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Dutch Elm Disease Resistance in American Elm: A Conceptual Framework and Case Study from Minnesota

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Abstract. Background: Dutch elm disease (DED) has reshaped the American elm (*Ulmus americana*) component in North American landscapes for nearly a century. Although breeding and selection programs have produced a small number of commercially available DED-resistant cultivars, uncertainty remains regarding the durability of their resistance under current pathogen virulence. Methods: This study presents a conceptual framework for screening and interpreting DED resistance based on historical breeding programs and long-term field studies. The framework was applied in a case study evaluating 3 commercially available American elm cultivars ('Valley Forge', 'Jefferson', and 'Lewis & Clark' [Prairie Expedition®]) inoculated with a locally derived isolate of *Ophiostoma novo-ulmi* ssp. *americana* in Minnesota. Trees were challenged with 3 inoculum concentrations, and resistance was assessed with 2 tree ages. Results: All cultivars exhibited low wilt severity one year after inoculation across all inoculum concentrations. No significant effects of cultivar, inoculum concentration, tree age, or their interactions were detected, indicating stable resistance across the tested doses and age range. Conclusions: These results are consistent with long-term North American and European studies showing that DED resistance in elm is quantitative and best expressed as functional survival or having the ability to limit pathogen spread, recover from localized wilt, and maintain canopy vigor over time. The conceptual framework and experimental results presented support the continued deployment and evaluation of DED-resistant American elm cultivars for urban and landscape restoration.

Keywords. Disease Resistance; *Ulmus*; Vascular Wilt.

INTRODUCTION

Dutch elm disease (DED) has been a dramatically destructive invasive pathogen affecting *Ulmus* spp. in North America since its introduction from the Netherlands in the early 1930s. Originally caused by the fungal pathogen *Ophiostoma ulmi* and later (and currently) by the more aggressive *O. novo-ulmi* ssp. *americana*, DED is very efficiently vectored by elm bark beetles (*Scolytus* spp.) (Brasier 2001). Once the dominant street and shade tree in much of the Midwest and Eastern United States, the American elm was valued for its form, environmental tolerance, and cultural importance. Its dominance in the urban landscape amplified the epidemic, and the disease resulted in millions of dead elms and enormous financial and ecological costs as it fundamentally altered the community structure and canopy cover across the United States.

Breeding and screening efforts began almost immediately after the pathogen was identified. In the Netherlands, Buisman and colleagues pioneered artificial inoculation techniques that led to the first resistant selections (Buisman 1928; Westerdijk and Buisman 1929; Heybroek 1993). Similar methodology was used in Europe and the United States, where the USDA and later university programs screened thousands of *U. americana* seedlings and clones (Smucker 1944; Clapper 1952; Smalley and Guries 1993). These programs demonstrated that reliable assessment of resistance required standardized inoculation protocols and highlighted key experimental variables like tree age, inoculum concentration, timing of inoculation, and isolate diversity (Tchernoff 1965; Schrieber and Stipes 1967; Sutherland et al. 1997; Solla et al. 2005; Townsend et al. 2005; Flower et al. 2017).

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Over decades of research, it has been shown that DED resistance is not immunity but a quantitative and dynamic trait (Smalley and Guries 1993; Townsend et al. 1995; Islam et al. 2022). Anatomical and physiological defenses, including narrower vessels, rapid tyloses development, and gum and extractive formation, as well as the induction of phenolics, slow the pathogen movement and preserve vascular function (Shigo and Marx 1977; Rioux and Ouellette 1991; Beier et al. 2017b; Beier and Blanchette 2018).

Although resistant cultivars of American elm including 'Jefferson', 'Valley Forge', 'Princeton', and 'Lewis & Clark' (here after Prairie Expedition®) as well as others are commercially available, questions remain about the durability of their resistance over time. Pathogen virulence may continue to evolve, and resistance may erode under stress or repeated exposure. While these cultivars have been studied in other inoculation studies and field trials, limited information is available on how resistance is affected by inoculum concentration or tree age when challenged with a current local strain of the pathogen (Sherald et al. 1994; Townsend et al. 2005; Beier et al. 2017b; Griffin et al. 2017).

The objective of this paper is twofold. First, to summarize historical, biological, and applied perspectives on DED resistance to provide a clear framework for what it means for an elm to be resistant; and second, to apply this framework in a Minnesota context by testing 3 commercially available *U. americana* cultivars against a current, local strain of *O. novo-ulmi* ssp. *americana*. By doing so, this work not only summarizes how resistance has been defined and interpreted over time but also examines whether cultivars that have been regarded as resistant remain resistant under present day field conditions.

Conceptual Framework for Screening and Interpreting Resistance to Dutch Elm Disease

The artificial inoculation of elm with the casual pathogen of DED, *Ophiostoma ulmi*, was initiated by the Dutch as they raced to control the pathosystem that was decimating the clonal population of *U.* × *hollandica* in the country. After successfully determining that *Ophiostoma ulmi* was the fungal pathogen causing the disease, they were the first to use controlled inoculations on clonal material for screening and breeding methods. This involved making a slit in the stem and placing a droplet(s) of a spore suspension of the pathogen which would enter the vascular system of the tree. The trees response was then rated over time (Heybroek 1993). This enabled the Dutch researchers to identify one of the first resistant elm selections *U.* × *hollandica* 'Christine Buisman'. Shortly after, the disease spread to the United States, and the United States Department of Agriculture (USDA) began screening American elm (*U. americana*) for resistance using a similar method (Smucker 1944; Clapper 1952). This early work laid the foundation for dedicated breeding efforts and resistant selections of *U. americana* (Townsend and Santamour 1993). Advances were made in developing and screening DED-resistant elms in programs in the United States and Europe. These programs relied on artificially inoculating selections with the pathogen and assessing the responses for disease resistance. Since that time, many studies have been duplicated, and key variables have emerged that focus on the importance of reliable screening methodology and what it means to have a resistant elm selection. Some of the key variables include the size/age of the trees at inoculation; the timing (season or phenological age) of inoculation; how the inoculum is produced; the concentration, volume, and number of isolates used in inoculum; the inoculation site and techniques used; the number and diversity of pathogen isolates applied; and methods for rating disease response. Table 1 describes several key variables used in major studies on DED resistance in *Ulmus* spp. (Smalley and Guries 1993; Townsend et al. 2005; Buiteveld et al. 2015; Beier et al. 2017b; Flower et al. 2017; Collin et al. 2022; Domínguez et al. 2022). Each one of these variables can influence how trees respond to inoculation, contributing to variability among studies.

Among these, inoculation timing, dose, and site are particularly important in affecting disease outcomes. Timing of inoculation relative to host phenology may influence disease development because seasonal changes in xylem development, vessel characteristics, and hydraulic function can alter the host's vascular response to infection. Multiple studies have shown host susceptibility is greatest in late spring/early summer and lessens throughout the growing season (Smalley and Kais 1966; Takai and Kondo 1979; Beier et al. 2017a). This corresponds to vessel size being largest early in the season, becoming smaller as dense summerwood is developed. Inoculum dose influences the rate of infection, although the

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Table 1. Comparison of inoculation techniques, inoculum concentrations and volumes, assessment timing, and evaluation criteria used by several DED-resistant elm screening programs in North America and Europe. The table highlights methodological variability among studies and identifies common elements used to standardize and interpret resistance to Dutch elm disease across programs.

Study / institution	Material / tree type	Inoculation method	Inoculum details	Assessment timing	Evaluation criteria
Smalley and Guries 1993 / University of Wisconsin-Madison, WI	*Ulmus americana* 3–6 year field trees	0.1-mm drill hole into crown branch	*Ophiostoma ulmi*, *O. novo-ulmi*; 1×10^6 spores/mL	Field: 2–3 months & 1 year	% crown wilt
Townsend et al. 2005 / US National Arboretum, Glenn Dale, MD	*U. americana* 2–9 year field trees	2.4-mm trunk drill hole	*O. ulmi* + *O. novo-ulmi*; 3×10^6 spores/mL	4 weeks, 1 & 2 years	Dieback & defoliation
Flower et al. 2017 / United States Forest Service, Delaware, OH	*U. americana* 3–7 year field trees	0.5-cm hole 30 cm above ground	Mixed inoculum; $6 \times 10^5 – 1.2 \times 10^6$ spores/tree	1 year	% crown wilt
Beier et al. 2017 / University of Minnesota, St. Paul, MN	*U. americana* 4–7 year field trees	2.3-mm hole in main stem	*O. novo-ulmi*; 1×10^6 spores/mL, 25µl	10–12 weeks & 1 year	% crown wilt
Buiteveld et al. 2013 / Applied Plant Research, Wageningen, The Netherlands	Field-grown commercial and Dutch clones	Blade cut main stem	*O. novo-ulmi*; 1×10^6 spores/mL / 0.12 mL	4–8 weeks & 1 year	% crown wilt
Domínguez et al. 2022 / Universidad Politecnica de Madrid, Madrid, Spain	*U. minor* clones (R × S crosses)	Blade cut at trunk base	*O. novo-ulmi* ssp. *americana*; 1×10^6 spores/mL / 0.1 mL	30, 60, 120 dpi	% crown wilt
Sutherland et al. 1997 / Forest Research Station, Surry, United Kingdom	*U. procera* / *U.* × *hollandica*	Blade cut main stem	*O. ulmi* / *O. novo-ulmi*; 1×10^6 spores/mL, 2 drops	12 weeks	% defoliation

relationship does not appear to be strictly linear and may plateau beyond certain thresholds (Schrieber and Stipes 1967; Flower et al. 2017). In addition, the site of inoculation (main stem vs. branches) affects the rate and extent of xylem colonization of the pathogen and subsequent defense reactions, as it is introduced into different portions of the vascular system (Hart and Landis 1971; Smalley and Guries 1993).

An additional source of variability in resistance assessment is tree age and size. Response to DED in elm has been reported to vary across tree age and is sometimes described as juvenile resistance, although results are inconsistent. Early work suggested reduced susceptibility in younger trees (Caroselli and Feldman 1951; Neely 1968; Wright 1968), while other studies have demonstrated substantial disease development in young trees depending on genotype and experimental conditions (Smalley and Guries 1993; Martín et al. 2023), with recent work demonstrating significant genotype-by-environment interactions in DED resistance that further complicate direct comparisons across studies (Domínguez et al. 2024). However, reduced disease severity has also been observed in larger, more mature trees of the same genotype under comparable inoculation conditions (Townsend et al. 2005). Even relatively small differences in tree age (1 or 2 years) has been shown to significantly influence disease severity, with susceptibility declining as trees mature, underscoring the importance of using trees of comparable age in resistance studies (Smalley and Kais 1966; Sutherland et al. 1997). These differences are likely influenced by variation in host vascular anatomy and physiology, including vessel diameter and hydraulic dynamics, which influence pathogen movement (Solla et al. 2005). These findings also demonstrate that long term field trials are the gold standard for durable resistance which should be carried out following small stem assays.

Together, these findings indicate that age related effects are context dependent and should be considered when comparing resistance across studies. And more broadly, similar sources of variability, including

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timing, dose, and site further complicate comparisons, emphasizing the need for a consistent approach to interpreting resistance.

Resistance Characteristics

Central in disease development in American elm is a race between pathogen virulence and host defenses. This is a dynamic process in which the pathogen (*O. novo-ulmi*) attempts to colonize the xylem of host elm species. Once it does, the tree employs a defense against the pathogen by way of structural, physiological, and biochemical processes. Anatomically, trees with smaller (narrower) xylem vessels seem to be able to slow the spread vertically by more efficiently producing tyloses (ballooning intrusions of parenchyma cells into the lumen of the vessel) and the production of gums and gels, both of which occlude infected vessels and provide a chemical barrier (Rioux and Ouellette 1991; Beier et al. 2017b; Beier and Blanchette 2018). The process of defense proposed can be summarized as compartmentalization of the pathogen, in which the tree "walls off" the fungus in order to slow or stop its spread from infected to healthy tissues (Shigo and Marx 1977). This is accomplished by inducing tyloses, gums, and gels in xylem vessels above and below infected areas limiting vertical spread (wall 1), phenolics and other compounds limiting tangential and radial spread (walls 2 and 3). A final barrier zone of cells formed after infection may also develop (wall 4), and if the response is rapid and effective, it can limit pathogen movement into new tissues, and the tree is able to put on healthy, functional cells and grow beyond the infection (Rioux and Ouellette 1991). Studies have shown that in resistant elm selections, this response is a more rapid and robust response that more effectively compartmentalizes the pathogen and continues to add healthy tissue (Beier et al. 2017b).

Advances have also been made on the molecular basis of resistance and the genetic underpinnings of these physiological processes. Sherif et al. (2016) showed that resistant *U. americana* 'Valley Forge' rapidly activates jasmonic acid (JA) signaling and a group of defense related genes within the first few days of infection while maintaining stable salicylic acid (SA) levels. As opposed to susceptible trees, this drives the expression of protective compounds like proteinase inhibitors, chitinases, and cytochrome P450 enzymes that restrict fungal growth and reinforce vessel walls. Transcriptome analysis by Islam et al. (2022) further revealed that resistant genotypes activate genes linked to effector triggered immunity, phenylpropanoid metabolism, and oxidative stress moderation. These processes enhance lignin and phenolic deposition and strengthen xylem barriers. Similar patterns were also observed in resistant Asian selections of *U. parvifolia*, which showed enrichment of cytochrome P450, brassinosteriod, and glutathione metabolism pathways associated with detoxification and hormonal crosstalk (Lyu et al. 2025). In addition to these specific responses, it appears that resistant selections shift energy and resources away from growth and toward upregulation of defense genes during infection (Perdiguero et al. 2018). These studies indicate that DED-resistant genotypes upregulate a coordinated response that acts early and systemically to contain infection and maintain vascular function.

Dutch elm disease resistance is best understood not as immunity but rather a quantitative and variable trait that is characterized by the tree's ability to limit pathogen spread, maintain vascular function, and ultimately survive infection. Wilt that does occur is normally exhibited by localized areas in the crown as opposed to overall or systemic wilt (personal observation). Although resistant trees may show some wilt symptoms, often in the range of 5% to 30%, they avoid total crown wilt and recover by producing new healthy growth while maintaining crown form and vitality (Townsend et al. 2005; Buiteveld et al. 2015). Long term field trials with *U. minor* show resistant clones as having functional survival or maintaining a functional role in the landscape or urban environments where susceptible genotypes experienced rapid decline and mortality (Martín et al. 2015; Collin et al. 2022). Further, resistance is not necessarily permanent. Studies on *U. americana* have shown that resistance is variable over time and conditions due to the complex nature of this pathosystem (Smalley and Guries 1993; Townsend et al. 2005). Trees may have repeated exposure to the pathogen, stress may play a role in making even resistant trees more susceptible, and the changing virulence of the pathogen may result in overcoming resistance.

The anatomical and physiological defenses described translate into phenotypic traits that form the practical basis for screening and interpreting resistance. In inoculation trials, resistant genotypes typically exhibited delayed onset of wilt, restriction of symptoms to individual branches or crown sections,

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and the capacity to recover and continue to grow healthy new tissues/shoots. These patterns reflect effective early defense upregulation that limits vascular dysfunction while maintaining canopy development and photosynthetic capacity (Sherif et al. 2016; Islam et al. 2022). As previous studies have shown, the rapid upregulation of defense genes corresponds with the limited, nonsystemic wilt often recorded in resistant *U. americana* cultivars. In contrast, susceptible trees show slower or uncoordinated responses, leading to systemic colonization and rapid canopy collapse. At the cellular level this translates into resistant genotypes displaying stronger compartmentalization of infected xylem by elevated synthesis of lignin and phenolics and enhanced production of detoxification enzymes and pathogenesis-related (PR) proteins (Beier et al. 2017b; Beier and Blanchette 2018; Islam et al. 2022; Lyu et al. 2025). These mechanisms sustain vascular function and can explain why resistant cultivars maintain high live-crown ratios even after inoculation. The resulting pattern, localized wilt followed by recovery, illustrates how molecular and anatomical defenses work together to produce durable, functional survival.

Collectively, resistance can be described by several recurring traits observed across studies and screening programs:

1. Localized wilt—symptoms confined to limited parts of the crown, indicating effective restriction of pathogen spread.
2. Delayed symptom onset—visible wilt develops more slowly in resistant trees, consistent with early activation of defense pathways.
3. Recovery capability—infected trees regenerate healthy tissue and resume growth following limited dieback.
4. Sustained functionality—vasculature and canopy function are maintained, continuing the tree's ecological and aesthetic role in the landscape.

Following inoculation, wilt percentages provide approximate thresholds that correspond to susceptibility classes widely used across programs (Townsend et al. 2005; Buiteveld et al. 2015; Collin et al. 2022). This can be summarized generally as susceptible, intermediate, and highly resistant, in which symptoms and outcomes progress from rapid death in susceptible to little to no wilt in highly resistant and intermediate (Table 2). These quantitative categories form the operational framework for interpreting resistance in inoculation studies. When combined with consistent protocols and an understanding of mechanistic defense, they allow reliable identification of clones exhibiting reproducible resistance across sites and years. Also, this framework reflects the consensus that resistance in elm is quantitative and dynamic rather than absolute, integrating anatomical and physiological defense processes and molecular signaling as well as field performance and long-term survival. In practice, this framework links controlled inoculation data to canopy level outcomes, providing a consistent reference for comparing resistance across programs, sites, and years (Smalley and Guries 1993; Townsend et al. 2005; Buiteveld et al. 2015; Collin et al. 2022). Disease severity has traditionally been assessed using visual ratings of wilt symptoms following inoculation. However, more recently hyper and multispectral leaf imaging has been used, combined with machine learning to distinguish elm genotypes relative to their susceptibility to DED (Wei et al. 2023). Future application of this technology could provide a more accurate rating method and screening process of the phenotypic response in the elm screening process following inoculation.

Functional resistance expressed through retained canopy health and recovery can also be interpreted through the concept of functional survival in which trees maintain their ecological and landscape roles

Table 2. Response types observed following inoculation with *Ophiostoma novo-ulmi*, categorized by symptom expression, expected outcome, and approximate percentage of crown wilt. Wilt thresholds are based on criteria commonly used in elm resistance screening and reflect the quantitative and continuous nature of DED resistance rather than strict resistance classes. DED (Dutch elm disease).

Response type	Symptoms	Outcome	Wilt rating
Susceptible	Rapid, systemic wilt	Death in weeks	High (> 75%)
Intermediate/tolerant	Partial wilt, recovery possible	Survives, may decline over years	Medium (30%–75%)
Highly resistant	Little to no wilt	Normal growth	Low (< 30%)

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despite the presence of the pathogen. The proportion of live crown (functional canopy) serves as a practical measure of sustained health, paralleling arboriculture standards that link live crown ratio to physiological performance (Lilly et al. 2019). Pruning guidelines caution against removing > 25% of the live crown in a single season, otherwise compromising photosynthetic capacity and stressing the tree (Lilly et al. 2019). However, *U. americana* is a resilient species and may likely tolerate more than this standard crown reduction.

Ultimately the goal of screening criteria is to confidently separate truly resistant from susceptible genotypes. Most elm programs err on the side of caution and typically designate a clone as "DED resistant" only after it has demonstrated consistent performance across multiple inoculations, years, and phenotypic plasticity (Townsend and Douglass 2004; Domínguez et al. 2024). Long term field trials remain the gold standard for durable resistance and should be carried out after small stem assays. This aids in accounting for variability in weather, phenology, and physiological condition and can help ensure durable resistance.

Implicit in this continuum is that resistance measured via aggressive stem inoculations likely underestimates performance under natural conditions. Townsend et al. (2005) also notes that systemic inoculation is inherently more severe than natural crown infections caused by beetle feeding, where defenses can act locally, making it a conservative but consistent test of host resistance.

Defining explicit thresholds helps to ensure that only the most DED-resistant elms are propagated and released. The literature shows a convergence of similar standards across independent programs when screening elms for DED resistance using controlled inoculation with high spore concentrations, multiyear evaluations, and resistance categorization based on crown wilt and recovery potential. These shared criteria have made it possible to distinguish susceptible clones that ultimately do not survive from resistant clones that can tolerate infection with minimal recoverable damage. This alignment of experimental methodology and interpretive framework provides a consistent global standard. Long term trials in North America and Europe show that the integration of consistent inoculation protocols with field validation enables meaningful comparison of genotypes across programs and sites. Collectively, these contributions have transformed DED research from disparate local efforts into a unified, evidence-based system capable of identifying and deploying resilient elms for urban and forest restoration.

Case Study: A Comparison of Commercially Available American Elm Cultivars to *Ophiostoma novo-ulmi* ssp. *americana* Inoculation

This case study evaluated whether DED resistance in three commercially available American elm cultivars remained effective against a current Minnesota isolate of *O. novo ulmi* ssp. *americana* under field conditions. The objectives were to compare resistance among three cultivars across different inoculum concentrations, and to determine whether tree age at the time of inoculation influenced disease severity.

MATERIALS AND METHODS

Ulmus americana cultivars 'Valley Forge', 'Jefferson', and 'Lewis and Clark' (Prairie Expedition®) were planted in a random block design in the Urban Forestry Outreach Research & Extension (UFORE) Nursery, University of Minnesota, St. Paul Campus. All trees were grown on their own root systems (nongrafted). Inoculations were performed at two time points across three spore concentrations. For each cultivar × inoculum concentration, 8 replicate trees were inoculated. Two water inoculated control trees were included per cultivar, and one susceptible wild type control was inoculated with the highest inoculum concentration at each time point to verify pathogen virulence.

The isolate used for the initial inoculation was isolated from an elm with DED symptoms in St. Paul, MN, USA, using a malt extract media (MEA) modified from Harrington (1981), which included 15-g malt extract, 15-g agar, and amended with 0.1-g cycloheximide following autoclaving per L. The identity of the isolate was confirmed in 2019 by sequencing the internal transcribed spacer (ITS) region of the rDNA and identified as *O. novo-ulmi* ssp. *americana*. Following the initial trial, the culture was maintained by culturing on sterilized sections of elm twigs and stored at −80 °C. This stored isolate was subsequently revived on MEA media supplemented with cycloheximide and used to prepare inoculum for the second year of inoculations. Inoculum was prepared in 150 mL of a

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liquid media containing 20-g dextrose; 2-g l-asparagine; 1.5-g KH_2PO_4; 1-g $MgSO_4 \times 7\ H_2O$; 0.00015-g $FeCL_3 \times 6\ H_2O$; 0.0001-g $ZnSO_4$; 0.00018-g $MnCl_2 \times 4\ H_2O$; 0.001-g thiamine HCl; and 0.001-g pyridoxal per L deionized water (Stennes and French 1987) and was inoculated with the culture of *O. novo-ulmi* ssp. *americana* and placed on a shaker for 3 days at 150 rpm. Following shaking, the spore concentration was adjusted to 1×10^4, 1×10^5, and 1×10^6 spores/mL. Inoculations took place 40 days after bud break (which corresponded to 300 growing degree days [ggd][base 50] in year 1 and 314 ggd in year 2) to ensure inoculum was delivered into expanding early wood vessels. A small hole (2.3 mm) was drilled in the main stem of the tree at breast height (1.37 m) and 25 µl of the adjusted spore suspension was injected into the hole with a pipette and wrapped with parafilm.

The age comparison inoculation used the same procedures described above using one spore concentration (1×10^6 spores/mL). In year 3, 11 trees per cultivar were inoculated except for Prairie Expedition®, which had 12 trees available.

Trees were monitored for symptom development and rated for percent wilt beginning at 4 weeks and continuing at 4 week intervals until the end of the growing season using a 0 to 11 ordinal scale: 0 = 0%; 1 = 1% to 9%; 2 = 10% to 19%; 3 = 20% to 29%; 4 = 30% to 39%; 5 = 40% to 49%; 6 = 50% to 59%; 7 = 60% to 69%; 8 = 70% to 79%; 9 = 80% to 89%; 10 = 90% to 99%; and 11 = 100%. Disease severity was monitored during the season following inoculation and rated one year following.

Table 3. Summary statistics for one year post inoculation wilt ratings of American elm cultivars 'Jefferson', 'Prairie Expedition', and 'Valley Forge' in year 1 and year 3. For each combination, the sample size (*n*), median wilt rating, and IQR are shown. Disease ratings were recorded on an ordinal scale from 0 to 11, where 0 = no wilt and 11 = tree death. JE (Jefferson); PE (Prairie Expedition); VF (Valley Forge); IQR (interquartile range).

Cultivar	Treatment	*n*	Median	IQR
JE	1	8	0.5	2
JE	3	11	0	0
PE	1	8	0	1.5
PE	3	12	0	1
VF	1	8	0	0
VF	3	11	0	0.5

Wilt ratings were analyzed to test the effects of cultivar and treatment factors (inoculum dose or inoculation year) as well as their interaction. Because ratings were recorded on an ordinal scale, cumulative link models (ordinal logistic regression) were used as the primary analysis, with model terms evaluated using Wald chi-square tests. The proportional odds assumption was assessed using nominal tests. Wilt ratings were visualized using boxplots with individual observations overlaid, and summary statistics are reported as medians with interquartile ranges (IQR). All analyses were conducted in R Studio (version 4.6.0)(R Foundation, Vienna, Austria) with significance assessed at $\alpha = 0.05$.

RESULTS

Across both experiments, wilt ratings were generally low, with similar median values across cultivars and treatments with broad overlap in wilt ratings (Table 3) (Figures 1 and 2). Statistical analysis indicated no significant effects of cultivar, inoculum dose, or year on wilt ratings. In the dose experiment, ordinal logistic regression showed no significant effects were detected for cultivar ($\chi^2(2) = 1.44$, $P = 0.49$); dose ($\chi^2(2) = 2.46$, $P = 0.29$); or their interaction ($\chi^2(4) = 2.47$, $P = 0.65$). Similarly, in the age experiment, no significant effects were observed for cultivar ($\chi^2(2) = 1.29$, $P = 0.53$); inoculation year ($\chi^2(1) = 0.63$, $P = 0.43$); or the cultivar *x* year interaction ($\chi^2(1) = 2.87$, $P = 0.24$). The proportional odds assumption was not violated for either model. Mock inoculated trees showed no symptoms throughout the experiment, while susceptible control inoculated trees progressed to complete wilt the first year, confirming a lack of response with water injection and pathogen virulence and inoculum viability, respectively.

DISCUSSION

Consistent low wilt across cultivars and inoculum doses indicated DED resistance in these cultivars was durable, while complete wilt was observed in susceptible controls indicating the efficacy of the inoculum and procedure. The absence of a significant dose effect suggests that, within the concentration range typically used (~25 µl of 1 to 3×10^6 spores/mL), the resistance mechanisms in these cultivars are sufficient to limit systemic infection. These findings align with long term trials in both North America and Europe, which demonstrate that resistance can function across diverse conditions when selection and

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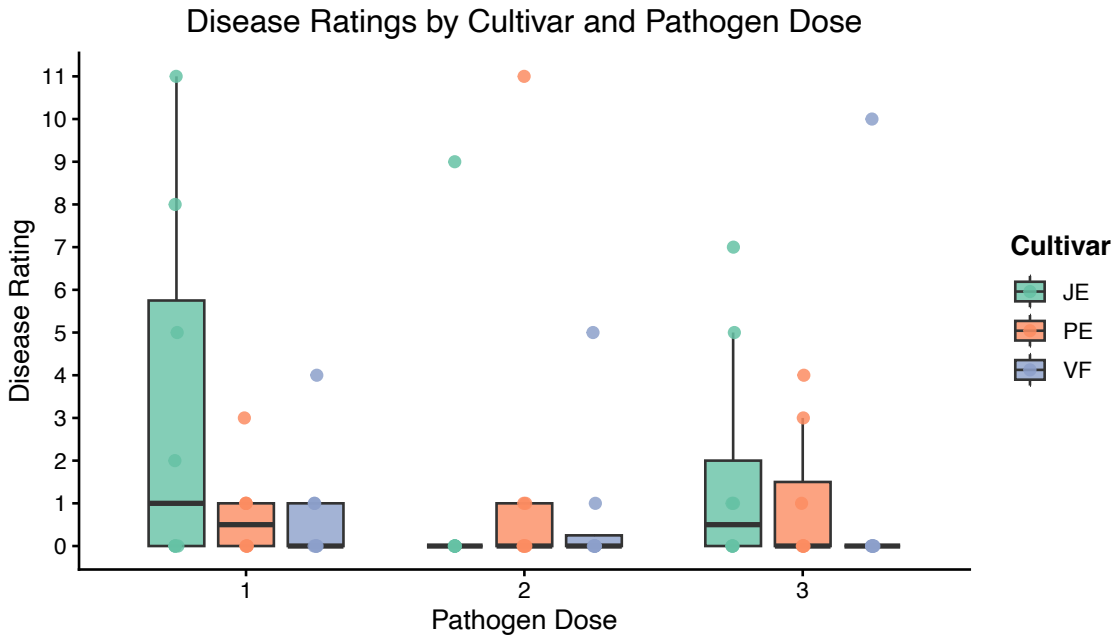

Figure 1. Boxplot showing the distribution of one year post inoculation disease ratings for 'Jefferson' (JE), 'Prairie Expedition' (PE), and 'Valley Forge' (VF) across three *Ophiostoma novo-ulmi* ssp. *americana* inoculum concentrations (1 = 1 × 10^4; 2 = 1 × 10^5; and 3 = 1 × 10^6 spores/mL). Boxes represent the interquartile range (IQR) with the median indicated by a horizontal line, and whiskers extend to the range of observed values excluding outliers. Individual points represent observations for each tree. Disease ratings were recorded on an ordinal scale from 0 to 11, with 0 = no wilt and 11 = tree death. Distributions overlapped among dose levels and cultivars and shows no consistent separation in disease severity across treatments.

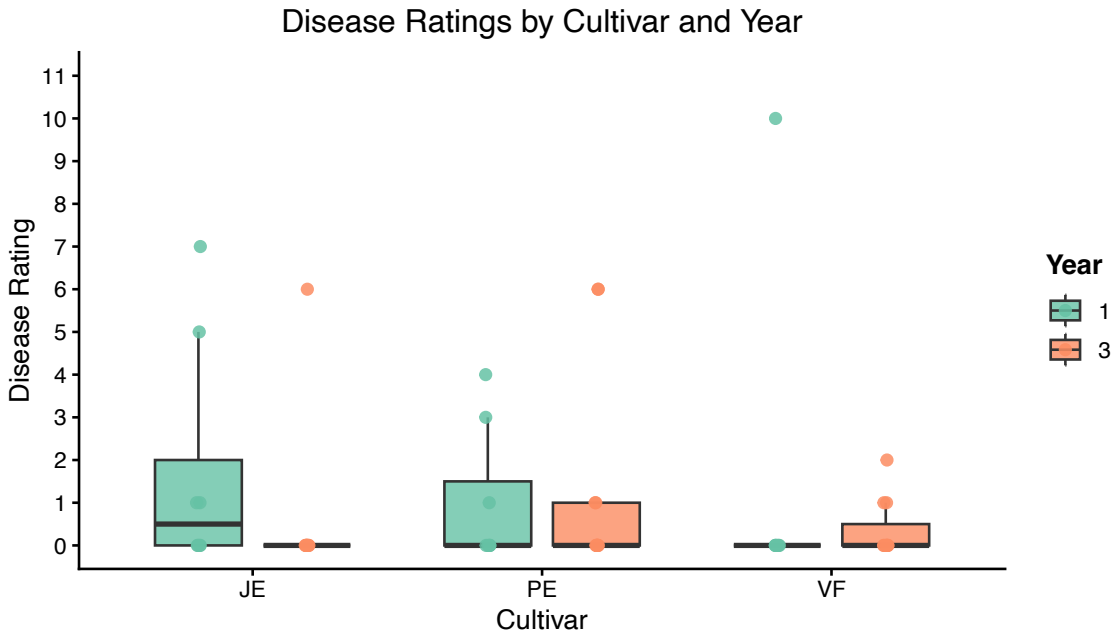

Figure 2. Boxplot showing the distribution of one year post inoculation disease ratings for 'Jefferson' (JE), 'Prairie Expedition' (PE), and 'Valley Forge' (VF) inoculated with *Ophiostoma novo-ulmi* ssp. *americana* in year 1 and year 3. Boxes represent the interquartile range (IQR) with the median indicated by a horizontal line, and whiskers extend to the range of observed values excluding outliers. Individual points represent observations for each tree. Disease ratings were recorded on an ordinal scale from 0 to 11, with 0 = no wilt and 11 = tree death. Distributions overlapped between years and among cultivars, indicating high within group variability and no clear separation between years.

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testing protocols are rigorous (Townsend et al. 2005; Buiteveld et al. 2015; Martín et al. 2023; Wei et al. 2023; Domínguez et al. 2024). *Ophiostoma novo-ulmi* ssp. *americana* used in this study is understood to predominate in the Upper Midwest and is considered highly aggressive (Brasier and Kirk 2010). The limited wilting observed in tested trees indicates that these cultivars maintained resistance under the conditions of this study when challenged with a contemporary, regional isolate.

Although overall disease severity was low, variability was observed with each cultivar having at least one tree with a score of ≥ 10. This variation has been reported in previous elm resistant studies (Smalley and Guries 1993; Townsend and Douglass 2004; Townsend et al. 2005; Martín et al. 2023; Domínguez et al. 2024) and can reflect the context dependent nature of DED resistance (Martín et al. 2023). Microenvironmental factors such as rooting depth, water availability, and localized vigor likely contribute to the observed differences among replicates. The results also highlight the challenge of interpreting resistance from single year trials, as environmental factors and physiological differences can influence symptoms expression. Repeated inoculations remain essential for confirming durable resistance (Townsend and Douglass 2004).

A lack of a dose response is notable, given that inoculum concentrations of 1 to 3×10^6 spores/mL are commonly used in elm resistance screening (Townsend and Douglass 2004; Townsend et al. 2005; Buiteveld et al. 2015; Beier et al. 2017b; Domínguez et al. 2022). Previous work has shown that a higher inoculum load can increase canopy decline, particularly in more susceptible genotypes (Flower et al. 2017), while Schrieber and Stipes (1967) showed that trees inoculated with 100 spores induced similar wilting as those inoculated with 3 times the concentration. Inoculation methods vary among programs, with some studies using stem slits as opposed to drilled injections. The volume of inoculum also varied in studies where some protocols use a larger volume (25 µl), which likely induces a more severe response than droplet-based methods (Heybroek 1993; Buiteveld et al. 2015; Domínguez et al. 2024). Expanded studies using a broader range of inoculum concentrations/volumes would help further resolve the relationship between dose and disease expression in tested genotypes.

Under the conditions of this study, the 2-year difference in tree age tested also did not show a significant effect on wilt symptoms in cultivars. The consistency in resistance over this time range suggests that disease progression is not highly influenced by this modest difference in age. These results align with previous studies and indicate differences in susceptibly in *U. americana* over 4 years was stable or sometimes decreased (Schrieber and Stipes 1967; Solla et al. 2005), while others have reported a difference in one or two years can significantly affect wilting (Smalley and Kais 1966; Sutherland et al. 1997) with susceptibility declining with age. On this evidence, using trees at least 4 years or older and of similar age in field inoculation studies is warranted.

From a management perspective, these results support the continued deployment of 'Jefferson', 'Valley Forge', and Prairie Expedition® as viable DED-resistant cultivars. Their performance under a standardized, high dose challenge highlights the resilience of currently available resistant cultivars and suggests that these genotypes maintain both structural and functional resistance under present day pathogen pressure. However, the potential for pathogen virulence evolution suggests the need for ongoing monitoring, expanded genetic diversity among deployed clones, and periodic reevaluation of resistance using contemporary pathogen isolates.

CONCLUSIONS

This case study illustrates the application of the conceptual framework outlined above to evaluate resistance in American elm in field inoculation screening and demonstrates that the currently available DED-resistant American elm cultivars 'Valley Forge', 'Jefferson', and Prairie Expedition® maintain stable, low wilt symptoms when challenged with an aggressive locally sourced isolate of *O. novo-ulmi* ssp. *americana*. No significant differences among cultivars, age differences, or inoculum doses were detected, indicating wilt ratings were consistent under the conditions of this study. These results reinforce the view that resistance in elm can remain durable, shown by the capacity to compartmentalize infection, recover, and maintain functional canopy over time.

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Résumé. Contexte: La maladie hollandaise de l'orme (MHO) a profondément remodelé la présence de l'orme d'Amérique (*Ulmus americana*) dans les paysages nord-américains depuis près d'un siècle. Bien que les programmes de sélection et d'amélioration génétique aient permis de produire un nombre restreint de cultivars résistants à la MHO disponibles sur le marché, des incertitudes subsistent quant à la pérennité de leur résistance face à la virulence actuelle de l'agent pathogène. Méthodes: Cette étude propose un cadre conceptuel permettant de dépister et d'interpréter la résistance à la MHO, basé sur des programmes d'amélioration génétique historiques et des études de terrain à long terme. Ce cadre a été appliqué dans le contexte d'une étude de cas visant à évaluer trois cultivars d'orme d'Amérique disponibles sur le marché ('Valley Forge', 'Jefferson' et 'Lewis & Clark' [Prairie Expedition®]) inoculés avec un isolat *d'Ophiostoma novo-ulmi* ssp. *americana* provenant de la région du Minnesota. Les arbres ont été exposés à trois concentrations d'inoculum et leur résistance a été évaluée en fonction de deux tranches d'âge. Résultats: Un an après l'inoculation, tous les cultivars ont présenté un faible degré de flétrissement, quelle que soit la concentration de l'inoculum appliqué. Aucun réaction significative en lien avec la variété, la concentration de l'inoculum, l'âge de l'arbre ou leurs interactions n'a été détectée, ce qui témoigne d'une résistance stable tant pour les concentrations testées que pour les tranches d'âge. Conclusions: Ces résultats concordent avec ceux d'études nord-américaines et européennes à long terme, montrant que la résistance de l'orme à la MHO est quantitative et s'exprime au mieux par la survie fonctionnelle, c'est-à-dire la capacité à limiter la propagation de l'agent pathogène, à se rétablir d'un flétrissement localisé et à maintenir la vigueur de la canopée au fil du temps. Le cadre conceptuel et les résultats expérimentaux présentés ici plaident en faveur du déploiement continu et de l'évaluation de cultivars d'orme d'Amérique résistants à la MHO dans le cadre de la restauration urbaine et paysagère.

Zusammenfassung. Hintergrund: Die Ulmenkrankheit (dutch elm disease - DED) hat den Bestand an Amerikanischen Ulmen (*Ulmus americana*) in nordamerikanischen Landschaften seit fast einem Jahrhundert grundlegend verändert. Obwohl Züchtungs- und Selektionsprogramme eine kleine Anzahl kommerziell erhältlicher, DED-resistenter Sorten hervorgebracht haben, besteht weiterhin Unsicherheit hinsichtlich der Dauerhaftigkeit ihrer Resistenz angesichts der aktuellen Virulenz des Erregers. Methoden: Diese Studie präsentiert einen konzeptionellen Rahmen für das Screening und die Interpretation der DED-Resistenz auf der Grundlage historischer Züchtungsprogramme und langfristiger Feldstudien. Der Rahmen wurde in einer Fallstudie angewendet, in der drei im Handel erhältliche Sorten der Amerikanischen Ulme ('Valley Forge', 'Jefferson' und 'Lewis & Clark' [Prairie Expedition®]) bewertet wurden, die in Minnesota mit einem lokal gewonnenen Isolat von *Ophiostoma novo-ulmi* ssp. *americana* beimpft wurden. Die Bäume wurden mit drei Inokulumkonzentrationen infiziert, und die Resistenz wurde bei zwei Baumalterstufen bewertet. Ergebnisse: Alle Sorten wiesen ein Jahr nach der Inokulation bei allen Inokulumkonzentrationen einen geringen Schweregrad der Welke auf. Es wurden keine signifikanten Effekte der Sorte, der Inokulumkonzentration, des Baumalters oder deren Wechselwirkungen festgestellt, was auf eine stabile Resistenz über die getesteten Dosen und den getesteten Altersbereich hindeutet. Schlussfolgerungen: Diese Ergebnisse stehen im Einklang mit langfristigen nordamerikanischen und europäischen Studien, die zeigen, dass die DED-Resistenz bei Ulmen quantitativ ist und am besten als funktionelles Überleben beschrieben wird – also als die Fähigkeit, die Ausbreitung des Erregers zu begrenzen, sich von lokal begrenztem Welken zu erholen und die Vitalität der Baumkrone über einen längeren Zeitraum aufrechtzuerhalten. Der vorgestellte konzeptionelle Rahmen und die experimentellen Ergebnisse sprechen für den weiteren Einsatz und die Bewertung von DED-resistenten amerikanischen Ulmensorten für die Stadt- und Landschaftsrenaturierung.

Resumen. Antecedentes: La enfermedad holandesa del olmo (DED, por sus siglas en inglés) ha transformado la presencia del olmo americano (*Ulmus americana*) en los paisajes de América del Norte durante casi un siglo. Aunque los programas de mejora genética y selección han generado un número reducido de cultivares de olmo americano resistentes a la DED disponibles comercialmente, persiste la incertidumbre sobre la durabilidad de dicha resistencia frente a la virulencia actual del patógeno. Métodos: Este estudio presenta un marco conceptual para evaluar e interpretar la resistencia a la DED, basado en programas históricos de mejora genética y estudios de campo a largo plazo. Dicho marco se aplicó en un estudio de caso que evaluó tres cultivares comerciales de olmo americano ('Valley Forge', 'Jefferson' y 'Lewis & Clark' [Prairie Expedition®]) inoculados con un aislado local de *Ophiostoma novo-ulmi* ssp. *americana* en Minnesota. Los árboles fueron expuestos a tres concentraciones de inóculo y la resistencia se evaluó en dos grupos de edad. Resultados: Todos los cultivares mostraron una baja gravedad de marchitez un año después de la inoculación, independientemente de la concentración del inóculo. No se detectaron efectos significativos atribuibles al cultivar, a la concentración del inóculo, a la edad del árbol ni a sus interacciones, lo que indica una resistencia estable en todas las dosis y rangos de edad evaluados. Conclusiones: Estos resultados concuerdan con estudios realizados a largo plazo en América del Norte y Europa, los cuales demuestran que la resistencia a la DED en los olmos es de naturaleza cuantitativa y se manifiesta mejor como supervivencia funcional; es decir, la capacidad de limitar la propagación del patógeno, recuperarse de la marchitez localizada y mantener el vigor de la copa a lo largo del tiempo. El marco conceptual y los resultados experimentales presentados respaldan la continuación del uso y la evaluación de cultivares de olmo americano resistentes a la DED para entornos urbanos y proyectos de restauración paisajística.

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