yes		2,3
Apocynaceae					
Metaplexis japonica (Thunb.) Makino	Rough potato		Yes		2,3
Araliaceae					
Aralia cordata Thunb.	Japanese spikenard		Yes		2,3
Aralia elata (Miq.) Seem.	Japanese angelica		Yes		2,3
Asteraceae					
Arctium lappa L.	Greater burdock		Yes		2,3
Betulaceae					
Alnus incana (L.) Moench	Grey alder		Yes		2,3
Betula platyphylla Sukaczev	Siberian silver birch		Yes		2,3
Bignoniaceae					
Catalpa bungei C.A. Mey.	Manchurian catalpa	Yes			1
Boxaceae					
Buxus sinica (Rehder & E.H. Wilson) M. Cheng	Chinese boxwood	Yes			1,10
Cannabaceae					
Canabis sativa L.	Industrial hemp	Yes			1,10
Cupressaceae					
Juniperus chinensis L.	Chinese juniper	Yes			11
Platycladus orientalis (L.) Franco	Chinese thuja	Yes			11
Euphorbiaceae					
Mallotus japonicus (L.f.) Mull. Arg.	East Asian mallotus			Yes	4
Fabaceae					
Albizia julibrissin Durazz	Persian silk tree	Yes			1
Glycine max (L.) Merr.	Soybean	Yes			10
Maackia amurensis Rupr.	Amur maackia		Yes		2,3
Robinia pseudoacacia L.	Black locust	Yes			1,3
Fagaceae					
Quercus aliena Blume	Oriental white oak		Yes		2,3
Quercus sp.	Oak	Yes			1
Hydrangeaceae					
Philadelphus schrenkii Rupr.	Mock orange		Yes		2,3
Juglandaceae					
Juglans hindsii (Jeps.) Jeps. Ex R.E. Sm.	California walnut	Yes			6
Juglans major (Torr.) A. Heller	Arizona walnut	Yes			6
Juglans mandshurica Maxim.	Manchurian walnut		Yes		2,3
Juglans microcarpa (Berlandier)	Texas walnut	Yes			6
Juglans nigra L.	Black walnut	Yes	Yes		2,3,6
Juglans regia L. = *J. sinensis* (C. DC) Dode	English walnut		Yes		2,3
Platycarya strobilacea Siebold et Zucc.		Yes			1
Pterocarya stenoptera C. DC.	Chinese wingnut	Yes	Yes		2,3,13
Lythraceae					
Punica granatum L.	Pomegranate	Yes			7
Magnoliaceae					
Magnolia kobus DC.	Kobus magnolia		Yes		2,3
Magnolia obovata Thunb.	Japanese bigleaf magnolia		Yes		2,3
Malvaceae					
Firmiana simplex (L.) W.F. Wight	Chinese parasoltree	Yes	Yes		1,2,3
Meliaceae					
Cedrela fissilis Vell.	Argentine cedar		Yes		2,3
Melia azedarach L.	Chinaberry	Yes		Yes	1,4,5
Toona sinensis (A. Juss.) M. Roem.	Chinese mahogany	Yes	Yes		1,2,3
Moraceae					
Morus alba L.	White mulberry		Yes		2,3
Morus australis Poir. = *Morus bombycis* Koidz.	Chinese mulberry		Yes		2,3

Oleaceae

Table 2. Continued

Family	Common name	China	South Korea	Japan	Ref.
Species					
Ligustrum lucidum W.T. Aiton	Chinese privet	Yes			1
Paulowniaceae					
Paulownia kawakamii Ito	Sapphire dragon tree	Yes			1
Platanaceae					
Platanus × acerifolia (Aiton) Willd.	London planetree	Yes			1
Rosaceae					
Malus spectabilis (Aiton) Borkh.	Asiatic apple	Yes			1
Prunus armeniaca L.	Armenian plum	Yes			1
Prunus mume Siebold & Zucc.	Japanese apricot	Yes			3, 14
Prunus persica (L.) Batsch	Peach	Yes			1,3
Prunus salicina Lindl.	Chinese plum	Yes			1,3
Rosa hybrid L.	Rose		Yes		2,3
Rosa multiflora Thunb.	Multiflora rose		Yes		2.3
Rosa rugosa Thunb.	Rugosa rose		Yes		2,3
Rubus crataegifolius Bunge	Korean raspberry		Yes		2,3
Sorbaria sorbifolia (L.) A. Braun	False spiraea	Yes	Yes		1,2,3
Sorbus commixta Hedl.	Japanese rowan		Yes		2,3
Rutaceae					
Phellodendron amurense Rupr.	Amur cork tree				2,3
Tetradium daniellii (Benn.) T.G. Hartley	Bee-bee tree		Yes		2,3
Zanthoxylum bungeanum Maxim.	Chinese pepper	Yes			8
Salicaceae					
Populus koreana J. Rehnder	Korean poplar		Yes		2,3
Populus sp.	Poplar	Yes			1,3
Salix babylonica L.	Weeping willow				9
Salix matsudana Koidz.	Chinese willow	Yes			9
Salix sp.	Willow	Yes	Yes		3
Sapindaceae					
Acer buergerianum Miq.	Trident maple	Yes			1
Acer pictum subsp. *mono* (Maxim.) H. Ohashi	Painted maple	Yes			1
Simaroubaceae					
Ailanthus altissima (Mill.) Swingle	Tree-of-heaven	Yes	Yes	Yes	1–5
Picrasma quassioides (D. Don) Benn.	Picrasma		Yes		2,3
Styracaceae					
Styrax japonicus Siebold & Zucc.	Japanese snowbell		Yes	Yes	2,3,4
Styrax obassia Siebold & Zucc.			Yes		2,3
Ulmaceae					
Ulmus sp.	Elm	Yes			1
Vitaceae					
Parthenocissus quinquefolia (L.) Planch.	Virginia creeper		Yes		2,3
Vitis amurensis Rupr.	Amur grape		Yes		2,3
Vitis vinifera L.	Common grape vine	Yes	Yes		1,2,3
Vitis spp.	Wild grapes		Yes		2,3

1. Zhou (1992), 2. Park et al. (2009), 3. Dara et al. (2015), 4. Tomisawa et al. (2013), 5. Chu (1930), 6. Zhang (2001), 7. Hou (2013), 8. Gao (1993), 9. Lieu (1934), 10. Chou et al. (1985), 11. Li et al. (2013), 12. Hong and Li (1994), 13. Chou (1946), 14. Han et al. (2008).

There is an urgent need for more information on *L. delicatula* biology, behavior, host range, seasonal development, life history, chemical control, and biological control for its effective management in North America. In this study, the oviposition substrate selection of *L. delicatula* females was investigated by the survey and collection of egg masses from multiple field study plots between 2016 and 2017. Collected egg masses were characterized through the measurement of density, size, and hatch success in the laboratory. Host preference, seasonal development, and life history were also studied through the monitoring of egg hatch, periodical surveys on various life stages, examination of the aggregation patterns of nymphs and adults, and random field observations. Cumulative degree-days were calculated for all *L. delicatula* life stages based on weather data within the study area.

Materials and Methods

Study Plots

Fourteen 0.4-ha plots in Berks County, Pennsylvania were selected to study oviposition substrate selection, including four (Rolling, ODSouth, Rock, and Lutz) from the core infested area in 2016, and 10 (Straub, Conrad, WSEast, ODNorth, WSWest, Nuss, Kulps, HCEast, Huffs, and HCWest) from the periphery of the core infested area in 2017. These study plots were selected to reflect the introduction history and dispersal pattern of this pest in Pennsylvania. Study plot Rolling is the infestation epicenter of *L. delicatula* in North America. All but two study plots (ODSouth and WSEast) were selected from mixed hardwood forests dominated or co-dominated by species such as red maple, black birch (*Betula lenta* L. [Fagales: Betulaceae]), black cherry, northern red oak, and tulip tree. Study plot ODSouth was in a farm with hedgerows of black cherry and flowering dogwood (*Cornus florida* L. [Cornales: Cornaceae]) while study plot WSEast was the backyard of a residence scattered with single tree-of-heaven and black walnut trees in the middle, and northern spicebush (*Lindera benzoin* L. [Laurales: Lauraceae]) along the edges. See Liu (2019) for details on locations and conditions of all study plots. Study plot ODSouth was also used for the egg hatch, host preference, and seasonal development studies in 2017.

Oviposition Substrate Selection

Oviposition substrate selection by *L. delicatula* was studied by recording the types of substrates where the egg masses were found. Methods are described in Liu (2019). Briefly, all potential surfaces (trunks of live or dead trees, shrubs, vines, stone, fence posts, building structures, etc.) at each study plot were searched for *L. delicatula* egg masses between late March and late April of each year. Egg masses found on any surface 200 cm above ground were collected using a bench chisel or a pair of forceps and the oviposition substrate labeled and recorded sequentially for each study plot. Each collected egg mass was placed in a 16-ml borosilicate clear glass vial with a black phenolic cap (Fisher Scientific, Hampton, NH) (2016) or a 50-ml centrifuge tube (VWR International, Radnor, PA) (2017) and labeled by location, substrate type number, and egg mass number (e.g., Kulps #1-1 represents the first egg mass collected from substrate type no. 1 at study plot Kulps). Damaged or incomplete egg masses were excluded from the collection. A total of 6 h (three skilled surveyors for 2 h) was spent at each study plot. Each study plot could have multiple instances of egg laying on a given substrate (e.g., six different black cherry trees had multiple egg masses at study plot ODSouth in 2016, resulted in six substrate replicates for black cherry at this location). Egg masses were sorted by substrate types for each study plot. The total number of *L. delicatula* egg masses found on each study plot (e.g., Lutz, Straub) and substrate type (e.g., tree-of-heaven, metal fence post) in each year were used for data analysis.

Egg Mass Density

Lycorma delicatula egg mass density was calculated by dividing the number of egg masses collected from each substrate replicate by its surface area measured in square meters. The diameter-at-meter height in centimeters (DMH) of the trunk was measured at 100 cm above ground for trees and shrubs, whereas two dimensions (average length and width in centimeters) were measured for nonliving materials (stone, metal fence post) after egg collection in the field. Surface area (A) is defined as: 1) trees and shrubs: $A = (\pi \times DMH \times 200)/10{,}000$, 2) stone: $A = (L \times W)/10{,}000$, where L is the length and W is the width, and 3) metal fence post: $A = 2 \times (L \times W)/10{,}000$, where L is length and W is the width of exposed portion, both sides. Egg mass density was then sorted by substrate type, study plot, and sampling year before subject to analysis.

Egg Mass Size

The number of eggs within each collected egg masses was counted in the laboratory two weeks after completion of incubation. Direct count was made for egg masses with little or no waxy cover on the top; however, most egg masses required removal of surface wax with a #2 camel hair brush (Grumbacher, Leeds, MA). Egg mass size (no. eggs/egg mass) was sorted by substrate type, study plot, and sampling year before analysis.

Egg Hatch in the Laboratory

Field-collected *L. delicatula* egg masses were brought back to the laboratory in 2016 and 2017 for incubation inside Percival incubators (model # DR-36VL, Percival Scientific, Perry, IA) at 22 ± 1°C, 40 ± 5% relative humidity (RH) and a 16:8 (light: dark) h photoperiod for 2 mo. Egg masses were monitored twice a week for hatch. Percent hatch success was calculated by dividing the number of hatched eggs by the total number of eggs of each egg mass and analyzed for effects of substrate type, study plot, and sampling year.

Egg Hatch in the Field

To monitor *L. delicatula* egg hatch in the field, a total of 41 egg masses (EM-1 to EM-41) were selected from four different types of substrates (live white ash, dead flowering dogwood, live black cherry, and live flowering dogwood) at study plot ODSouth in early April 2017. Each egg mass was circled with a red sharpie marker (New Brands, Atlanta, GA) and labeled by attaching a 1.9 × 8.9 cm aluminum tag with wires (Forestry Supplies, Jackson, MS) next to it. Extra wires were used to secure the tag in place when egg masses were found on tree trunks or large branches. Egg masses were monitored twice a week from 30 April to 18 June. Opening of an egg lid (1.8 mm in length and 0.5 mm in width) indicates hatch has occurred (Liu 2019). The total number of eggs for each egg mass was recorded 2 wk after the completion of hatch in the field. The per cent egg hatch success was calculated by dividing the number of hatched eggs by the total number of eggs of each egg mass and were analyzed for effect of substrate type.

Host Preference for Nymphs and Adults

Host preference of *L. delicatula* nymphs and adults was studied at study plot ODSouth in 2017 by examining their aggregation patterns throughout the season in the field. In total, 23 plants from nine host species were monitored twice a week from May 25 until the appearance of the first egg mass in the fall, including 13 trees (four tree-of-heaven, three dogwood, three black walnut, one black cherry, one sassafras—*Sassafras albidum* (Nuttall) Nees [Laurales: Lauraceae], and one white ash—*Fraxinus americana* L. [Lamiales: Oleaceae]), five shrubs (multiflora rose—*Rosa multiflora* Thunb. [Rosales: Rosaceae]), and five vines (four summer grape—*Vitis aestivalis* Michx. [Vitales: Vitaceae], and one oriental bittersweet—*Celastrus orbiculatus* Thun. [Celastrales: Celastraceae]). Previous observations at this study plot showed that these species were utilized either by females for oviposition or by nymphs and adults for feeding. All life stages (nymphs, adults, and eggs) from the current generation found on the lower 200-cm trunk of the trees or stem of the vines were counted, whereas for shrubs the entire plant was thoroughly inspected for *L. delicatula* life stages. Nymphs were separated into four instars based on size (first instars—4.0 × 2.0 mm; instars— 7.0 × 3.5 mm; third instars—10.0 × 4.5 mm; fourth instars—13.0 × 6.0 mm) and morphological characteristics (e.g., black body with white spots for the first–third instars, and black and red body with white spots for the fourth instars) (Zhou 1992, Dara et al. 2015).

Seasonal Development and Life History

Seasonal development of *L. delicatula* was studied at study plot ODSouth between 12 April and 15 Nov. 2017 through the monitoring of egg hatch and periodical surveys of various life stages in the field. Starting and ending dates for each life stage were recorded. Stage composition on each sampling date (i.e., proportion of each life stage observed) was calculated. Seasonal development was analyzed by comparing the change in stage composition over time for the entire field season. The highest proportion recorded for each stage indicates population peak for that specific stage. A life history table was then constructed to show critical dates for the seasonal development of all stages of *L. delicatula*. Cumulative growing degree-days were calculated based on simple average with a lower threshold of 10°C (50°F) and a high threshold of 35°C (95°F) at weather station D9872 APRSWXNET DW9872 in Oley, Pennsylvania (40.40000N, 75.71530W, elevation: 130 m (427 feet)). Growing season at this site started on 19 Feb. and ended on 6 Nov. 2017 (Online Phenology and Degree-day Models at http://uspest.org/wea/).

Data Analysis

A general linear model was used to analyze the relationship between the total number of egg masses collected and the substrate replicates. Shapiro–Wilk normality test was conducted on egg mass density and egg mass size data first. If the data were not normally distributed, Kruskal–Wallis test was used in the one-way ANOVA (analysis of variance) to detect effects of sampling year, study plot, and substrate type. Significant effects by ANOVA was followed by pairwise Wilcoxon rank-sum test with a *P*-value adjusted by the Benjamini–Hochberg method. For egg hatch success data in the laboratory, Pearson's chi-squared test on count data was used to detect effects of sampling year, study plot, and substrate type, followed by post-hoc pairwise comparison for significant effects. For egg hatch success data in the field, Pearson's chi-squared test on count data was initially used to detect the effect of substrate type. The mean hatch success was then separated by post hoc pairwise comparisons for significance (R Core Team 2019).

Results

Oviposition Substrate Selection

Oviposition substrates of *Lycorma delicatula* in North America observed in this study included 20 species of trees and 2 species of shrubs in 14 families and two kinds of nonliving materials, with a total of 663 egg masses were collected from 208 substrate replicates (Table 3). Significant positive correlation was detected between the number of substrate replicates utilized by *L. delicatula* females and number of egg masses collected (t = 6.169, P < 0.001), with a multiple R^2 of 0.634 (F = 38.05, df = 1, 22, P < 0.001). In general, the more the replicates of a giving substrate type, the higher the number of egg masses found. Tree-of-heaven was the most used substrate type with an average of 4.5 (159/35) egg masses/substrate replicate. However, black cherry, black birch, and sweet cherry (*P. avium* L. [Rosales: Rosaceae]) were also highly utilized when both the number of egg masses and number of substrate replicates were considered, with an average of 6.0 (131/22), 1.6 (99/62), and 5.9 (65/11) egg masses/

Table 3. *Lycorma delicatula* oviposition substrate types by egg masses collected and replicates utilized in North America 2016–2017

Substrate type		Egg masses		Replicates	
Scientific name (family)	Common name	*N*	%	*n*	%
Plants					
Ailanthus altissima (Mill.) Swingle (Simaroubaceae)	Tree-of-heaven	159	23.98	35	16.82
Prunus serotina Ehrh. (Rosaceae)	Black cherry	131	19.76	22	10.58
Betula lenta L. (Betulaceae)	Black birch	99	14.93	62	29.81
Prunus avium L. (Rosaceae)	Sweet cherry	65	9.81	11	5.29
Betula alleghaniensis(Britt.) (Betulaceae)	Yellow birch	29	4.38	15	7.21
Lindera benzoin L. (Lauraceae)	Northern spice bush	26	3.92	4	1.93
Acer rubrum L (Sapindaceae)	Red maple	23	3.47	13	6.25
Carpinus caroliniana Walter (Betulaceae)	American hornbeam	19	2.87	9	4.32
Liriodendron tulipifera L. (Magnoliaceae)	Tulip tree	17	2.57	7	3.36
Quercus rubra L. (Fagaceae)	Northern red oak	14	2.11	4	1.93
Robinia pseudoacacia L. (Fabaceae)	Black locust	7	1.06	3	1.44
Acer saccharinum L. (Sapindaceae)	Silver maple	5	0.75	1	0.48
Viburnum prunifolium L. (Adoxaceae)	Blackhaw	5	0.75	1	0.48
Carya ovata (Mill.) K. Koch (Juglandaceae)	Shagbark hickory	4	0.60	3	1.44
Fraxinus americana L. (Oleaceae)	White ash	3	0.45	2	0.96
Betula nigra L. (Betulaceae)	River birch	2	0.30	1	0.48
Acer platanoides L. (Sapindaceae)	Norway maple	2	0.30	1	0.48
Pinus strobus L. (Pinaceae)	Eastern white pine	2	0.30	1	0.48
Cornus florida L.(Cornaceae)	Flowering dogwood	2	0.30	2	0.96
Acer negundo L. (Sapindaceae)	Boxelder	1	0.15	1	0.48
Ostrya virginiana (Mill.) K. Koch (Betulaceae)	American hophornbeam	1	0.15	1	0.48
Sassafras albidum (Nutt.) Nees (Lauraceae)	Sassafras	1	0.15	1	0.48
Non-living materials					
Metal fence posts	Metal fence posts	31	4.68	4	1.93
Stone	Stone	15	2.26	4	1.93
Total		663	100	208	100

Note: Replicate is defined as an instance of egg laying by *L. delicatula* females on a given substrate. Percentage of egg masses and replicates is calculated for each type of oviposition substrate against all substrate types utilized.

substrate replicate, respectively. Black birch was the most used substrate type by the number of substrate replicates although the average number of egg masses per replicate was relatively low. These four species accounted for 62.5% (130/208) of the total substrate replicates utilized and 68.5% (454/663) of the total egg masses collected, respectively (Table 3). Occasional substrate types included metal fence posts, yellow birch (*B. alleghaniensis* (Britt.) [Fagales: Betulaceae]), northern spice bush, red maple, American hornbeam (*Carpinus caroliniana* Walter [Fagales: Betulaceae]), tulip tree, stone, and northern red oak, with an average number of egg masses/substrate replicate of 7.8 (31/4), 1.9 (29/15), 6.5 (26/4), 1.8 (23/13), 2.1(19/9), 2.4 (17/7), 3.8 (15/4), and 3.5 (14/4), respectively. Metal fence posts and northern spice bush yielded a higher number of egg masses per substrate replicate when compared with tree-of-heaven. These eight occasional substrate types combined for 28.8% (60/208) of the total substrate replicates utilized and 26.2% (174/663) of the total egg masses collected (Table 3). The remaining 12 substrate types (black locust—*Robinia pseudoacacia* L. [Fabales: Fabaceae], silver maple, blackhaw—*Viburnum prunifolium* L. [Dipsacales: Adoxaceae], shagbark hickory—*Carya ovata* (Mill.) K. Koch [Fagales: Juglandaceae], white ash river birch—*B. nigra* L. [Fagales: Betulaceae], Norway maple—*A. platanoides* L. [Sapindales: Sapindaceae], eastern white pine—*Pinus strobus* L. [Pinales: Pinaceae], flowering dogwood, boxelder—*A. negundo* L. [Sapindales: Sapindaceae], American hophornbeam—*Ostrya virginiana* (Mill.) K. Koch [Fagales: Betulaceae], and sassafras) were rarely utilized, with a total of 35 egg masses collected from 18 substrate replicates (Table 3).

Dominant oviposition substrate types varied from study plot to study plot. Tree-of-heaven dominated study plots Lutz, Straub, Conrad, Kulps, Huffs, and HCWest with 50, 40, 74, 35, 43, and 87% of the total egg masses collected from 46, 38, 29, 23, 29, and 43% of the total substrate replicates, respectively. Black cherry was the preferred substrate type at study plots ODSouth and HCEast with 81 and 65% of the total egg masses collected from 67 to 15% of the total substrate replicates, whereas black birch dominated study plots Rolling and Nuss with 78 and 41% of the total egg masses from 86 to 33% of the total substrate replicates, respectively (Fig. 1A and B). Sweet cherry was the only substrate type utilized at study plot WSWest (Fig. 1B). Yellow birch and metal fence post was the dominant substrate type at study plots Rock (40%) and WSEast (33%), accounting for 35 and 54% of the total egg masses collected, respectively (Fig. 1 A and B). Tulip tree and blackhaw were equally utilized as oviposition substrates at study plot ODNorth based on the number of egg masses collected and substrate replicates utilized (Fig. 1B).

Egg Mass Density

Trees, shrubs, and nonliving materials of all sizes were utilized as oviposition substrates by *L. delicatula* females. For tree-of-heaven, DMH ranged from 2.5 to 53.3 cm with a surface area of 0.16–3.35 m^2. For black cherry, black birch, and sweet birch, trees with a DMH of 5.1 to 27.9, 1.3 to 30.5, and 2.5 to 35.6 cm were used for oviposition, resulting in a surface area of 0.32–1.75, 0.08–1.91, and 0.16–2.23 m^2, respectively. For the eight occasional substrate types, DMH ranged from 5.1 to 35.6, 10.2 to 20.3, 2.5 to 12.7, 7.6 to 76.2, and 5.1 to 81.3 cm, with a surface area of 0.32–2.23, 0.64–1.28, 0.16–0.80, 0.48–4.79, and 0.32–5.10 m^2 for yellow birch, red maple, American hornbeam, tulip tree, and northern read oak, respectively. Northern spice bush had small surface areas (0.08–0.16 m^2) due to the smaller DMHs (1.3–2.5 cm). Small surface areas were also observed on stones (0.06–0.12 m^2 ranged from 30 to 40 cm in length and 20–30 cm in width) and metal fence posts (GRN UPC Green Steel Farm Fence T-Post Post) (0.23 m^2 with the dimension of 7.62 × 152.4 cm (width by length) for the above ground portion, both sides). The surface area ranged from 0.16 to 3.77 m^2 (DMH of 2.5–60.1 cm) for the 12 rarely used substrate types with one to three replicates per substrate type.

Lycorma delicatula egg mass density ranged from 0.2 to 75.2 egg masses/m^2 based on analysis of field-collected eggs in PA between 2016 and 2017. Average egg mass density was 6.0 and 6.7 egg masses/m^2 for 2016 and 2017, respectively, with no significant difference between sampling years (χ^2 = 0.489, df = 1, P = 0.489) (Fig. 2A). However, significant differences were observed by study plot (χ^2 = 39.511, df = 13, P < 0.001) and oviposition substrate type (χ^2 = 59.254, df = 23, P < 0.001), with the average density ranging from 2.3 to 32.5 egg masses/m^2 and 0.2 to 45.4 egg masses/m^2 for study plot and substrate type, respectively (Fig. 2B&C).

Egg mass density was higher at study plots ODSouth (32.5), WSWest (29.6), WSEast (23.1), and HCWest (10.5) while less than 10 egg masses/m^2 was observed at the rest of the study plots (Fig. 2B). Results of pairwise comparisons showed that a significant difference (α = 0.05) was found between study plots ODSouth and Rolling, as well as WSEast and Rock. No significant differences were found between any other study plots (Fig. 2B). WSWest was not included in any pairwise comparisons because a single substrate replicate was utilized at this study plot (Fig. 2B).

Results of pairwise comparisons showed no significant difference in egg mass density between oviposition substrate types (α = 0.05), although relatively higher densities were found on northern spice bush (45.4), stone (36.1), metal fence post (33.4), blackhaw (10.4), black cherry (9.6), black locust (8.6), American hornbeam (7.3), and sweet cherry (5.3) when compared with tree-of-heaven (5.1) (Fig. 2C). River birch, silver maple, Norway maple, boxelder, American hophornbeam, sassafras, eastern white pine, and blackhaw were not included in any pairwise comparisons because of single substrate replicate (Fig. 2C).

Egg Mass Size

Lycorma delicatula egg mass size ranged from 0 to 192 per egg mass in Pennsylvania based on the 2016–2017 field collections (Fig. 3). Three egg masses (one from Nuss and two from Kulps) contained no eggs although covered by a layer of wax. Most egg masses (91.8%) contained less than 50 eggs, with 73.8% having 20–50 eggs and 18% had < 20 eggs/egg mass (Fig. 3). Seven egg masses containing more than >100 eggs/egg mass were found at study plot WSWest, while six egg masses with more than 80 eggs/egg mass were collected at study plots ODSouth (3), WSEast (2), and Lutz (1) (Fig. 3). Significant difference in egg mass size was observed for sampling year (χ^2 = 4.189, df = 1, P = 0.041), study plot (χ^2 = 50.147, df = 13, P < 0.001) and oviposition substrate type (χ^2 = 63.488, df = 23, P < 0.001). Egg mass size is significantly larger (α = 0.05) in 2017 compared to 2016, with an average of 34.7 and 31.6 eggs/egg mass, respectively.

The average egg mass size ranged from 27.1 eggs/mass at study plot Straub to 49.4 eggs/mass at plot WSWest. Results of pairwise comparisons showed that egg masses at study plot WSWest were significantly larger (α = 0.05) than those at study plots HCWest (29.0), Straub (27.1), and Lutz (28.0); whereas egg masses were significantly larger at study plot HCWest compared with those at study plots Straub and Lutz. No significant differences in egg mass size were found between the other study plots.

Significantly larger (α = 0.05) egg masses were found on sweet cherry and black cherry than on tree-of-heaven, with an average size of 46.0, 36.4, and 27.6 eggs/mass, respectively. Other oviposition substrate types with large egg masses include eastern white

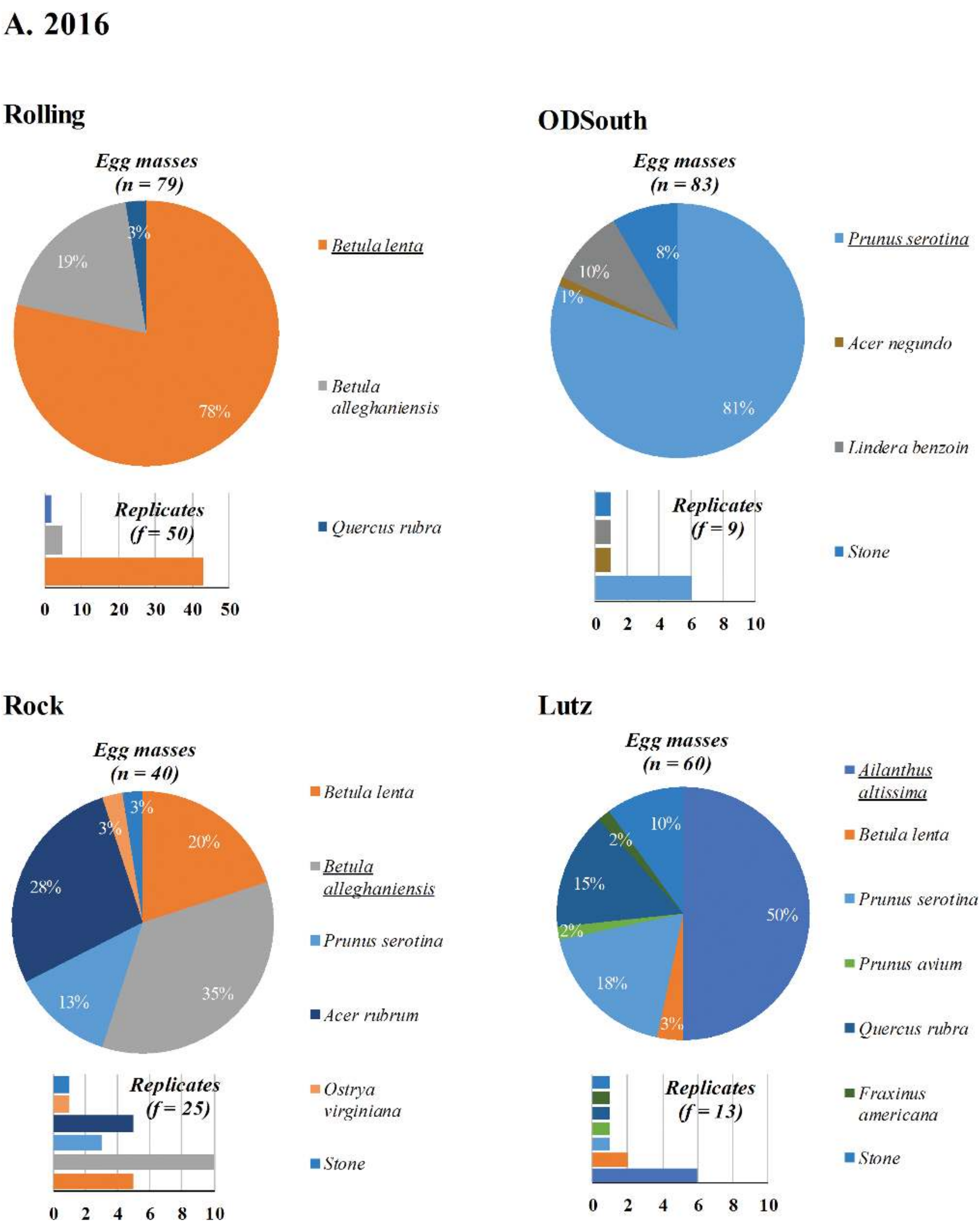


Fig. 1. Oviposition substrate selection for *Lycorma delicatula* based on number of egg masses collected and substrate replicates utilized in Pennsylvania. (A) 2016 and (B) 2017.

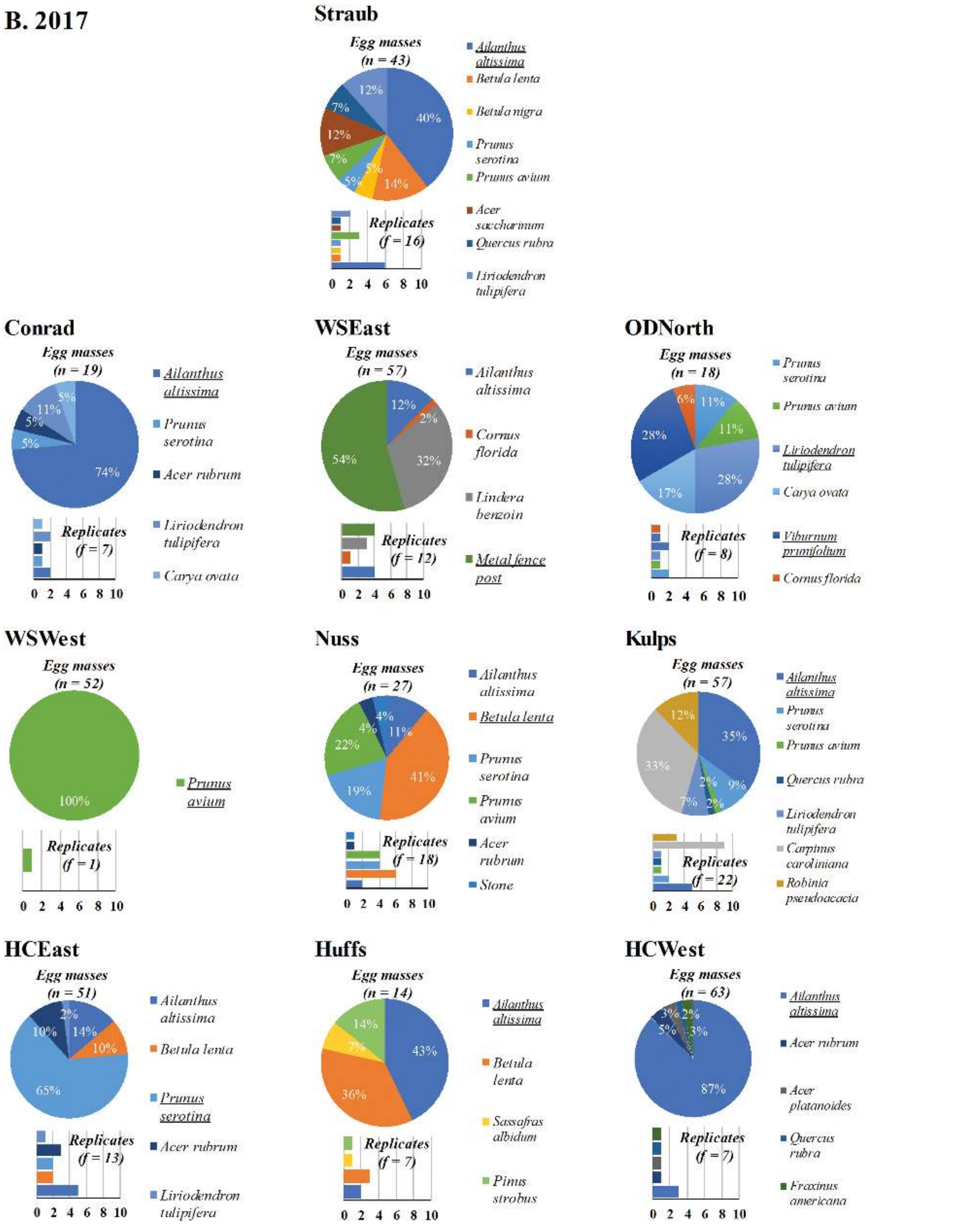


Fig. 1. Continued

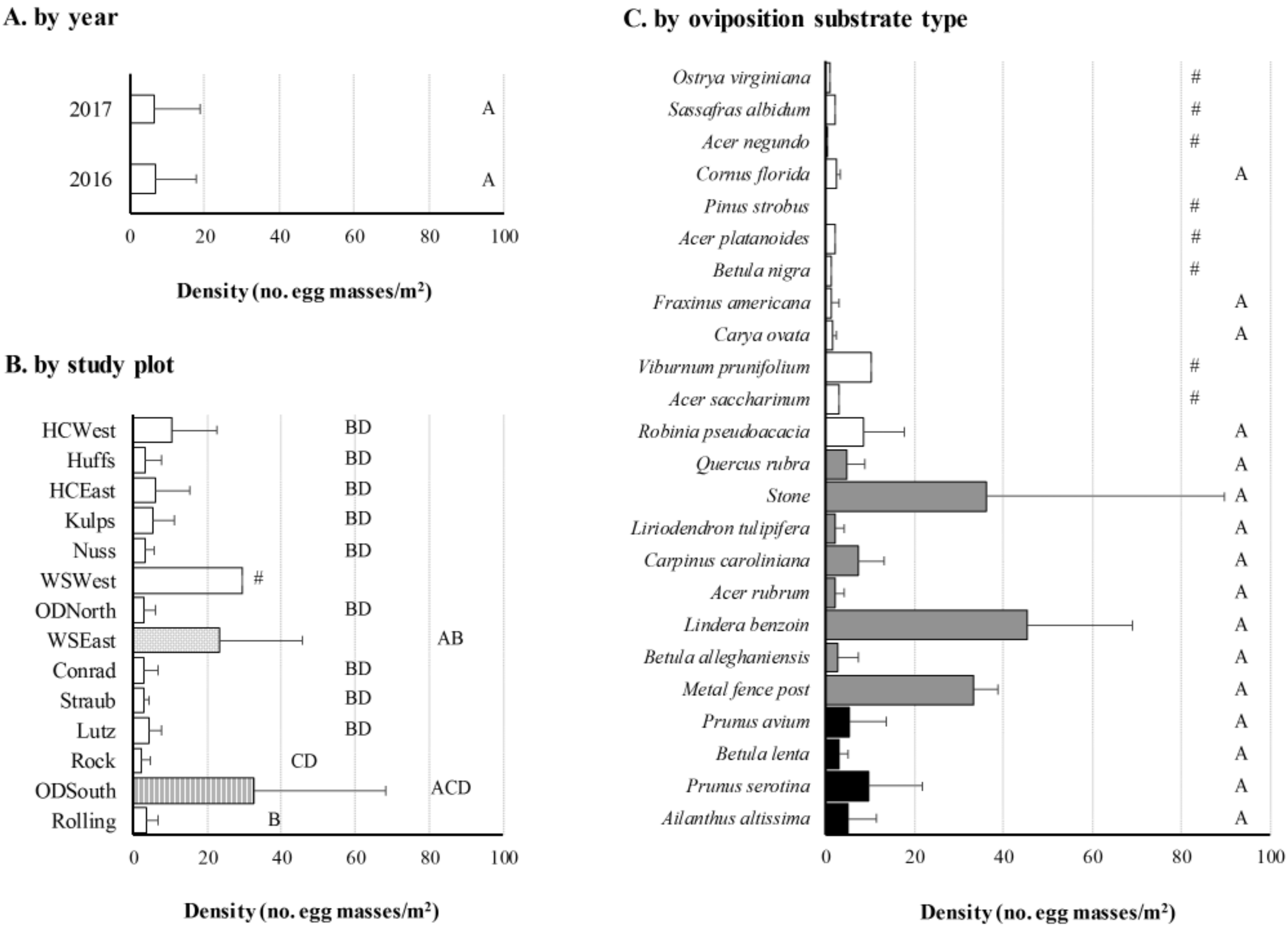


Fig. 2. *Lycorma delicatula* egg mass density (no. egg masses/m^2) by sampling year, study plot, and oviposition substrate type in Pennsylvania 2016–2017. (A) By year, (B) by study plot, (C) by oviposition substrate type. Means followed by the same uppercase letters within the same category are not significant different (pairwise Wilcoxon rank-sum test with the Benjamini–Hochberg adjustment, $P < 0.05$). Oviposition substrate type shaded differently to show selection preference by females for oviposition (black-highly utilized, gray-occasional, and none-rarely used). "#" sign indicates single substrate replicate.

pine (48.0), black locust (40.3), metal fence posts (39.0), flowering dogwood (37.5), northern spice bush (36.7), American hornbeam (36.6), and white ash (35.7). However, no significant difference was detected between any other pair of substrate types. Three substrate types (sassafras, American hophornbeam, and boxelder) yielded only a single egg mass.

Egg Hatch in the Laboratory

The three egg masses that contained no eggs were excluded from the egg hatch study in the laboratory. Egg hatch started within 2 wk after incubation and lasted for about 2 wk, with peak hatch at the mid-point of that period. Overall, the egg hatch success ranged from 0 to 100% for eggs collected in the spring of 2016 and 2017. Average egg hatch success was 23.4 and 34.0% for 2016 and 2017, respectively, with a significant difference between sampling years ($\chi^2 = 382.51$, df = 1, $P < 0.001$). Significant differences were also observed for study plot ($\chi^2 = 1{,}343.7$, df = 13, $P < 0.001$) and oviposition substrate type ($\chi^2 = 1{,}895.2$, df = 23, $P < 0.001$), with average egg hatch success ranged from 13.5 to 52.6% and 0 to 79.6% for study plot and substrate type, respectively (Fig. 4).

Results of pairwise comparisons show that egg hatch success was significantly higher ($\alpha = 0.05$) at study plot WSEast compared with other study plots except for Rolling and ODSouth, where 52.6% eggs hatched after 2 mo of incubation in the laboratory (Fig. 4B). On the other hand, egg hatch success was significantly lower at study plot Lutz (13.5%) than the rest (Fig. 4B). Significant differences in egg hatch success was also found between a few other study plots (Fig. 4B).

Only 23% of eggs from tree-of-heaven hatched, whereas 79.6% of eggs from black locust hatched after two months of incubation. No eggs from American hophornbeam and eastern white pine hatched (Fig. 4C). Significant differences ($\alpha = 0.05$) in egg hatch successes were observed between black locust and tree-of-heaven and the rest of the oviposition substrate types, while no significant differences were found among all other substrate types (Fig. 4C). Other substrate types with relatively high egg hatch success include metal fence posts (68.8%), silver maple (55.5%), flowering dogwood (46.2%), white ash (45.7%), sassafras (45.5%), northern spice bush (43.0%), and boxelder (42.9%). Less than 40% of the eggs hatched from all other substrate types, with only 15.4, 15.5, 15.9, and 18.0% of eggs hatched for collections made on blackhaw, northern red oak, river birch, and black cherry, respectively (Fig. 4C). Eastern white pine, boxelder, and American hophornbeam were not included in any pairwise comparisons because of single substrate replicate (Fig. 4C).

Egg Hatch in the Field

Lycorma delicatula egg hatch in the field was first observed on 2 May and last observed on 5 June at study plot ODSouth in 2017, with an overall peak on 18 May (Fig. 5). Egg hatch was observed

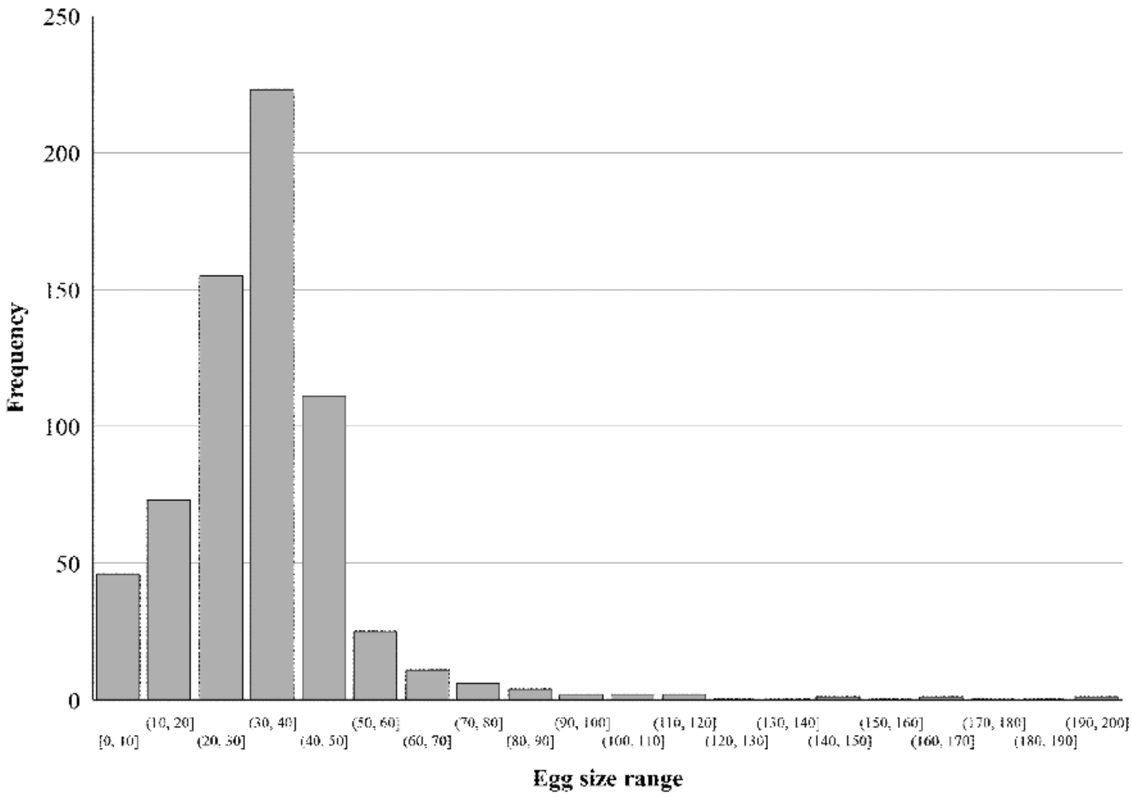


Fig. 3. *Lycorma delicatula* egg mass size (no. of eggs/egg mass) by frequency in Pennsylvania 2016–2017.

at about the same time on all four oviposition substrate types although lasted a little shorter on substrate type C, while variations in secondary peaks were observed for substrate types B and D compared with that of substrate types A and C (Fig. 5). Overall, 68.2% of the eggs hatched for the 41 egg masses monitored in the field at study plot ODSouth in 2017. Hatch success ranged from 0 to 100%, with an average of 66.3, 84.2, 51.2, and 66.3% (range 0–100%, 68.8–100%, 15.2–83.3%, and 38.8–90.7%) for live white ash, dead flowering dogwood, live black cherry, and live flowering dogwood, respectively (Table 4), Significant differences in egg hatch success were detected among different types of oviposition substrates (χ^2 = 130.970, df = 3, $P < 0.001$), with significantly higher and lower success observed on dead flowering dogwood and live black cherry, respectively ($P < 0.01$) (Table 4). No significant differences in egg hatch success were observed between live white ash and live flowering dogwood (Table 4).

Host Preference for Nymphs and Adults

Lycorma delicatula fed on a variety of hosts as early instars, gradually congregated on certain plants as they grew, and aggregated on a few favored tree species by the adult stage (Fig. 6). A total of nine host species (flowering dogwood, tree-of-heaven, black walnut, black cherry, sassafras, white ash, multiflora rose, summer grape, and oriental bittersweet) were recorded for the first instars (Fig. 6A). Only six of the host species were recorded in the second instars (Fig. 6B), and four of those species for third, fourth, and adults, respectively (Fig. 6C–E). Tree-of-heaven, summer grape, black walnut, and multiflora rose were favored for *L. delicatula* although their significance varied between stages. Black cherry, sassafras, and white ash were only used by the first instars, whereas flowering dogwood and oriental bittersweet were fed upon by both the first and second instars (Fig. 6A and B). Flowering dogwood and tree-of-heaven were the favored hosts for younger first instar nymphs in late May, but they gradually moved to multiflora rose and oriental bittersweet by mid-June. Summer grape appeared to be an important host in late June for older first instars (Fig. 6A). Most second instar nymphs fed on tree-of-heaven and multiflora rose in early to mid-June. They then moved almost exclusively to summer grape by late June (Fig. 6B). Summer grape became the most favored host for early third instar nymphs followed by tree-of-heaven in early to mid-July (Fig. 6C). Black walnut became the dominant host for fourth instar nymphs in late July and early August, although tree-of-heaven is a consistent host throughout the stage (Fig. 6D). By mid-August to late August, adults concentrated on tree-of-heaven while a sizable portion of the population remain on summer grape (Fig. 6E).

Seasonal Development and Life History

Results of field egg hatch at study plot ODSouth in 2017 showed that *L. delicatula* eggs first hatched on 2 May 2017 (Fig. 5), although first instar nymphs were not detected on the monitored host trees, shrubs, and vines until 25 May during periodical surveys in the field (Fig. 7). All *L. delicatula* nymphs observed in the field were first instars until 5 June. The second instar nymphs were first found on 8 June and peaked on 22 June and accounted for 99% of the population observed. The third instar nymphs were first found on 26 June and peaked on 6 July when they made up 95% of the population observed, and the fourth instar nymphs first found on 10 July and peaked on 31 July with 95% of the population observed (Fig. 7). The first adult was discovered on 24 July. By 22 August, 100% of the population observed were adults. The first egg mass was observed on 2 October (Fig. 7). Maturation feeding lasted for at least 2 mo between the emergence of the first adult in late July and the deposition of the first egg mass in early October.

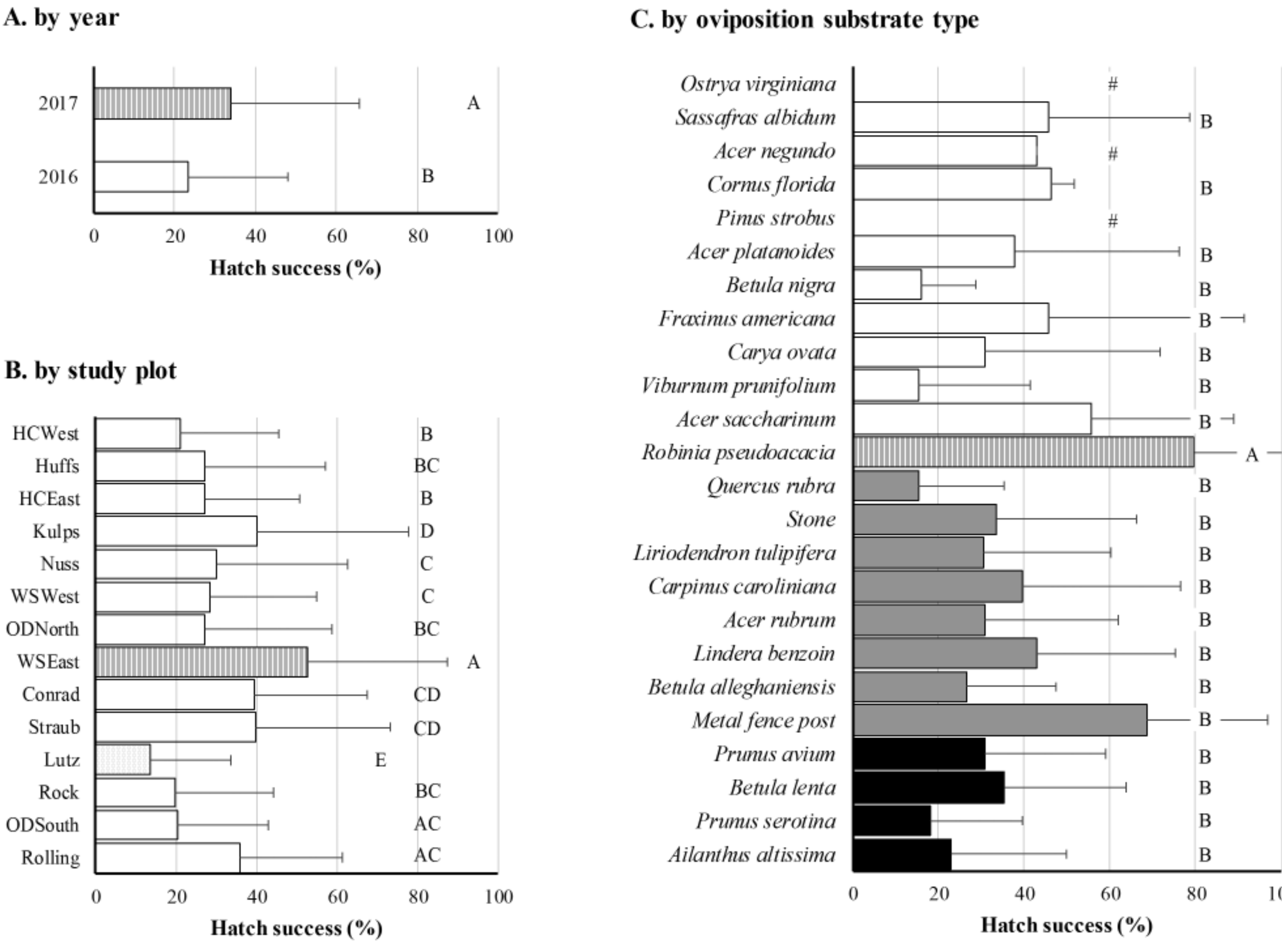


Fig. 4. *Lycorma delicatula* egg hatch success (%) in the laboratory by sampling year, study plot, and oviposition substrate type in Pennsylvania 2016–2017. (A) By year, (B) by study plot, (C) by oviposition substrate type. Means followed by the same uppercase letters within the same category are not significant different (Pearson's χ^2 pairwise comparison, $P < 0.05$). Count data were used in analysis although percent data were presented here. Oviposition substrate type shaded differently to show selection preference by females for oviposition (black-highly utilized, gray-occasional, and none- rarely used). "#" sign indicates single substrate replicate.

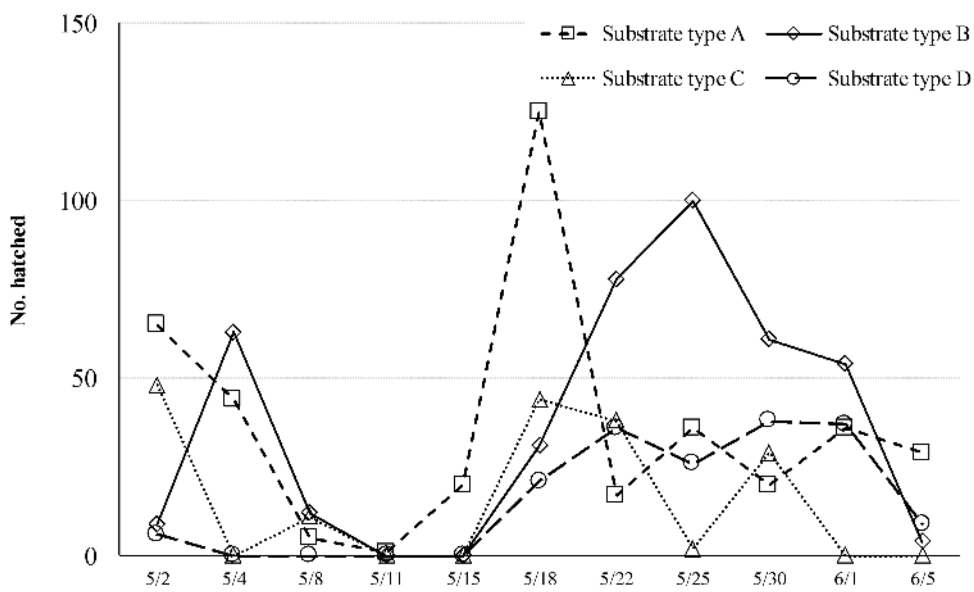


Fig. 5. *Lycorma delicatula* egg hatch on different substrate types at study plot ODSouth in Pennsylvania 2017.

Table 4. *Lycorma delicatula* egg hatch success (%) in the field by oviposition substrate type at study plot ODSouth in Pennsylvania 2017

Substrate type	Species	Diameter at breast height (cm)	No. egg masses	No. eggs	Egg hatch success (%) (Mean ± stdev)
A	White ash (live)	25.4	16	600	66.3 ± 33.8 b
B	Flowering dogwood (dead)	30.8	11	503	84.2 ± 9.7 a
C	Black cherry (live)	17.8	9	378	51.2 ± 24.7 c
D	Flowering dogwood (live)	35.6	5	245	66.3 ± 33.8 b
Total			41	1726	68.2 ± 28.5

Note: means followed by the same lowercase letters are not significantly different (Pearson's pairwise Chi-squared test with the Benjamini–Hochberg adjustment, $P < 0.001$).

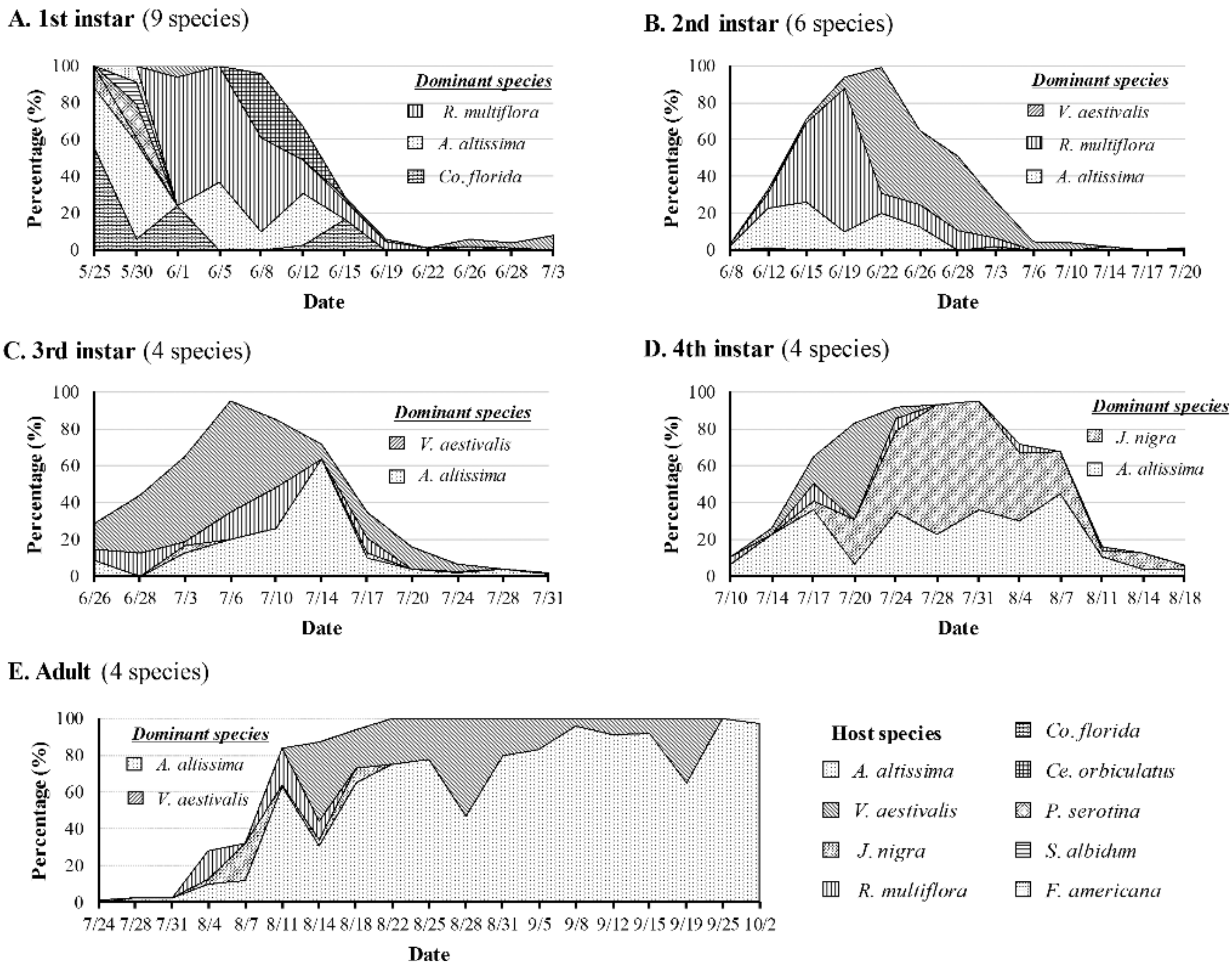


Fig. 6. Host preference of *Lycorma delicatula* nymphs and adults at study plot ODSouth in Pennsylvania 2017.

A life history table was constructed based on the combined information from the monitoring of egg hatch, seasonal development of nymphs and adults, as well as random field observations on all life stages throughout the year (Table 5). The life table shows that the first instar nymphs lasted for 62 d between 2 May and 3 July with peak population on 25 May, and the second instars lasted for 42 d from 8 June and 20 July, peaking on 22 June. The third and fourth instar nymphs and adults lasted for 35, 39, and 114 d between 26 June and 31 July (peak on 6 July), 10 July and 18 Aug. (peak on 31 July), and 24 July and 15 Nov. (peak on 22 Aug.), respectively (Table 5). Egg masses of the new generation were first observed on 2 October and could potentially last for 7–8 mo (Table 5, Figs. 5 and 7).

The $CUMDD_{10}$ for the egg stage ranged from 0 to 325 with peak hatch at 210. The $CUMDD_{10}$ for other life stages were 153–652 (peak at 254), 340–881 (peak at 519), 567–1,020 (peak at 690), 738–1,227 (peak at 1,020), and 942–1,795 (peak at 1,278) the first, second, third, fourth instar, and adult stage, respectively (Table 5).

Discussion

Oviposition substrate selection is crucial to the reproductive success of herbivorous insects. The optimal oviposition theory (i.e., preference-performance hypothesis) predicts correlation between oviposition preference by females and host suitability for offspring

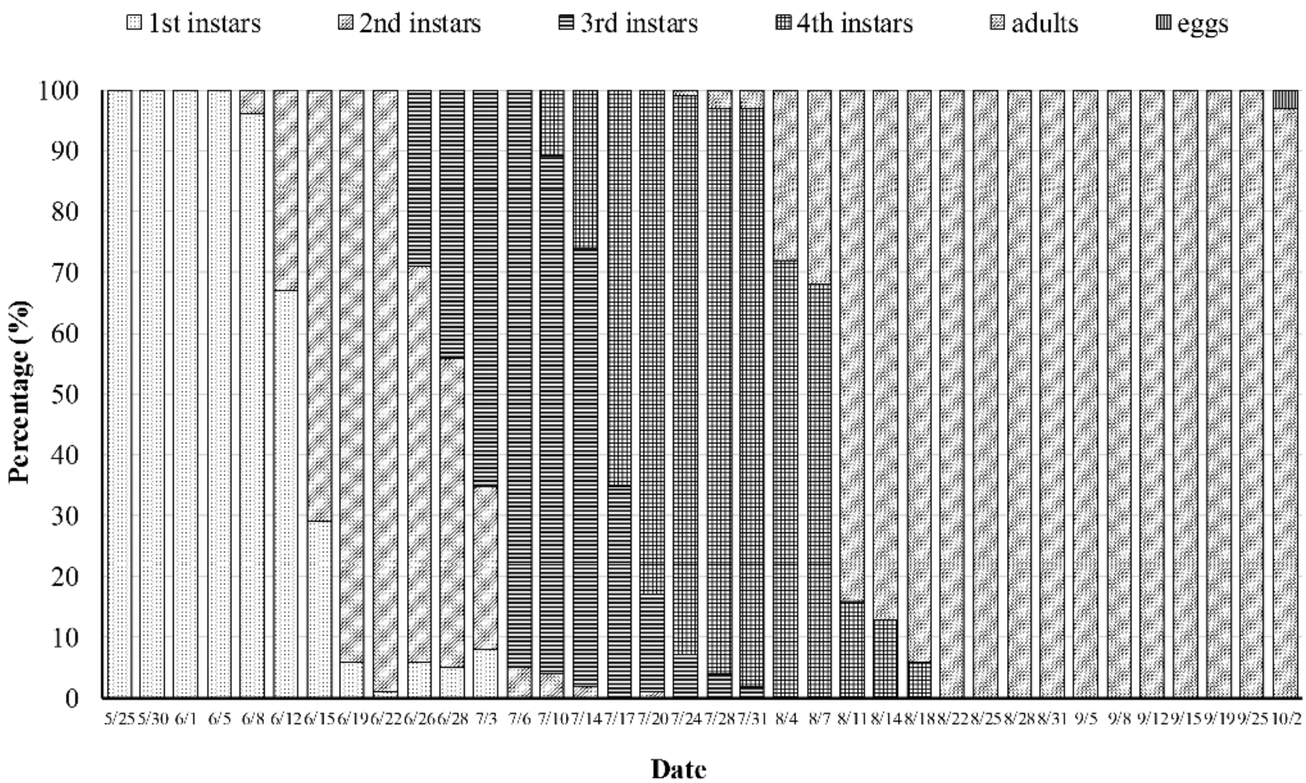


Fig. 7. Seasonal development of *Lycorma delicatula* at study plot ODSouth in Pennsylvania 2017.

development (Jaenike 1978). However, it does not work well for species in instances where the adults feed on different hosts from the immature life stages (Fujiyama 2008). Alternatively, the optimal foraging theory anticipates maximized female fitness through the optimization of adult performance (longevity and fecundity) on its preferred hosts, even at the expense of the offspring (Jaenike 1986; Scheirs et al. 2000, 2004; Mayhew 2001; Scheirs and De Bruyn 2002; Adar and Dor 2018). As a polyphagous species with mobile nymphs and adults, *L. delicatula* uses a wide range of substrates for oviposition (Tables 1 and 3). Nymphs and adults feed on a broad list of hosts at different stages (Table 2, Fig. 6). This kind of oviposition and development patterns could not be fully explained by either theory.

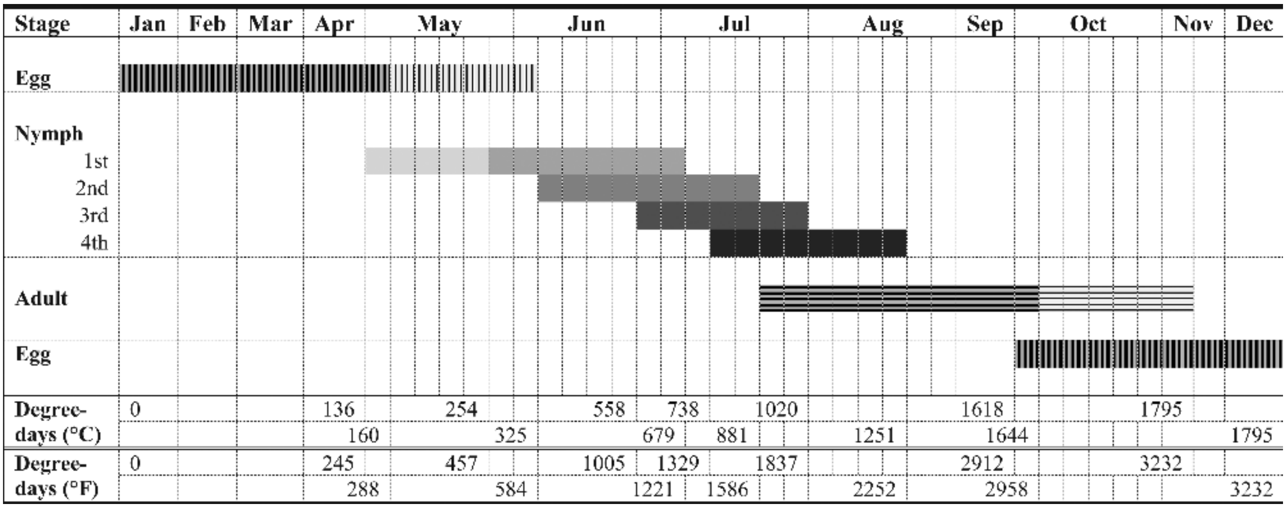
The list of the oviposition substrates reported by this study (Table 3) is a large expansion from what has been reported by Dara et al. (2015) in North America. Egg masses were also found on nonliving materials (Table 3). While the dominant substrate types varied from plot to plot, tree-of-heaven, black cherry, black birch, and sweet cherry were generally used more often by *L. delicatula* females (Table 3). Top substrate types in South Korea included tree-of-heaven, Japanese zelkova, Japanese maple, white poplar, oriental and Yoshino cherry, and Siberian silver birch (Kim et al. 2011), and egg masses were usually found on black locust and sawtooth oak in addition to tree-of-heaven in Japan (Tomisawa et al. 2013). Tree-of-heaven and black locust were the only two common substrate types between Asia and North America, although different species of birch, cherry, and oak were listed (Tables 1 and 3).

Surface-area-based egg mass density has been used previously to estimate egg massdensity for spruce budworm (*Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (Fowler and Simmons 1982) and Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Erebidae) (Luck and Dahlsten 1967). It is a useful tool in describing and comparing pest populations on specific oviposition substrate types. Results in this study is based on data from any surface 200 cm above ground and might not represent the complete picture of some substrate types where egg masses are found on higher locations. As a general field egg mass survey on *L. delicatula*, however, a gypsy moth (*Lymantria dispar* (L.) (Lepidoptera: Erebidae)) model might be more appropriate due to the obvious similarities in oviposition substrate selection patterns between these two species. In these surveys, egg mass density is measured by the total number of egg masses per hectare of land found during a fixed-radius or a timed walk survey (Kolodny-Hirsch 1986, Fleischer et al. 1991, Thorpe and Ridgway 1992, Carter et al. 1994, Carter and Ravlin 1995). Knowledge of the temporal and spatial distribution of *L. delicatula* egg masses in the field could provide a basis for the development of such a sampling scheme.

An average size of 30.7 eggs/egg mass was reported in Japan (Tomisawa et al. 2013). The significant difference in egg mass size between study plots and substrate types found in this study could be the result of the few extra-large egg masses. We do not know, however, why the extra-large egg masses appeared on specific trees at those plots. Significantly larger egg masses were found in 2017 compared with 2016, which could be indicative of increasing population based on the theory by Liebhold et al. (1994) on gypsy moth.

In China, about 80% of eggs on tree-of-heaven hatched, comparing to only 2–3% of eggs on pagoda tree and elms (Zhou 1992). Significantly higher hatch success in the laboratory was observed for egg masses collected from black locust compared with tree-of-heaven in this study, possibly the result of lower winter mortality due to its protective corky bark (Fig. 4C). A field egg hatch success of 33.1–84.3% was observed in South Korea, with a strong positive correlation between egg hatch success and the minimal and mean temperatures in January (Park 2015). Minimum winter temperature

Table 5. *Lycorma delicatula* life history table and age-specific cumulative growing degree-days (online phenology and degree-day models at http://uspest.org/wea/) in the field in Pennsylvania 2017.



Lycorma delicatula life history table was constructed based on data from studies on field egg hatch monitoring (2 May–5 June), seasonal development of nymphs and adults (25 May 25–2 Oct), as well as random field observations on all life stages throughout the year. Different shading patterns within the same life stage indicates different observation methods.

Cumulative growing degree-days were calculated based on simple average with a lower threshold of 10°C (50°F) and a high threshold of 35°C (95°F) at weather station D9872 APRSWXNET DW9872 in Oley, Pennsylvania (40.40000N, 75.71530W, elevation: 130 m (427 feet)). Growing season at this site started on 19 Feb. and ended on 6 Nov. 2017 (Online Phenology and Degree-day Models at http://uspest.org/wea/)

also had an impact on *L. delicatula* egg mortality (Lee et al. 2011). Field egg hatch success ranged from 51.5 to 84.2% on different trees at ODSouth in this study (Table 4). Variation in egg hatch success on different types of oviposition substrates and the role of extreme winter temperature in egg hatch of *L. delicatula* in the field deserves more investigation.

While tree-of-heaven was utilized by all stages of nymphs and adults based on results of these host preference studies, other hosts such as flowering dogwood, multiflora rose, oriental bittersweet, summer grape, and black walnut all played important roles in the life cycle of *L. delicatula* (Fig. 6). There was also a clear trend of a narrowing number of utilized host species from the younger nymph stages to adult stages (Fig. 6). Red maple was not a part of the current study but was nonetheless one of the highly-utilized hosts for adult aggregation at one location (Liu, personal observation). Massive feeding, mating, and dispersal flights were also recorded on apple trees in an orchard in northeast Pennsylvania in 2017 (Myrick and Baker 2019). The broad range of hosts that was observed for early instars may be related to the diverse oviposition substrate types and habitats selected by the *L. delicatula* females. More study on a balanced selection of species at multiple field plots could shed more light on host preference and aggregation patterns for nymphs and adults.

The proximity to suitable habitat for the offspring hypothesis states that oviposition decisions by females have a great impact on larval defense sequestration, predation evasion, mixed nutrient acquisition, host synchronization, and interspecific competition (Refsnider and Janzen 2010). It is a better model for species capable of migration as immatures. Ballabeni et al. (2001) showed that female alpine leaf beetle, *Oreina elongata* (Suffrian) (Coleoptera: Chrysomelidae), would select a less suitable host that was situated next to a preferred host to achieve maximum egg survival. Larval migration to the preferred host resulted in better development and the necessary sequestration of defensive chemical pyrrolizidine alkaloids that are found only on the preferred host. A similar argument could also be made for *L. delicatula* as eggs survived better on other types of oviposition substrates compared to tree-of-heaven based on egg hatch success (Fig. 4C). In addition, the color change in *L. delicatula* fourth instar is directly related to the defense sequestration as it congregates primarily on tree-of-heaven (Song et al. 2018). Tree-of-heaven contains large amount of quassinoids (De Feo et al. 2003). Quassinoids are a group of compounds possessing antimalarial, antifeeding, insecticidal, anti-flammatory, and anticancer properties extracted from plants in the Simaroubaceae family (Polonsky 1973, Vieira and Braz-Filho 2006, Fiaschetti et al. 2011). Predatory birds such as the great tit (*Parus major minor* L. [Passeriformes: Paridae]) would feed on *L. delicatula* nymphs and adults collected from Korean willow (*Salix koreensis* Andersson [Malpighiales: Salicaceae]) but generally avoid those from tree-of-heaven (Song et al. 2018). The ability to develop on a wide range of hosts in different life stages, to migrate freely between common hosts, and to aggregate on consistent hosts make this type of development pattern possible for *L. delicatula*.

Seasonal development of *L. delicatula* in North America is more in line with that of South Korea and Japan than China, especially if the starting dates of adult emergence and egg deposition are considered. Adults first appear in late July, and eggs were found in early October in Pennsylvania based on the current study, whereas those events occurred in mid-June and mid-August around Xi'an city (34.34160N, 108.93980E) in Shanxi, China (Zhou 1992); late July and mid-September in Komatsu city (36.40840N, 136.44590E) in Ishikawa, Japan (Tomisawa et al. 2013); early July and late September in Hongneung Arboretum (37.59350N, 127.04400E) in Seoul, South Korea (Park et al. 2009); and early August and mid-September in Okcheon county (36.30640N, 127.57130E) in Chungbuk, South Korea (Lee et al. 2011). Difference in climate conditions due to geographical locations in the study areas likely contribute to discrepancies.

In South Korea, a total of 355 cumulative degree-days based on the threshold of 8.1°C ($CUMDD_{8.1}$) was predicted for egg hatch by one study (Choi et al. 2012). In another study carried out in Cheonan city (36.86667N, 127.16667E) in South Chungcheong, the first, second, third, and fourth instars, and adults lasted from 11 May to 15 July, 25 May to 29 July, 15 June to 19 Aug., 6 July to Aug. 25, and 27 July to 26 Oct. between 2010 and 2012, with estimated cumulative degree-days based on the threshold of 11.1°C ($CUMDD_{11.1}$) of 271, 492, 620, 908, and 1,820 for the peak populations, respectively (Park 2015). If converted to the $CUMDD_{10}$ model, the development of *L. delicatula* in South Korea will be similar to that in North America for the nymphs while adults need more time to reach peak populations (Table 5).

Results from this study could have profound impacts on the development of survey and detection tools, biology and phenology, host preference, and integrated management of *L. delicatula* in North America. Egg mass detection surveys should start with tree-of-heaven since it is still one of the primary oviposition substrate types. However, other substrate types (highly utilized, occasional, and even rarely used) near tree-of-heaven within the habitat should also be examined carefully since *L. delicatula* does not need to lay eggs on tree-of-heaven to ensure offspring success. Standardized and quantifiable surveys of egg mass density could be used to describe infestation level and compare populations, and egg mass size is an important parameter in predicting population trends. While newly hatched nymphs are usually confined on or near the original oviposition substrates, older nymphs and adults feed on a wide range of hosts at different stages, migrate freely between highly utilized hosts, and aggregate on consistent hosts. Adults need at least a couple of months to mature while acquiring necessary nutrients. Seasonal development and life history data can help predict occurrence of specific pest stages in the field. Management approaches need to adapt to accommodate the oviposition selection strategies and development patterns of *L. delicatula*. Egg scraping and tree banding as mechanical control tools may not be very efficient due to variations in oviposition substrate types and migration between hosts for nymphs and adults. A host removal program that is concentrated on tree-of-heaven, however, could be very important as this tree serves as one of the primary hosts for *L. delicatula* throughout its life cycle. Chemical control should target adults aggregating on certain hosts before females starting to lay eggs. An integrated approach with selective host tree removal, focused mechanical control, targeted chemical control, and potential biological control could potentially bring *L. delicatula* populations under control in North America.

Acknowledgments

I thank Mary Rowse, George Lang, Steffan Helbig, Gary Weller, Mancini Robert, Dave Straub, Laszlo Lengyel, Paul Gierschick, William Blair, Adrianne Blank, Steve Moyer, Frank Morgan, Louis Farina, and Piper Sherbourne for access to the study plots; Zachary Clemens, Gina Peters, Paul Smith, Brian Liu, Mark Faulkenberry, Fengyou Jia, and Thomas Hall for laboratory and field assistance; Sven-Erik Spichiger and John Baker (Pennsylvania Department of Agriculture) for logistic support and tree-of-heaven distribution and treatment information; and two anonymous reviewers for valuable comments. This research was funded by USDA Farm Bill awards from 2016-2017 and Farm Bill #AP17PPQS&T00C057 and supported by the Pennsylvania Department of Conservation and Natural Resources.

References Cited

Adar, S., and R. Dor. 2018. Mother doesn't always know best: Maternal wormlion choice of oviposition habitat does not match larval habitat choice. Behav. Processes. 147: 1–4.

Ballabeni. P., D. Conconi, S. Gateff, and M. Rahier. 2001. Spatial proximity between two host plant species influences oviposition and larval distribution in a leaf beetle. Oikos. 92: 225–234.

Barringer L. E, and E. Smyers. 2016. Predation of the spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae) by two native Hemiptera. Entomol. News 126: 70–72.

Barringer, L. E., L. R. Donovall, S-E. Spichiger, D. Lynch, and D. Henry. 2015. The first New World record of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae). Entomol. News 125: 20–23.

Carter, J. L., and W. F. Ravlin. 1995. Evaluation of binomial egg mass sampling plans for low density gypsy moth populations in continuously forest habitats. J. Econ. Entomol. 88: 890–896.

Carter, J. L., W. F. Ravlin, D. R. Gra, M. R. Carter, and C. W. Coakley. 1994. Foliage presence and absence effect on gypsy moth (Lepidoptera: Lymantriidae) egg mass sample counts and the probability of exceeding action thresholds with foliage present. J. Econ. Entomol. 87: 1004–1007.

Choi, D. S., D. I. Kim, S. J. Ko, B. R. Kang, J. D. Park, S. G. Kim, and K. J. Choi. 2012. Environmentally-friendly control methods and forecasting the hatching time *Lycorma delicatula* (Hemiptera: Fulgoridae) in Jeonnam Province. Korean J. Appl. Entomol. 51: 371–376.

Chou I. 1946. A study on *Lycorma delicatula* White (Hemiptera: Fulgoridae). Entomol. ARS. 1(2–4): 31–54.

Chou I, J. Lu, J. Huang, and S. Wang. 1985. Economic insect fauna of China, Fasc. 36, (Homoptera: Fulgoroidea), pp. 104–119. Science Press, Beijing, China.

Chu, H. J. 1930. Notes on the life history of *Lycorma delicatula* White in Nanking. Peking Nat. Hist. Bull. 5: 33–35.

Clifton, E. H., L. A. Castrillo, A. Gryganskyi, and A. E. Hajek. 2019. A pair of fungal pathogens drives decline of a new invasive herbivore. Proc. Natl. Acad. Sci. USA. 116: 9178–9180. doi:10.1073/pnas.1903579116.

Cooperband, M. F., R. Mack, and S-E. Spichiger. 2018. Chipping to destroy egg masses of the spotted lanternfly, *Lycorma delicatula* (Hempitera: Fulgoridae). J. Insect Sci. 18: 7, 1–3.

Cooperband, M. F., J. Wickham, K. Cleary, S. E. Spichiger, L. Zhang, J. Baker, I. Canlas, N. Derstine, and D. Carrillo. 2019. Discovery of three kairomones in relation to trap and lure development for spotted lanternfly (Hemiptera: Fulgoridae). J. Econ. Entomol. 112: 671–682.

Dara, S. K., L. Barringer, and S. P. Arthurs. 2015. *Lycorma delicatula* (Hemiptera: Fulgoridae): a new invasive pest in the United States. J. Integr. Pest Manag. 6(1): 20.

De Feo, V., L. De Martino, E. Quaranta, and C. Pizza. 2003. Isolation of phytotoxic compounds from tree-of-heaven (*Ailanthus altissima* Swingle). J. Agric. Food Chem. 51: 1177–1180.

Domingue, M. J., and T. C. Baker. 2019. Orientation of flight for physically disturbed spotted lanternflies, *Lycorma delicatula*, (Hemiptera, Fulgoridae). J. Asia-Pacific Entomol. 22: 117–120.

Fiaschetti G, M. A. Grotzer, T. Shalaby, D. Castelletti, and A. Arcaro. 2011. Quassinoids: from traditional drugs to new cancer therapeutics. Curr. Med. Chem. 18: 316–328.

Fleischer, S. J., F. W. Ravlin, and R. C. Reardon. 1991. Implementation of sequential sampling plans for gypsy moth (Lepidoptera: Lymantriidae) egg masses in eastern hardwood forests. J. Econ. Entomol. 84: 1100–1107.

Fowler, G. W., and G. A. Simmons. 1982. Spruce budworm egg mass density on Balsam fir: lower to extreme populations levels (Lepidoptera: Tortricidae). Great Lakes Entomol. 15: 277–286.

Fujiyama, N., C. Torii, M. Akabane, H. Katakura. 2008. Oviposition site selection by herbivorous beetles: a comparison of two thistle feeders: *Cassida rubiginosa* and *Henosepilachna niponica*. Entomol. Exp. Appl. 128: 41–48

Gao, Y. 1993. Study on high yield cultivation technique of Chinese pepper *(Zanthoxylum bungeanum)*. Econ. For. Res. 11(S1): 255–261.

Han, J. M., H. J. Kim, E. J. Lim, S. H. Lee, Y. J. Kwon, and S. W. Cho. 2008. *Lycorma delicatula* (Hemiptera: Auchenorrhyncha: Fulgoridae: Aphaeninae) finally, but suddenly arrived in Korea. Entomol. Res. 38: 281–286.

Hao, Y., C. H. Dietrich, and W. Dai. 2016. Structure and sensilla of the mouthparts of the spotted lanternfly *Lycorma delicatula* (Hemiptera: Fulgoromorpha: Fulgoridae), a polyphagous invasive planthopper. PLoS One. 11: e0156640.

Hong, H., and B. Li. 1994. Occurrence and control of major insect pests on Chinese kiwi fruit. Hubei Plant Protect. (3): 17–18.

Hou, Z. 2013. Study on the *Lycorma Delicatula* and egg parasitoids. MSc Thesis. Chinese Academy of Forestry, Beijing, China.

Jaenike, J. 1978. On optimal oviposition behavior in phytophagous insects. Theor. Popul. Biol. 14: 350–356.

Jaenike, J. 1986. Feeding behavior and future fecundity in *Drosophila*. Am. Nat. 127: 118–123.

Kim, S. S., and T. W. Kim. 2005. *Lycorma delicatula* (White) (Hemiptera: Fulgoridae) in Korea. Lucanus 5: 9–10.

Kim, J. G., E. H. Lee, Y. M. Seo, and N. Y. Kim. 2011. Cyclic behavior of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae) on host plants. J. Insect Behav. 24: 423-435.

Kolodny-Hirsch, D. M. 1986. Evaluation of methods for sampling gypsy moth (Lepidoptera: Lymantriidae) egg mass populations and development of sequential sampling plans. Environ. Entomol. 15: 122–127.

Leach, H., D. Biddinger, and G. Krawczyk. 2018. Spotted lanternfly management for homeowners. Penn State Extension, State College, PA, USA. Available online: https://extension.psu.edu/spotted-lanternfly-management-for-homeowners (accessed 16 April 19).

Leach, H., D. Biddinger, G. Krawczyk, E. Smyers, and J. M. Urban. 2019. Evaluation of insecticides for control of the spotted lanternfly, *Lycorma delicatula,* (Hemiptera: Fulgoridae), a new pest of fruit in the Northeastern U.S. Crop Prot. 124: 104833. doi:10.1016/j.cropro.2019.05.027.

Lee, J. E., S. R. Moon, H. G. Ahn, S. R. Cho, J. O. Yang, C. Yoon, and J. H. Kim 2009. Feeding behavior of *Lycorma delicatula* (Hemiptera: Fulgoridae) and response on feeding stimulants of some plants. Korean J. Appl. Entomol. 48: 467–477.

Lee, D.-H., Y.-L. Park, and T. C. Leskey. 2019. A review of biology and management of *Lycorma delicatula* (Hemiptera: Fulgoridae), an emerging global invasive species. J. Asia-Pacific Entomol. 22: 589–596.

Lee J. S., I. K. Kim, S. H. Koh, S. J. Cho, S. J. Jang, S. H. Pyo, and W. I. Choi. 2011. Impact of minimum winter temperature on *Lycorma delicatula* (Hemiptera: Fulgoridae) egg mortality. J. Asia-Pacific Entomol. 14: 123–125.

Lee, K. Y., S. K. Kim, I. H. Kim, and K. S. Kim. 2011. Seasonal occurrence of spot clothing wax cicada, *Lycorma delicatula* (Hemiptera: Fulgoridae) and its control efficacy using EFAM at the vineyards. Korean J. Pestic. Sci. 15: 303–309.

Li, J., X. Li, and S. Li. 2013. The occurrence and control of *Semanotus bifasciatus* and *Lycorma delicatula* in cypress trees. Modern Agric. Sci. Technol. (1): 37–38.

Liebhold, A., K. Thorpe, J. Ghent, and D. B. Lyons. 1994. Gypsy moth egg mass sampling for decision-making: a user's guide. USDA Forest Service, Morgantown, West Virginia.

Lieu, K. 1934. External morphology and internal anatomy of a lantern-fly, *Lycorma delicatula* (White). 1933 Year Book of Bureau of Entomology, Hangzhou, Zhejiang, (3): 1–25.

Liu, G. 1939. Some extracts from the history of entomology in China. Psyche 46: 23–28.

Liu, H. 2019. Occurrence, seasonal abundance, and superparasitism of *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae) as an egg parasitoid of the spotted lanternfly (Lycorma delicatula) in North America. Forests 10(2), 79: 1–16.

Liu, H., and J. Mottern. 2017. An old remedy for a new problem? Identification of *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae), an egg parasitoid of *Lycorma delicatula* (Hemiptera: Fulgoridae) in North America. J. Insect Sci. 17(1): 18, 1–6.

Luck, R. F., and D. L. Dahlsten. 1967. Douglas-fir tussock moth (*Hemerocampa pseudotsugata*) egg-mass distribution on white fir in Northeastern California. Can. Entomol. 99: 1193–1203.

Mayhew, P. J. 2001. Herbivore host choice and optimal bad motherhood. Trends Ecol. Evol. 16: 165–167.

Myrick, A. J., and T. C. Baker. 2019. Analysis of anemotactic flight tendencies of the spotted lanternfly (*Lycorma delicatula*) during the 2017 mass dispersal flights in Pennsylvania. J. Insect Behav. doi:10.1007/s10905-019-09708-x

(NYS IPM) New York State Integrated Pest Management. 2019. Spotted lanternfly. https://nysipm.cornell.edu/environment/invasive-species-exotic-pests/spotted-lanternfly/ (accessed 18 June 19)

Park, J. D., M. Y. Kim, S. G. Lee, S. C. Shin, J. H. Kim, and I. K. Park. 2009. Biological characteristics of *Lycorma delicatula* and the control effects of some insecticides. Korean J. Appl. Entomol. 48: 53–57.

Park, M. 2015. Overwintering ecology and population genetics of *Lycorma delicatula* (Hemiptera: Fulgoridae) in Korea. PhD dissertation, Seoul National University, Seoul, South Korea.

(PDA) Pennsylvania Department of Agriculture. 2018. PA Agriculture Department adds seven counties to spotted lanternfly quarantine zone. Available online: http://www.media.pa.gov/pages/Agriculture_details.aspx?newsid=616 (accessed 05 April 19).

Polonsky, J. 1973. Chemistry and biogenensis of the quassinoids (Smaroubolides). Recent Adv. Phytochem. 6: 31–64.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria. Available online: http://www.R-project.org/. (accessed 05 August 2019).

Refsnider, J. M., and F. J. Janzen. 2010. Putting eggs in one basket: Ecological and evolutionary hypotheses for variation in oviposition-site choice. Annu. Rev. Ecol. Evol. Syst. 41: 39–57.

Scheirs, J., and L. De Bruyn. 2002. Integrating optimal foraging and optimal oviposition theory in plant-insect research. Oikos. 96: 187–191.

Scheirs, J., L. De Bruyn, and R. Verhagen. 2000. Optimization of adult performance determines host choice in a grass miner. Proc. Biol. Sci. 267: 2065–2069.

Scheirs, J., T. G. Zoebisch, D. J. Schuster, and L. De Bruyn. 2004. Optimal foraging shapes host preference of a polyphagous leafminer. Ecol. Entomol. 29: 375–379.

Song, S, S. Kim, S. W. Kwon, S-I. Lee, and P. G. Jablonski. 2018. Defense sequestration associated with narrowing of diet and ontogenetic change to aposematic colours in the spotted lanternfly. Sci. Rep. 8: 16831.

Thorpe, K. W., and R. L. Ridgway. 1992. Gypsy moth (Lepidoptera: Lymantriidae) egg mass distribution and sampling in a residential setting. Environ. Entomol. 21: 722-730.

Tomisawa, A., S. Ohimiya, H. Fukutomi, K. Hayashi, and T. Ishikawa. 2013. Biological notes on *Lycorma delicatula* (White) (Hemiptera: Fulgoridae) in Ishikawa prefecture, Japan. Japan J. Entomol. 16: 3–14.

Vieira, I. J. C., and R. Braz-Filho. 2006. Quassinoids: Structural diversity, biological activity and synthetic studies. Stud. Nat. Prod. Chem. 33: 433–492.

Wang, R. R., J. J. Liu, X. Y. Li, A. P. Liang, and T. Bourgoin. 2018. Relating antennal sensilla diversity and possible species behaviour in the planthopper pest *Lycorma delicatula* (Hemiptera: Fulgoromorpha: Fulgoridae). PLoS One. 13: e0194995.

White, A. 1845. Description of a new genus and some new species of homopterous insects from the East in the collection of British Museum. Ann. Mag. Nat. Hist. 15: 34–37.

Yang, R., Y. Wang, K. Zhang, and Y. Hao. 2015. Study on the occurrence and control of *Lycorma delicatula* on grape in areas of Lanzhou. Gansu Agric. Sci. Technol. 4: 87–88.

Zhang, W. 2001. Investigations on the insect pests of American black walnut in Henan province. For. Pest Dis. (1): 38–39.

Zhou, J. X. 1992. *Lycorma delicatula* (White) (Homoptera: Fulgoridae), pp. 169–170. In G. R. Xiao (ed.), Forest Insects of China, 2nd ed. Chinese Forestry Publishing House, Beijing, China.

Zu, X. 1992. Studies of persimmon proliferation disease. Hebei Fruits (3): 23–26.