

Research

Life History of *Allokermes galliformis* (Hemiptera: Kermesidae) in Colorado

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Abstract

Allokermes galliformis (Riley) (Hemiptera: Kermesidae), sometimes referred to as the ‘pin oak kermes’, has emerged as a significant pest of red oaks grown in the Front Range area of eastern Colorado. Although kermes scales infrequently cause significant tree damage, a novel association exists between the pin oak kermes and the pathogenic bacterium *Lonsdalea quercina* subsp. *quercina*. Together, they produce drippy blight disease of red oaks which is characterized by significant branch dieback. Field studies were conducted in Boulder, CO during 2015–2016 to better understand the life history of *A. galliformis* and identify points when this insect may be best managed. *A. galliformis* has a 1-yr life cycle. Upon egg eclosion in September and October, crawlers migrated to textured places on limbs to overwinter. In May, a second migration occurred with the great majority of first instar females moving to new growth and the base of the current season growth where they permanently settled, became sessile and resembled plant galls. Immature male scales remained active and ultimately migrated to the trunk or solid surfaces in the near vicinity of the trunk, produced a cocoon, and subsequently emerged as winged forms in early summer. After mating, females began to produce eggs and peak egg production occurred between mid-August and mid-September when adult females produced an average of 2,488 and 4,726 eggs in 2015 and 2016, respectively.

Key words: pin oak kermes, scale insect, drippy blight, feeding location

Kermes scales (Hemiptera: Kermesidae) are a family of gall-like insects that feed primarily on oak twigs and branches throughout the Northern Hemisphere. In natural ecosystems, predators and parasitoids typically suppress kermes scale populations to levels that rarely cause noticeable damage to their host (Kosztarab 1996, Spodek et al. 2012, Spodek and Ben-Dov 2014). However, in some landscape plantings kermes scale feeding has been shown to cause significant plant injury in the form of substantial branch dieback that can lead to tree decline and in some cases contributes to mortality (Hamon 1977, Solomon et al. 1980, Turner and Buss 2005, Turner et al. 2005, Pellizzari et al. 2012, Podsiadlo 2012).

Allokermes galliformis (Riley) (Hemiptera: Kermesidae) is the most abundant and widespread species of kermes scale in North America. It is present in 34 of the contiguous United States, in addition to being documented in Canada, Japan, and Mexico (Bullington and Kosztarab 1985, Gill 1993, Kosztarab 1996, García Morales et al. 2016). *A. galliformis* reportedly feeds on more than 40 species of oak trees as well as several species of chinquapin, but tentative identifications are common because *A. galliformis* morphology often changes based on its host plant (Baer and Kosztarab 1985, Kosztarab 1996). Despite this, previous documentation of *A. galliformis* is

extensive, but information on this species is not detailed (Cockerell 1894, Bullington and Kosztarab 1985, Kosztarab 1996, García Morales et al. 2016). For example, although there are taxonomic descriptions for the second instar male and all stages of the female (Baer and Kosztarab 1985, Bullington and Kosztarab 1985), the adult male is not described and critical information on the life history of *A. galliformis* is lacking (Kosztarab 1996).

The outbreak of *A. galliformis* in Colorado deserves special attention. Not only is *A. galliformis* often present in high abundance in landscape plantings along the urban corridor in Colorado, but it is also associated with development of drippy blight disease of red oaks (Snelling et al. 2011, Caballero et al. 2014, Sitz et al. 2018). Feeding wounds are entry and exit courts for a pathogenic bacterium, *Lonsdalea quercina* subsp. *quercina*. The combination of scale feeding and the bacterial infection exacerbates the impact of typical kermes scale infestations, producing intensified symptoms involving extensive branch dieback and tree decline. For example, in one community experiencing drippy blight disease, approximately 25% of the public red oak tree plantings have been removed in the last decade (Sitz et al. 2018). Due to the increased risk to red oak trees, several municipalities are looking for detailed life history information

to identify the most vulnerable life stage of the insect in order to guide best treatment practices for *A. galliformis*. In a disease similar to drippy blight, the incidence of the bacterium, *Brenneria quercina*, decreased when efforts were put forth to control the phytophagous insect causing plant damage (Myhre 1988). Similarly, identifying the means to best manage *A. galliformis* associated with drippy blight of red oak may be the best way to manage the bacterium. The aim of this research is to 1) describe the life history of *A. galliformis* in Colorado and 2) provide a more detailed understanding of the overwintering placement and settled feeding locations of kermes scale insects.

Materials and Methods

Life History Observations

Branch sampling was used to describe overwintering stages of *A. galliformis*. Branch samples were obtained from four trees each year (2014–2015 and 2015–2016) during city tree trimmings and removals of northern red oaks affected by drippy blight disease in Boulder, CO, on 18 December 2014, 12 February 2015 (40°00′02.61″N, –105°26′49.98″W, and 40°01′57.16″N, –105°27′86.53″W, and two trees at 40°01′57.42″N, –105°27′88.07″W), and in the following season on 22 March 2016, and 21 April 2016 (40°01′06.63″N, –105°28′20.98″W, and 40°00′02.42″N, –105°27′76.36″W, and two trees at 40°02′52.11″N, –105°28′19.79″W). Mature trees were used in this survey and ranged in size from 50 to 75 cm diameter breast height. Sampling focused on the terminal 5 yr of branch growth, which involved branch lengths averaging approximately 50 cm. The number and distribution of Instar I scales were recorded from these branches with specific sites noted including bark fissures, branch unions, bud scars, buds, growth rings, around venters of dead female scales, and wounds with callus tissue (Fig. 1). A total of 55 branches were examined in 2014–2015 and 42 in 2015–2016.

All of the additional life history observations continued throughout the year in 2015 and 2016 on six red oak trees at two sites in Boulder, CO (40°01′02.4″N, –105°27′04.9″W and 40°01′72.9″N, –105°25′99.0″W). Kermes scale size was used to determine life stage, as kermes scales approximately double in width each life stage (Hamon et al. 1976). Instar III can be discriminated from Instars I and II by the size discrepancy and the presence of three dorsal white longitudinal stripes (Fig. 2A–C). Further recording of scale distribution occurred following the second migration of the scales in spring when Instars I and II were present (7 and 27 May 2015, $n = 23$; 18 May 2016, $n = 30$). Samples included the terminal 3 yr of branch

growth, averaging approximately 20 cm in length, and the number and distribution of Instars I and II were recorded.

Subsequent sampling continued through mid-October and involved weekly collections of approximately 50 female specimens to determine female development (2015, $n = 624$; 2016, $n = 545$). From late July through mid-October an additional approximately 50 female scales were collected and cut open weekly to document the timing of egg development (2015, $n = 332$; 2016, $n = 257$). In September 2015 and 2016 we conducted estimates of total egg production, based on numbers of eggs or residual exuvium of hatched eggs contained within a venter (2015, $n = 19$; 2016, $n = 19$). Eggs and exuvium were floated in 75% EtOH, 25 out of 250 cells of a gridded 10-mm Petri dish were counted, and the total number of offspring was estimated. During the winter, venters remaining on trees were opened to determine the percent of females that successfully produced offspring (2015, $n = 229$; 2016, $n = 167$).

Histological sectioning was used to visualize the feeding damage sustained by kermes scales. In August of 2015, two samples containing three females feeding on 2-yr-old branch tissue were fixed, embedded, and sectioned according to Womack et al. (2016). The woody samples were dehydrated through week-long soaks (Ruzin 1999) in each grade of ethanol (30, 50, 70, 90, 95, and 100%), then embedded in hydroxypropyl methacrylate (HPMA) plastic (Electron Microscopy Sciences, Hatfield, PA), and sectioned at a 5- μ m thickness using a microtome (RM1265, Leica, Wetzlar, Germany). Every other section was mounted onto Fisher Superfrost Plus microscope slides and stained using Eosin and Toluidine Blue (Fisher Scientific, Pittsburgh, PA). Therefore, the depth of an attribute could be calculated by determining the number of mounted sections in which it was present.

In June and July of 2015 and 2016, targeted collections were made of approximately 500 cocoons containing maturing males on the main trunk. Collections were made using an aspirator and the insects were then held in the lab to record emergence of adult male scales as well as parasitoids. Insect voucher specimens are housed in the C.P. Gillette Museum of Arthropod Diversity.

Statistical Analysis

To determine differences in overwintering and migration locations of first instar scales, mixed effects models were fit using JMP software (11.1.0v, SAS Institute 2012). Log of scale insect number was the response variable in two models to determine first instar abundance at overwintering locations, and second settled feeding locations. To account for blocking in the experimental design, branches within the trees were random effects. In the first model (overwintering locations),

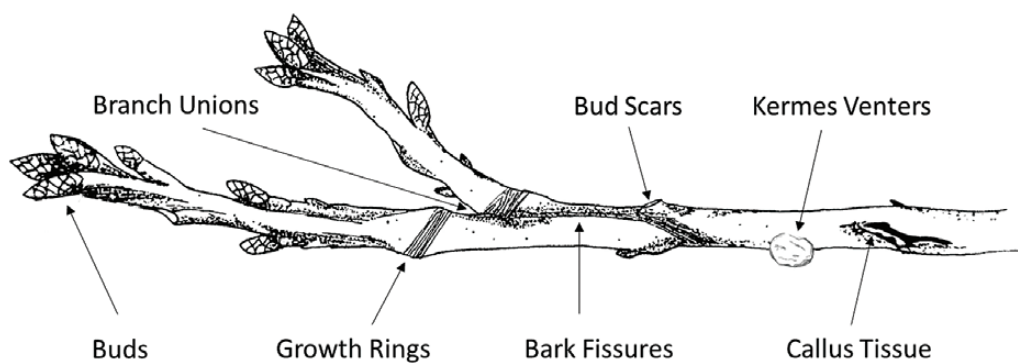


Fig. 1. A red oak branch showing the locations where overwintering *A. galliformis* crawlers were observed. These locations include around the base of buds, branch unions, growth rings, bark fissures, bud scars, callus tissue/ wounds, and around old kermes venters.

branch age and branch location were considered fixed effects. In the second model (settled feeding location), branch location was a fixed effect. Pairwise comparisons were obtained for both models using a Tukey HSD method, but the data were separated by year.

Results and Discussion

A. galliformis exhibited a univoltine life cycle (Fig. 3) that for females involved three nymphal instars (Fig. 2A–C) and an adult (Fig. 2D). Males were observed to produce two nymphal male instars, a ‘pupal stage’ within a white cocoon (Fig. 4A), and an adult male (Fig. 4B). Typical of Kermesidae, *A. galliformis* displayed extreme sexual dimorphism in the adult stage; females developed into large wingless insects that resembled twig galls while males were minute and winged (Gullan and Kosztarab 1997).

Eclosion started in September and lasted through October, when the rust-colored crawlers (Instar I) moved to protective crevices on the bark of branches to overwinter (Fig. 3). *A. galliformis* spent approximately 8 mo as crawlers (Fig. 3) migrating twice during this time. Male and female crawlers are not sexually dimorphic like the other life stages, and therefore cannot be discerned from one another.

The distribution of overwintering crawlers was affected by the age of the branch material where crawlers settled. Overwintering occurred on wood of various ages with an average of 10% noted on 5-yr-old wood, 33% on 4-yr-old wood, 32% on 3-yr-old wood, 19% on 2-yr-old wood, and 5% on 1-yr-old wood (Table 1). Furthermore, in 2014–2015 significantly more first instars overwintered on older, 2- to 3-yr-old branch growth (2011–2013) than 1-yr-old branch

growth (2014) (Table 1; $F_{4,1807} = 5.90$, $P = 0.0105$, $P < 0.001$, and $P = 0.0021$ for 2014 compared to 2011, 2012, and 2013, respectively). In 2015–2016 the same trend occurred, but preferences were not significant (Table 1; $F_{4,1416} = 1.90$, $P = 0.1006$). There was large variation in the abundance of *A. galliformis* between the two study seasons, with more than ten times as many crawlers detected per branch in 2015 (129 ± 67) than in 2016 (10 ± 6) ($F_{1,318} = 215.20$, $P < 0.001$). Despite this variation, the trend for overwintering crawlers to avoid the most recent growth was consistent across sampling years (Table 1). Very few crawlers were observed to settle on branch material older than 5 yr; large branches were not evaluated.

There were also clear patterns as to the sites within the branch regions where scales overwintered (Table 2). Across both years, the number of first instars overwintering around growth rings was higher when compared to all other locations (Fig. 1; Table 1; 2014: $F_{6,1805} = 57.31$, $P = 0.0022$, $P = 0.0052$, $P < 0.001$, $P = 0.0001$; $P < 0.001$, and $P < 0.001$ for growth rings compared to bark fissures, bud scars, branch unions, wounds/callus, around venters, and around buds, respectively; 2015: $F_{4,1146} = 53.08$, $P < 0.001$ for all comparisons), where an average of 35% were observed on the growth rings. Additionally, 26% were found at bark fissures of the samples from both years and less common sites for overwintered scales were wound areas with callus tissue (17%), bud scars (13%), branch unions (6%), around old female scale venters (2%), and on buds (1%).

After overwintering, a second migration occurred following bud break in May. Across both years, a large majority of first instars migrated to new growth (86 and 97% in 2015 and 2016, respectively) and either resettled around the new growth ring (29 and 45%

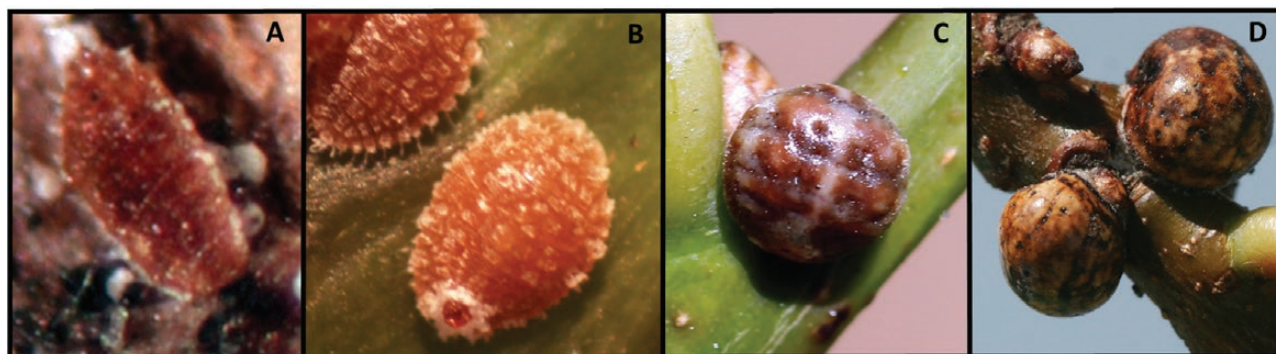


Fig. 2. Life stages of female *A. galliformis* including (A) first instar, (B) second instar, (C) third instar, and (D) post-reproductive adult female.

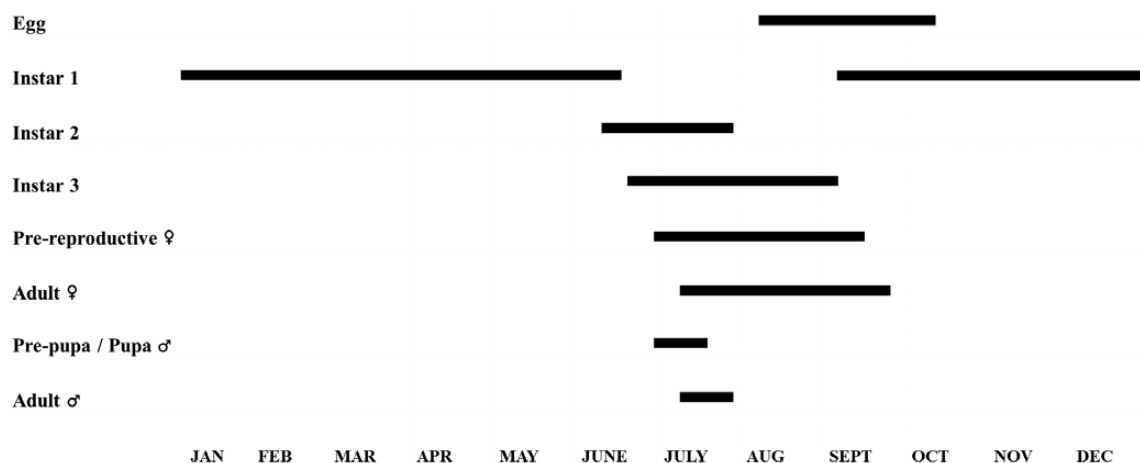


Fig. 3. Seasonal life history of *A. galliformis* obtained from drippy blight diseased Northern red oak (*Quercus rubra*) from parks in Boulder, CO throughout 2015 and 2016.

in 2015 and 2016, respectively) or on current season growth (62 and 49% in 2015 and 2016, respectively) (Table 3). A smaller percentage (9 and 6% in 2015 and 2016, respectively) remained on older growth when compared to new growth (Table 3; 2015: $F_{2,106} = 15.27$, $P < 0.001$ and 2016: $F_{2,56} = 59.60$, $P < 0.001$). Molting to Instar II subsequently occurred at these sites, and the scales present in the upper canopy were determined to be female due to their sessile habit. Instar II females appeared the orange color of bud scales (Fig. 2A and B) and increasingly came to resemble plant galls during further

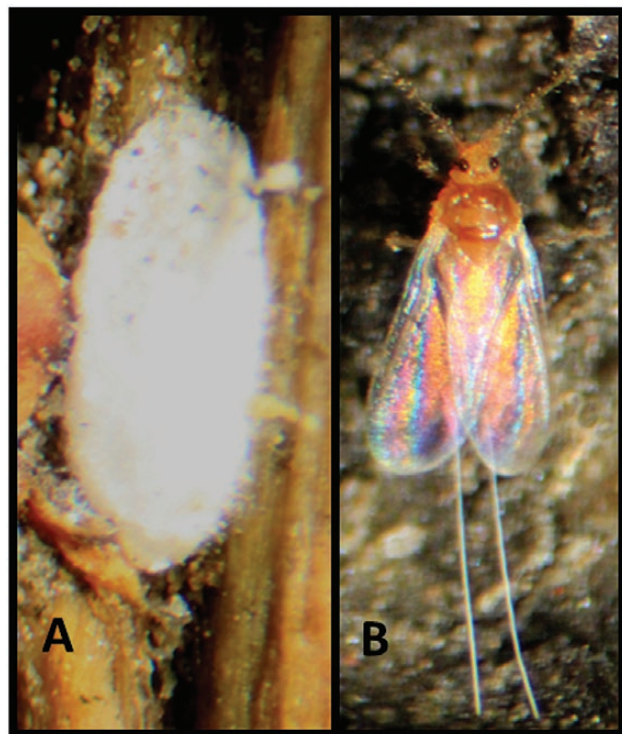


Fig. 4. *A. galliformis* male (A) pupal case, and (B) adult life stage.

development. Differences in populations of scales on plants between the two seasons continued through Instar II, with almost fivefold more scales noted per branch in 2015 (52 ± 5) than 2016 (11 ± 5) ($F_{1,201} = 73.12$, $P < 0.001$). In both years, the great majority of female scales ultimately settled around the new growth ring or on the current season growth. Later, branch breakage and dieback were often observed at these sites.

Instar II and each successive female life stage persisted for 1 to 2 mo (Fig. 3). The majority of Instar II females were present in mid-to-late June, and the majority of Instar III females occurred in early and mid-July. Instar III and early adult females turned maroon to brown (Fig. 2C).

Females histologically sectioned were found to produce injuries associated with their feeding, and potentially the plant pathogenic bacterium *Lonsdalea quercina* subsp. *quercina* (Fig. 5). All three sectioned kermes scales were adult females, as seen by the presence of fully developed false venters that separated the kermes scale true venter from the oak branch (Fig. 5) (Bullington and Kosztarab 1985). The sections indicative of life stage were also indicative of feeding location. Although the stylets were not visualized using this technique, the kermes scale mouthparts were consistently found directly above a mass of cells that stained a deeper color than the surrounding cortex cells. Additionally, light blue stained tissues, likely periderm, were observed to extend around portions of the damaged cortex cells (Fig. 5). Only the cortex in the histological sections directly under the kermes scale sections containing the false venter and mouthparts exhibited darkened tissues indicative of damaged cells. The accumulation of damaged tissues averaged 0.16 ± 0.05 mm wide and 0.35 ± 0.02 mm deep.

Some Instar I crawlers were observed overwintering on the trunk of the tree. This was a habit noted to occur with males of *Allokermes kingii* Cockerell (Hemiptera: Kermesidae) (Hamon et al. 1976), and it is likely that some males of *A. galliformis* similarly move to trunks at this time. Adult males of *A. galliformis* were short-lived compared to females, and the pre-pupae and adults were only present in July (Fig. 3). In early and mid-July, pre-pupae created white waxy pupal cocoons (Fig. 4A) which were most abundant on the trunk, but also frequently found on rocks, mulch, fencing, and plants or debris

Table 1. The number of first instar *A. galliformis* (mean $\pm$ standard error) that settled on the most recent 5 yr of branch growth

Year sampled	No. ^a	Year of branch growth					
		2010	2011	2012	2013	2014	2015
2014–2015	55	1.83 $\pm$ 0.28ab	2.67 $\pm$ 0.51a	2.65 $\pm$ 0.39a	2.36 $\pm$ 0.37a	0.82 $\pm$ 0.12b	.
2015–2016	42	.	0.30 $\pm$ 0.08a	0.22 $\pm$ 0.04a	0.27 $\pm$ 0.06a	0.36 $\pm$ 0.06a	0.19 $\pm$ 0.04a

Four trees were evaluated each winter (2014–2015 and 2015–2016). All branch material was obtained from trees located on public grounds in Boulder, CO. Means followed by the same letter in a row are not statistically different ($P < 0.05$, Tukey HSD).

^aNumber of branches counted.

Table 2. The number of first instar *A. galliformis* (mean $\pm$ standard error) that overwintered on red oak branches (in either bark fissures, bud scars, branch unions, wounds with callus tissue, buds, and growth rings, or around old female kermes scale venters)

Year	No. ^a	Bark fissures	Bud scars	Branch unions	Wounds / callus	Buds	Growth rings	Around venters
2014–2015	55	3.97 $\pm$ 0.83b	1.67 $\pm$ 0.20b	0.88 $\pm$ 0.22bc	2.34 $\pm$ 0.37b	0.10 $\pm$ 0.05c	4.99 $\pm$ 0.48a	0.49 $\pm$ 0.13c
2015–2016	42	0.30 $\pm$ 0.08b	0.14 $\pm$ 0.03b	0.14 $\pm$ 0.05b	0.15 $\pm$ 0.40b	0.01 $\pm$ 0.01b	1.14 $\pm$ 0.14a	0.00 $\pm$ 0.00b

Five years of branch growth was evaluated each winter (2014–2015 and 2015–2016). All branch material was obtained from trees located on public grounds in Boulder, CO where four trees were evaluated each winter (2014–2015 and 2015–2016). Means followed by the same letter in a row are not statistically different ($P < 0.05$, Tukey HSD).

^aNumber of branches counted.

around the base of the tree. Pupal cases were documented up to 6 feet away from the base of the tree. From mid-July to August, males developed into the adult stage and were tan with clear to iridescent wings (Fig. 4B). Adult males were weak fliers (Gullan and Kosztarab 1997) with one pair of wings and hamulohalteres, and they lacked functional mouthparts.

The peak time for reproductive female development is from mid-August through mid-September, and post-reproductive females were easily identifiable because their protective venter turned tan with three rows of dark spots (Fig. 2D). During the middle of August, female scales began to develop eggs that were tightly packed within the interior of the venter. Oviposition was complete by late October and the eggs began to hatch by mid-September.

Examination of the content of female venters remaining on the tree in the winter indicated either egg exuvium produced by viable eggs that had hatched, or dead eggs, barren venters, and/or a white powdery material indicative of non-viable offspring. In total, an average of 65% of adult females survived to produce viable offspring. Of these, females produced an average of $2,488 \pm 592$ eggs in 2015 (range 43–7,210) and $4,726 \pm 701$ eggs in 2016 (range 1,400–9,850). These levels of egg

production are consistent with that reported by other *Allokermes* species. For example, Hamon et al. (1975) reported an average of 2,820 eggs being produced by *A. kingii*. The highest number of eggs recorded from *A. galliformis* (9,850) exceeded the record of 6,676 eggs reported by Himebraugh (1904) from a female of *Allokermes gillettei* Cockerell (Hemiptera: Kermesidae) collected in Manitou, CO.

Although scale populations fluctuated during this study and were lower in 2015–2016, *A. galliformis* was still present in high densities in both years. At the study sites, it was common to see groups of 10 to 15 individuals packed together feeding in a similar location. Even though *A. galliformis* occurred in sustained high population densities, little evidence of natural enemy activity was observed. Some lady beetles and scavenging vespid wasps were seen on infested trees, but rather than showing predatory behavior, they were observed feeding on scale excrement and bacterial exudates. No parasitism of females was observed, but approximately 5% of male scales were parasitized in the pre-pupae stage by a minute wasp in the family Encyrtidae, which are known kermes scale parasitoids (Guerrieri and Viggiani 1990, Japoshvili and Karaca 2003, Japoshvili and Noyes 2006, Japoshvili et al. 2015). On three separate occasions during the experiment, a predatory thrips species was collected inside newly exited venters which may have fed on developing eggs. Also, in about 5% of female scales the body contents were reduced to a white, powdery substance suggestive of pathogen infection. The absence of natural enemies of *A. galliformis* in Colorado, and the relatively high populations of the insect that occur in contrast to areas where the insect and host are native, suggest that an exploration of natural enemies in areas of origin and their introduction into Colorado may be valuable for long-term management of *A. galliformis* in the state. Another kermes scale, *A. gillettei* (Cockerell), native to gambel oak (*Quercus gambelii*) stands in Colorado (Bullington and Kosztarab 1985), does not cause economic damage which is likely, in part, due to the presence of natural enemies.

Although the life history of *A. galliformis* is similar in some respects to *A. kingii*, the only other kermes scale in North America that has been studied similarly, there are important differences. Geographic location and climate impact the life history of kermes scale insects, as *A. kingii* exhibits a 1-yr life cycle in most of its range (Hamon et al. 1976), but in warmer regions *A. kingii* can exhibit

Table 3. The number of immature *A. galliformis* (mean $\pm$ standard error) that migrated onto either new growth, current season growth ring, or previous growth on the most terminal 20 cm of red oak branch material

Year	No. ^a	Previous growth	Current season growth rings	New growth
2015	23	$4.55 \pm 0.86b$	$16.13 \pm 2.51a$	$16.21 \pm 2.32a$
2016	30	$0.24 \pm 0.13c$	$6.83 \pm 1.16a$	$4.00 \pm 1.28b$

Immatures were counted immediately following bud break (2015, $n = 45$; 2016, $n = 30$). All branch material in 2015 was obtained from two trees located on public grounds in Boulder, CO, and all branch material in 2016 was collected from five red oak trees on University of Colorado, Boulder grounds. Means followed by the same letter in a row are not statistically different ($P < 0.05$, Tukey HSD).

^aNumber of branches counted.

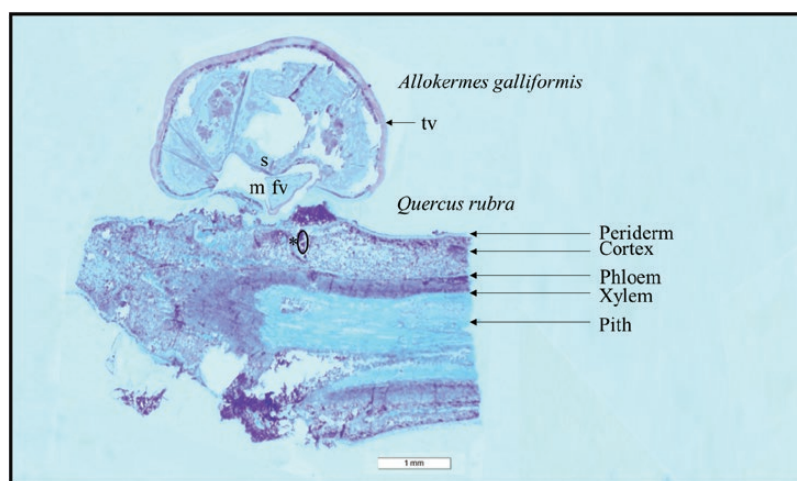


Fig. 5. Histological section showing an adult female kermes scale, *A. galliformis*, feeding on a Northern red oak (*Quercus rubra*) branch collected from public grounds in Boulder, CO. Insect and plant cells were stained using Eosin and Toluidine Blue. The adult kermes scale has true venter (tv) encasing the insect body, as well as a false venter (fv) separating the sternum (s) from the oak branch. The location of the mouthparts (m) is labeled. The branch morphology includes the periderm (pd), cortex (c), phloem (ph), xylem (x), and pith (p). The asterisk indicates the light blue stained plant tissue, likely periderm, which extends into the cortex and surrounds a mass of darker stained tissue. Tissues that stained darker are circled, and are thought to be damaged from kermes scale feeding as well as the necrotrophic phytopathogenic bacterium *Lonsdalea quercina* subsp. *quercina*.

a bivoltine life cycle (Turner and Buss 2005). Where a univoltine life cycle occurs, the period in which the successive life stages are present in Colorado are delayed by approximately 1 mo compared to the univoltine life cycle of *A. kingii* in Virginia (Kosztarab 1996). Furthermore, *A. galliformis* female life stages were commonly observed throughout 1 or 2 mo during the summer and showed more overlap in life stages than *A. kingii*.

Our study identified specific sites where *A. galliformis* can be found during its development and plant tissues damaged by its feeding. This information can be useful in targeting treatments for its management. Due to the low efficacy of pesticides against this pest, techniques used to manage kermes scale should include mechanical removal of infested branches or individual scales, and treating trees with horticultural oils, and/or contact insecticides (Turner and Buss 2005, Turner et al. 2005). In the late summer, before egg eclosion, adult female scales are easily seen which makes this an ideal time for mechanical removal of individual pin oak kermes on accessible branches. Dormant season applications of horticultural oils should target overwintering crawlers, which this study found are concentrated on 2- to 4-yr-old wood of branches. In Colorado, dormant season oil applications would be best completed between November and mid-May. Following spring bud break, the crawlers move to current season growth or aggregate at the growth ring. Oils, with or without insecticides documented to control scales, may also be useful at this stage.

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