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Drippy Blight, a Disease of Red Oaks in Colorado, U.S., Produced from the Combined Effect of the Scale Insect *Allokermes galliformis* and the Bacterium *Lonsdalea quercina* subsp. *quercina*

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Abstract. Drippy blight is an emergent disease of red oaks, caused by the interaction between a kermes scale insect (*Allokermes galliformis*) and a bacterium (*Lonsdalea quercina* subsp. *quercina*). Multi-locus sequence analysis was used to confirm the bacterial pathogen's identity and its relationship to other phylogenetically related Enterobacteriaceae species. Further, Koch's postulates were performed on sapling red oaks. Prior to the discovery of drippy blight disease in Colorado, in the United States, the bacterium was reported on oak trees in California but was limited to acorn infections. The scale insect, *A. galliformis*, was previously known to occur on pin oak in the eastern United States but was not previously associated with either this bacterium or the production of significant branch dieback associated with drippy blight. In addition to a description of this new disease, this research documents a host range expansion of *L. quercina* subsp. *quercina* to northern red oak (*Quercus rubra*), Shumard oak (*Q. shumardii*), and pin oak (*Q. palustris*) and extends the reported host range of *A. galliformis* to include northern red and Shumard oaks.

Key Words. *Allokermes galliformis*; Bacteria; Colorado; Drippy Blight; *Lonsdalea quercina,* Red Oak; Scale Insect.

Northern red oak (*Quercus rubra*), pin oak (*Q. palustris*), and Shumard oak (*Q. shumardii*) comprise a small but important component of the urban tree landscape along the eastern urban corridor adjacent to the Rocky Mountains in Colorado, U.S. Since the early 2000s, some municipalities within this region have noted sites where all ages of these oak species and their hybrids have experienced significant dieback of unknown origin. The disease incidence has accelerated in some locations. For example, in Boulder, which has the largest concentration of northern red oaks on public property in the state of Colorado, trees showing extensive twig dieback throughout the crown more than doubled over three years, from 11% (50/450) in 2012 to 24% (110/450) in 2015. As the trees have shown progressive decline, there has been a resultant increase in tree removals (K. Alexander, personal communication, 2016).

Affected trees initially exhibit leaf scorching and leaf drop, followed by dieback of small-diameter twigs throughout the canopy (Figure 1a; Figure 1b). As branch cankers form or as twigs die, tree parts become brittle and snap off the tree, especially during windstorms. At the point of breakage, new shoot growth often results in small witch's brooms, or twig dieback from successive years may result in major limb dieback. Another feature associated with the disease, particularly in northern red oak, is copious gummosis that drips from cankered, damaged twigs, and onto sidewalks and parked cars, creating a nuisance (Figure 1c; Figure 1d). This combination of symptoms has led to this condition being described as "drippy blight" of red oak.

Initially, it was considered that these symptoms resulted from a species of kermes scale insect, *Allokermes galliformis*, consistently found on damaged branches (Figure 1c). Kermes scales are insect gall mimics that develop almost exclusively on oak (Gill 1993). *Allokermes galliformis* has been reported from several *Quercus* species but is most often found in association with pin oak, leading to it sometimes being called "pin oak kermes" (Bullington and Kosztarab 1985).

Kermes scales are generally considered minor pests of oak, occasionally causing some twig dieback, and can be associated with excretion of waxy substances (Bullington and Kosztarab 1985). However, the extensive production of gummosis and the presence of small cankers noted regularly at scale feeding sites (Figure 1c; Figure 1d) led to suspicions that there may be pathogen involvement. The objectives of this report were to identify the microbe(s) associated with the twig cankers, establish their potential pathogenicity, and to better understand interactions of pathogens and *A. galliformis* in producing the symptoms of drippy blight disease on red oaks.

MATERIALS AND METHODS

Pathogen Identification

Cream-colored bacterial colonies were isolated from canker margins in northern red and pin oaks at several locations in Boulder and Denver, Colorado. For molecular identification of the bacteria, single-spore cultures were grown in nutrient broth for 24 hours on a rotary shaker, and genomic DNA was extracted using an Invitrogen™ Easy-DNA™ kit (Invitrogen, Carlsbad, California, U.S.). The 16S ribosomal DNA was amplified using the methods of Jiang et al. (2006). Amplified products were Sanger-sequenced at Colorado State University's Proteomics and Metabolomics Facility (Fort Collins, Colorado, U.S.), and compared to the NCBI Nucleotide Database using BlastN search (Altschul et al. 1990) in order to identify the pathogen.

To ensure each sequence belonged to *Lonsdalea quercina* subsp. *quercina*, multiple genomic regions of other closely related species were also used for comparison (Table 1). Sequences were retrieved from the NCBI Nucleotide Database, either from individual gene submission (Gen-

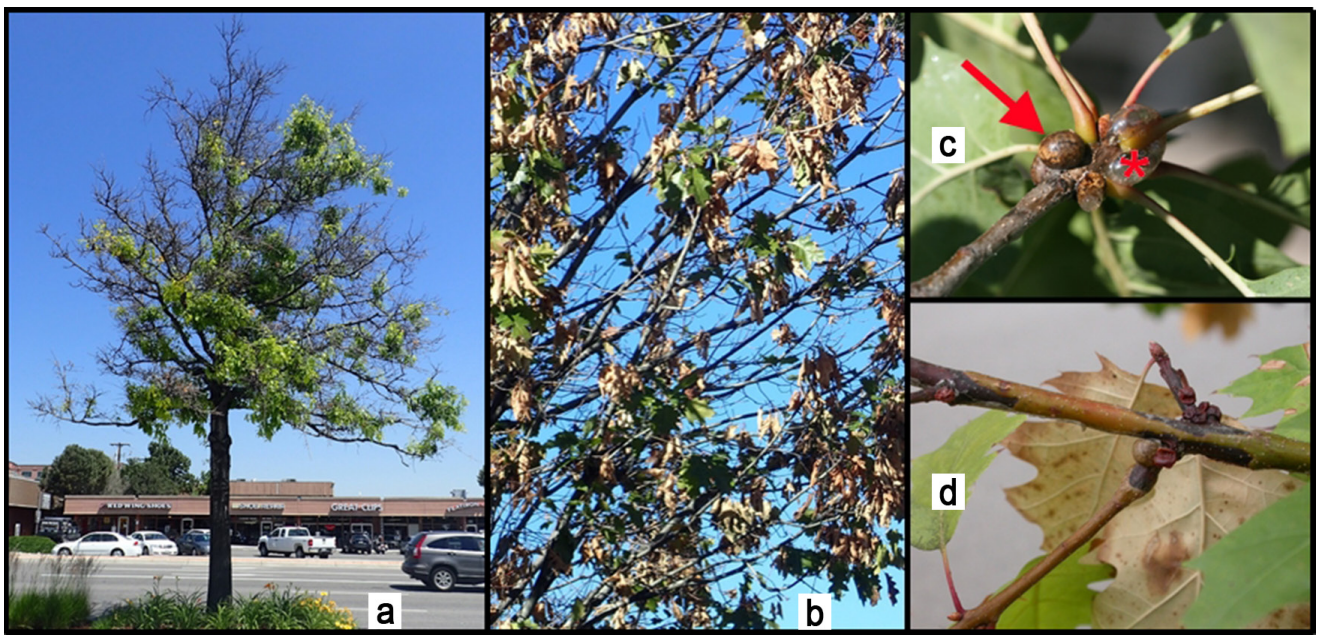

Figure 1. Signs and symptoms of drippy blight disease: a) a symptomatic pin oak showing witch's brooms and dieback as a result of drippy blight disease, b) northern red oak branches exhibiting flagging and dieback from drippy blight disease, c) an adult kermes scale insect (*Allokermes galliformis,* arrow) next to bacterial exudates (*Lonsdalea quercina* subsp. *quercina,* star), and d) dead (shriveled) and live (round) kermes scales surrounded by bacterial cankers.

bank accession numbers in Table 1) or from complete genome sequences (Caballero et al. 2014; Zhao et al. 2014). These were trimmed and aligned using ClustalW (Larkin et al. 2007) and Mega5 (Tamura et al. 2011), respectively. Bayesian phylogenetic analyses were performed in MrBayes using the general time-reversible model, with inverse-gamma rates of evolution for 500,000 generations, and a burn-in equal to 0.25 (Huelsenbeck and Ronquist 2001). *Erwinia piriflorinigrans* was used as the outgroup.

Pathogenicity Studies

One-year-old potted northern red, pin, and Shumard oaks were grown in a shade house at Colorado State University, and used to confirm microbe pathogenicity. Trees were inoculated with a northern red oak isolate of *L. quercina* subsp. *quercina* (NCCB100490) collected in Boulder, Colorado. Two experiments were conducted with different inoculation sites: emerging leaf whorls and one-year-old stems. A single colony was streaked onto full-strength nutrient agar, incubated for two days at 26°C, then diluted in 1 mL of sterile water for each inoculation experiment. In the first experiment, five trees of each species were used, and each tree was inoculated three times (n = 45). Emerging leaf whorls were mechanically wounded with a 1 cc syringe needle as trees broke dormancy, then 50 µl of the 5x108 CFU bacterial suspension was injected between the layered whorls. In a second experiment, three trees of each species were inoculated three weeks post budbreak with 5 µl of a bacterial suspension injected into one-year-old stems. Each tree was inoculated twice (n = 18). In each experiment, control inoculations using sterile water were also made twice, slightly (3–4 cm) above the inoculation sight, or on a different twig. Each site was wrapped (Parafilm®, Bemis Company, Inc., Oshkosh, Wisconsin, U.S.). The canker lengths were recorded and the pathogen was re-isolated from cankers on nutrient agar five to fifteen days after inoculation.

Data were analyzed using JMP software (11.1.0v; SAS Institute). For each inoculation experiment, a mixed model was fit using canker lesion length as the response variable with tree species as a fixed effect. Tukey's HSD was used to obtain pairwise comparisons between lesion lengths on the different tree species.

Table 1. GenBank Accession Numbers. The species, isolate number, and GenBank accession numbers are provided for the species used to compare the pathogen *Lonsdalea quercina* subsp. *quercina* to closely related Enterobacteriaceae species. The species comparison was based off of several loci, including 16S ribosomal RNA, DNA gyrase subunit B genes (*gyr*B), beta subunit of ATP synthase (*atp*D), and translational initiation factor genes (*inf*B) sequences.

Species	Isolate number	16S ribosomal DNA	DNA gyrase subunit B genes (*gyr*B)	Beta subunit of ATP synthase (*atp*D)	Translational initiation factor genes (*inf*B)
Cronobacter sakazakii	CMCC 45402	retrieved from genome: NC_023032	retrieved from genome: NC_023032	retrieved from genome: NC_023032	retrieved from genome: NC_023032
Erwinia piriflorinigrans	CFBP 5882	GQ405203	JF311583	JF311470	JF311696
E. toletana	LMG 24162	FN547375	EU145274	EU145258	EU145290
Lonsdalea quercina subsp. *britannica*	LMG 26267T	JF311442	JF311666	JF311553	JF311779
	LMG 26268	JF311443	JF311667	JF311554	JF311780
	LMG 26269	JF311444	JF311669	JF311556	JF311782
	R-43661	JF311445	JF311671	JF311558	JF311784
	LMG 6054	JF311446	JF311672	JF311559	JF311785
Lonsdalea quercina subsp. *iberica*	LMG 26264T	JF311441	JF311665	JF311552	JF311778
	LMG 26265	JF311439	JF311662	JF311549	JF311775
	LMG 26266	JF311440	JF311663	JF311550	JF311776
	R-43277	JF311438	JF311661	JF311548	JF311774
Lonsdalea quercina subsp. *quercina*	NCCB100490	KX537747	retrieved from genome: JIBQ01000000	retrieved from genome: JIBQ01000000	retrieved from genome: JIBQ01000000
	NCCB100489	KX537748	retrieved from genome: JIBP01000000	retrieved from genome: JIBP01000000	retrieved from genome: JIBP01000000
	ATCC 29281	KX537749	retrieved from genome: JIBO01000000	retrieved from genome: JIBO01000000	retrieved from genome: JIBO01000000

Disease Description

Three drippy-blight-diseased trees measuring 50–75 cm diameter at breast height located in Boulder, Colorado, parks were felled in December 2010. Approximately 100 twigs <1 cm diameter were collected from each tree, and evaluated for the presence of kermes scales and cankers. In 2015 and 2016, diseased trees throughout Boulder were monitored weekly from May to October to document the disease progression.

RESULTS AND DISCUSSION

The red oak (NCCB100490) and pin oak (NCCB100489) isolates of *L. quercina* subsp. *quercina*, shared 100% of nucleotide identity when the four gene sequences were compared (Caballero et al. 2014), and formed a monophyletic clade with *L. quercina* subsp. *quercina* ATCC 29281, based on the multi-locus sequence analysis (Figure 2). The Colorado strains are closely related to, but genetically distinct from, *L. quercina* subsp. *quercina* ATCC 29281 found in California. Strains are less closely related to *L. quercina* subsp. *iberica* (LMG 26264T, LMG 26265, LMG 26266, R-43277) or *L. quercina* subsp. *britannica* (LMG 26267T, LMG 26268, LMG 26269, R-43661, LMG 6054). *Lonsdalea quercina* subsp. *iberica* causes bark cankers and drippy bud on holm oak and Pyrenean oak in Spain (*Q. ilex* and *Q. pyrenaica*, respectively) (Biosca et al. 2003; Poza-Carrión 2008), whereas in the United Kingdom, *L. quercina* subsp. *britannica* is thought to contribute to acute oak decline of *Q. robur* and *Q. petraea* (Brady et al. 2012; Denman et al. 2012). Oozing bark cankers on hybrid poplar (*Populus* × *euramericana*) have been attributed to *L. quercina* subsp. *populi* (Tóth et al. 2013; Li et al. 2014).

Following inoculation with *L. quercina* subsp. *quercina*, canker development associated with copious production of bacterial exudates was noted in tested trees involving all three red oak species (northern red, pin, and Shumard), except for one of eight Shumard oak saplings. *Lonsdalea quercina* subsp. *quercina* was consistently re-isolated from canker margins on each oak species. Trees inoculated on leaf whorls exhibited bacterial ooze within five to seven days of inoculation (Figure 3a), and small lesions formed as the shoots elongated. Shoot and leaf dieback were also observed. Cankers on red oak were significantly longer than cankers on pin oak ($P = 0.04$), with lengths of 1.02 cm and 0.55 cm, respectively. Shumard oak cankers measured 0.77 cm and did

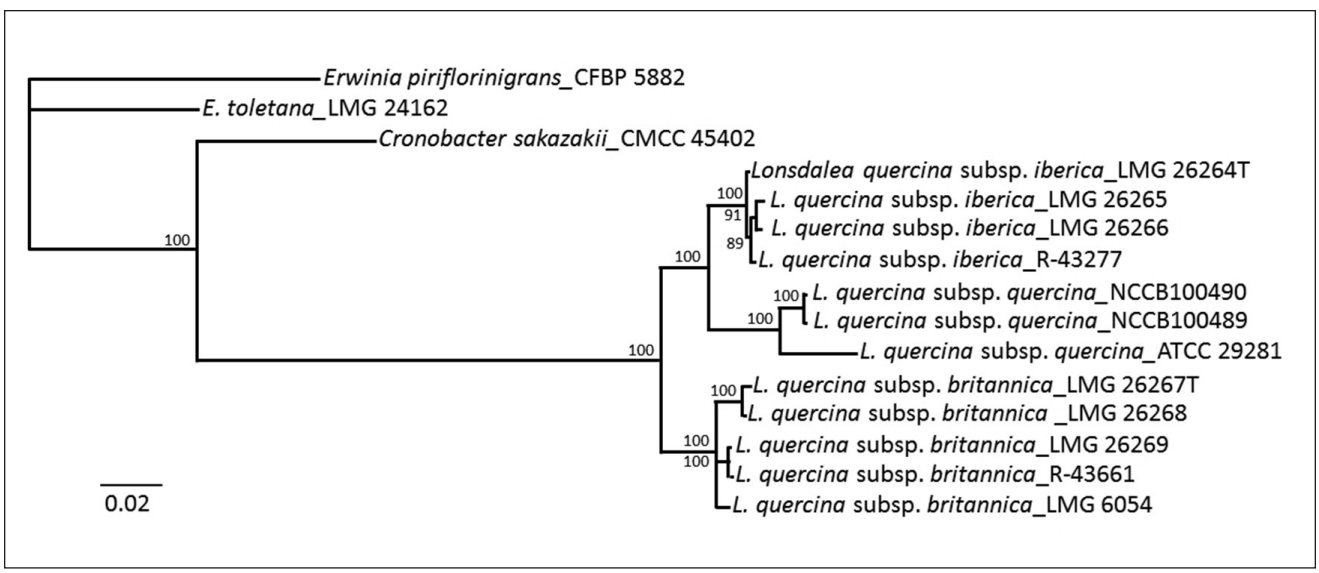

Figure 2. Phylogenetic tree of Enterobacteriaceae species based on 16S ribosomal RNA, DNA gyrase subunit B genes (*gyr*B), beta subunit of ATP synthase (*atp*D), and translational initiation factor genes (*inf*B) sequences. A Bayesian analysis was performed for 500,000 generations using a GTR / gamma distributed with invariant sites model of evolution. Bayesian probabilities are shown next to each branch. Species: *Cronobacter sakazakii*; *Erwinia piriflorinigrans* (CFBP 5882); *Lonsdalea quercina* subsp. *iberica* (LMG 26264T, LMG 26265, LMG 26266, R-43277); *Lonsdalea quercina* subsp. *quercina* (red oak isolate NCCB100490, pin oak isolate NCCB100489, ATCC 29281); *Lonsdalea quercina* subsp. *britannica* (LMG 26267T, LMG 26268, LMG 26269, R-43661, LMG 6054); *Pantoea calida*; and *Erwinia toletana*.

not differ from cankers on northern red or pin oaks (P = 0.53 and P = 0.35, respectively). Oaks inoculated on stems three weeks post budbreak developed bacterial exudates within ten to fifteen days of inoculation, and small cankers formed on stems within 21 days of inoculation (Figure 3b). Although the cankers on northern red oak trees averaged 1.25 cm and were over twice as long as cankers on Shumard and pin oak trees, there were no statistical differences in the canker lengths (P = 0.12 and P = 0.47, respectively). Cankers found on Shumard and pin oaks were also similar in size (0.53 cm and 0.57 cm, respectively, P = 0.76).

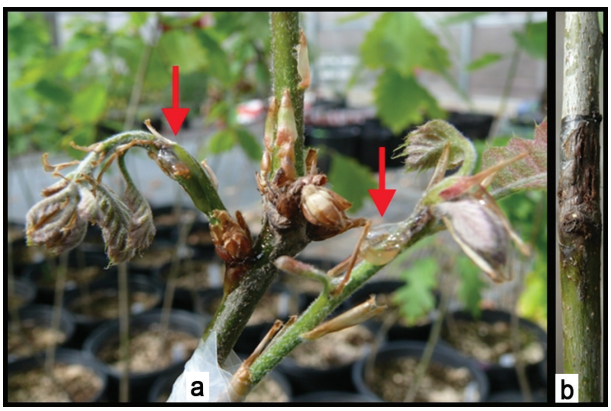

Figure 3. Inoculation experiment: a) Shumard oak, 14 days post leaf whorl inoculation with *Lonsdalea quercina* subsp. *quercina* (note the bacterial ooze at inoculation sites, arrows); b) canker formation in northern red oak on one-year-old stems.

In the course of field collections of three northern red oak trees in 2010, *A. galliformis* was found on 70%–81% of the twigs. Cankers typical of those produced by *L. quercina* subsp. *quercina* were present at one or more feeding sites of scales on 51%–57% of the kermes-scale-infested twigs. Further, cankers were only present at scale insect feeding sites, which strongly supports an interaction between *A. galliformis* and *L. quercina* subsp. *quercina*. This combination of kermes scale feeding and subsequent bacterial canker formation resulted in 30%–42% twig dieback.

The occurrence of twig cankers associated with the production of large amounts of bacterial ooze from infection with *L. quercina* has not previously been reported. In California, *L. quercina* subsp. *quercina* infections are limited to acorns of coast live oak (*Q. agrifolia*) and interior live oak (*Q. wislizenii*), producing a condition sometimes described as "drippy nut of acorns" because of the copious bacterial ooze manifesting at acorn wound sites (Hildebrand and Schroth 1967).

Although *L. quercina* causes infections of acorns in California (Hildebrand and Schroth 1967), a canker disease of *Populus* in China and Hungary (Tóth et al. 2013; Li et al. 2014), and contributes to oak decline in Britain and Spain (Biosca et al. 2003; Brady et al. 2012; Denman et al. 2012), drippy blight of red oak differs from these previous documentations. Branch dieback, canker formation, twig abscission at the junction to the current season's growth, leaf drop, epicormic branching, and witch's brooms are symptoms associated with this newly described condition. Furthermore, during the spring and summer, bacterial oozing occurs throughout the canopy. Exudates may be so copious that dripping ooze results in large sticky areas on sidewalks and other surfaces under the canopy throughout the middle of the summer. Twig cankers, indicated by maroon discoloration and clear margins (Figure 1d), appear in the late summer near kermes-scale-feeding sites and wounds. If the bacterium is present in the fall, it dries and hardens.

Historically, tree damage accompanying kermes scale infestations was attributed exclusively to the insect feeding (Turner and Buss 2005; Turner et al. 2005; Kosztarab 1996; Pellizzari et al. 2012). In contrast, these results document a situation in which the combined activity of a kermes scale insect and a bacterium produce the tree decline symptoms described as drippy blight of red oak (Snelling et al. 2011; Caballero et al. 2014). The exact manner of how these two organisms interact to produce drippy blight disease remains unclear. In drippy nut of acorns, the bacterium establishes at wound sites caused by seed-feeding weevils, filbertworms, and cynipid gall wasps (Swiecki and Bernhardt 2006). Similarly, in drippy blight of red oak, the wounding associated with kermes-scale-feeding injuries may provide entry or exit courts for the pathogen. Alternatively, the interaction may be more indirect, where kermes scales act as a stressor to facilitate growth and spread of the pathogen within the host.

Additional outstanding questions on drippy blight disease remain. For example, efforts to manage this disease complex have been disappointing and are complicated by the presence of two causal

agents. Although effective scale management programs, such as removing scales by hand, pruning and destroying infested materials, treating with horticultural oils, and applying contact or systemic insecticides are likely the best way to control drippy blight disease (Turner and Buss 2005; Turner et al. 2005), studies to quantify the efficacy of control treatments are pertinent to maintaining red oaks in drippy-blight-diseased regions. If horticultural oils or insecticides are used to control drippy blight disease, monitoring for the most susceptible life stage of *A. galliformis* is necessary to determine the proper timing of applications. The life history of *A. galliformis* is similar to *A. kingii* (Hamon et al. 1976; Kosztarab 1996), but checking for *A. galliformis* egg hatch is pivotal to ensuring that the timing of application targets susceptible life stages (Turner et al. 2005).

Drippy blight disease of red oaks is an emergent disease caused by the interaction between *A. galliformis* and *Lonsdalea quercina* subsp. *quercina*. In addition to a description of this new disease, this report documents a host range expansion of *L. quercina* subsp. *quercina* to northern red oak, Shumard oak, and pin oak, and extends the reported host range of *A. galliformis* to include northern red and Shumard oaks.

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Résumé. La Drippy Blight (aucun nom commun) est une maladie émergente du chêne rouge, causée par l'interaction d'une cochenille de type kermès (*Allokermes galliformis*) et d'une bactérie (*Lonsdalea quercina* subsp. *quercina*). L'analyse séquentielle multi-locus fut utilisée pour confirmer l'identité de l'agent pathogène bactérien et sa relation avec d'autres espèces d'entérobactéries apparentées phylogénétiquement. En plus, les postulats de Koch furent appliqués à des semis de chêne rouge. Préalablement à la découverte de la Drippy Blight au Colorado, USA, la bactérie avait été observée sur des chênes en Californie mais s'était limitée à des infections de glands. Cette cochenille, *A. galliformis*, était précédemment connue pour être présente sur le chêne des marais dans l'est des États-Unis mais elle n'était cependant associée, ni à cette bactérie, ni à la production de dépérissement significatif de branches en lien avec la Drippy Blight. Au delà de la description de cette nouvelle maladie, cette recherche documente également l'expansion de plantes hôtes pour la bactérie *L. quercina* subsp. *quercina* vers le chêne rouge (*Quercus rubra*), le chêne de Shumard (*Q. shumardii*) et le chêne des marais (*Q. palustris*) tout en élargissant la gamme d'hôtes connus de *A. galliformis* afin d'inclure les chênes rouges ainsi que de Shumard.

Zusammenfassung. Die Tropffäule ist eine zunehmende Erkrankung von Roteichen, die aus der Interaktion zwischen einer gall-bildenden Schildlaus (*Allokermes galliformis*) und einem Bakterium (*Lonsdalea quercina* subsp. *quercina*) entsteht. Multi-Lokus-Sequenz-Analytik wurde verwendet, um die Identität des pathogenen Bakteriums zu bestätigen und seine Beziehungen zu anderen phytogenetisch verwandten Enterobacteriaceae species. Darüber hinaus wurden Kochs Postulate an jungen Roteichensprossen. Bevor der Entdeckung der Tropffäule in Colorada, in den USA, wurde über das Bakterium in Kalifornien an Eichenbäumen berichtet, aber es war begrenzt auf Eichelinfektionen. Die Schildlaus *A. galliformis*, war vorher dafür bekannt, auf Sumpfeichen in den östlichen Vereinigten Staaten aufzutreten, aber es war vorher nicht mit diesem Bakterium oder der Produktion von signifikantem Triebsterben in Verbindung mit Tropffäule assoziiert. Zusätzlich zu einer Beschreibung dieser neuen Krankheit dokumentiert dieser Bericht eine Ausdehung des Wirtsspektrums von *L. quercina* subsp. *quercina* auf Amerikanischen Roteiche (*Quercus rubra*), Shumard -Eiche (*Q. shumardii*), und Sumpfeiche (*Q. palustris*) und dehnt das berichtete Wirtsspektrum von *A. galliformis* auf die Amerikanische und Shumard-Eiche aus.

Resumen. El tizón por goteo es una enfermedad emergente de los robles rojos, causada por la interacción entre un insecto escama de kermes (*Allokermes galliformis*) y una bacteria (*Lonsdalea quercina* subsp. *quercina*). Se utilizó el análisis de secuencia múltiple para confirmar la identidad del patógeno bacteriano y su relación con otras especies de Enterobacteriaceae relacionadas filogenéticamente. Además, se llevaron a cabo los postulados de Koch en árboles jóvenes de robles rojos. Antes del descubrimiento de la enfermedad del tizón por goteo en Colorado, Estados Unidos, se reportó la bacteria en robles en California, pero se limitó a infecciones de bellota. El insecto escama, *A. galliformis*, se conocía previamente en roble americano en el este de los Estados Unidos, pero no se había asociado con esta bacteria ni con la producción de muerte regresiva significativa asociada con la plaga por goteo. Además de una descripción de esta nueva enfermedad, esta investigación documenta una expansión del rango de huéspedes de *L. quercina* subsp. *quercina* al roble rojo del norte (*Quercus rubra*), roble Shumard (*Q. shumardii*), y roble (*Q. palustris*) y extiende el rango de hospedante reportado de *A. galliformis* para incluir robles del norte y robles Shumard.