Life History and Potential Hosts of Zapatella davisae (Hymenoptera: Cynipidae), a Recent Invader on Black Oak in the Northeastern United States

Monica Davis¹*, Joseph Elkinton¹, and Russell Norton²

Abstract - Quercus velutina (Black Oak) is a dominant deciduous tree in Cape Cod, Martha’s Vineyard, and Nantucket, MA. In recent years, Black Oak trees in these regions have experienced severe canopy loss due to the infestation of a stem-gall wasp, Zapatella davisae. In addition to infestations first documented in the Cape Cod region in 2012, Zapatella davisae has been present in Long Island, NY, since the 1990s. We investigated the life cycle of Z. davisae, specifically emergence patterns and timing of development. We evaluated differences in the severity of the infestations in Long Island and Cape Cod. We also identified towns in Cape Cod that contained Z. davisae infestations to better estimate the geographic extent of the infestation in the region. We found that Zapatella davisae completes 1 generation per year and emerges throughout the month of May. The severity of the infestation was the greatest in Cape Cod, an indication that something is controlling the population in Long Island. We concluded that Z. davisae is widespread and present in all towns in Cape Cod, Nantucket, and Martha’s Vineyard. Our research will lay the foundation for future biological control efforts and will help arborists and landowners make management decisions regarding Z. davisae in the Cape Cod region and Long Island.

Introduction

Oaks are a major component of New England forests, therefore oak pests can have lasting economic and ecological impacts on the region. In particular, a stem gall wasp, Zapatella davisae Buffington and Melika (Hymenoptera: Cynipidae), has caused extensive mortality and canopy damage to Quercus velutina Lam. (Black Oak) in Cape Cod, Nantucket, and Martha’s Vineyard, MA (Buffington et al. 2016). Cape Cod is the largest protected coastal area of oak–pine forest or sandplain vegetation in New England (Eberhardt et al. 2003). It is composed of sandy soil that is often nutrient poor and does not retain water; thus, trees that can adapt to dry, low-nutrient conditions are the most successful competitors (Neil et al. 2007). Drought-resistant tree species, such as Pinus rigida Mill (Pitch Pine.), Black Oak, and Quercus coccinea Muenchh. (Scarlet Oak) make up most of the trees in this forest (Eberhardt et al. 2003). A decline in Black Oak tree canopy cover is of high conservation concern in the Cape Cod region.

Zapatella davisae was discovered on Martha’s Vineyard in 2012, but infestations can be tracked back to ca. 2008 based on the inferred ages of damaged twigs and branches (Buffington et al. 2016). Zapatella davisae creates woody stem galls

¹University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, MA 01002.
²Cape Cod Extension, 3195 Main Street, Barnstable, MA 02563. *Corresponding author - mjdavis@eco.umass.edu.

Manuscript Editor: Daniel Pavuk
underneath the bark and causes extensive node swelling and twig disfiguration (Fig. 1; Buffington et al. 2016). Other symptoms include flagging, leaf clumping, canopy dieback, and tree mortality (Fig. 2; Pike et al. 2001). Although the damage caused by *Z. davisae* has been documented in individual trees, its life cycle, severity of damage, and host specificity have remained unknown (Buffington et al. 2016).

Part of our research parallels a previous study of an oak-gall wasp (previously misidentified as *Bassettia ceropteroides* Bassett) that caused damage and mortality to Black Oak on Long Island in 1990 (Melika and Abrahamson 2007). Over the past
5 years, there has been much speculation as to whether *B. ceropteroides* is the same species that is causing extensive tree mortality in Cape Cod, Martha’s Vineyard, and Rhode Island. In 2016, molecular analyses confirmed that the gall wasp on Long Island is the same species that is on Cape Cod (Buffington et al. 2016), and not long after, taxonomists determined that the gall wasp is a new species, *Zapatella davisaee* (Buffington et al. 2016). Differences between the 2 populations, specifically host trees and the severity of the infestation have not been previously evaluated.

*Zapatella davisaee* is a member of the Cynipini, a host-specific tribe that contains over 87% of all gall makers on oaks (Abrahamson 1998, Stone et al. 2008). Life-cycle descriptions are available for only 85 of 900 species in the Cynipini tribe worldwide (Pujade-Villar et al. 1999). The life cycle of *Z. davisaee* is still unknown; however, the biology of other species of *Zapatella* may help identify potential life-cycle patterns. All Cynipini, also known as oak-gall wasps, reproduce through either cyclic or obligate parthenogenesis (Stone et al. 2008). Cyclic parthenogenesis in Cynipini consists of the strict alternation between 1 parthenogenetic generation and 1 sexual generation (Stone et al. 2008). The alternating generations may occur in the same year or in alternating years and may attack different hosts or different tissues of the same host (Hood and Ott 2001, Stone et al. 2002). Obligate parthenogenesis is also common in Cynipini, having evolved many times from cyclic parthenogenesis by deletion of the sexual generation (Herbert 1981, Rispe and Pierre 1998).

Most *Zapatella* species exhibit obligate parthenogenesis; however, they have various hosts, gall-tissue types, and generation times. For example, *Zapatella nievesaldreyi* Melika and Pujade-Villar induces stem galls on *Quercus humboldtii* Bonpl. (Andean Oak) in Colombia, whereas *Zapatella oblata* Weld creates bud galls on both Scarlet Oak and *Quercus falcata* Michx (Southern Red Oak) in Virginia (Pujade-Villar et al. 2012). Preliminary microsatellite data (J. Andersen, University of California Berkley, Berkley, CA, unpubl. data) suggest that sampled populations of *Z. davisaee* are obligately parthenogenetic, but it is unclear whether cyclic parthenogenesis also occurs.

An understanding of the life cycle, severity of the infestation, and potential hosts of *Z. davisaee* will aid in determining future management efforts and help answer ecological questions regarding *Z. davisaee* community and population dynamics. Our first objective was to describe the life cycle of *Z. davisaee*, specifically its emergence patterns and the phenology of its developmental stages. Our second objective was to compare levels of infestation between Cape Cod and Long Island, and identify any additional host trees in each region. Our final objective was to document the distribution of *Z. davisaee* in Cape Cod. Our research will inform the implementation of different management strategies, as well as identify the geographical distribution and potential hosts of *Z. davisaee*.

**Field-site Description**

We conducted all field collections and surveys in coastal sand-plain vegetation communities in New England and Long Island, NY. We completed infestation surveys in Cape Cod, Nantucket, and Martha’s Vineyard, MA, as well as Long
Island, NY, and coastal Rhode Island. All locations were in close proximity to the coast and contained oak–pine forest vegetation. We undertook the life-cycle study at 2 sites: 1 in Dennis, MA (41°44'12.33" N, 70°11'38.78"W) and the other in Riverhead, NY (40°57'44.26"N, 72°42' 59.57"W).

Methods

Life cycle

To determine emergence patterns of *Z. davisae*, we captured adult gall wasps as they emerged from stem galls in Cape Cod, MA. We covered new and last year’s growth on 100 branches of 20 infested trees with 11.4 cm x 17.7 cm organza bags. We made visual inspections of the bags each month from November 2013 to March 2014, and then weekly during April and May 2014. At each check, we scored every bag for the presence or absence of *Z. davisae*. We completed the same schedule of bag deployment and visual checks the following year, from November 2014 to May 2015. To determine date of emergence, we recorded dates when live gall wasps were found and calculated a range based on the first and last record.

We collected branch samples biweekly from Dennis, MA, and Riverhead, NY, to document the stages of development of the stem-gall generation. Every other week, we haphazardly collected and stored in separate 3.79-L (1-gallon) plastic bags 5 branches from the crown of 10 trees at 1 of the 2 sites. We performed dissections of the galls on new and last year’s growth under a dissecting microscope (Wild M5A, 6X-50X), and scored each sample for the presence or absence of each life stage of *Z. davisae*. We did not conduct statistical analyses of these data because we used the binomial data only to identify the timing of certain life stages.

Tree infestation survey

During the spring and summer of 2016, we completed field surveys on Long Island and Cape Cod. We randomly chose GPS coordinates of 7 sites per region that contained Pitch Pine and oak forest vegetation on a GIS topographical map; all locations were at least 10 km from any other site. We checked each site, and if Black Oak trees were not present, we drove no more than an additional 3 km in search of trees. If we were unable to find Black Oak, we randomly chose a new site in the same manner. At each of the 7 sites in both regions, we scored 20 Black Oak trees for the presence or absence of gall-wasp infestation. At each site, we identified to species each oak tree that was not a Black Oak and was scored for the presence or absence of gall-wasp infestation. We scored level of infestation on field observations. We defined low-infested trees as those with small galls that were difficult to find, moderately infested trees had obvious galls and noticeable canopy damage, and heavily infested trees had >80% of branches galled and severe canopy damage. We used RStudio Version 0.99.491 (R Core Team 2015) to run a chi-squared test comparing the number of trees at each infestation level between both regions, and to perform a 2-sample test for equality of proportions and chi-square to compute the proportion of trees infested in each region.
Estimation of gall-wasp distribution

We surveyed by car and on foot towns in Rhode Island, Cape Cod, Martha’s Vineyard, and Nantucket to identify places where *Z. davisaee* was present in New England. We and extension personnel completed visual surveys in each region. The main focus of this project was Cape Cod, Martha’s Vineyard, and Nantucket; however, we also documented infestations reported in Rhode Island. We surveyed all towns in Cape Cod, Martha’s Vineyard, and Nantucket, MA. In Rhode Island, we searched only coastal areas for *Z. davisaee* with local extension personnel. *Zapatella davisaee* was scored as being present in a town if observers detected *Z. davisaee* damage on at least 5 trees. We overlaid a GIS layer from the Massachusetts Department of Conservation and Recreation to compare defoliation levels with town-level infestation detection. We created a map in QGIS Version 2.180 to identify the current extent of the *Z. davisaee* infestation.

Results

Life cycle

We detected no gall wasp emergence in the fall of 2013 and 2014 of the bag experiment, confirming that *Z. davisaee* does not have an autumnal generation. In the spring of 2014, *Z. davisaee* adults emerged 7–25 May on Cape Cod. We observed the same pattern in 2015 and concluded that *Z. davisaee* emerges between the 1st and 3rd week of May depending on the year.

The life cycle of 1 generation of *Z. davisaee* from August to May is illustrated diagrammatically in Figure 3. The *Z. davisaee* life stages we recognized included early and late larval stages, pupae, and fully formed adults. We first detected gall cavities in July, and the early larval stage was present by mid-August, with the late larval stage present in early September. We did not determine the number of larval instars. Pupation occurred in mid-September, when both larval stages were still present. In early October, we detected pharate adults. Mature adults were present in early spring of the following year and they emerged in May. *Zapatella davisaee* overwintered in several life stages, and individuals became adults by May prior to emergence.

Tree-infestation surveys

There was a significant difference in the level of gall-wasp infestation on Long Island versus Cape Cod ($\chi^2 = 30.6; \text{df} = 3; P < 0.0001$; Fig. 4). Long Island had significantly more trees with low-level infestations than trees with medium or heavy infestations. Cape Cod showed the opposite trend, with more heavy infestations, followed by medium and then low infestations. There was a site effect on both Cape Cod and Long Island, confirming that infestation levels varied across both regions (Cape Cod: $\chi^2 = 95.633; \text{df} = 18; P < 0.0001$; Long Island: $\chi^2 = 53.438$, df = 18, $P < 0.0001$). No other oak species besides Black Oak was infested by *Z. davisaee* (Table 1). Most Black Oaks in both regions harbored some infestation, and the proportion of trees infested in Cape Cod versus Long Island was not different (Table 1) ($\chi^2 = 3.745; \text{df} = 1; P = 0.052$).
Estimation of gall wasp distribution

All towns on Cape Cod contained a *Z. davisae* infestation (Fig. 5). *Zapatella davisae* was present in all towns on Nantucket and Martha’s Vineyard. In Rhode Island, documented infestations were in primarily coastal areas of oak–pine forest, where Black Oak was the dominant deciduous tree. *Zapatella davisae* defoliation levels reported by the Massachusetts Department of Conservation and Recreation (DCR) in 2015 and 2016 [REFERENCE?] were consistent with our survey results;

Table 1. Number of trees surveyed for each oak species at sites on Cape Cod and Long Island and the proportion of trees of each species that were infested with *Zapatella davisae* (all zero except for Black Oak)

<table>
<thead>
<tr>
<th>Oak species</th>
<th>Cape Cod</th>
<th>Long Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>White</td>
<td>24 (0.00)</td>
<td>0 (0.00)</td>
</tr>
<tr>
<td>Red</td>
<td>9 (0.00)</td>
<td>4 (0.00)</td>
</tr>
<tr>
<td>Scarlet</td>
<td>11 (0.00)</td>
<td>1 (0.00)</td>
</tr>
<tr>
<td>Chestnut</td>
<td>0 (0.00)</td>
<td>2 (0.00)</td>
</tr>
<tr>
<td>Pin</td>
<td>0 (0.00)</td>
<td>2 (0.00)</td>
</tr>
<tr>
<td>English</td>
<td>4 (0.00)</td>
<td>0 (0.00)</td>
</tr>
<tr>
<td>Black</td>
<td>120 (0.89 ± 0.027 SE)</td>
<td>120 (0.79 ± 0.037 SE)</td>
</tr>
</tbody>
</table>

Figure 3. Timing and stages of development for the twig-gall generation of *Zapatella davisae*. 

![Diagram of life cycle of Zapatella davisae](image-url)
Figure 4. Average proportion of trees at each gall-wasp infestation level (low, medium, and high) across all sites on Long Island and Cape Cod.

Figure 5. Map of towns in New England with known Zapatella davisae infestations documented by ground surveys. Includes Z. davisae defoliation data from DCR mapping flyovers in 2015 and 2016.
However, *Z. davisae* was found in 12 additional towns where the overhead defoliation data of the DCR survey did not detect *Z. davisae*.

**Discussion**

We found that *Z. davisae* completes one stem-gall generation per year, and emerges in May. This life cycle is congruent with the biology of several other *Zapatella* species (Pujade-Villar et al. 2012). Identifying the life cycle of *Z. davisae* will allow managers to determine the appropriate timing for biological-control release or pesticide application. *Z. davisae* only has 1 life cycle per year; thus, it should be easier to manage than other gall wasp pests with multiple generations (Bhandari and Zhiqiang 2016). We have conducted a follow-up study to evaluate the efficacy of systemic insecticides as control agents of *Z. davisae* and intend to give application date recommendations based on *Z. davisae’s* life cycle (M. Davis and J. Elkinton, unpubl. data).

*Zapatella davisae* was first noted on Martha’s Vineyard in 2008 and has continued to be detected in significant portions of the oak–pine forest in coastal New England. We observed *Z. davisae* only attacking Black Oak in the field; thus, its potential for range expansion throughout New England may be limited by the distribution of Black Oak. In New England, Black Oak occurs widely, but it is only a dominant deciduous tree in coastal oak–pine forests. Our results indicate that *Z. davisae* may not have the capacity to establish inland, but will continue to be a coastal pest in areas with sand-plain vegetation. Thus far, we have encountered *Z. davisae* only in this forest type.

Native species whose ranges are expanding have the capacity to alter native plant communities and population dynamics (Prior and Hellmann 2013, Schonrogge et al. 1995). Some native insect herbivores have little impact on their host plant due to the suppression of population densities by natural enemies (i.e., top-down control; Keane and Crawley 2002, Strong et al. 1984). Other species may experience natural-enemy release during a lag period after initial expansion, which can lead to population outbreaks and extensive plant damage (Prior and Hellman 2013). Our results imply that temporal and spatial differences between Long Island and Cape Cod populations have influenced the population dynamics of *Z. davisae*. It is evident that *Z. davisae* causes significantly more damage on Cape Cod than Long Island. Based on the enemy-release hypothesis, these new populations on Cape Cod may be causing more damage, because they are released from their natural enemies, which would otherwise keep them in check. As for next steps, we have identified parasitoids in both regions and plan to utilize population-ecology methods to evaluate their effect on *Z. davisae’s* population dynamics.

Extensive Black Oak mortality in coastal New England has caused significant ecological and economic impacts, including the cost of removing and replacing dead trees. We identified preliminary information about *Z. davisae’s* biology, specifically its life cycle, symptoms, and distribution. This information provides a strong foundation for integrated pest management practices and helps describe a pest that was once unknown to science. In addition, our study revealed the need to
evaluate factors that influence *Z. davisae* populations on Long Island and Cape Cod, including pesticide control and natural-enemy regulation.

**Acknowledgments**

We thank H. Broadley, T. Murphy and J. Boettner, from the University of Massachusetts-Amherst, for manuscript review and feedback. We are grateful to D. Gilrein, from the Cornell Horticultural station, and H. Faulbert, from the University of Rhode Island, for help finding field sites. We appreciate undergraduate students E. Mooshain, C. Camp, G. Hepsler, and K. Donahue for field collection and processing help. We thank Arborjet Inc., the Woodbourne Arboretum, and the University of Massachusetts-Amherst Department of Environmental Conservation for funding support.

**Literature Cited**


