ELISA Testing, Lab Culturing, DNA Sequencing (All Studies)

All fine root samples for all of the rural and urban oak surveys were prepared as per standard ELISA testing methods. Roots testing positive for *Phytophthora* infection were baited to isolate the oomycete using leaf pieces of the same oak tree species The leaf pieces are grown on a semi-selective medium for *Phytophthora* and sub-cultured until they were single isolate cultures. The mycelia were harvested and well plates were delivered to Ball Horticulture-Helix Labs for DNA extraction and amplification, and then sent to Oklahoma State University for Sanger Sequencing. The sequences were then returned to Ball Horticulture-Helix for identification for genus and species.

RESULTS

IDNR Statewide Oak Decline Study (Rural Oak Forests: 2023-2025)

To date, over 400 white, northern red, bur, shingle, and black oak tree root samples have been taken at approximately 40 different sites statewide (**Figure 2**). Preliminary results have revealed that more than 80% of the root samples taken from declining white oak, northern red oak, bur, black, and swamp white oaks have tested positive for the presence of oomycetes in the roots. **Please note: this is a qualitative measure and only indicates the presence of oomycetes (infection) in the roots of the sampled oak trees.**

Our root infection rates (>80%) are consistent with findings obtained by **Remsen (2024), Watson and Adams (2024), and Remsen et al., (2025)** for oak species growing in urban sites in the Chicagoland area. In contrast, in other studies, root infection rates for European oaks have been found to be somewhat lower (60%) compared with our studies.

Rooting depth. Overall, there was no difference in the percentage of trees (86%) with oomycetes present at sites with a rooting depth of <10" compared with trees with a rooting depth of > 10 inches. Apparently, in rural forests, rooting depth is not a major factor in oak decline but according to Remsen's (2024) study, soil compaction is a major predisposing factor for urban oaks.

Topography (Slope, Aspect). Overall, slope does not appear to be a significant factor in oak decline, but there was nearly a 20% difference in roots testing positive on flat sites compared with sloping sites. Infection rates were more consistent between different flat sites compared with sloping sites. For oak species growing on flat (<5% slope) and sloping (>15%) sites, 92% and 83% of white oak roots tested positive, respectively. For northern red oak roots 83% and 90% of roots tested positive, respectively.

Consistent with our study, Remsen (2024), found that slope was not a major factor for urban oaks growing in the Chicagoland area.

Restrictive Soil Layer (RSL), perched water tables (PWTs), and Seasonal High-Water Tables (SHWTs). Soils with restrictive layers (RLs) (i.e. clay or plow pan layers), perched water tables (PWTs) or seasonal high-water tables (SHWTs) within the soil profile or near the soil surface can impede drainage, and root growth and penetration. Additionally, PWT and SHWTs in spring and early summer months, along with flooding, can facilitate the spread of oomycetes, leading to root rots and tree decline. In this study, trees growing on flat sites with RLs, PWTs, and SHWTs within 1-3 feet of the soil surface had a higher incidence of roots testing positive for oomycetes. These results are consistent with the Watson and Adams (2024) study.

Soil Texture. Soil texture may play a major role as well. The vast majority of the study sites were silt loams (SLs) and/or silty clay loams (SCLs) with some sites having very fine textured soils (i.e. clay content >35%). Clay and clayey soils are notorious for holding water and are usually slow to drain. Soils with high clay content (>35%) in the B horizon (subsoil) usually stay wetter longer and are slower to drain. Many of the flat sites had silty-clay-loam (SCL) soils at a depth of 7 to 15 inches, with 30-40% clay content in the subsoil (B-Horizon), a restrictive soil layer (RSL) at a depth of 1 to 3 feet, perched water table (PWT), and a seasonal high-water table (SHWT) within three feet of the surface.

In contrast, sloping sites also had SL and SCL soils, but at great depths of 15 to 20 inches with 30-40% clay content in the B-Horizon; and RSLs and SHWTs greater than six feet. The sites with soil layers with higher clay content closer to the soil surface could potentially be slower to drain particularly during excessively wet springs and summers, and during periodic flooding. RSLs, PWTs, and SHWTs within the rooting zone of trees (18-24 inches) probably contribute to the high incidence of oomycetes and the potential for subsequent root-rotting events. Our findings are consistent with Remsen (2024) and Watson and Adams (2024).

In contrast, white, bur, and swamp white oak roots sampled from flat sites (i.e. Mason State Nursery) had much lower (<40%) levels of infected oak roots. Additionally, white and black oak roots sampled at the nearby Sandridge state forest were not infected. One possible reason is both sites have predominately sand and/or sandy-silt soils that are excessively well-drained and can be droughty. In contrast, northern red oaks, growing at a different location at the Mason State Nursery (MSN), on more silty soils, had a higher root infection rate (60%).

DNA Sequencing (All Studies). A summary of oomycetes sequenced to date for rural and urban oak species is presented in **Tables 1 and 2.** Not surprisingly, there appears to be a complex of oomycetes associated with oak roots including over 20 different *Phytophthora*, *Phytopythium*, and *Pythium* spp.

Recent related studies on urban oak trees by Remsen (2024), Watson and Adams (2024), Remsen et al., 2025) have found additional oomycete spp. including *Phytophthora pini* (**white oak**), *Phytophthora gonapodyides* (**white and swamp white oak**), *Phytopythium plurivora* (**white oak**), *Pythium littorale* (**white oak**), *Pythium latarium* (**northern red oak**), *Pythium* sp. 824b (**bur oak**), *Pythium nodosum* (**bur oak**), *Globisporangium heterothallicum* (**white oak**), *Globisporangium (Pythium) macrosporum* (**northern red oak**), and *Elongisporangium anandrum* (**northern red oak**) (**Table 2**).

In our study and Remsen (2024), *Phytopythium vexans* was found to be the predominate known root pathogen for both rural and urban oak trees with white oaks having the highest infection rates compared with bur (distant second), northern red, and black oaks (**Table 2**). *Phytopythium vexans* was also more prevalent on poorly-drained, flat sites (**Table 3**).

Comparing our studies, other North American studies, and European studies, *s*ome of the aforementioned oomycetes are known pathogens on herbaceous and woody plants, and a few have been found in forest soils associated with declining oaks (**Table 4**) (Balcì and Halmschlager 2003a,b; Corcobado et al., 2013; Cordier et al. 2009; Gaertig et al. 2002, Gosling et al. 2024; Jung et al. 1996, 2000, Jonosson et al. 2003; McConell and Balci 2024; Nagle et al. 2010; Watson and Adams 2024). However, in some studies, the evidence is circumstantial (i.e. oomycetes were found associated with roots of declining oaks, but pathogenicity was not been confirmed). Further testing with Koch's postulate will be required to determine if any of these oomycetes are pathogenic or are just saprophytes of oaks.

Soil nutrients, pH, and pathogenic oomycetes. A summary of soil nutrient levels for all statewide rural forest sampling sites is presented in **Table 5**. Very low to low P and Ca levels were found on 60% and 51%, of all sampling sites, respectively. Also, very low to low levels of S and Zn were found on 33% and 40% of sampling sites, respectively. High to very high levels of Mn and Fe were detected for all sampling sites.

A summary of white and northern red oaks roots growing in soils with *Phytopythium vexans* with low macro- and micro-nutrient levels is presented in **Table 6.** Of all of the oomycetes sequenced to date in this study, the world-wide pathogenic *Phytopythium vexans* was found associated with a high percentage of white and bur oak roots growing in P, Ca, S, and Zn deficient soils (very low to low levels) for 100%, 80%, 40%, and 60% of root sampling sites, respectively. Additionally, oaks growing on poorer sites with <3% organic matter (OM) and low fertility (CEC<10) tended to have a higher percentage of roots testing positive.

Studies have shown there is a relationship between low Ca levels and the incidence of infection by *Phytophthora* spp. where it is suspected that Ca levels may prevent the development of zoospores. Further, Ca plays multiple roles in plant defense against pathogens and has been found to be important in "Ca signaling" for initiating various biochemical and physiological responses in plant defense. The role of P has been found to be more variable, but it is a well-known player in cell energy, via phosphorylation, DNA, and RNA. More recently, studies focusing on Zn have revealed its importance in overall plant health particularly in photosynthesis, but also in diseases resistance (Cabot et al. 2019; Tripathi et al. 2022).

Watson and Adams (2024) Urban Oak Study: ELISA results were positive in 87% of the samples. All sites had fine textured soils classified as moderately to poorly drained, and with high spring water tables. Topography was always very flat. The water table was near the surface for most of the spring on poorly drained sites with declining trees, and significantly higher than in the slightly elevated sites with better drainage and healthy trees. From 2018 to 2020, the region experienced the highest average spring rainfall for any three consecutive years in the last 70 years. This created soil conditions conducive to root disease development.

Remsen et al. 2025) Urban Oak Study: Low micronutrient levels, compaction, elevated soil sodium, and poor drainage appear to be the most relevant predisposing abiotic site characteristics for white oak decline. **Remsen (2024) and Remsen et al., 2025)** found that Zn was a major factor in the health of oaks meaning that trees growing on soils with Zn deficiencies were more prone to infection by oomycetes (i.e. *P. vexans*) leading to oak decline.

SUMMARY (All Studies): What Have We Learned to Date?

- To date, over 20 different oomycete species have been identified
- Visual tree assessments do not necessary reflect root infection and is consistent with other studies
- Oomycete infestation rates >80% are much higher than results from European studies (60%)
- White oaks tend to have higher infestation rates compared WITH bur, northern red, swamp white and black oaks
- A variety of known oak root pathogens have been identified with *P. vexans* being the predominate root rotting pathogen

- Site and soil characteristics appear to be important for rural and urban oak tree decline in Illinois
- Flat sites with poor to moderate drainage, fine textures, clayey sub-soils, perched or seasonally high-water tables, and compaction may be important predisposing soil factors for oak decline for both rural and urban Illinois oak forests
- Slope, depth to restrictive layers, and rooting depth do not appear to be related to root infection levels in rural oak forests
- Multiple consecutive years (2018 to 2020) of far above normal rainfall appear to have facilitated the development of root disease leading to rapid decline of oaks in the region
- Oak roots growing in sandy to sandy-silt soils have no or very low infestation levels
- Soils with low levels of P Ca, S, or Zn and elevated Na levels (deicing salts) may contribute to altered nutrient cycling associated with declining oaks

CONCLUSIONS (Future Research, and Oak Management Recommendations).

Watson and Adams (2024) conclude that if *Phytophthora* spp., and perhaps other soil-borne pathogens, are widely present in soils and oak root systems, a better understanding of the conditions that will lead to serious disease would help us to anticipate it in the future and treat trees to control disease before the infection kills trees. Unusually high rainfall that is conducive to root disease development is becoming a consistent trend in Illinois in the last century. Over the last 120 years, mean precipitation has increased by 5% to 20% across the state (Wuebbles et al. 2021). Understanding this pathosystem will increase in importance in the future as Northern Illinois is expected to see further increases in winter and spring precipitation in the coming decades as the climate warms (Wuebbles et al. 2021).

Positive ELISA test results indicate that species of *Phytophthora* is present in the root systems, but identification of pathogenic species can only be confirmed by isolating them into culture from the roots, morphological or molecular identification, and completing Koch's postulates. Species identification work is currently underway. Preliminary results have identified several species of *Phytophthora*, *Pythium*, and *Phytopythium*. Most of them have previously been reported to cause root disease on different hosts, but not necessarily oaks.

Roots of non-declining trees growing on soils with better drainage also ELISA tested positive. During sampling, the fine roots appeared healthy, though sometimes sparse in density. Do *Phytophthora* or other Oomycete species have a role in oak root growth life cycle under normal conditions that are not severe enough to cause rapid decline? Could root pathogens like *Phytophthora* spp. be contributing to normal fine root turnover?

Remsen et al., 2025 suggests that a slow decline over several years is not uncommon on mature oaks in the built environment. Is a less severe infection of *Phytophthora* spp. contributing to this decline under less extreme soil conditions? If better understood, could that disease be managed to reverse or prevent decline? Further, site and soil characteristics appear to be important for the white oak decline spiral in the Chicago region. Our results support that poor drainage, fine textures, and compaction may be important predisposing soil characteristics for white oak decline in the Chicago region. Lower micronutrient levels, especially zinc, and elevated sodium levels are also associated with declining oaks. It appears that these two factors may be associated with urban stressors like deicing salts and altered nutrient cycling. Further research is necessary to investigate the mechanisms behind these relationships.

Remsen et al. (2025) concludes these applications include planting white and bur oaks on sites that have less intense urban pressures, loamy textures, and better drainage, where predisposing factors can be minimized. Soil quality for these vulnerable species needs to be monitored, maintained, and improved following BMPs. Appropriate irrigation and drainage management are essential to maintain mature white oak health in the face of continued inciting climate factors.

Future research on contributing and predisposing factors will further our understanding of white oak decline in this region. We believe this study's findings can help provide guidance for management and future research during this period of widespread loss and decline of mature white oak trees.

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Figure 1: Manion's tree decline spiral (Taken from Manion, 1981)

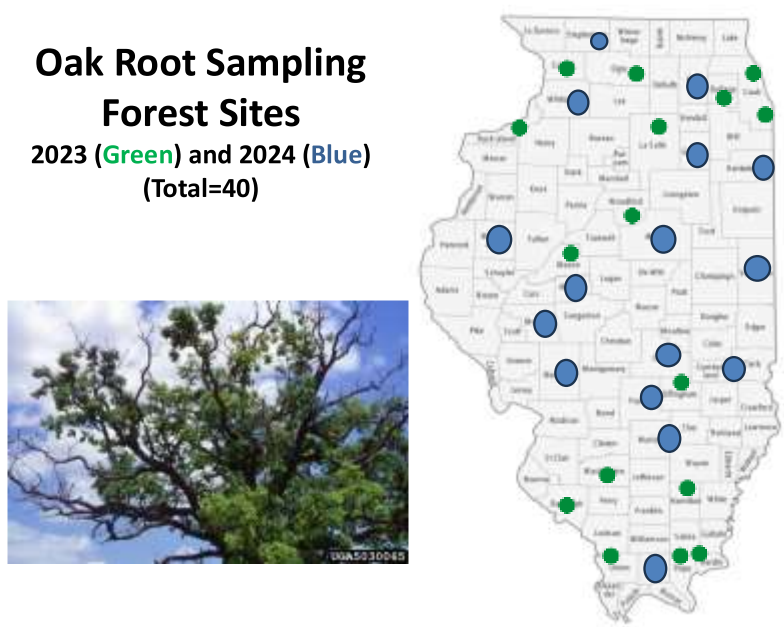

Figure 2: Rural oak forest root sampling sites (2023-2024)

Table 1. Summary of identification of oomycetes associated with oak species

Oak Species	Oomycetes Sequenced
White Oak, Northern Red Oak	***Phytophthora chlamydospora*** *Pythium sp.* Isolate Pyt726 ***Pythium torulosum*** **(oaks associated with turf)** *Pythium vanterpoolii* ***Phytopythium vexans*** **(rural and urban oak trees)**
Bur, Black, Shingle Oaks	***Phytopythium vexans*** **(rural and urban oak trees)** ***Pythium aff. diclinum***
White, Swamp White, Northern Red Oaks **Urban Oak Studies** by Adams, Watson, and Resmen (2021-2023)	***Phytophthora pini*** **(WO)** ***Phytophthora gonapodyides*** **(WO/SWO),** ***Phytopythium plurivora*** **(WO)** *Pythium littorale* (WO) *P.ythium latarium* (NRO) ***Globisporangium heterothallicum*** **(WO)** ***Globisporangium (Pythium) macrosporum*** **(NRO)** ***Elongisporangium anandrum*** **(NRO)**

Table 2. Summary of oomycete spp. associated with oak roots of rural and urban oak species (2023)

Oomycete spp.	% of Total	% Rural	% Urban	Means
P. chamydospora	2	7	0	4%
P. vexans	**18**	**35**	**25**	**30%**
P. citrinum	7	17	6	12%
P. torulosum	15	10	**41**	**26%**
Pythium #726	10	17	16	17%
P. dissotocum	2	7	0	4%
P. aff. diclinum	2	7	0	4%
Means		**12%**	**13%**	
Oak Taxa				
Q. velutina	2	3	0	2%
Q. alba	**57**	**55**	**59**	**57%**
Q. rubra	10	21	0	11%
Q. macrocarpa	30	17	**41**	**29%**

Oomycete spp.	Rural Forests	Urban Forests
Phytophthora chlamydospora	**WO**	
Phy. pini (*Phy. citricola* complex)	**WO**	
Phy. gonapodyides	WO, SWO	
Pythium dissotocum	NRO, BO	
Pyt. sp. Isolate Pyt726	WO, BO	WO
Pyt. sp. 824b	BO	
Pyt. torulosum (TMA)	WO	WO, BO
Pyt. vanterpoolii (TMA)	WO	
Pyt. litorale	WO	
Pyt. nodosum	BO	
Elongisporangium (*Pyt.*) *anandrum* (TMA)	NRO	

Oomycete spp.	Rural Forests	Urban Forests
Pyt. irregulare		WO
Pyt. barbulae	WO	
Pyt. aff *diclinum*	BO,SHO	
Globisporangium (*Pyt.*) *macrosporum*	WO, NRO, BO	
G. heterothallicum (TMA)	WO, BLO	
G. intermedium	WO, NRO, BLO	WO
G. acanthophoron		WO, BO
Phytopythium plurivora (*P. citricola* complex)	**WO**	
Phytopythium vexans	**WO, NRO, BO, BLO**	BO
Phytopythium citrinum	**WO, NRO, BO**	

Table 3. Percent of oak species infested by oomycetes by site and hydrology (2023)

Oomycetes	% Bur Oaks	% NROs	% White Oaks	Means	Site and Hydrology
P. chamydospora	0	0	6	3%	Flat, Poor Drainage
P. vexans	**56**	**50**	**13**	**40%**	**Flat, Poor Drainage**
P. citrinum	11	16	9	13%	Flat, Perched Water Table
P. torulosum	17	0	40	20%	
Pythium #726	0	0	26	13%	Flat, Poor-Well Drained
P. dissotocum	0	16	0	13%	

Table 4. Summary of oomycetes known to cause disease in agronomic crops and oak forests (per the literature)

Oomycetes Known to Cause Disease

(***Jankowiak et al.*** **2015**)

- *Phytophthora chlamydospora* — Global soil-borne pathogen
- ***P. pini*** — Found in MO oak decline study
- ***P. plurivora*** (new taxon) — Highly virulent root pathogen

- ***Pythium aff. diclinum*** — Virulent pathogen in oak forests
- *P. torulosum* — Soil-borne in oak forests
- ***Pyt. (Elongisporangium) anandrum*** — Virulent root pathogen in Europe

- *Phytopythium citrinum* — Soil borne in oak forests
- *Phytopy. littorale* — Aquatic root rot pathogen
- ***Phytopythium vexans*** — Highly virulent root pathogen

Less Oomycetes Known to Cause Disease

(***Jankowiak et al.*** **2015**)

• *Pyt. irregulare*	• Root rot pathogen
• *Pyt. sp. Isolate Pyt-726*	• Root rot pathogen
• *Pyt. sp. Isolate Pyt-824b*	• Root rot pathogen
• *P.yt. latarium*	• Root rot pathogen
• *Pyt. (Globisporangium) acanthophoron*	• Root rot pathogen
• *Pyt.* (*G.*) *heterothallicum*	• Root rot pathogen
• *Pyt.* (*G.*) *intermedium*	• Root rot pathogen
• *Pyt.* (*G.*) *macrosporum*	• Found in Japanese soils
• *Pyt.* (*G.*) *nodosum*	• Root rot pathogen

Table 5. Summary of rural oak forest root sampling sites with Low (L) to Very Low (VL) soil nutrients levels (2023-2024)

Soils Nutrients (VL-L)	% of All Oak Root Sampling Sites
Phosphorus (P)	**60%**
Potassium (K)	< 2%
Magnesium (Mg)	18%
Calcium (Ca)	**51%**
Sulfur (S)	**33%**
Zinc (Zn)	**40%**
Manganese (Mn)	0%
Iron (Fe)	0%

Table 6. Summary of rural forest oak species growing on soils with low nutrient levels with roots infected by *Phytopythium vexans*

Soils Nutrients (VL-L)	% White-Bur Oaks	% Northern Red Oaks
Phosphorus (P)	**100%**	0%
Potassium (K)	**0%**	0%
Calcium (Ca)	**80%**	0%
Sulfur (S)	**40%**	0%
Zinc (Zn)	**60%**	0%
Manganese (Mn)	0%	0%
Iron (Fe)	0%	0%