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## A review of Dutch elm disease and new prospects for *Ulmus americana* in the urban environment

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### ABSTRACT

American elm (*Ulmus americana*) is an important cultural and historic symbol of the North American landscape. Its graceful form and resilience to harsh growing conditions made it ideal for widespread planting as an urban tree. However, with the initial introduction of Dutch elm disease (*Ophiostoma ulmi*) to the United States in the late 1920's, and the later appearance of the more virulent *O. novo-ulmi*, American elm populations commenced a sudden and precipitous decline due to mortality associated with *Ophiostoma* spp. The absence of this tree created a gap in riparian areas of native forests and resulted in a substantial reduction in urban tree canopy cover throughout communities of the United States and Canada. Here we highlight the prevalence of the American elm in the U.S., and the affiliated impacts of Dutch elm disease (DED). We also discuss important factors including mode of DED introduction and transmission, and challenges associated with DED management in the urban environment. Results from ongoing evaluation of putatively resistant American elms are detailed.

### KEYWORDS

American elm; Dutch elm disease; disease resistance; urban forestry; elm mortality

## Introduction

The American elm (*Ulmus americana* L.) is a keystone tree species in riparian ecosystems throughout North America. Its habitat range stretches from Saskatchewan, Canada in the north, south to the Mississippi Alluvial Valley (Marks, 2017), west to Montana and east to the Atlantic coast (Schlesinger, 1952). The American elm comprises late-successional forests, first replacing willow (*Salix* spp.) and poplar (*Populus* spp.) and soon co-dominating the subcanopy with other hardwoods that include ash (*Fraxinus* spp.) and maple (*Acer* spp.). American elm is tolerant to stressful growing conditions, thriving in temperate floodplains that are exposed to seasonally saturated soils and severe flooding. Similar ecological roles are shared by red maple (*Acer rubrum*), silver maple (*A. saccharinum*), and green ash (*F. pennsylvanica*) (Swain & Kearsley, 2000). As one of the first flowering trees of the spring, it is estimated that elm trees may be host to over 500 species of insects, pollinators, and herbivores (Marks, 2017). Associated wildlife

include the North American porcupine (*Erethizon dorsatum*), American wood duck (*Aix sponsa*), eastern grey squirrel (*Sciurus carolinensis*), and several species of early-season migratory birds (Flower et al., 2017; Pinchot, Flower, Knight, & Slavicek, 2019).

For millennia, elm trees were cultivated for their application in agriculture and building construction (Bey, 1990; Newhouse, Kaczmar, Powell, & Maynard, 2009). In the U.S., native Americans fashioned rope from elm bark (Bey, 1990; Newhouse et al., 2009). As early colonists settled New England, mature elm trees were often spared the axe and were planted as windbreaks for farms, shade for livestock, shelter for homes, and for their distinct aesthetic value (Bey, 1990; Campanella, 2003; Newhouse et al., 2009). Colonists associated mature trees as being landmarks of peace treaties, charters, and sites of public protest, exemplified by the Liberty tree in Boston and the Washington elm in Cambridge, Massachusetts (Schlesinger, 1952; Campanella, 2003). Throughout the 19th century, mature and graceful American elm trees attracted tourists from near and far, even capturing the attention of famed writers Charles Dickens and Henry David Thoreau (Campanella, 2003). The American elm was designated the state tree of Massachusetts in 1941 and North Dakota in 1947 (McPherson, 2013). The vase-like form, spreading canopy (Figure 1), and resilience to adverse conditions, made it an ideal candidate as a shade and ornamental tree (Jonnes, 2017); by 1971 nearly half (45%) of all street trees in Chicago were an elm (Bassuk, 1990).

By 1918, a wilt pathogen, known as Dutch elm disease (DED) (*Ophiostoma ulmi*), spread through northwest Europe causing outbreaks of elm mortality (Brasier, 1990, 1991, Brasier, 2000a). The DED fungus and its lethal effects were rapidly noted across the northern hemisphere, as it spread into eastern North America and southwestern Asia (Brasier, 2000a; Santini et al., 2012b; Marcotrigiano, 2017). In the U.S, DED (*O. ulmi*) was first introduced from Europe to the Baltimore Port around 1933 and quickly spread to more than thirty states (Jonnes, 2017; Marcotrigiano, 2017). Beginning as early as the 1940's, an even more aggressive form of the fungus (*O. novo-ulmi*) had developed concurrently in eastern Europe (ssp. *novo-ulmi*) and the Great Lakes region of the U. S. (ssp. *americana*) (Brasier, 1979, 1990, 1991, 1996, 2000a, 2001). Pomerleau (1961) stated that the second outbreak was noticeable in Canada by 1945, in a port city named Sorel just south of Quebec City. *O. novo-ulmi* subsp. *americana* was introduced from Canada into Britain on diseased elm logs during the 1960's spreading to the Netherlands, France, Spain and many other countries of western Europe (Brasier, 2001; Brasier & Gibbs, 1973). The ensuing absence of elm trees created an ecological gap in native forests, negatively impacted urban tree canopy cover, and posed a substantial financial and operational challenge to urban forest managers (Holmes, 1990; Hubbes, 1999; Marcotrigiano, 2017; Marks, 2017).

American elm is a long-lived species, known to persist for up to 300 years (Bey, 1990). Dutch elm disease, however, was noted to severely impact moderate-to-old-growth elms, limiting its age distribution throughout its native range. In a study of forest demographics in the Connecticut River basin, Marks and Canham (2015) concluded that mortality rates were typically a function of tree size and that DED mortality increased at 15 years and when elm trees obtained a diameter of >30 cm (12") measured at 1.4 m (4.5'). The loss of large numbers of these elm trees in mature size classes changed the long-term structure of specialised, vulnerable ecosystems (Marks, 2017).



**Figure 1.** A specimen of American elm in Massachusetts, USA. Photo credit: N. Brazee.

Widespread outbreak of DED and the associated mortality of elm trees growing in the urban environment meant costly tree care for municipalities (Harper, Bloniarz, DeStefano, & Nicolson, 2017; Jonnes, 2017). By the mid-1970's, less than half of the 77 million urban elms in the U.S. were estimated to have remained (Hubbes, 1999). At this time, the elm population of Toronto, Ontario, Canada (approximately 35,000 trees), was estimated to have declined by 80% (Hubbes, 1999; Huntley, 1982). Intense periods of diseased tree removal substantially impacted tree care budgets and compromised the funding of other routine maintenance activities (Hauer, 2016). In a 40-year economic modelling analysis of DED management in Milwaukee, WI, Hauer, Hanou, and Sivyer (2020) estimated that the removal and planting costs were more than double when comparing no-management regimes to active DED-management scenarios. By the 1970's, the cost of DED in the U. S. was estimated to be billions of dollars per year (Campana & Stipes, 1981; Sinclair & Campana, 1978).

In this paper we detail the history and biology of Dutch elm disease – one of the most important contemporary invasive diseases relative to tree populations. We review the modes of disease transmission and the challenges associated with DED-management in the urban environment. Understanding and application of host plant resistance as an important management tool is also discussed, including the latest information pertaining to putatively disease-resistant American elm cultivars as suitable urban trees.

## Methods

Literature outlining the ecology and natural history of American elm, origins and understanding of DED and its management, and anatomy and physiology of American elm and the feasibility of the use of putatively resistant elm trees was reviewed. Publications included in this review originated from scientific journals, books, anthologies, government technical reports, fact sheets, and conference proceedings. Databases searched included the UMass Library Database, Google Scholar, UMass Scholarworks, HOLLIS of Harvard Library, International Society of Arboriculture publication database, and United States Forest Service Treearch tool. Common keywords included in the database searches were emergent from initial scans of the research literature and included “*Ulmus americana*”, “Dutch elm disease”, “elm mortality”, “urban elm trees” and “resistance”. We consulted the bibliographies of many key references to incorporate related sources of literature. Finally, methodologies and results of American elm resistance trials were also included (see [Table 1](#)).

## History and ecology of Dutch elm disease (DED)

With the onset of DED in Europe in 1918, important research ensued in the Netherlands at the Willie Commelin Scholten Phytopathological Laboratory (WCS Laboratory) (Holmes, 1990; Schippers & Roosje, 1997). Originally founded in 1894, this institution pioneered research in plant pathology, as it drew from academic expertise and resources provided by the University of Utrecht, the University of Amsterdam, and the Free University at Amsterdam (Schippers & Roosje, 1997). Diagnostic work at the WCS Laboratory, led by Dr. Johanna Westerdijk, confirmed the taxonomy and biology of the fungus (Holmes, 1990; Schippers & Roosje, 1997). Dr Dina Spierenburg of the Plant Protection Service in Wageningen first isolated the causal agent, and Dr Bea Schwarz, WCS Laboratory, first classified and characterised the asexual stage of the fungus, then known as *Graphium ulmi* in 1922 (Brasier, 1991; Holmes, 1990, 1990; Jonnes, 2017; Mitterpergher & Santini, 2004). Her inoculations were observed to infect the xylem of elm wood and consistently cause diagnostic wilt symptoms associated with DED. In 1932, fellow scientist Dr Christine Buisman identified the sexual stage of the fungus, *Ophiostoma ulmi* (Holmes, 1990).

## Vector transmission and prevention

Dutch elm disease results from a multifaceted relationship between host elms, elm bark beetles, introduced fungal pathogens, and the environment. The DED fungus infects the susceptible host tree in two ways: it may be introduced via root grafts from diseased to

**Table 1.** American elm cultivar performance.

Selection	Release	Resistance	Form
“American Liberty”	<ul style="list-style-type: none"> <li>• Multiclone selected in 1980s by E. Smalley &amp; R. Guries at University of Wisconsin<sup>11, 16</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Not considered resistant to modern strains of <i>O. novo-ulmi</i><sup>4, 11, 15, 19</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Favourable form, vigorous, upright main stem in youth<sup>11</sup></li> <li>• Older branches becoming more horizontal at maturity<sup>11, 16</sup></li> </ul>
“Valley Forge”	<ul style="list-style-type: none"> <li>• Released in 1995 by the U.S. National Arboretum<sup>11</sup></li> <li>• Used primarily in breeding &amp; research<sup>11, 20</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Most DED resistant selection from the National Arboretum trials<sup>19, 20</sup></li> <li>• Has demonstrated resistance to elm yellows<sup>1</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Broad canopy when young<sup>11</sup></li> <li>• Requires extensive juvenile pruning<sup>4, 12, 18, 22</sup></li> </ul>
“New Harmony”	<ul style="list-style-type: none"> <li>• Selected in Ohio by the U.S. National Arboretum in 1995<sup>10, 19</sup></li> </ul>	<ul style="list-style-type: none"> <li>• High DED tolerance, often rated second to “Valley Forge”<sup>12</sup></li> <li>• Has demonstrated resistance to elm yellows<sup>1</sup></li> <li>• Tolerant to air pollution, poor soil conditions<sup>12</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Broad canopy, vase shape<sup>9</sup></li> <li>• Canopy is rounder than “Valley Forge”<sup>1</sup></li> <li>• May retain central leader with moderate juvenile pruning<sup>22</sup></li> </ul>
“Delaware 2”	<ul style="list-style-type: none"> <li>• Selected in 1940’s by the New Jersey Bureau of Plant Industry<sup>10</sup></li> <li>• Parent tree of North Dakota provenance<sup>10</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Moderate-high DED resistance<sup>1</sup></li> <li>• 0–3% foliar symptoms at four weeks post inoculation<sup>19</sup></li> <li>• Susceptible to elm yellows<sup>1, 14</sup></li> <li>• Hardy to USDA Zone 3<sup>1</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Fast-growing with broad asymmetrical form<sup>1</sup></li> </ul>
“Washington”	<ul style="list-style-type: none"> <li>• A triploid selection by the National Park Service in 1960s<sup>10, 11, 21</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Moderate-high DED resistance<sup>1</sup></li> <li>• Moderately susceptible to elm yellows<sup>1</sup></li> <li>• Hardy to USDA Zone 3<sup>1</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Vase-shape<sup>1</sup></li> </ul>
“Princeton”	<ul style="list-style-type: none"> <li>• Introduced in 1922 by Princeton Nurseries, New Jersey<sup>14</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Moderate-high DED resistance<sup>1</sup></li> <li>• 0–3% foliar symptoms at four weeks post inoculation<sup>19</sup></li> <li>• 80% + survival rate from the National Elm Trial<sup>9</sup></li> <li>• Hardy to USDA Zone 3<sup>1</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Dense, symmetrical, upright form<sup>7</sup></li> <li>• Vigorous, narrow branch attachments<sup>12</sup></li> <li>• Prone to storm damage<sup>8</sup></li> <li>• Requires extensive juvenile pruning<sup>5, 22</sup></li> </ul>
“Jefferson”	<ul style="list-style-type: none"> <li>• A 2004 triploid selection by the National Park Service and National Arboretum<sup>10, 14</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Moderate-high DED resistance<sup>1</sup></li> <li>• High DED tolerance in association with twig inoculation<sup>14</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Slower growth rate, wider branch unions, overall better structure than “Princeton”<sup>1, 7, 22</sup></li> <li>• Early bud break and late leaf drop<sup>7</sup></li> </ul>
“Colonial Spirit”	<ul style="list-style-type: none"> <li>• Selection by Princeton Nurseries from a survivor tree in New Jersey<sup>10, 11</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Resistance evaluation is ongoing<sup>6, 10</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Vase shape<sup>11</sup></li> <li>• Maintains a central leader<sup>10</sup></li> </ul>
“St. Croix”	<ul style="list-style-type: none"> <li>• Selected in 2003 by M. Stennes, Minnesota State University, from a large parent tree in Afton, MN<sup>3, 11</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Expressed DED symptoms during trials but survived when wild types did not<sup>3, 11</sup></li> <li>• Hardy to USDA Zone 2<sup>3</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Vase shape<sup>11</sup></li> <li>• Wide canopy<sup>3, 10, 11</sup></li> </ul>

(Continued)

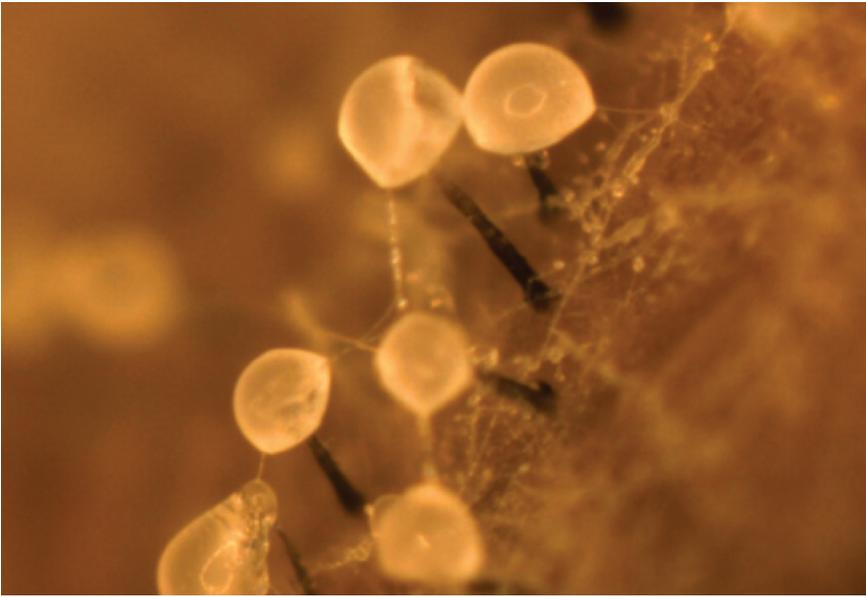
**Table 1.** (Continued).

Selection	Release	Resistance	Form
"Prairie Expedition"; Lewis and Clark®	<ul style="list-style-type: none"> <li>Released by the North Dakota State University Research Foundation in 2004 <sup>10, 13</sup></li> <li>Collected from a survivor tree in southwest North Dakota <sup>10</sup></li> </ul>	<ul style="list-style-type: none"> <li>High DED resistance at 90 days post-inoculation <sup>2</sup></li> <li>Hardy to USDA Zone 3 <sup>13</sup></li> </ul>	<ul style="list-style-type: none"> <li>Vase shape, wide canopy <sup>13</sup></li> <li>Best planted in large, open greenspaces <sup>13</sup></li> </ul>

References: <sup>1</sup> Bassuk,(2009); <sup>2</sup> (Beier et al. 2017); <sup>3</sup> Bliska et al. (2009); <sup>4</sup> (Costello et al. 2004); <sup>5</sup> (Dirr 2011); <sup>6</sup> Flower et al. (2017); <sup>7</sup> (Fraedrich 2015); <sup>8</sup> (Giblin 2017); <sup>9</sup> (Griffin et al. 2017); <sup>10</sup> Haugen & Bentz (2017b); <sup>11</sup> (Marcotrigiano 2017); <sup>12</sup> (McPherson et al., 2009); <sup>13</sup> (Zeleznik, Morgenson, Walla, and West 2018); <sup>14</sup> Santamour & Bentz (1995); <sup>15</sup> (Slavicek and Knight 2012); <sup>16</sup> Smalley & Lester (1988); <sup>17</sup> (Smalley and Guries 1993); <sup>18</sup> (Townsend and Douglass 2001); <sup>19</sup> (Townsend et al. 2005). <sup>20</sup> U.S. National Arboretum 21(Whittemore and Olsen 2011). <sup>22</sup> (Zetterstrom 2017)

healthy trees or it may be transmitted by insect vectors (Cuthbert, 1975; Karnosky, 1979; Newbanks, Roy, & Zimmermann, 1982). Ten beetle species from the genus *Scotylus* are known to feed on elms (Lanier & Peacock, 1981). The native elm bark beetle (*Hylurgopinus rufipes*) and the introduced European elm bark beetle (*Scolytus multistriatus*) are responsible for carrying DED spores (*Ophiostoma* spp.) on their bodies among American elm populations (Karnosky, 1979). The introduction of the European elm bark beetle to North America is believed to have preceded *O. ulmi* by several years, having been first observed in Massachusetts in 1909 (Sinclair & Campana, 1978). Entomologist J. J. Franzen was the first to attribute the European elm bark beetle as a vector (Jonnes, 2017). It is smaller, more aggressive, and often out-competes the native beetle when colonising susceptible elm hosts. The native elm bark beetle, however, is adapted to colder climates and has been more prominent in the northern part of its range (Childs, 2011). As of 2010, a third beetle species, *Scolytus schevyrewi*, was observed in 28 U.S. states (LaBonte, 2010). This beetle, native to China, was introduced to the western U.S. and is hosted by five families of woody plants including members of *Salicaceae*, *Fabaceae*, *Rosaceae*, *Elaeagnaceae*, and *Ulmaceae*. Research in Fort Collins, Colorado, USA, reported significant DED transmission only on trees with pre-existing stress (Negrón et al., 2005). In 2013, it was concluded that *S. schevyrewi* was no more effective at transmitting disease than *S. multistriatus* (Jacobi, Koski, Negrón, & Gibbs, 2013).

Elm bark beetles attack healthy elm trees when they engage in maturation feeding. In late spring, young adult beetles emerge from infected elms and fly to healthy specimens, feeding in the crotches of juvenile twigs (Childs, 2011; Comeau et al., 2015). In ring-porous species such as elms, the production of earlywood coincides with the maturation feeding of bark beetles. The beetles take advantage of the increased vessel activity occurring near the twig surface (Hubbes, 1999). Fungal spores (Figure 2) carried by the beetle can directly inoculate the feeding wounds; this is known as primary transmission (Newbanks et al., 1982). After the inoculation event, *Ophiostoma* spp. will infect the xylem and cause disease. Later in the season, the adult beetles travel to weakened trees to lay eggs (Childs, 2011; Santini & Faccoli, 2015). Galleries are created throughout the inner bark, serving as pupal chambers and sites of sporulation. Effective vectoring often requires a high degree of sporulation inside the insect galleries, as well as sufficient depth of the galleries under the bark.



**Figure 2.** Fruiting bodies of *Ophiostoma novo-ulmi*. Photo credit: N. Brazee.

In urban areas, beetle vector management emerged in the 20th century as a potential strategy to control DED (Santini & Faccoli, 2015). Population suppression of beetles through mass trapping was attempted but was unfortunately, largely ineffective (Cuthbert, Peacock & Cannon, 1977; Lanier & Peacock, 1981). Through the years, ongoing gains were made in relation to the understanding of beetle ecology (i.e. life cycle, feeding behaviour) (Parker, 1947; Brasier, 1990; Webber, 2000), and this information did contribute to more effective vector management programmes. Conventional sanitation programmes included seasonal surveys to locate infected trees, with the goal of early-stage removal of dead or dying trees before the following spring. Sanitation with higher intensity was found to be effective when trees were removed within 20 days of observed symptoms of DED infection (Barger, 1977; Cannon, Barger, & Worley, 1977). Insecticide applications for treatment of adult bark beetles may be implemented by spraying twigs and crotches of susceptible trees in early-spring and mid-summer with insecticides (Lamb, 2014). It is important to note that chemical treatments may be costly to implement, and in urban areas, may be met with widespread aversion by the broader public (Harper, Autio, Finn, & Rossi, 2016).

### **Pathogenic phase**

The physical infection and spread of *Ophiostoma* spp. through the host plant is known as the pathogenic phase. When the fungus is vectored to the tree during beetle feeding, it spreads vertically within the xylem vessels – a consequence of passive transpiration (Comeau et al., 2015). At the feeding sites, competition between spores is fierce, where only successful genotypes may colonise the host elm. The depth of feeding grooves as well as the hydraulic activity of the xylem may affect how many spores inoculate the tree

(Büchel & Cornelissen, 2000). Filamentous growth facilitates lateral spread into secondary vessels (Comeau et al., 2015). Host cell walls are destroyed by mycelial growth, others punctured by germ tubes (Büchel & Cornelissen, 2000). Hubbes (2004) concluded that most mycelial growth occurred between plant cells.

The onset of infection triggers a mechanism within the host xylem that enacts a network of protective barriers, compartmentalising the pathogen from the lower parts of the tree. This reaction disrupts the functioning of the vascular system, producing visual symptoms of disease infection. Branch ends of an infected tree are restricted from accessing water within the plant system, and quickly become chlorotic and wilted. These external symptoms are described as “flagging” and represent an important visual indicator of the disease. Eventually, xylem vessels die and become discoloured. The darkening of the vascular cambium can be seen when bark is removed from sampled twigs. This internal “staining” is a more conclusive diagnostic tool than foliar symptoms (Büchel & Cornelissen, 2000; Newbanks et al., 1982).

### **Saprophytic phase**

The outward movement of *Ophiostoma* spp. into the cambium represents the commencement of the saprophytic phase of infection (Büchel & Cornelissen, 2000; Webber et al., 1987). Fungal colonies may originate from previous infections or recent beetle activity (Santini & Faccoli, 2015). The sexual recombination of these distinct sources of inoculum within the bark is critical to the disease cycle and may help determine the pathogen’s fitness (Büchel & Cornelissen, 2000; Santini & Faccoli, 2015). Fruiting bodies are released as soon as spring temperatures begin to rise, coinciding with beetle emergence and feeding (Büchel & Cornelissen, 2000). The sticky conidial spores encounter new generations of beetle larvae as they emerge from pupal chambers and disperse to nearby elm trees (Lea & Brasier, 1983).

### **Root graft transmission and prevention**

Root grafting is a natural, physiological process that can occur between closely related plant taxa (Figure 3). Root grafting may provide benefits such as nutrient sharing between the connected vasculature of individual trees, as well as increased anchorage (Watson, Hewitt, Cusic, & Lo, 2014). In urban situations, American elms growing in proximity (Figure 4) may transmit pathogens directly from infected trees to healthy trees via root grafts (Cuthbert, 1975; Epstein, 1978).

*Ophiostoma* spp. pathogens cause vascular wilt disease, which disrupts the passive uptake of water within a tree (D’Arcy, Eastburn, & Schumann, 2001). Vascular wilt pathogens have a weak ability to infect living tissue and are better suited in the nutrient-poor conditions of the water-conducting vessels (Schumann & D’Arcy, 2006). *Ophiostoma* initially grows from the vector feeding site and into the living xylem (Newbanks et al., 1982; Webber et al., 1987). Vegetative structures of the fungus produce spores that are distributed vertically in the xylem tissue through passive osmotic transport (Gibbs & Webber, 2004; Taiz et al., 2015). During the infection’s saprophytic phase, the fungus moves laterally through the secondary xylem, which consists of dead vessel cells, and into the inner bark (Webber et al., 1987). However, *Ophiostoma* spp., and other



**Figure 3.** Root grafting between American elms. Photo credit: N. Tisserat, Kansas State University, Manhattan, KS, USA.



**Figure 4.** Elms growing within root-graft proximity. Photo credit: postcard collections, special collections, Bailey-Howe library, university of Vermont, Burlington, VT, USA.

vascular wilts, are unable to colonise parenchyma cells, ray cells, vascular cambium, and the inner bark until it is necrotic (Gibbs & Webber, 2004; Yadeta & Thomma, 2013). *Ophiostoma* spp. are only able to progress downward in a tree as the host plant succumbs to vascular failure and dies back.

Eventually, contents of the host xylem are taken up by neighbouring, root-grafted trees. Root graft infections often result in more rapid death of the recipient tree, which then perpetuates fungal and vector populations. Thus, stumps may be a common source of root graft transmission (Cuthbert, 1975). Root graft transmission was a major factor in municipal outbreaks and has been proven difficult to manage among hedgerow plantings (Epstein, 1978). As a control measure, root graft severance is strongly recommended when American elm tree specimens are planted within 25 to 50 feet of one other (Stipes, 2017). Soil fumigation has been documented as a traditional method for the treatment of root grafts, however, results were found to be inconsistent (Epstein, 1978).

### Virulence of *Ophiostoma novo-ulmi*

*Ophiostoma* spp. are highly adaptable wilt pathogens, having established associations with several species of insect vectors as they are introduced to new regions (Brasier, 2000a). *Ophiostoma ulmi* behaves invasively throughout the northern hemisphere. By the 1940's, the closely related, *O. novo-ulmi*, emerged in the U.S. and Europe (Brasier, 1991; Brasier & Webber, 2019). *Ophiostoma novo-ulmi* has been observed to be superiorly virulent, outcompeting the prevailing *O. ulmi*. The pathogenicity factors of *O. novo-ulmi* include a superior growth rate and heightened ability to suppress the host defence response (Brasier & Webber, 2019; Martin et al., 2019).

The successful growth rate of *O. novo-ulmi* can be attributed in part to its ability to grow and survive in more temperate climates; in comparison, *O. ulmi* is better-suited to warmer, subtropical growing conditions (Kerling & Elgersma, 1970; Brasier, 1990, 2001). Once introduced to North America, *O. novo-ulmi* successfully established a relationship with the native elm bark beetle (*H. rufipes*), thus enabling it to expand its range northward (Webber, 2000).

Fitness of *O. novo-ulmi* may also be related to its chemically antagonistic nature against lesser fit species of bark-colonising fungi and its heightened ability to infiltrate the cambium and inner bark. After sequencing the genome of *O. novo-ulmi*, six exported peptidases were discovered that may disarm plant defence peptides and enhance the pathogen's ability to cause disease (Comeau et al., 2015). Strains of *O. ulmi* also have varying degrees of aggressiveness for degrading host cell walls. *Ophiostoma novo-ulmi* can more actively penetrate cell walls through pit membranes (Comeau et al., 2015). Research in the mid-20th century posited that a wilt-inducing compound known as cerato-ulmin (CU) was found to translocate from the xylem and accumulate in destination leaf tissues, reducing transpiration and increasing respiration (Scala et al., 1997; Guries & Smalley, 2000). Cerato-ulmin has been additionally reported to increase the capacity of conidia spores that can be vectored to bark beetles (Temple et al., 1997). Other researchers posit that CU production does not appear to affect the ability to cause disease, or at least is not the sole means of causing a serious infection (Bowden et al., 1996).

### Host plant resistance mechanisms

In highly susceptible American elm specimens, *Ophiostoma* spp. can readily translocate and cause systemic disruptions in the xylem. Infection can both directly and indirectly result in the cavitation and plugging of vessels (Bowden et al., 1996; Newbanks et al., 1982; Santini & Faccoli, 2015), often escalating to total vascular failure. Trees exhibiting disease tolerance effectively limit the establishment of the DED pathogen in the xylem using constitutive, anatomical barriers (McNabb, Heybroek, & MacDonald, 1970; Shigo & Marx, 1977), and an induced production of chemicals. The following mechanical factors have been associated with the expression of resistance: bud burst phenology, group and size of vessel elements (McNabb et al., 1970), and timing of barrier wall formation with metabolite production (Beier, Held, Giblin, & Blanchette, 2017).

### Timing of leaf emergence

A potential factor of importance related to DED tolerance involves phenology and disease avoidance. Studies have suggested that early leaf-out may set in motion asynchrony between the host tree and scolytid beetle (*Scolytus* spp.) feeding (Ghelardini, 2007; Buchel et al., 2016). Beetles feed during a period in the growing season when the host is most vulnerable to vascular infection. The period of maximum susceptibility to infection coincides with the timing of leaf expansion and the formation of spring vessels, known as earlywood. Clones of European field elm (*U. minor*) originating from a southern latitude were determined to be less susceptible than their northern counterparts that leafed out later (Ghelardini, 2007). Trees that leaf out earlier in the season may have completed earlywood production and commence producing latewood before inoculation can occur (Solla et al., 2005; Ghelardini, 2007; Buchel et al., 2016). The date of bud break may be an important observation point for resistance screening programmes in relation to environmental conditions and elm bark beetle activity.

### Size and arrangement of vessels

Compartmentalisation of decay in trees (CODIT) is a survival process that involves dynamic response from the sapwood during fungal colonisation (Shigo & Marx, 1977), or other damaging events (Morris et al., 2020). It has been observed that American elm is able to restrict infection through this process (Shigo & Tippett, 1981). During CODIT, the sapwood resists the spread of infection by conceptually walling-off healthy tissue and pathways of vascular transport (Shigo & Marx, 1977). This series of walls are formed in order of increasing strength. The first wall represents the occlusion of the xylem and limits vertical spread. Structures called tyloses balloon from living parenchyma cells in response to a change in water potential, ultimately obstructing vascular transport. This prevents the pathogen from invading through vessel pits (Ouellette & Rioux, 1992). The second wall resists the spread of decay into the heartwood, while the third manages radial spread through the sapwood (Shigo & Marx, 1977).

The ability of a susceptible elm to limit the spread of spores to the immediate site of infection is associated with the diameter of the water-conducting vessels within which they travel (Buchel et al., 2016). Some species of woody plants have long vessel cells

with large diameters. The elm, with its ring-porous wood, has vessels four times wider than species with diffuse-porous wood (Newbanks et al., 1982). The diameter of xylem vessels is proportional to the rate of sap flow, and in times of infection, the rate of spore conductance (Solla & Gil, 2002). Since vessel pores must remain open to conduct nutrients, this creates a substantial vulnerability relative to invading pathogens (Shigo, 1985). Cavitation occurs when there is excessive pressure difference between pores and the air. This dysfunction in the xylem is characteristic of DED (Newbanks et al., 1982), and is also more likely to occur in large-diameter vessels (Sinclair & Brener, 1974; Solla & Gil, 2002).

Vessel group size has also been surmised as a metric for tolerance to infection (McNabb et al., 1970; Sinclair, Zahand, & Melching, 1975). Shigo, Campana, Hyland, and Anderson (1980) observed over 500 samples of discoloured wood and inspected vascular arrangement in infected elms. Vessels that were grouped closely together could enable lateral movement of a pathogen into the stem (Shigo et al., 1980). Widely spaced vessel groups could more easily compartmentalise. The timing of compartmentalisation in the xylem may be under genetic influence and contribute to host resistance of vascular disease (Lester & Smalley, 1972; Shigo et al., 1980; Solla & Gil, 2002).

### **Barrier wall and chemical defence**

The fourth wall of compartmentalisation is crucial to the success of CODIT (Beier & Blanchette, 2018; Li et al., 2016) in elm trees. This barrier zone is formed by the vascular cambium and prevents decay from entering new sapwood using specialised parenchyma cells and phenolic compounds (Shigo et al., 1980; Li et al., 2016; Morris et al., 2020). The barrier prevents outward transmission and protects the necessary functioning of the xylem amidst an infection (Martín, Sobrino-Plata, Rodríguez-Calcerrada, Collada, & Gil, 2019). Starch is stored in the barrier zone as non-structural carbon (Shigo & Tippet, 1981) and contributes to the rapid production of secondary metabolites. Starch deposits have been observed to accumulate 48 hours post-inoculation (hpi) in cells near the infection site. Suberin and lignin, which have high molecular weights and are slower to be produced (Morris et al., 2020), have been correlated with increased host plant resistance to DED (McNabb et al., 1970).

Secondary metabolites are chemical compounds with low molecular weight and are produced rapidly in response to stress (Morris et al., 2020). These include, but are not limited to, terpenoids (i.e. mansonones) and phenolic compounds (i.e. flavonoids) (Duchesne, Jeng, & Hubbes, 1985; Duchesne, Jeng, Hubbes, & Sticklen, 1990; Aoun, Jacobi, Boyle, & Bernier, 2010; Comeau et al., 2015; Buchel et al., 2016). Analyses *in vitro* and *in planta* have shown that antimicrobial metabolites called phytoalexins are produced by the American elm in specific response to *O. novo-ulmi* infection. One molecule, phenylalanine ammonia-lyase (PAL) is activated during the defence response. Compared to controls, PAL increased 1.3 (24 hpi) to 7.2 (144 hpi) times in callus samples (Aoun, Rioux, Simard, & Bernier, 2009).

Early research focused on mansonones, which were associated with phytoalexin production in response to *O. ulmi*. These compounds are linked to the disruption of fungal membranes, ribosomes, and mitochondria (Hubbes, 1993). Mansonones are passively produced in the heartwood, but during times of infection are activated within

the sapwood (Morris et al., 2020). Studies conducted by Elgersma (1970), and Proctor and Smalley (1988) found increased mansonone production in resistant American elms. Elgersma (1970) isolated fungicidal compounds from wood infected with *O. ulmi* and identified them as mansonones E and F (Elgersma & Overeem, 1971). The difference in mansonone induction compared to aggressive and non-aggressive *O. ulmi* isolates was also studied (Duchense et al., 1985). Maximum accumulation of phytoalexins was present at 4 weeks with the non-aggressive strain compared to 6 weeks with the aggressive strain (Ouellette, 1978; Duchesne et al., 1985). Because different types of mansonones were elicited in response to different aggressive strains of *O. ulmi*, Duchense et al., (1985) suggested that more aggressive *O. ulmi* strains may have a suppressive effect on the production of mansonones in American elm.

Biosynthesis pathways and molecular signalling mechanisms of host plants are not comprehensively understood but may play important roles in early detection and in inducing a defence response. The accumulation of endogenous hormones such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) assist in the expression of pathogenesis-related proteins (Pieterse et al., 2014; Taiz, et al., 2015; Morris et al., 2020; Martínez-Arias et al., 2021). Specific secondary metabolites are deployed in response to stress (Morris et al., 2020; Vivas, Martín, Gil, & Solla, 2012). In American elm, this could mean coding for the enzymes that produce mansonones (Sherald, Santamour Jr., Hajela, Hajela, & Sticklen, 1994). Sherif et al. (2017) investigated the molecular detection of fungal pathogens by American elm hosts and observed that the tolerance of “Valley Forge” was influenced by a peak induction of jasmonic acid and defence-related genes that occurred at 96–122 hours (hpi). The results suggest that the host tree’s precise timing to compartmentalise the fungal pathogen is essential to resistance (Sherif et al., 2017).

Naturally occurring fungi that grow within host stem tissues, known as endophytic fungi, have been observed to assist in plant resistance to biotic stresses in forest trees (Martínez-Arias et al., 2021). In a 2021 study, stem fungal endophytes were selected from 210 isolates for their potential as enhancers of resistance for European elm (*U. minor*) by inhibiting *O. novo-ulmi* within the host (Martínez-Arias et al., 2021). *In vitro* expressions of phenotypic traits were characterised as releasing antipathogenic compounds, enzymes like chitinases, and directly competing with *O. novo-ulmi* for nutrient utilisation. Field-grown elms pre-inoculated with the endophyte isolates experienced reduced DED wilting symptoms and suggest that certain species impact physiological processes within the elm endobiome (Martínez-Arias et al., 2021). Further, Martin et al., (2013) observed a loss in diversity and frequency of fungi within the xylem of resistant European elms (*U. minor*) and Asian elms (*U. pumila*). Trade-offs between DED immunity and relationships between naturally occurring fungal species may occur depending on the phenolic characteristics of the xylem of resistant elm selections (Martin et al., 2013).

### **Elm improvement programmes**

American elm improvement selections are typically evaluated by assessing crown health, tree growth rate, and maintenance requirements (Costello, Scott, & Drake, 2004; Hubbes, 2004; Townsend, Bentz, & Douglass, 2005). Researchers often establish and examine metrics that include percent crown wilt (Townsend et al., 2005), to classify and rank

expressions of disease tolerance (Bowden, 1996). Most trials inoculate their selections annually with *Ophiostoma* spp. and inspect at various intervals post-inoculation (i.e. 2, 4, 6, and 8 weeks) (Beier et al., 2017; Knight, Haugen, Pinchot, Schaberg, & Slavicek, 2017). In the U.S, there have been large-scale evaluation trials conducted by land grant universities, Cooperative Extension, USDA Agricultural Research Service, and the USDA Forest Service (Griffin et al., 2017; Mittempergher & Santini, 2004; Smalley & Guries, 1993; Townsend et al., 2005).

The selection and production of resistant elms was pioneered at the WCS Lab in 1928 (Heybroek, 1957). Dr Johanna Westerdijk, the Director during the initial DED outbreak, observed variation in response to infection among elms and commenced the search to identify resistance traits within the genus (Swingle, Whitten, & Brewer, 1949; Holmes & Heybroek, 1990). Under her direction, Dr Christine Buisman led the “Committee for the Study and Control of the Elm Disease” and initiated a large collection of elm samples from across Europe for the purposes of propagation (Jonnes, 2017). Buisman developed a standard method of seedling inoculation, evaluation, and in 1935 discovered resistance in a selection of field elm (*U. minor*) (Figure 5) (Swingle et al., 1949; Holmes & Heybroek, 1990; Jonnes, 2017). When released to the public, the tree was widely planted but demonstrated poor resistance to wind and disease susceptibility (Martin et al., 2019).

The ability of elms to cross between species has made hybridisation a popular breeding method for the introduction of disease-and insect-resistant elm varieties



**Figure 5.** Included bark in *U. americana* “Princeton” (352–91\*A). Arnold Arboretum of Harvard University, Boston, MA, USA. Photo credit: C. Copeland.

(Ware, 2000). In 1972, the Morton Arboretum initiated an elm breeding programme to evaluate Asian elms in relation to their hardiness, growth form, and resistance to elm yellows, phloem necrosis, elm leaf beetles, and leaf miners (Ware, 2000). The physical attributes most popular in American elms (i.e. upright, arching structure, cold hardiness) are uncommon in European and Asian elm species, and hybrids. Chromosomal differences (i.e. polyploidy) within the *Ulmus* genera also make hybridisation a challenge (Bey, 1990).

Selections of potentially resistant American elm commenced in 1933 by Cornell University and the Boyce Thompson Institute in Yonkers, NY. By 1957, Dr Eugene Smalley of University of Wisconsin developed greenhouse and field inoculation standards, where small inoculation wounds were made on elm twigs to mimic natural pathogen introduction by a vector (Haugen, Beier, Bentz, Guries, & Slavicek, 2017; Smalley & Guries, 1993). Smalley and Guries (1993) introduced the multiclone “American Liberty”, but upon further inoculation it was found to lack the resistance observed in Asian elm species (Costello et al., 2004). Several successful clones, “R18-2” and “Delaware 2” are still utilised in research (Jonnes, 2017; Sinclair & Brener, 1974; Smalley & Guries, 1993; Townsend et al., 2005). The second wave of DED in 1970 (Li et al., 2016) renewed interest in elm selection and improvement programmes (Townsend et al., 2005). The National Park Service (NPS) conducted twig inoculation trials throughout the 1960’s and 1970’s. Wester (1972) selected several putatively resistant elms from the National Mall. From this effort, “Jefferson” and NPS 3–178 “Washington” were released by the USDA and NPS (Haugen et al., 2017; Warren, 2000).

The USDA breeding, selection, and evaluation programme commenced in 1937, when much of the focus was on identifying DED-resistant European and Asian elms (Townsend, Bentz, & Johnson, 1995). In 1989, Dr Alden (Denny) Townsend of the Agricultural Research Service National Arboretum began field-testing 287 American elm cultivars in Glenn Dale, Maryland (Jonnes, 2017). Townsend diverged from the methodology applied at the University of Wisconsin where researchers inoculated tree twigs, and he challenged young elms with more aggressive stem wounding techniques (Jonnes, 2017). In these trials, “Valley Forge” and “New Harmony” demonstrated DED-resistance that was statistically similar to non-American National Arboretum introductions “Frontier” (*U. wilsoniana*) and “Prospector” (*U. carpinifolia* x *U. parvifolia*) (Jonnes, 2017; Townsend, 2000; Townsend et al., 1995).

From 1992 to 2002, the University of California conducted an evaluation of American elm cultivated varieties (cultivars): “Frontier”, “Prospector”, “Valley Forge” and “American Liberty”. Cultivars “American Liberty” and “Valley Forge” demonstrated poor structure and the need for widespread corrective pruning. As a result of this trial, Costello et al. (2004) also confirmed a high degree of DED susceptibility in “American Liberty”. Furthermore, this study also concluded that the growth rate of “Valley Forge” was difficult to manage in a subtropical climate and would be better suited for temperate zones (Costello et al., 2004; McPherson et al., 2009).

In 2005, the U.S. National Arboretum initiated the National Elm Trial, a ten-year study on nineteen selections across sixteen states (Griffin et al., 2017; Pinchot et al., 2019; Townsend et al., 2005). The goal of this study was to monitor DED-resistant elm cultivars across various hardiness climates, observe growth rates, and determine biotic and abiotic tolerances (Jacobi, Klett, & Walla, 2018). Across the study, the best performing

cultivars included “Princeton”, “New Harmony”, and many of the Asian hybrids (Griffin et al., 2017). Although many varieties of resistant elm trees are selected for rapid growth, the growth rate of genotypes may lead to issues associated with branch attachment over time (Giblin, 2017; Gilman, 2003). Young populations of DED-resistant American elm cultivars are often predisposed to branch failure in association with bark inclusion (Gilman, 2003). A study generated in the aftermath of two major storms in St. Paul, MN, availed that “Princeton” and “Valley Forge” failed at a rate substantially higher than other tree species (Giblin, 2017). Branch failure was also noted among elms at younger ages than other urban tree species (Giblin, 2017).

More recent American elm production and selection efforts at the USDA Northern Research Station have focused on plant adaptations to long-term forest threats (Knight et al., 2017), as well as the need to increase the genetic variation among tree selections (Slavicek & Knight, 2012; Flower et al., 2017). Wild-type survivor trees (mature elms, 0.9 to 1.2 m diameter) have demonstrated themselves to be important sources for genetic resistance (Slavicek & Knight, 2012), and are now routinely utilised in breeding programmes to introduce tolerance mechanisms that may only be present in natural populations. In 2016, plant material from survivor elms was collected throughout distinct upper Midwest and New England watersheds (Pinchot et al., 2017) to produce selections that are adapted to a variety of regional and location conditions including temperature (i.e. cold tolerance), water availability and drainage, and shade (Slavicek & Knight, 2012; Knight et al., 2017; Pinchot et al., 2017). Controlled breeding strategies combine desirable features from maternal lines of DED resistant stock – usually “New Harmony”, “Delaware 2”, “Princeton”, R18-2, and “Valley Forge” – with wild-type paternal lines that exhibit strong resistance genes (Pinchot et al., 2017; Knight et al., 2017). Similar methods were used by Slavicek et al., (2009) using survivor trees in the Chippewa National Forest, located in northern Minnesota. Researchers at the USDA Elm Research Lab. in Delaware, OH, continue to screen the progeny of Chippewa National Forest and New England crosses (Haugen et al., 2017; Slavicek & Knight, 2012).

In 2016 and 2018, the University of Massachusetts established 200 putatively resistant American elm trees at the Agricultural Learning Center in Amherst, MA (Figure 6). These trees were derived from a total of 9 genotypes from the USDA Elm Research Lab. Representing crosses that include “New Harmony”, “Valley Forge”, “Delaware 2”, as well as local wild types from Northampton, MA. These trees will be further evaluated for tolerance to DED, growth form, and other urban-related stress factors (Harper, Brazee, Copeland, & McElhinney, 2021).

## Discussion and conclusion

Once considered the go-to shade tree in association with their appearance and ability to tolerate difficult urban environment (Jonnes, 2017), the presence of DED extirpated populations of American elm trees that had once been established throughout the streets and parks of communities of the Northeastern and Midwestern regions of the U.S. and Canada. While much has been learned regarding the life cycles, behaviour, and pathogenicity of DED, much remains to be discovered concerning its ecology and long-term ramifications on plant communities.



**Figure 6.** American elm research plot at the Agricultural Learning Center in Amherst, MA, USA. Photo credit: C. Copeland.

Effective management of DED relies on scouting for external symptoms, removing infected branches, preventing grafting of root systems underground, and installing disease-resistant elm specimens (Stipes, 2017). These practices are often resource intensive and difficult to conduct relative to large populations of trees. Since the presence of this pathogen is ubiquitous and municipal forest management plans are often constrained by budget limitations, there is little likelihood that this disease will ever be eradicated from the landscape; consequently, American elm populations will always be at risk of infection. Vigorous scouting programmes and management interventions, including chemotherapy treatments and pruning, may be more effective if conducted at the earliest signs of infection. Innovative methods of identifying early-stage symptoms of wilt using new approaches and new technologies will require exploration and testing.

Geographic information systems (GIS) have been used for several decades to map landscapes, collect data on trees, and perform spatial analysis. At Portland State University, a GIS was used to explore possible relationships between DED outbreaks, vector range, and tree proximity in the city of Portland (Fiebich, Montegna, & Del Rey, 2008). On the Swedish island of Gotland, the Swedish Forest Agency collected DED infection data from 2005–2013 and monitored flight patterns by trapping elm bark beetles (*S. multistriatus*) (Menkis, Östbrant, Wågström, & Vasaitis, 2016). The agency was able to educate landowners and authorities on restricting the transportation of elm wood (Menkis et al., 2016). In addition to traditional sanitation measures, this applied control strategy also included removing healthy trees growing within root-grafting distance of infected trees (Menkis et al., 2016). Although spatial analyses often only occur after an outbreak has impacted an urban forest, aerial survey technology may assist in the early detection of external DED symptoms. Unmanned aerial systems (UAS) have been increasingly used to collect high-resolution and

multispectral imagery to conduct aerial canopy assessments of forests and crops (Lin, Huang, Wang, Huang, & Liu, 2019; Tu, Johansen, Phinn, & Robson, 2019).

Over the years, many selections of American elm cultivars have been produced featuring varying degrees of DED-resistance, and many are still commercially available that are reported to have questionable levels of tolerance (Marcotrigiano, 2017). Because disease tolerance is not a fixed trait, American elm maintenance costs can be much higher than other landscape trees (Del Tredici, 1998). Due to the virulence of the DED fungus, resistant and genetically diverse elm varieties must be continuously evaluated (Slavicek & Knight, 2012; Townsend et al., 2005). Genetic crosses between the most reliably resistant cultivated varieties (i.e. “Valley Forge”, “New Harmony”), and local genotypes derived from survivor trees, offer the promise of enhancing the combinations of resistance traits. Some programmes are exploring the manipulation of defence responses (Hubbes, 2004; Sherif, Shukla, Murch, Bernier, & Saxena, 2016), as well as the ecological impacts of selecting DED-resistant genotypes (Martin et al., 2013; Blumenstein, 2015).

If resistant selections are to be successfully introduced and made available for planting in commercial and residential settings, they must also possess criteria that make them suitable for use as ornamental trees. This may include structural integrity, aesthetic appeal, and persistence under stressful urban conditions. Long-term elm trials have assessed survivability, growth rate, branching patterns, and crown condition post-inoculation (Griffin et al., 2017). Reports of structural integrity of limbs and branches require further formal investigation into how growth rate may affect branch formation and limb failure. Tree-related failures, after all, are known to be associated with instances of human injury and fatality, as well as damage to property (Schmidlin, 2009; Van Haaften et al., 2021). According to Gilman (2003), branch-to-stem diameter ratio is an important factor to consider, and a key indicator related to branch failure. Tree measurements and canopy inspections across large areas may be more accurate using imagery and GIS.

Much of the practice of contemporary urban forest management has been shaped by the devastating effects of DED. Chemotherapeutic treatment programmes remain an important option for the management of DED but are costly and may be met with resistance by local residents. Though perhaps more palatable by community members, DED management through mechanical means (e.g. pruning, root severing) may be limited relative to their efficacy and offer only a very narrow window of application. The use of DED-resistant specimens may be the most practical long-term strategy to maintain elm trees as part of the urban tree canopy, however, success with various genotypes has been mixed. Though elm improvement programmes show promise, critical knowledge gaps remain regarding specific factors that influence host plant resistance. Ongoing research to understand these factors and to continuously assess performance and ecological impacts of DED-resistant selections in urban landscapes will be critical. Innovative, integrated, and proactive approaches will be required to preserve existing elm specimens and to establish new, healthy populations for generations to come.

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