INTRODUCTION

A new, late-season leaf disease on bur oak (Quercus macrocarpa) had been observed in southern Minnesota, southwest Wisconsin, eastern Nebraska, and Iowa since the mid-1990s. Symptoms of the new disease included necrosis of the leaf tissue along the veins and death of entire leaves, usually starting in late July (Pokorny and Harrington 2011). Branches in the lower crown were generally the most severely affected, and severity of the disease tended to increase year to year in individual trees. Distinctive fruiting bodies (conidiomata) of a fungus were found along the veins of affected leaves, and the fungus was tentatively identified as Tubakia dryina. However, the cause of the disease had not been established before this project, and the incidence of the disease appeared to be increasing.

When investigations began in 2008, it became apparent that there are a number of Tubakia species on bur oak and other oak species in Iowa. A fungus that matched the description of T. dryina was found on white oak (Q. alba) but rarely on bur oak, and the Tubakia sp. associated with the new disease appeared to be distinct. The new disease was named bur oak blight (BOB). The spotty nature of BOB initially suggested that pathogen was invasive and had not fully expanded its potential range. Alternatively, an increase in early-season rain events (climate change) over the past two decades could explain the apparent elevated incidence and severity of the disease (Harrington 2011). To help resolve these questions and characterize the diversity of Tubakia spp. on oaks in the Upper Midwest, the following objectives were developed: (1) determine the distribution of BOB and follow within-tree intensification and spread to new trees in Story County, Iowa; (2) determine the geographic distribution of bur oak blight in Iowa and the Midwest; (3) collect specimens and isolates of Tubakia spp. from diseased Quercus spp. and other hosts across the Eastern United States; (4) delineate species of Tubakia using morphology and DNA sequences and determine their host and geographic ranges; and (5) provide a review of Tubakia spp. with descriptions of new and old species.

METHODS

An informal survey of the Tubakia spp. on oaks and distribution of BOB in Iowa and the Midwest was conducted through examination of specimens in herbaria and collections of symptomatic oak leaves provided by numerous collaborators in Iowa and other States. We and our cooperators sampled extensively in late summer and early fall in 2009 through 2014 to determine the distribution of BOB in Iowa, Minnesota, and surrounding States. For all samples, we examined leaves for necrosis and presence of fruiting bodies; if Tubakia fruiting bodies were present, we conducted isolations and confirmed the species identification using polymerase chain reaction (PCR) and ribosomal DNA (rDNA) sequencing. Morphological features and further DNA sequence comparisons using other genes were used to help delineate putative species of Tubakia.
We conducted detailed epidemiological studies in a grove of 39 mature bur oak on a bottomland site at Brookside Park in Ames, IA, from 2009 through 2012. We monitored the progress of symptoms and isolated healthy twigs and leaves from affected ones. For disease ratings, the top and bottom half of the tree crown were separately evaluated for the crown area with symptomatic branches: 0 = no symptoms, 1 = less than 1/3 of the area with symptomatic branches, 2 = less than 2/3 of the area symptomatic, and 3 = 2/3 or more of the branches symptomatic. The disease rating for the whole tree was the sum of the lower and upper crown ratings, resulting in a scale ranging from 0 to 6.

We also determined September disease ratings and amount of overwintering inoculum on all trees in seven mature bur oak groves (four upland and three bottomland sites) in and around Ames.

### RESULTS AND DISCUSSION

We sequenced the rDNA of more than 250 isolates of *Tubakia* spp. from oak trees in Iowa and adjacent States and identified six species of *Tubakia* (table 7.1). Each of the species was

<table>
<thead>
<tr>
<th>Tubakia sp.</th>
<th>Hosts</th>
<th>States</th>
<th>Leaf symptoms</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tubakia iowensis</em></td>
<td><em>Q. macrocarpa</em>, rarely <em>Q. bicolor</em></td>
<td>Illinois, Iowa, Kansas, Minnesota, Missouri, Nebraska, South Dakota, Wisconsin</td>
<td>Vein necrosis, petiole necrosis, small necrotic spots</td>
</tr>
<tr>
<td><em>Tubakia dryina</em></td>
<td><em>Q. alba</em>, <em>Q. macrocarpa</em></td>
<td>Illinois, Iowa, Missouri, Wisconsin</td>
<td>Leaf spots</td>
</tr>
<tr>
<td><em>Tubakia</em> sp. A</td>
<td><em>Q. macrocarpa</em></td>
<td>Illinois, Iowa, Missouri, New Jersey, Wisconsin</td>
<td>Leaf spots, vein necrosis</td>
</tr>
<tr>
<td><em>Tubakia</em> sp. B</td>
<td><em>Q. macrocarpa</em>, <em>Q. muehlenbergii</em>, <em>Q. stellata</em>, rarely <em>Q. alba</em>, <em>Q. bicolor</em></td>
<td>Arkansas, Iowa, Kansas, Minnesota, Missouri, Wisconsin</td>
<td>Leaf spots, vein necrosis</td>
</tr>
<tr>
<td><em>Tubakia</em> sp. C</td>
<td><em>Q. ellipsoidalis</em>, <em>Q. imbricaria</em>, <em>Q. rubra</em></td>
<td>Iowa, Minnesota, Wisconsin</td>
<td>Discrete circular leaf spots, vein necrosis</td>
</tr>
</tbody>
</table>
isolated at least once from surface-sterilized, healthy leaves, showing that they were all endophytes in oak, but they were also isolated from necrotic leaf tissue, necrotic twigs, or acorns. All six species were isolated at least once from bur oak, but only one was associated with the extensive late-season leaf mortality that is characteristic of BOB.

The European *T. dryina* was the least common fungus in the region. A second uncommon fungus, *Tubakia* sp. A, appears to be the species originally described as *Actinopelte americana*, which was mostly isolated from healthy twigs and leaves of bur oak at our Brookside Park study site. Two undescribed species were leaf pathogens on members of the red oak (*Q. rubra*) group; one of these was occasionally found on *Q. rubra* trees with severe symptoms of veinal leaf necrosis, and the second species was less common and caused discrete, circular leaf spots as well as veinal necrosis. The causal agent of bur oak blight was described as *T. iowensis*, and a closely related species was tentatively named *Tubakia* sp. B (Harrington and others 2012). The latter appeared to have a broader host range on members of the white oak group and was more often associated with leaf spots than veinal necrosis. Besides bur oak, *T. iowensis* was found rarely on swamp white oak (*Q. bicolor*).

Bur oak blight was found to be a very host-specific disease, and the survey work at Brookside Park showed that it has a unique disease cycle. *T. iowensis* forms two types of asexual fruiting bodies (Harrington and others 2012). The most common type of fruiting body forms on necrotic leaf veins during the summer and serves as secondary inoculum during wet summers. But the most important type of fruiting body develops on petioles of leaves that remain attached to the twig through the winter months and mature the next spring.

Extensive sampling of naturally infected trees and greenhouse inoculation studies (West 2015) confirmed that the overwintering inoculum (from crustose fruiting bodies on petioles) leads to infection of emerging shoots during spring rains, latent infections without symptoms, and petiole necrosis 2 months later (Harrington and McNew, in press). The necrosis of the petiole prevents leaf abscission, and the fruiting bodies develop slowly on the dead petiole tissue for release of spores the next spring. Unusually wet springs for the last 20 years and buildup of overwintering inoculum in individual trees may be why the disease recently became conspicuous (Harrington 2013). Eradicative fungicide (propiconazole) injections of mature, blighted bur oak trees in early June reduced the number of dead leaves hanging on twigs through the winter and reduced disease severity for up to 3 years in a majority of trees in a study in Ames (Harrington 2012).

Bur oak blight was found to be most severe on mature trees on upland, former savanna sites, where the fire tolerant *Q. macrocarpa* var. *oliviformis* is well adapted (Deitschmann 1965, Great Plains Flora Association 1986). We identified *T. iowensis* throughout the geographic...
range of this small-acorn variety of bur oak (fig. 7.1). The disease was found in almost every Iowa county, though only low incidence of disease was found in the southeast corner of the State, and BOB was less common at some locations in the Loess Hills (western Iowa) and the denser forests of eastern Iowa than elsewhere. The disease also was very widespread in Minnesota, where, like in Iowa, *Q. macrocarpa* var. *oliviformis* is common.

The disease also was found on upland bur oak in States bordering Iowa and Minnesota (fig. 7.1). It was found in eastern South Dakota but not in North Dakota, where *Q. macrocarpa* var. *depressa* occurs on well-drained soils. Bur oak blight was not found on the large-acorned *Q. macrocarpa* var. *macrocarpa*, which is a bottomland variety common in the eastern and southern ranges of bur oak (Deitschmann 1965). In central Iowa, planted bur oak with small acorns may show severe BOB symptoms, but planted bur oak trees with larger acorns did not. *Tubakia iowensis* appears to be very specific to the upland variety of bur oak, and we suspect that there was little selection pressure for disease resistance in this variety when the climate was drier.

In seven permanent plots of mature, natural groves around Ames, IA, disease severity was found to be generally increasing from 2009 through 2014. The trend for more disease over the years is associated with consistently wet springs, a change in Iowa climate (Takle 2011) that appears to lead to buildup of the disease in individual trees. The disease severity was higher on the four upland sites than on the three bottomland sites (fig. 7.2). All trees on these sites had relatively small acorns and appeared to be *Q. macrocarpa* var. *oliviformis*, but there may have been more introgression of *Q. macrocarpa* var. *macrocarpa* into the bottomland sites than on the upland sites.

Severe BOB occurs in remnant savanna stands, and the bur oak ecotype adapted to thin, upland soils appears to be particularly vulnerable. However, even on upland sites, there
appears to be a wide variation in susceptibility within a stand, with severely affected trees next to healthy trees. In preliminary studies (West 2015), seedlings from acorns on trees with bur oak blight were not more susceptible to *T. iowensis* in inoculation trials than were seedlings from acorns on nearby healthy bur oak trees. The apparent resistance of some trees may be related to timing of bud break and inoculum release during warm spring rains.

**CONCLUSIONS**

Although six species of *Tubakia* were found on oaks in Iowa and elsewhere, only the newly described species, *T. iowensis*, causes bur oak blight. *T. iowensis* was found to be very host specific and widespread throughout the assumed geographic range of *Quercus macrocarpa* var. *oliviformis*, a fire-tolerant variety adapted to upland savannah forests. Genetic variation in the pathogen and apparent variation in susceptibility in the host suggest that *T. iowensis* is native and not invasive. Nonetheless, disease severity was found to be generally increasing in natural groves. The most important phases in the BOB disease cycle include infection of developing shoots, a long latent phase, late season necrosis of petioles, failure of abscission, and development of primary (spring) inoculum on the petioles of leaves that remain attached to the tree. Consecutive springs of high rainfall during bud break and shoot expansion are believed to increase severity of disease in individual trees. An increase in spring rainfall during the last two decades may explain the sudden recognition of BOB, and the apparent shift in climate in this region raises concerns about the future health of bur oak in the region.
**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


Front cover map: Ecoregion provinces and ecoregion sections for the conterminous United States (Cleland and others 2007) and for Alaska (Nowacki and Brock 1995).

Back cover map: Forest cover (green) backdrop derived from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery by the U.S. Forest Service Remote Sensing Applications Center.

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