

Relative Resistance of Ulmaceae for Host Susceptibility, Feeding Preference, and Suitability for the Adult Japanese Beetle (Coleoptera: Scarabaeidae)¹

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Abstract

Laboratory feeding and fecundity bioassays, and field defoliation surveys were conducted on 73 *Ulmus* and eight *Zelkova* taxa to determine their relative susceptibility, preference, and suitability for the adult Japanese beetle (*Popillia japonica* Newman). *Ulmus alata* Michx., *U. crassifolia* Nutt., *U. davidiana* Planch., *U. elliptica* K. Koch., *U. glabra* Hudson, *U. laevis* Pall., *U. microcarpa*, L.K. Fu, *U. multinervis* (syn. *U. castaneifolia*) Hemsl., *U. parvifolia* Jacq., *U. propinqua* Koidz., *U. prunifolia* Cheug and L.K. Fu., *U. rubra* Muhlenb., *U. suberosa* Henry, *U. sukaczewii* Andr., *U. szechuanica* Fang., *U. taihangshensis* S.Y. Wang, *U. thomasi* Sarg., *U. wilsoniana* Schneid., ‘Frontier’, ‘Homestead’, ‘New Horizon’, ‘Pioneer’, ‘Patriot’, *U. ‘Morton’* Accolade, and *U. ‘Morton’* Triumph, and *Zelkova serrata* (Thunb.) Mak. cultivars ‘Green Valley’ and ‘Village Green’, and *Z. schneideriana* Hand.-Mazz were the least susceptible to feeding and/or the least suitable for reproduction. Percent leaf tissue removed was highly correlated with field defoliation ratings, but was not a good predictor of fecundity. Asian and European elm leaves were thicker compared with North American elms, and Asian elm leaves were tougher compared with European and North American elm leaves. Host susceptibility and suitability were not related to leaf thickness or toughness. Adult female beetles laid significantly more eggs when feeding on Asian elm taxa compared with European, Eurasian, and North American elm taxa. Hybridization appears to affect host susceptibility. Results reported here provide new insight for the use of Ulmaceae taxa for future reforestation and tree breeding programs.

Species used in this study: *Ulmus alata* Michx., *U. americana* L., *U. bergmaniana* var. *lasiophylla* Schneid., *U. canescens* Melville, *U. carpinifolia* Gled., *U. castaneifolia* Hemsl., *U. changii* Hangchow, *U. chenmoui* Cheng, *U. crassifolia* Nutt., *U. davidiana* Planch., *U. elliptica* K.Koch., *U. foliaceae* Gilbert, *U. gaussonii* Cheng., *U. glabra* Hudson, *U. glaucescens* Franch., *U. glaucescens* Franch. var. *lasiocarpa* Rehd., *U. japonica* Sarg., *U. laevis* Pall., *U. lanceaefolia* Roxb., *U. lamellosa* C. Wang et S.L. Chang et L.K. Fu, *U. macrocarpa* Hance, *U. microcarpa* L.K. Fu, *U. multinervis* (syn. *U. castaneifolia*) Cheng, *U. parvifolia* Jacq., *U. procera* Salisb., *U. propinqua* Koidz., *U. propinqua* var. *suberosa* Henry, *U. prunifolia* Cheng et L.K. Fu, *U. pseudopropinqua* Wang et Li, *U. pumila* L., *U. rubra* Muehl., *U. serotina* Sarg., *U. suberosa* Henry, *U. sukaczewii* Andr., *U. szechuanica* Fang, *U. taihangshanensis* S.Y. Wang, *U. thomasi*, *U. wallichiana* Planch., *U. wilsoniana* Schneid., *Zelkova serrata* (Thunb.) Mak., *Z. carpinifolia* (Pall.) K. Koch., *Z. schneideriana* Hand.-Mazz., *Z. sinica* C.K. Schneid, *Sassafras albidum* (Nutt.) Nees.

Index words: Host plant resistance, *Popillia japonica*, preference, suitability, susceptibility, Ulmaceae.

Significance to the Horticulture Industry

Seventy-three *Ulmus* and eight *Zelkova* taxa were evaluated in a series of no-choice and multiple-choice laboratory feeding bioassays and field defoliation studies for susceptibility, preference, and suitability for the adult Japanese beetle (*Popillia japonica*). North American elms *Ulmus alata* Michx., *U. crassifolia* Nutt., *U. rubra* Muhlenb., *U. thomasi* Sarg.; European elms *U. elliptica* K. Koch., *U. glabra* Hudson, *U. laevis* Pall., *U. suberosa*

Henry, *U. sukaczewii* Andr., Asian elms *U. davidiana* Planch., *U. microcarpa*, L.K. Fu, *U. multinervis* (syn. *U. castaneifolia*) Hemsl., *U. parvifolia* Jacq., *U. propinqua* Koidz., *U. prunifolia* Cheug and L.K. Fu., *U. szechuanica* Fang., *U. taihangshensis* S.Y. Wang, *U. wilsoniana* Schneid., cultivars ‘New Harmony’, ‘Valley Forge’, ‘Frontier’, ‘Homestead’, ‘New Horizon’, ‘Pioneer’, ‘Patriot’, *U. ‘Morton’* Accolade, and *U. ‘Morton’* Triumph, and *Zelkova serrata* (Thunb.) Mak. cultivars ‘Green Valley’ and ‘Village Green’, and *Z. schneideriana* Hand.-Mazz. were the least susceptible to feeding and/or the least suitable for reproduction. Laboratory no-choice feeding studies were correlated with field defoliation ratings, but were not a good predictor of adult female fecundity. Physical leaf characteristics (i.e. leaf thickness and toughness) differed by geographic origin. Asian and European elm leaves were thicker than North American elms, and Asian elm leaves were tougher than European and North American elm leaves, but leaf thickness and toughness was not related to host susceptibility or adult female fecundity. Hybridization significantly affected host susceptibility and appears to contribute to an “*U. pumila* and *U. carpinifolia* factor” for host preference, susceptibility, and suitability. Results from this study suggests there is a rich pool of *Ulmus* and *Zelkova* taxa for future breeding programs and for reforestation efforts due to loss

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of landscape trees and urban forest cover by lethal insect pests (i.e. Asian longhorn beetle [*Anoplophora glabripennis* (Motschulsky, 1853)], emerald ash borer (*Agrilus planipennis* Fairmaire, 1888) and diseases (i.e. Dutch elm disease [*Ophiostoma ulmi* (Buisman) Nannf. and *Ophiostoma novo-ulmi* Brasier]), and for their broad hardiness range, ability to tolerate variety of soil conditions, and minimal maintenance in harsh urban environments.

Introduction

Since its introduction into the United States around 1916, the Japanese beetle, *Popillia japonica* Newman has become one of the most destructive and hard to control pests of nursery crops and landscape plants. Adult beetles feed on over 300 species of wild and cultivated plants including but not limited to members of Rosaceae, Malvaceae, Vitaceae, Polygonaceae, Aceraceae, Ulmaceae, and Salicaceae (Fleming 1972, Ladd 1986, 1987, 1989, Miller and Ware, 1999, Miller et al. 1999, Miller 2000, Miller et al. 2001a, Potter and Held 2002, Held 2004). Highly preferred hosts include lindens (*Tilia* spp. L.), sassafras [*Sassafras albidum* (Nuttall) Nees], and purple plum (*Prunus cerostifera* Erhart), all of which may be completely defoliated by adult beetles (Fleming 1972, Ladd 1986, 1987, 1989, Potter and Held 2002, Held 2004).

Common to most woody landscape plants, host plant resistance to *P. japonica* is poorly documented (Raupp et al. 1992), with susceptible or resistant plant lists being compiled from anecdotal descriptions and field observations (Hawley and Metzger 1940, Fleming 1972). No-choice laboratory bioassays conducted by Ladd (1987, 1989) have revealed considerable variations in feeding preference by *P. japonica* among plant species listed by Fleming (1972) as being either favored hosts, minor hosts, or non-host species.

Little or very limited information is available on *P. japonica* feeding preference among cultivars or varieties of common hosts with the exception of a few flowering woody ornamental plants and shade trees. Variation in host susceptibility, preference, and suitability can be quite distinct even within genera (Ranney and Walgenbach 1992, Spicer et al. 1995, Loughrin et al. 1996, 1997, Potter et al. 1998, Miller and Ware 1999a, Miller et al. 1999, 2001b, Rowe and Potter 2000, Potter and Held 2002, Held 2004, Potter and Redmond 2013). Feeding damage ratings for *P. japonica* was conducted by Ranney and Walgenbach (1992) on selected cultivars of birch (*Betula* spp. L.), cherry (*Prunus* spp. L.), and crabapple (*Malus* spp. Mill.) during one growing season. In addition, Spicer et al. (1995) found consistent differences in defoliation to 42 different cultivars of flowering crabapples and Potter et al. (1998) observed significant relative differences in susceptibility of flowering crabapples, lindens, and roses (*Rosa* spp. L.).

The Ulmaceae are considered a preferred host of the Japanese beetle (Fleming 1972). With the recent renewed interest and success in development of new American elm taxa and cultivars for Dutch elm disease (DED) and elm yellows resistance (Carter and Carter 1974, Rauscher et al. 1974, Townsend and Schreiber 1975, Townsend 1979, Smalley and Guries, 1993, Townsend et al. 1995a,b, 2005,

Sinclair et al. 2000, Townsend 2000, Townsend and Douglass, 2001, Sinclair and Lyon, 2005, Townsend et al. 2005) and reduced feeding susceptibility and preference by herbivorous insects (Cunningham and Dix 1983, Hall 1986, Hall and Young 1986, Hall and Townsend 1987, Hall et al. 1987, Miller 2000, Miller et al. 2001b, Miller and Ware 2014) elms have the potential once again to be included in landscape and shade tree plantings (Warren 2000, Dirr 2009). More recently, the accessibility and procurement of Asian elm seed sources has greatly added to the number of potential elm genotypes available for breeding and hybridization (Fu 1980, Ware 1992, 1995, Warren 2000). Simple and complex Eurasian and Asian elm taxa have shown to have varied resistance to DED, elm yellows, elm leaf beetle, spring and fall cankerworm, Japanese beetle, and elm leaf miner (Ware 1992, Gurries and Smalley 1994, Miller and Ware 1994, Ware 1995, Miller and Ware 1997, 1999b, Miller and Ware 2001a,b,c,d, Miller 2000, Miller and Ware 2002, 2003, Sinclair and Lyon 2005, Miller and Ware 2014, Griffin et al. 2017). Previous laboratory and field studies by Miller et al. (1999, 2001a), Condra et al. (2010), and Potter and Redmond (2013) have provided valuable information on the relative susceptibility and preference of recently acquired and developed *Ulmus* taxa of North American, European, and Asian elm parentage for feeding by *P. japonica*.

Plants protect themselves from herbivores by using either physical plant traits, chemical defenses, or a combination of both. In all likelihood, that is the case here with *Ulmus* taxa and Japanese beetles (Hoxie et al. 1975, Meredith and Schuster 1979, Johnson et al. 1980a,b, Ryan et al. 1982, Southwood 1986, Tingey and Laubengayer 1986, Matsuda and Senbo 1986, Doss et al. 1987, Potter and Kimmerer 1988, Ranney and Walgenbach 1992, Patton et al. 1997, Fulcher et al. 1998, Rowe and Potter 2000, Dalin and Bjorkman 2003, War et al. 2012). However, information is lacking on the suitability of many of these elm taxa for Japanese beetle reproduction, and possible physical leaf factors responsible for feeding susceptibility and preference.

In this study, our objectives were to evaluate the relative susceptibility, preference, and suitability of North American, European, and Asian elm, and *Zelkova* taxa and related cultivars and varieties, simple elm hybrids (a plant resulting from the crossing of two taxa), including *U. pumila* x *U. japonica*, and Asian elm hybrids, complex Asian elm hybrids (a plant in which three or more taxa are parents), and complex Eurasian elm hybrids for adult Japanese feeding and reproduction. *Ulmus americana* is genetically heterogeneous and most *U. americana* are reported to be tetraploid ($2n = 4x = 56$, where $x=14$). However, the diploid form of *U. americana* ($2n = 2x = 28$) was included in this study because both diploids and tetraploids may grow in proximity to each other and because further studies are needed to determine the potential for defoliation of diploid forms by herbivorous insect pests (Santamour 1993, Whittemore and Olsen 2011, Whittemore and Xia 2017). Additionally, we examined physical elm leaf characteristics, namely leaf thickness,

toughness, and pubescence, and their possible role in adult feeding susceptibility, preference, and suitability. Results from this study will contribute to the potential use of additional *Ulmus* and *Zelkova* taxa for comprehensive tree breeding programs for disease and insect pest host plant resistance.

Materials and Methods

No-Choice (NC) laboratory feeding bioassays (Susceptibility). Laboratory no-choice bioassay feeding studies were conducted on adult Japanese beetles as previously described by Miller and Ware, 1999a, Miller et al. (1999, 2001a), and Miller and Wiegrefe (2021). Seventy-three elm taxa and eight *Zelkova* taxa were evaluated. Refer to Table 1 for a list of *Ulmus* and *Zelkova* taxa evaluated. Sassafras [*Sassafras albidum* (Nutt.) Nees], a highly favored host of the Japanese beetle (Fleming 1972, Miller et al. 2001a, Miller and Wiegrefe 2021), served as the standard. Candidate *Ulmus* and *Zelkova* taxa growing in the Ulmaceae and geographic collections at The Morton Arboretum, Lisle, IL, ranged in height from 3 to 10 m (10-33 ft.), with diameters at breast height of 8-40 cm (3-16 in).

Ulmus and *Zelkova* taxa leaves for the no-choice (NC) and multiple-choice (MC) laboratory feeding bioassays were randomly collected from ground level from all four cardinal directions and held in cold storage in plastic bags at 5 C (41 F) for a maximum of 2 d. Leaves collected from each test tree were combined for the NC and MC laboratory feeding bioassays. Depending on availability, one to three individual trees of each *Ulmus* and *Zelkova* taxon were evaluated.

Adult beetles used in the NC and MC studies were field-collected from plants at The Morton Arboretum, Lisle, IL and The Chicago Botanic Garden, Glencoe, IL. Upon collection, the adult beetles were held in clear plexiglass cages under a photoperiod of 16:8 (L:D) h at 25 C (77 F). While being held in the cages (no longer than 12 hours), the beetles were allowed to feed on fresh crabapple (*Malus* spp.) foliage to ensure predisposition to feeding. Prior to the beginning of the feeding trials, the Japanese beetles were sexed, and one adult male/female Japanese beetle pair was placed into each of 10 clear plastic petri dishes (10.0 cm diam by 0.6 cm depth) along with one leaf of the specific *Ulmus* or *Zelkova* taxon to be tested. Each beetle pair was used only once. There were 10 dishes (sub-replicates) for each tree for each taxon evaluated for a total of 10 to 30 male/female beetle pairs per taxon. Petri dishes were examined daily for beetle mortality and evidence of feeding. Foliage was replaced every 2 d. At the time of leaf removal, the leaves were visually rated (nearest 5%) for the percent of leaf tissue removed, by two independent estimators using a defoliation template. Petri dishes were placed in clear plastic bags to prevent drying of the foliage and were held in a growth chamber under a 16:8 (L:D) h photoperiod at ~25 C (77 F). Condensation of water on the lid of the petri dish indicated a high relative humidity. At the end of seven days, the remaining foliage and fecal pellets were removed from each petri dish and the fecal pellets were oven dried and weighed (nearest mg). The NC

feeding bioassays were terminated after 7 days. The measure of the susceptibility for each taxon was defined by mean percent leaf tissue removed and mean dried fecal pellet weights.

Multiple-Choice (MC) laboratory feeding bioassays (Preference). Laboratory multiple-choice bioassay feeding studies were conducted on adult Japanese beetles as previously described by Miller and Ware, 1999a, Miller et al. (1999, 2001a) and Miller and Wiegrefe (2021). One adult female Japanese beetle was placed into each of 10 plastic petri dishes (15.0 by 0.6 cm) with each petri dish serving as a replicate. Depending on the number of elm selections tested in each study, (including the reference taxon), four to seven *Ulmus* and/or *Zelkova* leaf discs, representing four to seven different elm selections, were placed around the perimeter of each petri dish. The leaf discs were taken from the center of each leaf for each taxon and were 2.54 cm in diameter. Beetles had access to all leaf discs. The petri dishes were examined daily for seven days. Each day, the foliage discs were removed from the dishes, replaced, and visually evaluated (nearest 5%) by two independent estimators using a defoliation template for the amount of leaf tissue removed. New foliage discs were arranged randomly in the dish each day to eliminate possible bias. The measure of preference for each *Ulmus* and *Zelkova* taxon was defined by the mean percent of leaf tissue removed.

Field defoliation survey. In late August, after all adult beetle feeding had ceased, a field defoliation survey was conducted by visually examining the tree canopy from all four cardinal directions of all available *Ulmus* and *Zelkova* taxa. Trees were rated by two independent estimators for evidence of feeding using a scale of 0-4 as follows: 0=no feeding, 1=very light feeding, 2=light feeding, 3=moderate feeding, and 4=heavy feeding. Depending on the availability of *Ulmus* and *Zelkova* taxa, three to five single tree replicates were evaluated per taxon. Host susceptibility and preference was defined by using the feeding damage scale.

No-Choice (NC) laboratory fecundity bioassays (Suitability). A male/female pair of field-collected adult Japanese beetles was placed into a 5.7 L (6 qt) capacity Clear-View™ plastic container (Sterilite^R, Townend, MA) with approximately 5.0 cm. of finely sifted moist silt-loam soil, and foliage of the candidate *Ulmus* or *Zelkova* taxon to be tested. Sassafras (*Sassafras albidum*), a highly favored host of the Japanese beetle (Fleming 1972, Miller et al. 2001a, Miller and Wiegrefe 2021), served as the standard. Foliage was kept turgid and fresh using floral water piks. The boxes containing the beetles and foliage were kept at room temperature in the laboratory under natural day-length. The boxes were examined every third day and elm foliage was replaced if wilted or defoliated. At 7, 14, and 21 days from the initiation of the study, the soil in each container was visually examined for eggs, and the total number of eggs per container and adult beetle mortality was recorded. After each egg counting, the original male/female beetle pair was returned to the container. Ten single containers (replicates) containing one male/female pair

Table 1. Ulmaceae and *Zelkova* taxa evaluated in no-choice, multiple-choice, fecundity, and field defoliation studies for susceptibility, preference and suitability for the adult Japanese beetle.

Taxa, Hybrid, Cultivar, Variety	Parentage
North American elm taxa and cultivars	
'Jefferson'	<i>U. americana</i> (triploid as per Sherald et al., 1994)
'Valley Forge'	<i>U. americana</i>
'New Harmony'	<i>U. americana</i> '
<i>U. americana</i> (diploid form)	
<i>U. americana</i>	
Simple and complex Eurasian elm hybrids	
'Frontier'	<i>U. carpinifolia</i> x <i>U. parvifolia</i>
'Homestead'	<i>U. pumila</i> x (<i>U. x hollandica</i> 'Vegeta' x <i>U. carpinifolia</i>) x <i>U. pumila-pinnato-ramosa</i> x <i>U. carpinifolia</i> 'Hoersholmiensis'
'Pioneer'	<i>U. glabra</i> x <i>U. carpinifolia</i>
'Regal'	(<i>U. x hollandica</i> 'Vegeta' x <i>U. carpinifolia</i>) x (<i>U. pumila</i> x <i>U. carpinifolia</i> 'Hoersholmiensis')
'Patriot'	'Urban Elm' x <i>U. wilsoniana</i> 'Prospector'
'Urban Elm'	N-148 <i>U. x hollandica</i> 'Vegeta' x <i>U. carpinifolia</i> x <i>U. pumila</i>
<i>Ulmus pumila</i> and <i>U. japonica</i> hybrids	
'Sapporo Autumn Gold'	<i>U. pumila</i> x <i>U. japonica</i>
'Cathedral'	<i>U. pumila</i> x <i>U. japonica</i>
'New Horizon'	<i>U. japonica</i> x <i>U. pumila</i>
<i>U. parvifolia</i> and cultivars	
<i>U. parvifolia</i>	
'Dynasty'	<i>U. parvifolia</i>
'Athena'	<i>U. parvifolia</i>
Simple Asian hybrids	
<i>U. davidiana</i> x 'Accolade'	
<i>U. davidiana</i> x <i>U. japonica-wilsoniana-pumila</i>	
'Columnar'	<i>U. japonica</i> x <i>U. pumila</i>
'Single Stem'	<i>U. japonica</i> x <i>U. wilsoniana</i>
<i>U. japonica</i> x <i>U. americana</i>	
<i>U. japonica-wilsoniana-rubra</i>	
<i>U. japonica-pumila</i> x <i>U. wilsoniana</i>	
<i>U. japonica</i> x <i>U. wilsoniana</i>	
<i>U. pumila</i> x <i>U. americana</i>	
'Accolade' x <i>U. japonica</i>	(<i>U. japonica</i> x <i>U. wilsoniana</i>) x <i>U. japonica</i>
'Accolade' x <i>U. pumila</i>	(<i>U. japonica</i> x <i>U. wilsoniana</i>) x <i>U. pumila</i>
<i>U. szechuanica</i> x <i>U. japonica</i>	
'Vanguard' x <i>U. americana</i> -diploid	(<i>U. pumila</i> x <i>U. japonica</i>) x <i>U. americana</i> (diploid)
'Vanguard' x <i>U. davidiana</i>	(<i>U. pumila</i> x <i>U. japonica</i>) x <i>U. davidiana</i>
'Vanguard' x <i>U. japonica-wilsoniana-pumila</i>	(<i>U. pumila</i> x <i>U. japonica</i>) x <i>U. japonica</i> x <i>U. wilsoniana</i> x <i>U. pumila</i>
Complex Asian hybrids	
<i>Ulmus</i> 'Morton' Accolade™	<i>U. japonica</i> x <i>U. wilsoniana</i>
<i>Ulmus</i> 'Morton Stalwart' Commendation™	<i>U. carpinifolia</i> x <i>U. pumila</i> x <i>U. wilsoniana</i>
<i>Ulmus</i> 'Morton Red Tip' Danada Charm™	<i>U. japonica</i> x <i>U. wilsoniana</i>
<i>Ulmus</i> 'Morton Glossy' Triumph™	<i>U. pumila</i> x <i>U. japonica</i> x <i>U. wilsoniana</i>
<i>Ulmus</i> 'Morton Plainsman' Vanguard™	<i>U. pumila</i> x <i>U. japonica</i>
North American elm taxa	
<i>U. alata</i>	
<i>U. crassifolia</i>	
<i>U. rubra</i>	
<i>U. serotina</i>	
<i>U. thomasii</i>	
European elm taxa	
<i>U. canascens</i>	
<i>U. elliptica</i>	
<i>U. foliaceae</i>	
<i>U. glabra</i>	
<i>U. laevis</i>	
<i>U. suberosa</i>	
<i>U. sukaczewii</i>	
Asian elm taxa, cultivars, and varieties	
<i>U. bergmaniana</i> var. <i>lasiophylla</i>	
<i>U. castaneifolia</i>	
<i>U. changii</i>	
<i>U. chenmoui</i>	
<i>U. davidiana</i>	
<i>U. gaussenii</i>	
<i>U. glaucescens</i>	
<i>U. glaucescens</i> var. <i>lasiocarpa</i>	

Table 1. Continued.

Taxa, Hybrid, Cultivar, Variety	Parentage
<i>U. japonica</i>	
<i>U. lanceaefolia</i>	
<i>U. lamellosa</i>	
<i>U. macrocarpa</i>	
<i>U. microcarpa</i>	
<i>U. multinervis</i> (syn. <i>U. castaneifolia</i>)	
<i>U. parvifolia</i>	
<i>U. propinqua</i>	
<i>U. propinqua</i> var. <i>suberosa</i>	
<i>U. prunifolia</i>	
<i>U. pseudopropinqua</i>	
<i>U. pumila</i>	
<i>U. szechuanica</i>	
<i>U. taihangshanensis</i>	
<i>U. wallichiana</i>	
<i>U. wilsoniana</i>	
<i>U. wilsoniana</i> ‘98’	
<i>U. wilsoniana</i> ‘Prospector’	
Zelkova taxa and cultivars	
<i>Zelkova. carpinifolia</i> (D-Russia)	
<i>Z. carpinifolia</i> (T-Russia)	
<i>Z. schneideriana</i> (T-Russia)	
<i>Z. schneideriana</i> (N-China)	
<i>Z. serrata</i>	
<i>Z. serrata</i> ‘Green Vase’	
<i>Z. serrata</i> ‘Village Green’	
<i>Z. sinica</i>	
Reference Taxa	
<i>Sassafras albidum</i> (reference)	

were used for each of three single trees per *Ulmus* or *Zelkova* taxon for a total of 30 beetle pairs per taxon. The study was terminated after 21 days.

Trichome density and morphology. Ten mature leaves, for each of the 11 pubescent *Ulmus* taxon, were used to determine trichome density on the upper and lower leaf surfaces. The leaves were positioned under a light microscope and a 1cm² template was placed halfway between the leaf blade and midrib on both the adaxial and abaxial leaf surfaces. The total number of trichomes within the 1 cm² sampling area was counted and recorded. Scanning electron microscopy (SEM) was performed at The Morton Arboretum (TMA) electron microscopy laboratory, to observe trichome morphology, as previously described by St.-Laurent et al. (2000) and Bosu and Wagner (2007). The trichomes were examined in scanning electron microscopy (LEO 1430 VP) at an acceleration voltage of 10.6 kV. Trichomes were characterized as either simple (non-glandular) trichomes, and further divided into short (50-100 microns) and long (1-3 mm), or as bulbous (glandular) trichomes as previously detected and described on soybean [*Glycine max* (L.) Merrill] leaves (Peter et al. 1995), on 20 elm taxa (Bosu and Wagner 2007), and on birch leaves (Ventralla and Marinho 2008).

Effect of trichomes on host preference and suitability. In order to determine the effect of trichomes or lack of trichomes on beetle feeding preference, a MC laboratory feeding bioassays were conducted for 11 pubescent *Ulmus* taxa. The MC studies were conducted as described previously except that only one *Ulmus* taxon was tested

in paired choices. The trichomes were removed from leaves of each respective taxon using a microscope slide and gently scraping the upper and lower leaf surfaces exerting enough pressure to remove the trichomes but not enough to tear or rupture the leaf epidermis.

To determine the effect of trichomes or lack of trichomes on adult female fecundity, a NC fecundity study was initiated for the same 11 pubescent elm taxa mentioned previously. Methods and materials for this study were the same as mentioned above for trichome removal, and the NC laboratory fecundity bioassays.

Measuring elm leaf thickness and toughness. Prior to using the leaves for the NC laboratory feeding bioassays, 10 leaves for each taxon were measured for leaf thickness, and inner and outer leaf toughness. Leaves were collected in the field as previously described. Leaf thickness was determined by using a Vernier caliper to measure the thickness of each leaf (nearest mm) approximately one-half the distance from the leaf margin to the mid-rib. Inner and outer leaf toughness was determined to the nearest gram using a Chatillon™ digital force meter (pentrometer) (Greensboro, N.C.) applied to within 0.5 cm from the edge of the leaf for measuring outer toughness, and in the center of the leaf adjoining the mid-rib for inner toughness, respectively.

Measures of susceptibility, preference, and suitability. Measures of susceptibility for adult Japanese beetles feeding on *Ulmus* and *Zelkova* taxa was defined as the percent leaf tissue removed, and the dry fecal pellet weight in the NC feeding bioassays, and the field defoliation

ratings. Preference was determined by the amount of leaf tissue removed in the MC feeding bioassays. Host suitability was determined by the total number of eggs (fecundity) laid by females for each taxon, percent of females ovipositing, and male and female longevity.

Statistical analysis. Measures of susceptibility, preference, and suitability were subjected to analysis of variance (ANOVA) using taxon as the main effect. Means of significant effect (5%) were compared with the Dunn's test. Coefficients of correlation were determined by regression analysis for the rankings for comparing measures of susceptibility, preference, and suitability, and for leaf thickness, toughness, and pubescence. Percent leaf tissue removed for each taxon was arcsine transformed before analysis to correct for non-normality. All data are presented as original means + standard error of the mean (SE). Data were analyzed using the SigmaStat for Windows (Jandel Scientific 1992).

Results and Discussion

No-Choice (NC) laboratory feeding bioassays (Susceptibility). Adult Japanese beetles removed significantly more leaf tissue (>80%) from the North American taxa of *U. americana*-diploid form and *U. americana* as compared with *U. americana* cultivars 'Jefferson', 'Valley Forge', and 'New Harmony' ($F=56.5$, $P<0.0001$). Adult beetles produced significantly less dry fecal weight ($F=92.4$, $P<0.0001$) when feeding on 'Valley Forge', and 'New Harmony', and the greatest amount when feeding on the diploid form of *U. americana* and *U. americana*. Adult beetles produced an intermediate amount of dry fecal weight when feeding on 'Jefferson' (Table 2). American elm is very unusual in the *Ulmus* genus cytologically with the majority being tetraploids, but also diploids in some cases. *Ulmus americana* 'Jefferson' [National Park Service (NPS)-3-487] is considered to be triploid and is considered a hybrid between diploid and tetraploid elms (Sherald et al. 1994, Whittemore and Olsen 2011). 'Jefferson' has shown to be less susceptible to DED along with 'Valley Forge' and 'New Harmony'. It is possible that some of the same genetic traits have been extended to reflect reduced feeding by adult Japanese beetles. Conversely, the *U. americana*-diploid form was equally susceptible to adult Japanese beetle feeding as *U. americana*, and both have been shown to be highly susceptible to DED. It appears that ploidy may confer some level of resistance to both DED and feeding by the Japanese beetle. Further research is needed to understand the origin and relations of the different ploidy levels, and the potential for pest and disease resistance (Santamour 1993, Whittemore and Olsen 2011, Whittemore and Xia 2017).

Adult Japanese beetles feeding on simple and complex Eurasian elm hybrids removed significantly more leaf tissue (>80%) when feeding on 'Pioneer', 'Regal', and 'Patriot' and removed the least amount of leaf tissue (50%) when feeding on 'Homestead' ($F=68.0$, $P<0.0001$). Adult beetles removed an intermediate amount of leaf tissue when feeding on 'Frontier' and 'Urban' elm. Dry fecal

pellet weights followed the same ranking order as mean percent leaf tissue removed ($F=19.2$, $P<0.0001$) (Table 2).

For simple *U. pumila* and *U. japonica* hybrids, beetles removed significantly more leaf tissue (>77%) from 'Sapporo Autumn Gold' and 'New Horizon' compared with beetles feeding on 'Cathedral' ($F=23.0$, $P<0.0001$). Mean dry fecal pellet weights followed the same ranking as the mean percent leaf tissue removed ($F=15.8$, $P=0.006$) (Table 2).

Significantly more leaf tissue (>37%) was removed by adult beetles when feeding on *U. parvifolia* cultivars of 'Athena' and 'Dynasty' as compared to *U. parvifolia* ($F=17.1$, $P<0.0002$). Japanese beetles feeding on 'Athena' and 'Dynasty' produced 2X more dry fecal pellet weights compared with *U. parvifolia*. Dry fecal pellet weights were not significantly different among the three *U. parvifolia* taxa. It is possible that the two *U. parvifolia* cultivars were more nutritious contributing to greater dry fecal pellet production. Dirr (2009) states that 'Athena' leaves are a darker green, almost black, compared with the *U. parvifolia* phenotype which would suggest higher chlorophyll levels and better overall nutrition which was reflected in the higher dry fecal pellet weights.

Adult Japanese beetles removed significantly more leaf tissue (>40%) when feeding on simple Asian hybrids of *U. japonica* x *U. pumila* 'Columnar', *U. japonica* x *U. wilsoniana* 'Single Stem', *U. japonica* x *U. wilsoniana* 'Arnold', *U. pumila* x *U. americana*, and 'Vanguard' x the diploid form of *U. americana* compared with beetles feeding on *U. japonica-wilsoniana-rubra* ($F=19.7$, $P<0.012$). Adult beetles produced significantly more frass ($F=18.1$, $P<0.001$) when feeding on *U. japonica* x *U. wilsoniana* 'Arnold' compared with *U. japonica* x *U. wilsoniana* 'Single Stem', *U. japonica-wilsoniana-rubra*, *U. pumila* x *U. americana*, and 'Vanguard' x diploid form of *U. americana*. Intermediate amounts of dry fecal pellets were produced when feeding on *U. japonica* x *U. pumila* 'Columnar' (Table 2).

Adult Japanese beetles feeding on North American elms of *U. alata* and *U. americana*, removed significantly more leaf tissue (>80%) as compared with beetles feeding on *U. rubra*. *Ulmus crassifolia*, *U. serotina*, and *U. thomasi* were moderately fed upon ($F=90.8$, $P<0.0001$). Rankings for dry fecal pellet weights were consistent with the percent of leaf tissue removed ($F=71.7$, $P<0.0001$) (Table 2).

Japanese beetles removed significantly more leaf tissue (>70%) when feeding on the European elms of *U. canescens*, *U. carpinifolia*, *U. foliacea*, and *U. laevis* as compared with *U. elliptica*, *U. glabra*, *U. suberosa*, and *U. sukaczewii* with < 60% of leaf tissue removed ($F=63.5$, $P<0.0001$). Rankings for dried fecal pellet weight were consistent with the percent of leaf tissue removed ($F=44.8$, $P<0.0001$) (Table 2).

Adult beetles removed significantly more leaf tissue ($F=81.9$, $P<0.0001$), and produced significantly more dry fecal pellets ($F=29.5$, $P<0.0001$) when feeding on the Asian elms of *U. changii* and *U. wallichiana* compared with *U. prunifolia*, *U. wilsoniana* 'Prospector', and *U. wilsoniana-98*. *Ulmus lanceaefolia*, *U. pseudopropinqua*,

Table 2. Percent leaf tissue removed and dry fecal pellet weight for adult female Japanese beetles feeding on Ulmaceae in no-choice (NC) feeding studies.

Taxa or Cultivar ²	Mean % leaf tissue removed (\pm SE)	Mean dry fecal pellet weight (mg) (\pm SE)
North American elm cultivars		
<i>U. americana</i> ‘Jefferson’	48 \pm 0.0a	84.0 \pm 5.6ab
<i>U. americana</i> ‘Valley Forge’	35 \pm 0.1a	41.6 \pm 1.6a
<i>U. americana</i> ‘New Harmony’	16 \pm 0.1a	31.0 \pm 2.0a
<i>U. americana</i> -diploid form	83 \pm 0.0b	90.6 \pm 3.4b
<i>U. americana</i> (reference)	85 \pm 0.0b	97.2 \pm 11.5b
Significance	F=56.5, P<0.0001	F=92.4, P<0.0001
Simple and complex Eurasian hybrids		
‘Frontier’ (<i>U. carpinifolia</i> x <i>U. parvifolia</i>)	63 \pm 0.1ab	50.5 \pm 4.3a
‘Homestead’ (<i>U. pumila</i> x (<i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x <i>U. pumila-pinnato-ramosa</i> x <i>U. carpinifolia</i> ‘Hoersholmiensis’)	50 \pm 0.1a	18.9 \pm 3.2a
‘Pioneer’ (<i>U. glabra</i> x <i>U. carpinifolia</i>)	86 \pm 0.0b	72.3 \pm 7.6ab
‘Regal’ (<i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x (<i>U. pumila</i> x <i>U. carpinifolia</i> ‘Hoersholmiensis’)	83 \pm 0.1b	123.2 \pm 9.2b
‘Urban Elm’ (N-148 <i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x (<i>U. pumila</i>)	57 \pm 0.1ab	42.6 \pm 14.0a
‘Patriot’ (‘Urban elm’ x ‘Prospector’)	82 \pm 0.1b	72.3 \pm 3.8ab
Significance	F=68.0, P<0.0001	F=19.2, P<0.0001
Ulmus pumila and U. japonica hybrids		
‘Sapporo Autumn Gold’ (<i>U. pumila</i> x <i>U. japonica</i>)	88 \pm 0.0b	51.8 \pm 8.9b
‘Cathedral’ (<i>U. pumila</i> x <i>U. japonica</i>)	41 \pm 0.1a	21.9 \pm 3.7a
‘New Horizon’ (<i>U. japonica</i> x <i>U. pumila</i>)	78 \pm 0.1b	58.0 \pm 5.8b
Significance	F=23.0, P<0.0001	F=15.8, P=0.006
U. parvifolia taxa and cultivars		
<i>U. parvifolia</i>	7 \pm 0.0a	6.3 \pm 1.1a
‘Dynasty’ (<i>U. parvifolia</i>)	38 \pm 0.1b	12.3 \pm 2.0a
‘Athena’ (<i>U. parvifolia</i>)	46 \pm 0.1b	13.1 \pm 2.1a
Significance	F=17.1, P<0.0002	(NS)
Simple Asian hybrids		
<i>U. japonica</i> x <i>U. pumila</i> ‘Columnar’	61 \pm 0.1b	59.0 \pm 6.0ab
<i>U. japonica</i> x <i>U. wilsoniana</i> ‘Single Stem’	51 \pm 0.1b	31.6 \pm 4.1a
<i>U. japonica-wilsoniana-rubra</i>	37 \pm 0.1ab	43.6 \pm 4.5a
<i>U. japonica</i> x <i>U. wilsoniana</i> ‘Arnold’	52 \pm 0.1b	73.0 \pm 7.6b
<i>U. pumila</i> x <i>U. americana</i>	43 \pm 0.1b	43.2 \pm 4.2a
‘Vanguard’ x <i>U. americana</i> -diploid	45 \pm 0.1b	35.3 \pm 3.6a
Significance	F=19.7, P=0.012	F=18.1, P<0.0001
North American elm taxa		
<i>U. alata</i>	85 \pm 0.1b	39.2 \pm 3.8b
<i>U. americana</i>	80 \pm 0.1b	95.0 \pm 9.0c
<i>U. crassifolia</i>	41 \pm 0.1ab	67.3 \pm 6.5b
<i>U. rubra</i>	3 \pm 0.0a	2.4 \pm 0.1a
<i>U. serotina</i>	35 \pm 0.1ab	2.5 \pm 0.1a
<i>U. thomasii</i>	35 \pm 0.1ab	47.1 \pm 0.3b
Significance	90.8, P<0.0001	F=71.7, P<0.0001
European elm taxa		
<i>U. canescens</i>	99 \pm 0.2c	32.4 \pm 6.4a
<i>U. carpinifolia</i>	84 \pm 0.1b	97.0 \pm 9.0b
<i>U. elliptica</i>	59 \pm 0.2a	49.7 \pm 5.0a
<i>U. foliacea</i>	75 \pm 0.1b	78.8 \pm 8.0ab
<i>U. glabra</i>	34 \pm 0.1a	51.7 \pm 4.9a
<i>U. laevis</i>	71 \pm 0.1b	73.3 \pm 6.9ab
<i>U. suberosa</i>	10 \pm 0.1a	6.3 \pm 6.3a
<i>U. sukaczewii</i>	62 \pm 0.1a	44.4 \pm 4.3a
Significance	F=63.5, P<0.0001	F=44.8, P<0.0001
Asian taxa and cultivars		
<i>U. changii</i>	81 \pm 0.03b	33.8 \pm 3.6b
<i>U. lanceafolia</i>	37 \pm 0.05ab	6.5 \pm 0.0a
<i>U. prunifolia</i>	11 \pm 0.02a	1.7 \pm 0.0a
<i>U. pseudopropinqua</i>	28 \pm 0.05ab	5.3 \pm 0.1a
<i>U. taihangshanensis</i>	23 \pm 0.03ab	0.9 \pm 0.0a
<i>U. wallichiana</i>	75 \pm 0.04b	28.2 \pm 2.8b
<i>U. wilsoniana</i> ‘Prospector’	26 \pm 0.1a	12.7 \pm 3.8a
<i>U. wilsoniana</i> -98	6 \pm 0.0a	37.2 \pm 3.8a
<i>Sassafras albidum</i> (reference)	90 \pm 0.07b	60.1 \pm 4.2c
Significance	F=81.9, P<0.0001	F=29.5, P<0.0001

²Values within a column followed by the same letter are not significantly different (P<0.05, Dunn’s test)

Table 3. Percent leaf tissue removed, dry fecal pellet weight, and percent field defoliation for adult female Japanese beetle feeding on *Zelkova* taxa and cultivars in no-choice laboratory feeding bioassays, and field defoliation study.

Taxa and cultivars ^z	Mean % leaf tissue removed (\pm SE)	Mean dry fecal pellet weight (mg) (\pm SE)	Mean % field defoliation (\pm SE)
<i>Zelkova carpinifolia</i> (D-Russia)	58 \pm 0.1b	28.1 \pm 4.5b	28 \pm 4.5b
<i>Z. carpinifolia</i> (T-Russia)	20 \pm 0.0a	22.0 \pm 4.8ab	22 \pm 4.8ab
<i>Z. schneideriana</i> (T-Russia)	17 \pm 0.0a	27.4 \pm 11.8ab	27 \pm 11.8ab
<i>Z. schneideriana</i> (N-China)	19 \pm 0.0a	14.4 \pm 1.7ab	14 \pm 1.7ab
<i>Z. serrata</i>	39 \pm 0.1b	31.0 \pm 3.8b	13 \pm 0.0b
<i>Z. serrata</i> 'Green Vase'	11 \pm 0.0a	10.1 \pm 1.4a	10 \pm 1.5
<i>Z. serrata</i> 'Village Green'	10 \pm 0.0a	8.2 \pm 1.8a	12 \pm 1.3
<i>Z. sinica</i>	40 \pm 0.1b	39.3 \pm 5.6b	3 \pm 0.0a
<i>Sassafras albidum</i> (reference)	90 \pm 0.07c	60.1 \pm 4.2c	80 \pm 5.6c
Significance	F=26.3, P<0.0004	F=32.0, P<0.0001	F=28.4, P<0.0001

^zValues within a column followed by the same letter are not significantly different ($P<0.05$, Dunns's test).

and *U. taihangshanensis* were immediate in susceptibility and production of dry fecal pellets by Japanese beetles.

Evaluating eight different *Zelkova* taxa, adult Japanese beetles removed significantly more leaf tissue ($>40\%$) ($F=26.7, P<0.0001$) when feeding on *Z. serrata*, *Z. sinica*, and *Z. carpinifolia* (D-Russia) compared with *Z. serrata* cultivars 'Green Vase' and 'Village Green', *Z. carpinifolia* (T-Russia), and *Z. schneideriana* (T-Russia and N-China). Mean dry fecal pellet weight rankings were consistent with the percent of leaf tissue removed ($F=32.0, P<0.0001$) (Table 3).

Dry fecal pellet weights (Susceptibility). Dry fecal pellet weights were strongly correlated with the percent of leaf tissue removed ($R=0.84, P<0.001$) for all *Ulmus* and *Zelkova* taxa evaluated in this study,

Field defoliation survey (Susceptibility). Overall, highly significant differences in feeding damage were observed among the 30 *Ulmus* and six *Zelkova* taxa evaluated on the grounds of The Morton Arboretum ($F=118.3, P<0.0001$) (Table 4). *Ulmus americana*-diploid, *U. carpinifolia*, 'Urban' elm, *U. pumila*, the hybrids *U. japonica* x *U. wilsoniana* 'Single Stem', *U. pumila* x *U. americana*, 'Commendation', *U. elliptica*, *U. foliacea*, and *U. americana* (reference) had $>30\%$ feeding damage compared with the remaining taxa with $<25\%$ feeding damage (Table 4). Overall, the field feeding damage ratings were moderately correlated with the percent leaf tissue removed in the no-choice (NC) laboratory feeding studies ($R=0.38, P=0.02$). This could be due to a number of variables found in natural environments including leaf phenology, adult feeding habits, and environmental conditions compared with the controlled laboratory feeding studies.

Multiple-Choice (MC) laboratory feeding bioassays (Preference). Overall, there was no correlation between the percent leaf tissue removed in the no-choice (NC) and multiple-choice (MC) laboratory feeding studies. A significant difference ($F=6.36, P=0.009$) in feeding preference was observed in MC study #1 where adult beetles were presented *U. americana* 'Jefferson', *U. americana* 'Valley Forge' and the reference species *U. americana* (Table 5). The least amount of leaf tissue removed (12%) occurred on the diploid form of *U. americana*. Results from MC-1 were not consistent with the field defoliation

survey. These differences could be due to the greater preference for *U. americana* by adult Japanese beetles in a controlled MC experiment with limited choices compared to field conditions where beetles would have to search for a more preferred species. These findings are consistent with other studies involving herbivorous insects where a highly preferred host tends to dominate preference in controlled multiple-choice (MC) studies (Miller, and Ware, 1994, 1997, Miller and Ware, 1999a, b, Miller et al., 1999, 2000b).

In multiple-choice (MC) study #2, a significant difference ($F=41.9, P=0.0001$) in feeding preference was observed. 'Pioneer' and *U. carpinifolia* were the most preferred with *U. glabra* being least preferred. The cultivar, 'Frontier' was intermediate in preference (Table 5). Like MC-1 study, the amount of leaf tissue removed and the field defoliation ratings were not related to feeding preference for the same taxa (Tables 2 and 5). *Ulmus carpinifolia* was found to be highly susceptible to feeding both in the NC and field defoliation studies which might have contributed to the greater preference for 'Frontier' and 'Pioneer' in this MC study. Like *U. americana* in MC-1, and for the same reasons mentioned previously, *U. carpinifolia* may have dominated preference in this controlled MC study compared with feeding preference in a more natural setting. Conversely, *U. glabra* was found to be much less susceptible and/or preferred for feeding in both the NC and MC studies, and the field defoliation studies, but in the case of 'Pioneer', may have had only minimal genetic contribution to feeding susceptibility and preference.

In MC study #3, Japanese beetles fed significantly less on 'Homestead', 'Regal', and 'Urban' elm ($F=39.8, P<0.0001$). *Ulmus* x *hollandica* 'Vegeta', and *U. carpinifolia* were more preferred and *Ulmus pumila* was intermediate in preference (Table 5). In this study, the percent leaf tissue removed was very strongly correlated with leaf thickness ($R=0.93, P<0.0001$) but not for inner or outer leaf toughness for these same taxa.

MC study #4 revealed highly significant differences ($F=44.7, P<0.0001$) in feeding by adult beetles when they were allowed to choose between 'Sapporo Autumn Gold', 'Cathedral', 'New Horizon', *U. japonica*, *U. pumila*, and the reference species, *U. americana*. Beetles removed significantly more leaf tissue on *U. americana* compared

Table 4. Percent field defoliation of selected elm (*Ulmus*) taxa for adult Japanese beetles feeding .

Taxa ^z	Mean percent field defoliation (±SE)
North American elms and cultivars	
<i>U. americana</i> ‘Jefferson’	18 ± 0.0a
<i>U. americana</i> -diploid form	43 ± 0.0b
<i>U. americana</i>	55 ± 0.0c
Simple and complex Eurasian hybrids	
‘Frontier’ (<i>U. carpinifolia</i> x <i>U. parvifolia</i>)	0 ± 0.0a
‘Homestead’ (<i>U. pumila</i> x (<i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x <i>U. pumila</i> - <i>pinnatoramosa</i> x <i>U. carpinifolia</i> ‘Hoersholmiensis’)	8 ± 0.0a
‘Pioneer’ (<i>U. glabra</i> x <i>U. carpinifolia</i>)	8 ± 0.0a
‘Regal’ (<i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x (<i>U. pumila</i> x <i>U. carpinifolia</i> ‘Hoersholmiensis’)	23 ± 0.0b
‘Urban Elm’ (N-148 <i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x (<i>U. pumila</i>)	33 ± 0.0b
<i>Ulmus pumila</i> and <i>U. japonica</i> hybrids	
‘Sapporo Autumn Gold’ (<i>U. pumila</i> x <i>U. japonica</i>)	28 ± 0.0b
<i>U. parvifolia</i> taxa and cultivars	
<i>U. parvifolia</i>	0 ± 0.0a
‘Dynasty’ (<i>U. parvifolia</i>)	0 ± 0.0a
‘Athena’ (<i>U. parvifolia</i>)	0 ± 0.0a
Simple and complex Asian hybrids	
<i>U. japonica</i> x <i>U. pumila</i> ‘Columnar’	15 ± 0.0a
<i>U. japonica</i> x <i>U. wilsoniana</i> ‘Single Stem’	43 ± 0.0b
<i>U. japonica</i> - <i>wilsoniana</i> - <i>rubra</i>	8 ± 0.0a
<i>U. japonica</i> x <i>U. wilsoniana</i> ‘Arnold’	8 ± 0.0a
<i>U. pumila</i> x <i>U. americana</i>	43 ± 0.0b
‘Vanguard’ x <i>U. americana</i> - diploid	23 ± 0.0ab
North American elm taxa	
<i>U. americana</i>	97 ± 9.6c
<i>U. crassifolia</i>	3 ± 0.0a
<i>U. serotina</i>	8 ± 0.0ab
<i>U. thomasi</i>	10 ± 0.0b
European elm taxa	
<i>U. canescens</i>	5 ± 0.0a
<i>U. carpinifolia</i>	38 ± 0.0b
<i>U. elliptica</i>	34 ± 0.0b
<i>U. foliacea</i>	32 ± 0.0b
<i>U. glabra</i>	23 ± 0.0ab
<i>U. laevis</i>	8a ± 0.0
<i>U. suberosa</i>	5a ± 0.0
<i>U. sukaczewii</i>	5a ± 0.0
<i>Sassafras albidum</i> (reference)	80 ± 0.4 c
Significance	F=118.3, P<0.0001

^zValues within a column followed by the same letter are not significantly different (P<0.05, Dunn’s test).

with ‘Cathedral’, ‘New Horizon’, and *U. japonica* where <12% of leaf tissue was removed. ‘Sapporo Autumn Gold’ and *U. pumila* were intermediate in preference (Table 5). In this study, the mean percent leaf tissue removed was very strongly correlated with mean percent field defoliation ($R = 0.93$, $F=13.9$, $P=0.06$). When the highly preferred reference species of *U. americana* was not included in MC study #5, preference shifted to *U. pumila* with 56% of leaf tissue consumed compared to <22% of leaf tissue consumed for beetles presented with ‘Sapporo Autumn Gold’, ‘Cathedral’, ‘New Horizon’, and *U. japonica* ($F=44.7$, $P<0.0001$) (Table 5).

In MC study #6, *U. americana* was highly preferred over the six Asian taxa ($F=47.2$, $P,0.00010$) (Table 5). In MC study #7, adult female beetles removed significantly more

Table 5. Percentage of leaf tissue removed by adult Japanese beetles in multiple-choice (MC) laboratory feeding preference studies on Ulmaceae.

Taxa ^z	Mean percent leaf tissue removed (±SE)
	Study #1
<i>U. americana</i> ‘Jefferson’	32 ± 0.1b
<i>U. americana</i> ‘Valley Forge’	18 ± 0.0b
<i>U. americana</i> -diploid	12 ± 0.0a
<i>U. americana</i> (reference)	29 ± 0.1b
	Study #2
‘Frontier’ (<i>U. carpinifolia</i> x <i>U. parvifolia</i>)	26 ± 0.1ab
‘Pioneer’ (<i>U. glabra</i> x <i>U. carpinifolia</i>)	38 ± 0.1b
<i>U. glabra</i>	6 ± 0.0a
<i>U. carpinifolia</i>	35 ± 0.1b
	Study #3
‘Homestead’ (<i>U. pumila</i> x (<i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x <i>U. pumila</i> - <i>pinnatoramosa</i> x <i>U. carpinifolia</i> ‘Hoersholmiensis’)	13 ± 0.0a
‘Regal’ (<i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x (<i>U. pumila</i> x <i>U. carpinifolia</i> ‘Hoersholmiensis’)	8 ± 0.0a
‘Urban Elm’ (N-148 <i>U. x hollandica</i> ‘Vegeta’ x <i>U. carpinifolia</i>) x (<i>U. pumila</i>)	12 ± 0.1a
<i>U. x hollandica</i> ‘Vegeta’	42 ± 0.1b
<i>U. carpinifolia</i>	38 ± 0.1b
<i>U. pumila</i>	17 ± 0.6ab
	Study #4
‘Sapporo Autumn Gold’ (<i>U. pumila</i> x <i>U. japonica</i>)	36 ± 0.1ab
‘Cathedral’ (<i>U. pumila</i> x <i>U. japonica</i>)	3 ± 0.0a
‘New Horizon’ (<i>U. japonica</i> x <i>U. pumila</i>)	10 ± 0.0a
<i>U. japonica</i>	11 ± 0.1a
<i>U. pumila</i>	35 ± 0.1ab
<i>U. americana</i> (reference)	48 ± 0.1b
	Study #5
‘Sapporo Autumn Gold’ (<i>U. pumila</i> x <i>U. japonica</i>)	17 ± 0.1a
‘Cathedral’ (<i>U. pumila</i> x <i>U. japonica</i>)	3 ± 0.0a
‘New Horizon’ (<i>U. japonica</i> x <i>U. pumila</i>)	14 ± 0.0a
<i>U. japonica</i>	21 ± 0.1a
<i>U. pumila</i>	56 ± 0.1b
	Study #6
<i>U. changii</i>	20 ± 0.2a
<i>U. lanceaefolia</i>	12 ± 0.0a
<i>U. prunifolia</i>	9 ± 0.0a
<i>U. pseudopropinqua</i>	16 ± 0.1a
<i>U. taihangshanensis</i>	13 ± 0.1a
<i>U. wallichiana</i>	23 ± 0.1a
<i>U. americana</i> (reference)	42 ± 0.2b
	Study #7
<i>Z. carpinifolia</i> (D-Russia)	2 ± 0.0a
<i>Z. carpinifolia</i> (T-Russia)	15 ± 0.0c
<i>Z. schneideriana</i> (T-Russia)	2 ± 0.0a
<i>Z. schneideriana</i> (N-China)	1 ± 0.0a
<i>Z. serrata</i>	8 ± 0.0b
<i>Z. sinica</i>	0 ± 0.0a
<i>U. americana</i> (reference)	61 ± 0.1d

^zFor each respective study, values within a column followed by the same letter are not significantly different (P<0.05, Dunn’s test).

Table 6. Fecundity of adult female Japanese beetles by geographic origin of Ulmaceae.

Taxa by Geographic Origin ^z	Total eggs laid (±SE)
Asia	318±0.2c
Europe	95±0.1b
Eurasia	88±0.1b
North America	22±0.1a
Significance	F=123.0, P<0.0001

^zValues within a column followed by the same letter are not significantly different (P<0.05, Dunn's test).

leaf tissue when presented with *Z. serata*, *Z. carpinifolia* (T-Russia) and the reference, *U. americana* (F=35.2, P<0.0001). Less than 3% of leaf tissue was removed on the remaining four *Zelkova* taxa (Table 5). Results from

Table 7. Fecundity of adult female Japanese beetles ovipositing when feeding on Ulmaceae leaves.

Elm Taxa	Total eggs laid (±SE) ^z
North American elm taxa	
<i>U. alata</i>	9 ± 0.23a
<i>U. americana</i>	37 ± 0.29c
<i>U. crassifolia</i>	0 ± 0.00a
<i>U. serotina</i>	18 ± 0.31b
<i>U. thomasi</i>	1 ± 0.10a
<i>U. americana</i> 'Jefferson'	1 ± 0.10a
Significance	F=86.1, P=0.02
Simple and complex Eurasian hybrids	
'Frontier' (<i>U. carpinifolia</i> x <i>U. parvifolia</i>)	9 ± 0.30b
'Homestead' <i>U. pumila</i> x (<i>U. x hollandica</i> 'Vegeta' x <i>U. carpinifolia</i>) x <i>U. pumila-pinnato-ramosa</i> x <i>U. carpinifolia</i> 'Hoersholmiensis'	3 ± 0.10a
'Pioneer' (<i>U. glabra</i> x <i>U. carpinifolia</i>)	2 ± 0.07a
'Regal' (<i>U. x hollandica</i> Vegeta x <i>U. carpinifolia</i>) x (<i>U. pumila</i> x <i>U. carpinifolia</i> 'Hoersholmiensis')	12 ± 0.24b
'Patriot' ('Urban Elm' x <i>U. wilsoniana</i> 'Prospector')	0 ± 0.00a
'Urban Elm' (N-148 <i>U. x hollandica</i> 'Vegeta' x <i>U. carpinifolia</i> x <i>U. pumila</i>)	10 ± 0.17b
Significance	F=129.0, P<0.001
Ulmus pumila and U. japonica hybrids	
'Sapporo Autumn Gold' (<i>U. pumila</i> x <i>U. japonica</i>)	21 ± 0.34ab
'New Horizon' (<i>U. japonica</i> x <i>U. pumila</i>)	5 ± 0.11ab
Significance	t=143, P<0.01
Simple Asian hybrids	
<i>U. davidiana</i> x "Accolade"	16 ± 0.17a
<i>U. davidiana</i> x <i>U. japonica-wilsoniana-pumila</i>	25 ± 0.20ab
<i>U. szechuanica</i> x <i>U. japonica</i>	57 ± 0.57b
'Accolade' x <i>U. japonica</i>	37 ± 0.40ab
'Accolade' x <i>U. pumila</i>	10 ± 0.10a
'Vanguard' x <i>U. davidiana</i>	6 ± 0.10a
'Vanguard' x <i>U. japonica-wilsoniana-pumila</i>	50 ± 0.52b
Significance	F=47.2, P<0.001
Complex Asian hybrids	
<i>U.</i> 'Morton' Accolade	20 ± 0.22a
<i>U.</i> 'Morton Stalwart' Commendation	38 ± 0.42ab
<i>U.</i> 'Morton Red Tip' Danada Charm	42 ± 0.29ab
<i>U.</i> 'Morton Glossy' Triumph	22 ± 0.25a
<i>U.</i> 'Morton Plainsman' Vanguard	54 ± 0.50b
Significance	F=43.8, P<0.0001
European elm taxa	
<i>U. carpinifolia</i>	48 ± 0.68b
<i>U. elliptica</i>	6 ± 0.14a
<i>U. glabra</i>	7 ± 0.23a
<i>U. laevis</i>	7 ± 0.14 a
<i>U. sukaczewii</i>	8 ± 0.23a
Significance	F=117.2, P<0.0001

Table 7. Continued.

Elm Taxa	Total eggs laid (±SE) ^z
Asian taxa, cultivars and varieties	
<i>U. bergmaniana</i> var. <i>lasiophylla</i>	40 ± 0.28b
<i>U. castaneifolia</i>	16 ± 0.17a
<i>U. chenmoui</i>	51 ± 0.32b
<i>U. davidiana</i>	26 ± 0.22ab
<i>U. gausseii</i>	24a ± 0.20ab
<i>U. glaucescens</i>	21 ± 0.19ab
<i>U. glaucescens</i> var. <i>lasiocarpa</i>	10 ± 0.10a
<i>U. japonica</i>	38 ± 0.25ab
<i>U. lamellosa</i>	50 ± 0.31b
<i>U. macrocarpa</i>	71 ± 0.43c
<i>U. microcarpa</i>	6 ± 0.09a
<i>U. multinervis</i> (syn. <i>U. castaneifolia</i>)	21 ± 0.19a
<i>U. parvifolia</i>	56 ± 0.52b
<i>U. propinqua</i>	11 ± 0.12a
<i>U. propinqua</i> var. <i>suberosa</i>	35 ± 0.26ab
<i>U. prunifolia</i>	9 ± 0.07a
<i>U. pseudopropinqua</i>	19 ± 0.17a
<i>U. pumila</i>	21 ± 0.19a
<i>U. szechuanica</i>	9 ± 0.08a
<i>U. taihangshanensis</i>	4 ± 0.05a
<i>U. wilsoniana</i>	17 ± 0.18a
<i>U. wilsoniana</i> 'Prospector'	3 ± 0.10 a
<i>Sassafras albidum</i> (reference)	200 ± 0.56c
Blank	1 ± 0.00a
Significance	F=53.8, P<0.0001
Zelkova taxa	
<i>Z. schneideriana</i> (N-China)	9 ± 0.18a
<i>Z. serrata</i>	0 ± 0.00a
<i>Z. serrata</i> 'Green Vase'	0 ± 0.00a
<i>Z. serrata</i> 'Village Green'	1 ± 0.03a
<i>Z. sinica</i>	38 ± 0.78b
Significance	F=75.1, P<0.001

^zValues within a column followed by the same letter are not significantly different (P<0.05, Dunn's Test).

this multiple-choice study were very strongly correlated with the field defoliation survey (R=0.98, P=0.005)

No-Choice (NC) laboratory fecundity bioassays (Suitability). Overall, adult female Japanese beetles laid significantly more eggs (> 300 eggs) on Asian elm taxa compared with European (95 eggs), Eurasian (88 eggs), and North American (22 eggs) elm taxa (F=123.0, P<0.0001) (Table 6).

North American taxa. *Ulmus americana* and *U. serotina* was significantly more suitable for egg laying (>18 eggs) compared with *U. alata*, *U. crassifolia*, *U. thomasi*, and *U. americana* 'Jefferson' with <4 total eggs laid (F=86.1, P=0.02) (Table 7).

Simple and complex Eurasian hybrids. Adult females feeding on simple and complex Eurasian hybrids laid significantly more eggs on 'Regal' (12 eggs), 'Urban' elm (10 eggs), and 'Frontier' (9 eggs) compared with 'Homestead', 'Pioneer', 'Patriot', and 'Prospector' with <4 eggs per taxon (F=129.0, P<0.001) (Table 7).

Complex Asian hybrids. 'Morton Plainsman' Vanguard was significantly more suitable (total eggs = 54) (F=43.8, P<0.0001) compared with 'Morton' Accolade, and 'Morton Glossy' Triumph (<23 eggs produced). 'Morton

Table 8. Summary of leaf thickness, and inner and outer leaf toughness by geographic origin for Asian, European, and North American *Ulmus* taxa.

TAXA	Thickness ^z (microns) (±SE)	Toughness (g)	
		Inner (±SE)	Outer (±SE)
Asian ^y	282 ± 0.02b	30.71 ± 0.03b	29.71 ± 0.28b
European ^y	325 ± 0.04b	24.90 ± 0.03a	23.32 ± 0.26a
North American	198 ± 0.02a	25.31 ± 0.04a	20.73 ± 0.24a
Significance	F=70.0 P<0.001	F=31.1 P<0.001	F=39.1 P<0.001

^zValues within a column followed by the same letter are not significantly different ($P<0.05$, Dunn's Test).

^yIncludes simple and complex Eurasian hybrids.

Stalwart' Commendation and 'Morton Red Tip' Danada Charm were intermediate in suitability with a total of 38 and 42 eggs laid, respectively (Table 7).

Ulmus pumila x *U. japonica* hybrids. 'Sapporo Autumn Gold' was found to be more suitable for egg laying by adult female beetles (total of 21 eggs) compared with 'New Horizon' with a total of only five eggs laid ($t=143$, $P<0.01$) (Table 7).

European elm taxa. Adult female beetles laid significantly more eggs on *U. carpinifolia* (48 eggs) compared with the other five European elm taxa (< 20 eggs laid) ($F=117.2$, $P<0.0001$) (Table 7).

Asian taxa and simple hybrids. Adult female beetles laid significantly more eggs (>40 eggs) ($F=53.8$, $P<0.0001$) when feeding on *U. bergmaniana* var. *lasiophylla*, *U. chenmoui*, *U. lamellosa*, *U. macrocarpa*, *U. parvifolia*, *U. szechuanica* x *U. japonica*, and 'Vanguard' x *U. japonica-wilsoniana-pumila*. Adult female beetles laid an intermediate number of eggs (mean=30 total eggs) when feeding on *U. davidiana*, *U. davidiana* x. *U. japonica-wilsoniana-pumila*, *U. gaussenii*, *U. glaucescens*, *U. japonica*, *U. multinervis* (syn. *U. castaneifolia*), and *U. propinqua* var. *suberosa*. Adult female Japanese beetles laid significantly fewer eggs (<20 total eggs) on the remaining Asian elm taxa (Table 7).

Zelkova taxa. For the *Zelkova* taxa (Ulmaceae), *Z. sinica* was the most suitable for egg laying with a total of 38 eggs compared with *Z. schneideriana* (N-China), *Z. serrata*, and the cultivars of *Z. serrata* 'Green Vase', and 'Village Green' with <2 total eggs laid ($F=75.1$, $P<0.001$) (Table 7). Not surprisingly, the highly preferred sassafras (*Sassafras albidum*) was by far the most suitable with females producing a total of 200 eggs. These results are consistent with previous studies by Keathley and Potter (2008) and Miller and Wiegrefe (2021). One adult female beetle laid one egg in the blank reference container without foliage.

For all of the elms tested in this study, percent leaf tissue removed and dry fecal pellet weight were not good predictors of fecundity (percent leaf tissue removed, $R=0.36$, $P=0.10$ and dry fecal pellet weight, $R=0.05$, $P=0.82$, respectively). However, fecundity was strongly correlated with percent females ovipositing ($R=0.72$,

$P<0.001$). Our findings are consistent with a study by Miller and Wiegrefe (2021) evaluating the suitability of *Carpinus* taxa for Japanese beetle reproduction.

Adult longevity. Overall, adult male and female beetles lived an average of 20 days on all *Ulmus* taxa evaluated in this study. Results presented here are consistent with other studies (Potter et al. 1998, Miller et al. 1999, 2001a, Miller and Ware 1999a, 2001, Potter and Held 2002, Miller and Wiegrefe 2021). However, adult male Japanese beetles feeding on *Zelkova* taxa lived significantly longer (21 days) on 'Green Vase' and 'Village Green' compared to the other *Zelkova* taxa (males: 17-18 days, $F=13.6$, $P<0.009$ and females: 16-18 days, $F=12.2$, $P<0.016$) (Data not shown).

Elm leaf thickness and toughness. A summary of elm leaf thickness and toughness by geographic origin and taxa is presented in Tables 8 and 9. Asian and European elms had significantly thicker leaves (1.5X) than North American elms ($F=70.0$, $P<0.001$), and Asian elm leaves were significantly tougher than European and North American elms by a factor of 1.3X and 1.4X for inner and outer leaf toughness, respectively (inner toughness, $F=31.1$, $P<0.001$ and outer toughness, $F=39.1$, $P<0.001$, respectively) (Table 8). There was no significant difference between inner and outer leaf toughness for all of the *Ulmus* taxa evaluated in this study, Leaf thickness was moderately and strongly correlated with inner and outer leaf toughness (inner toughness, $R=0.43$, $P<0.006$, outer toughness, $R=0.52$, $P<0.001$), respectively, and inner leaf toughness was very strongly correlated with outer leaf toughness ($R=0.93$, $P<0.001$).

For the 20 Asian and complex hybrids, evaluated, *U. castaneifolia* had significantly thicker leaves and *U. gausenii*, *U. glaucescens*, *U. japonica*, *U. pumila*, and the complex hybrids of 'Accolade', 'Commendation', and 'Vanguard' had significantly thinner leaves. Leaves of the remaining Asian elm taxa and hybrids were intermediate in thickness ($F=353.3$, $P<0.001$). Leaves of *U. gausenii*, *U. japonica*, and *U. pumila* were the most tender (least tough) compared to the toughest leaves of *U. lamellosa*, *U. macrocarpa*, *U. parvifolia*, *U. taihangshanensis*, *U. wilsoniana*, 'Accolade', 'Commendation', 'Danada Charm', and 'Triumph'. Leaves of the remaining Asian elm taxa were intermediate in inner and outer leaf toughness (inner toughness, $F=254.4$, $P<0.001$, outer toughness, $F=303.0$, $P<0.001$).

For the simple and complex Eurasian hybrids, 'Frontier', 'Homestead' and 'Regal' had significantly thinner and more tender leaves than 'Patriot' and 'Pioneer' (thickness, $F = 47.4$, $P<0.001$, inner leaf toughness, $F=17.2$, $P<0.001$, outer leaf toughness, $F=17.8$, $P <0.001$).

Among European elms, *U. foliaceae* had the thinnest leaves and *U. procera* and *U. sukaczewii* had significantly thicker leaves ($F=44.2$, $P<0.001$). *Ulmus elliptica* and *U. procera* had significantly tougher leaves compared with *U. sukaczewii* (inner leaf toughness, $F=30.6$, $P<0.001$, outer leaf toughness, $F=4.9$, $P<0.001$).

The North American elm, *U. thomasi* had significantly thinner leaves compared with *U. alata* and *U. crassifolia* ($F=40.4$, $P<0.001$). There was no significant difference in

Table 9. Summary of elm (*Ulmus*) leaf thickness, and inner and outer leaf toughness.

TAXA ²	Thickness (microns) (±SE)	Toughness (g)	
		Inner (±SE)	Outer (±SE)
Asian taxa and complex hybrids			
<i>U. castaneifolia</i> .	411 ± 12.3c	30.98 ± 1.24c	28.85 ± 1.15d
<i>U. chenmoui</i>	373 ± 11.2bc	28.17 ± 1.13c	24.04 ± 0.96c
<i>U. davidiana</i>	274 ± 8.23b	31.66 ± 1.27d	28.12 ± 1.12d
<i>U. gauseinii</i>	173 ± 5.18a	12.79 ± 0.51a	12.61 ± 0.50a
<i>U. glaucescens</i>	213 ± 6.40a	22.59 ± 0.90b	19.19 ± 0.77b
<i>U. japonica</i> .	178 ± 5.33a	12.93 ± 0.52a	10.57 ± 0.42a
<i>U. lamellosa</i>	378 ± 11.4bc	58.97 ± 2.36g	59.88 ± 2.40h
<i>U. macrocarpa</i>	368 ± 11.0bc	37.83 ± 1.51e	44.72 ± 1.79g
<i>U. parvifolia</i>	269 ± 8.08b	38.65 ± 1.55e	30.35 ± 1.21e
<i>U. propinqua</i>	305 ± 9.14b	29.08 ± 1.16c	22.23 ± 0.89b
<i>U. prunifolia</i>	318 ± 9.53b	30.89 ± 1.24c	28.99 ± 1.16d
<i>U. pseudopropinqua</i>	371 ± 11.1b	25.31 ± 1.01c	24.72 ± 0.99c
<i>U. pumila</i>	203 ± 6.10a	14.92 ± 0.60a	14.42 ± 0.58a
<i>U. taihangshanensis</i>	257 ± 7.70b	38.15 ± 1.53e	35.06 ± 1.40f
<i>U. wilsoniana</i>	302 ± 9.07b	33.43 ± 1.34d	29.98 ± 1.20e
‘Accolade’	206 ± 6.17a	33.20 ± 1.33d	34.88 ± 1.40f
‘Commendation’	198 ± 5.94a	29.03 ± 1.16c	29.80 ± 1.19e
‘Danada Charm’	272 ± 8.15b	56.70 ± 2.27g	36.47 ± 1.46f
‘Triumph’	310 ± 9.30b	47.63 ± 1.91f	48.99 ± 1.96g
‘Vanguard’	216 ± 6.48a	26.67 ± 1.07c	25.08 ± 1.00c
Significance	F = 353.3	F = 254.4	F = 303.0
	P < 0.001	P < 0.001	P < 0.001
Simple and complex Eurasian hybrids			
‘Frontier’	213 ± 6.40a	22.77 ± 0.91a	22.68 ± 0.81a
‘Homestead’	196 ± 5.78a	24.22 ± 0.97a	20.14 ± 1.73a
‘Patriot’	770 ± 23.1b	42.55 ± 1.70c	43.27 ± 1.32c
‘Pioneer’	394 ± 11.8b	33.11 ± 1.32c	33.11 ± 1.72b
‘Prospector’	363 ± 10.9b	48.08 ± 1.92c	43.00 ± 0.79c
‘Regal’	206 ± 6.17a	22.68 ± 0.91a	19.87 ± 0.70a
Significance	F = 47.4	F = 17.2	F = 17.8
	P < 0.001	P < 0.001	P < 0.001
European elms			
<i>U. carpiniifolia</i>	254 ± 7.62b	18.05 ± 0.72c	17.60 ± 0.83b
<i>U. elliptica</i>	335 ± 10.1c	20.87 ± 0.83d	20.68 ± 0.66b
<i>U. foliaceae</i>	221 ± 6.63a	17.96 ± 0.72d	16.51 ± 0.54ab
<i>U. glabra</i>	277 ± 8.31c	14.52 ± 0.58b	13.52 ± 0.70ab
<i>U. procera</i>	345 ± 10.4d	21.23 ± 0.85d	17.42 ± 0.47b
<i>U. sukczewii</i>	338 ± 10.1d	12.34 ± 0.49a	11.70 ± 0.95ab
Significance	F = 44.2	F = 30.6	F = 4.9
	P < 0.001	P < 0.001	P < 0.001
North American elms			
<i>U. alata</i>	218 ± 6.55c	26.44 ± 1.06a	23.63 ± 0.88b
<i>U. americana</i>	178 ± 5.33a	24.40 ± 0.98b	18.55 ± 0.74b
<i>U. serotina</i>	193 ± 5.79b	23.32 ± 0.93a	20.87 ± 0.69ab
<i>U. thomasii</i>	157 ± 4.72a	25.17 ± 1.01a	17.15 ± 0.74ab
Significance	F = 40.4	NS	F = 4.84
	P < 0.001		P = 0.005

²Values within a column followed by the same letter are not significantly different (P < 0.05, Dunn’s Test).

inner leaf toughness for all of the North American elms tested in this study, but outer leaf toughness for *U. alata* was significantly greater compared with *U. americana* and *U. thomasii* (F=4.8, P<0.005).

Elm leaf thickness, toughness, and susceptibility. Overall, the percent leaf tissue removed in the no-choice (NC) laboratory feeding studies was not correlated with leaf thickness (R=0.06, P=0.70), inner leaf toughness (R=0.25, P=0.13), or outer leaf toughness (R=0.22, P=0.18). Likewise, leaf thickness and inner and outer leaf toughness were not good predictors of the amount of dry frass pellet weight produced (thickness R=0.0, P=0.95, inner R=0.18, P=0.27, outer R=0.18, P=0.37).

Elm leaf thickness, toughness, and suitability. Leaf thickness for Asian elms and complex hybrids was not correlated with adult female fecundity (R=0.09, P=0.68), but fecundity was moderately related with both inner and outer leaf toughness for Asian elms (inner toughness, R=0.44, P=0.04, outer toughness, R=0.48, P=0.02) (i.e. the more tender the leaf, the more eggs that were laid). Conversely, fecundity was not related to leaf thickness or inner or outer leaf toughness for simple and complex Eurasian hybrids (leaf thickness, R=0.69, P=0.13, inner toughness, R=0.69, P=0.13, outer toughness, R=0.71, P=0.11), European taxa (thickness, R=0.53, P=0.29, inner toughness, R=0.27, P=0.61, outer toughness, R=0.21, P=0.69), or North American taxa (thickness, R=0.06,

Table 10. Leaf trichome density per mm² of leaf surface for Asian elm taxa.

Taxa ^z	Mean # of leaf trichomes per mm ² (±SE)
<i>U. chenmoui</i>	211 ± 10.1ab
<i>U. davidiana</i>	247 ± 12.6ab
<i>U. gausennii</i>	184 ± 9.7a
<i>U. glaucescens</i>	581 ± 30.2b
<i>U. glaucescens</i> var. <i>lasiocarpa</i>	147 ± 6.9a
<i>U. lamellosa</i>	512 ± 26.2b
<i>U. macrocarpa</i>	310 ± 18.2ab
<i>U. propinqua</i>	171 ± 8.8a
<i>U. propinqua</i> var. <i>suberosa</i>	486 ± 26.2b
<i>U. prunifolia</i>	187 ± 9.2a
<i>U. pseudopropinqua</i>	352 ± 17.6ab
Significance:	F=91.9, P<0.0001

^zValues within a column followed by the same letter are not significantly different (P<0.05, Dunn's Test).

P=0.93, inner toughness, R=0.68, P=0.21, outer toughness, R=0.18, P=0.78).

Elm leaf trichome density. A summary of trichome density per mm² of leaf surface, by taxon, is presented in Table 10. *Ulmus glaucescens*, *U. lamellosa*, and *U. propinqua* var. *suberosa* had significantly greater trichome density per mm² (581, 512, 486, respectively) compared with *U. gausennii*, *U. glaucescens* var. *lasiocarpa*, *U. propinqua*, and *U. prunifolia* with 184, 147, 171, 187 leaf trichomes per mm², respectively. The remaining taxa had intermediate leaf trichome density (F=91.9, P<0.0001) (Table 9).

Elm leaf trichome density and host susceptibility. Collectively, for the 11 pubescent Asian elms evaluated here, there was no significant difference in percent leaf tissue removed when adult beetles were feeding on leaves with leaf trichomes present or when trichomes were removed, and percent leaf tissue removed was not correlated with leaf trichome density (R=0.16, P=0.64). However, in single taxon, paired no-choice (NC) feeding studies, adult female beetles removed significantly more leaf tissue when trichomes were removed from leaves of *U. chenmoui* (t=215.3, P=0.03), *U. gausennii* (t=423.4, P<0.001), *U. glaucescens* var. *lasiocarpa* (t=230.0,

P=0.02), *U. lamellosa* (t=199.2, P=0.048), and *U. macrocarpa* (t=575.0, P<0.0001) (Table 11). There was no significant difference in percent leaf tissue removed for beetles feeding on *U. davidiana*, *U. propinqua*, *U. propinqua* var. *suberosa*, *U. prunifolia*, *U. pseudopropinqua* leaves with or without trichomes present (Table 11). Additionally, there was no significant difference in dry fecal pellet weights for all 11 taxa evaluated for beetles feeding on leaves with trichomes present or removed.

Effect of trichomes on host suitability. For all Asian elms evaluated in this study, with either glabrous or pubescent leaves, there was no significant difference in total eggs produced, (t=0.23, P=0.82), eggs produced per female (t=0.51, P=0.62), or eggs produced per ovipositing female (t=1.32, P=0.20) (Data not shown).

For these same 11 highly pubescent Asian elm taxa mentioned above, pubescence or lack thereof, did not have a significant effect on the total number of eggs laid for females feeding on leaves with trichomes present (440 eggs) or where trichomes had been removed (407 eggs) (t=0.227, P=0.82) or number of eggs per ovipositing female (t=1.32, P=0.20). However, there was a significant difference in the percentage of females ovipositing when feeding on leaves with trichomes present (46%) versus leaves with trichomes removed (74%) (t=3.31, P=0.003). There was no relationship between total eggs produced with leaf trichomes present (R=0.27, P=0.42) or without trichomes, (R=0.21, P=0.54), eggs per female with trichomes present (R=0.00, P=0.99) or without trichomes (R=0.05, P=0.89), percent females ovipositing with trichomes present (R=0.11, P=0.74), or eggs per ovipositing female with trichomes present (R=0.19, P=0.58) and without trichomes (R=0.02, P=0.95).

However, in the single paired taxon, no-choice (NC) feeding studies, adult female beetles laid significantly more eggs when feeding on *U. gausennii*, (t=12.1, P=0.0001), *U. propinqua* var. *suberosa* (t=24.3, P=0.0001), and *U. prunifolia* (t=16.4, P=0.0001) leaves where trichomes had been removed compared with leaves with trichomes present (Table 12). Conversely, adult beetles feeding on *U. davidiana* (t=10.7, P=0.001), *U. glaucescens*, (t=9.8, P=0.001), *U. lamellosa*, (t=6.6, P=0.008), *U. macrocarpa*, (t=7.2, P=0.004) and *U. propinqua* (t=7.6, P=0.005) laid

Table 11. Paired single taxon no-choice (NC) feeding (% leaf tissue removed) studies for adult female Japanese beetles feeding on pubescent Asian elms with leaf trichomes present and with trichomes removed.

Taxa	Mean percent leaf tissue removed ^z		Significance
	With trichomes (±SE)	Trichomes removed (±SE)	
<i>U. chenmoui</i>	64 ± 6.8a	84 ± 5.2b	t=215.3, P=0.03
<i>U. davidiana</i>	36 ± 6.8a	46 ± 7.0a	NS
<i>U. gausennii</i>	46 ± 7.8a	79 ± 6.3b	t=423.4, P<0.0001
<i>U. glaucescens</i>	31 ± 6.6b	17 ± 3.9a	t=4.2, P=0.0002
<i>U. glaucescens</i> var. <i>lasiocarpa</i>	12 ± 3.5a	33 ± 5.6b	t=230.0, P=0.02
<i>U. lamellosa</i>	16 ± 4.7a	31 ± 5.4b	t=199.0, P=0.048
<i>U. macrocarpa</i>	0 ± 0.0a	13 ± 2.4b	t=575.0, P<0.0001
<i>U. propinqua</i>	44 ± 6.7a	42 ± 7.1 a	NS
<i>U. propinqua</i> var. <i>suberosa</i>	39 ± 6.0a	29 ± 6.6a	NS
<i>U. prunifolia</i>	24 ± 5.6a	38 ± 5.9a	NS
<i>U. pseudopropinqua</i>	41 ± 6.5 a	54 ± 6.2a	NS

^zValues across rows followed by the same letter are not significantly (NS) different. (P<0.05, Student's t-test)

Table 12. Paired single taxon fecundity studies for adult female Japanese beetles feeding on pubescent Asian elms with leaf trichomes present and with trichomes removed.

Taxa ^z	Total eggs laid (±SE)		Significance ¹
	With trichomes	Trichomes removed	
<i>U. chenmoui</i>	52 ± 0.32a	54 ± 0.28a	NS
<i>U. davidiana</i>	42 ± 0.22b	11 ± 0.12 a	<i>t</i> =10.7, <i>P</i> =0.001
<i>U. gausseii</i>	17 ± 0.18a	31 ± 0.36b	<i>t</i> =12.1, <i>P</i> =0.0001
<i>U. glaucescens</i>	38 ± 0.41b	21 ± 0.19a	<i>t</i> =9.8, <i>P</i> =0.0001
<i>U. glaucescens</i> var. <i>lasiocarpa</i>	10 ± 0.10a	10 ± 0.10a	NS
<i>U. lamellosa</i>	82 ± 0.86 b	50 ± 0.31a	<i>t</i> =6.6, <i>P</i> =0.008
<i>U. macrocarpa</i>	71 ± 0.50 b	25 ± 0.21a	<i>t</i> =7.2, <i>P</i> =0.004
<i>U. propinqua</i>	75 ± 0.52b	34 ± 0.32 a	<i>t</i> =7.6, <i>P</i> =0.005
<i>U. propinqua</i> var. <i>suberosa</i>	59 ± 0.54a	99 ± 0.83b	<i>t</i> =24.3, <i>P</i> =0.0001
<i>U. prunifolia</i>	9 ± 0.08a	69 ± 0.61b	<i>t</i> =16.4, <i>P</i> =0.0001
<i>U. pseudopropinqua</i>	11 ± 0.12a	27 ± 0.30a	NS
<i>Sassafras albidum</i> (reference)	—	64 ± 0.35b	
Blank	—	1 ± 0.0a	

^zValues across rows followed by the same letter are not significantly (NS) different (*P*<0.05, Student's *t*-test).

significantly more eggs on leaves with trichomes present compared with leaves where trichomes were removed (Table 12). There was no significant difference in total eggs laid, for adult beetles feeding with or without trichomes present, on *U. chenmoui*, *U. glaucescens* var. *lasiocarpa*, and *U. pseudopropinqua*. Results from this study provide new insight into the relative susceptibility, preference, and suitability of *Ulmus* and *Zelkova* taxa for feeding and reproduction by adult Japanese beetles, and for their potential use in tree breeding programs. Leaf tissue chemical analysis, and its influence on host susceptibility, preference, and suitability, was beyond the scope of this study, and was not examined; however, we did attempt to examine, and will discuss possible physical plant traits (i.e. leaf thickness, toughness, and pubescence) of *Ulmus* and *Zelkova* leaves that affect relative host plant resistance to adult Japanese beetles.

Leaf thickness and toughness, and host susceptibility and preference. Physical plant traits, such as leaf toughness and thickness, can greatly influence invertebrate feeding and usually correlate with leaf fiber and lignin content (Graca and Zimmer 2005). Agrawal and Fishbein (2006) found leaf toughness could be used to predict herbivory of many plants including milkweeds (*Asclepias* spp.), and Raupp (1985) found that the toughness of willow (*Salix* spp.) leaves reduced leaf beetle feeding due to mandibular wear. In field defoliation trials, Bosu et al. (2007) observed that the thicker and tougher leaves of Asian elm taxa and taxa experienced much less defoliation by the elm leaf beetle (*Pyrrhalta luteola* Muller). Potter and Kimmerer (1988) found that the thick glabrous cuticle and tough leaf margins of the American holly (*Ilex opaca* Ait.) leaves were more important than leaf margin spines in deterring edge feeding caterpillars. Miller and Ware (2014), determined that the thicker and tougher leaves of most Asian elm taxa and hybrids were less susceptible to feeding by the elm leafminer (*Fenusa ulmi* Sundevall).

In earlier field defoliation studies and no-choice (NC), and multiple-choice (MC) laboratory bioassay feeding studies, evaluating Ulmaceae for feeding host susceptibility and preference for the Japanese beetle, Miller et al. (1999,

2001a), Condra et al. (2010), Potter and Redmond (2013), and Griffin et al. (2017) found that the thicker and tougher leaves of certain Asian elm species such as *U. parvifolia* and cultivars, *U. propinqua*, *U. lamellosa*, *U. macrocarpa*, *U. pseudopropinqua*, *U. prunifolia*, and *U. taihangshanensis* were much less susceptible to feeding by Japanese beetles. The complex Asian hybrids of ‘Accolade’, ‘Commendation’, ‘Danada Charm’, ‘Triumph’, and ‘Vanguard’ were more susceptible to feeding even though they had variable leaf thickness and toughness (Miller et al. 1999, Condra et al. 2010, Potter and Redmond 2013, Griffin et al. 2017). Miller, et al. (1999) found that the thicker leaves of *U. castaneifolia* were equally appealing as the thinner leaves of *U. gausseii*, *U. japonica*, and *U. szechuanica*.

Results from the ten-year national elm field trial revealed that ‘Homestead’ and ‘Pioneer’ had the highest Japanese feeding damage while *U. parvifolia*, *U. propinqua*, ‘Valley Forge’, ‘New Harmony’, ‘Prospector’, ‘New Horizon’, and ‘Frontier’ were the most resistant to Japanese feeding damage (Griffin et al. 2017). In this study, ‘Homestead’ and ‘Frontier’ had significantly thinner and more tender leaves compared to ‘Pioneer’, but all three taxa were much less preferred in the field study. However, in our multiple-choice (MC) studies, ‘Pioneer’ was more preferred, but ‘Homestead’ was one of the least preferred. Our results are also consistent with studies by Rowe and Potter (2000) who found that Japanese beetles fed the same on sun and shade leaves of rose (*Rosa variety floribunda* ‘Class Act’) of equal toughness as well as the thicker sun and thinner shade rose leaves. Similar conflicting results with regard to leaf thickness and toughness were reported by Keathley and Potter (2008) for both preferred and non-preferred hosts of Japanese beetle, and for *Carpinus* taxa by Miller and Wiegrefe (2021). It appears that in this study, leaf thickness and inner and outer leaf toughness are not good indicators of host susceptibility for Japanese beetle feeding.

Hybridization, susceptibility, preference, and suitability. Hybridization may have both a positive and/or negative influence on susceptibility, preference, and suitability for adult Japanese beetles and may be polygenic, and not the

result of a single gene expression (Paige and Capman 1993, Fritz et al. 1999, Cheng et al. 2011). It is well known that secondary metabolites are a common chemical defense employed by plants against herbivorous insects and hybridization may increase the variation of secondary metabolites affecting herbivore resistance (Patton et al. 1997, Fulcher et al. 1998, Orians 2000, Cheng et al. 2011). Most secondary metabolites (SMs) may be present in the parents, but hybrids may miss some parental SMs or have novel ones (Paige and Capman 1993, Cheng et al. 2011, Lopez-Caamal and Tovar-Sanchez 2014). In this study, *U. carpinifolia*, *U. pumila*, and members of the David (*U. davidiana*) complex (i.e. *U. japonica*, *U. wilsoniana*, *U. propinqua*) appear to either increase, decrease, and/or have no effect on feeding preference. For example, in the multiple-choice (MC) laboratory feeding bioassays and field defoliation studies, when a susceptible or preferred species such as *U. carpinifolia* or *U. pumila* is crossed with a much less susceptible or preferred species (i.e. *U. parvifolia* or *U. glabra*), the resulting hybrids of ‘Frontier’ and ‘Pioneer’ are more preferred. Further, when highly preferred *U. pumila* is crossed with *U. japonica*, preference increased for the ‘Sapporo Autumn Gold’ hybrid (*U. pumila* x *U. japonica*), but the opposite is also true for the *U. pumila* x *U. japonica* hybrids of ‘Cathedral’ and ‘New Horizon’ where preference decreased. However, in the case of ‘Homestead’ and ‘Urban elm’, both complex hybrids including *U. pumila*, *U. carpinifolia*, and *U. x hollandica* ‘Vegeta’ parentage, there was a reduction in preference. When *U. wilsoniana* is crossed with the less preferred *U. japonica* (i.e. ‘Accolade’, ‘Danada Charm’), there is no appreciable change in preference, but preference decreases when combined with *U. carpinifolia* and *U. pumila* parentage for ‘Commendation’. It appears that *U. carpinifolia* and *U. pumila* tend to increase preference in simple and complex elm hybrids, but members of the David elm (*U. davidiana*) complex (i.e. *U. wilsoniana* and *U. japonica*) tend to decrease preference.

The reason for this hybrid effect is not clear but is probably related to leaf chemistry and to a lesser extent, leaf pubescence. A similar phenomenon, the “*U. pumila* and *U. carpinifolia* factor” has been observed in elms (*Ulmus* spp.), where when Siberian elm (*U. pumila*) is incorporated into hybrids with other taxa it appears to affect the susceptibility, preference, and suitability of elms to an extensive defoliating insect guild including Japanese beetle, elm leaf beetle (*Pyrrhalta luteola*), spring cankerworm (*Paleacrita vernata* Peck), fall cankerworm (*Alsophila pometaria* Harris), and elm leafminer (*Fenusa ulmi*) (Miller and Ware 1994, 1997, 1999a, 2014, Miller et al. 1999, 2001a,b,c, 2014, Bosu et al. 2007, Bosu and Wagner 2007, Condra et al. 2010, Griffin et al. 2017).

Leaf thickness and toughness, and host suitability. There does not appear to be a clear relationship between leaf thickness and host suitability (i.e. fecundity). However, inner and outer leaf toughness was related to suitability. For example, adult female beetles feeding on the thicker leaves of *U. lamellosa*, *U. macrocarpa*, and *U. propinqua* laid significantly more eggs compared to female beetles feeding on the thinner leaves of *U. gausenii*, *U. japonica*,

and *U. szechuanica*. Keathley and Potter (2008) found that the fecundity of Japanese beetles feeding on the tougher leaves of susceptible Virginia creeper [*Parthenocissus quinquefolia* (L.) Planch] was comparable to *S. albidum*, a highly preferred host. Similarly, Miller and Wiegrefe (2021) determined that adult Japanese beetles feeding on the thicker leaves of *Carpinus caroliniana*, and the hybrids of *C. betulus* x *C. tschonoskii* and *C. caroliniana* x *C. betulus* laid a similar number of eggs as *S. albidum*. Keathley and Potter (2008) also reported that Japanese beetles feeding on the resistant, and thin leaves of *Cornus florida* L. laid far fewer eggs. In contrast, Miller and Wiegrefe (2021) found that beetles feeding on the thinner and more-tender *C. laxiflora* leaves were significantly more fecund, but in the same study, Japanese beetles feeding on the thinner and more-tender leaves of *C. japonica* and *C. cordata* laid fewer eggs. Conversely, in the same study by Miller and Wiegrefe (2021), adult beetles feeding on thicker and tougher leaves of *C. coreana*, *C. fargesii*, *C. turczaninari*, and the hybrids of *C. caroliniana* x *C. cordata*, *C. caroliniana* x *C. coreana*, and *C. caroliniana* x *C. orientalis* laid significantly fewer eggs. It appears that leaf characteristics (i.e. leaf chemistry) other than thickness and toughness are more important for determining suitability for adult Japanese beetles (Ladd 1986, Barbosa and Krischik 1987, Ladd 1988, Stamp and Harmon 1991, Fulcher et al. 1996, 1998, Keathley et al. 1999, Potter and Held 1999, Paluch et al. 2006).

Leaf trichomes and host susceptibility. While leaf trichomes may provide a general defense, the effect of pubescence may be positive, negative, or non-existent depending on the herbivore species, and can be influenced by genotype, the environment, leaf development stage, and previous feeding (Levin 1973, Roberts et al. 1979, Southwood 1986, Peter et al. 1995, Hare and Elle 2002, Bosu and Wagner 2007, Handley et al. 2005, Dalin et al. 2008, Kariyat et al. 2018). Trichomes may also help protect plants from insect herbivores specifically as it relates to feeding, growth, survival, and oviposition. Feeding may be negatively correlated with trichome density, but is generally considered a “soft weapon” in plant defense compared to other plant traits (Levin 1973, Potter et al. 1998, Miller and Ware 1999a, Miller 2000, Miller et al. 2001a,b,c, Dalin et al. 2008).

In this study, leaf trichome density does not appear to be a good indicator of feeding susceptibility. For example, of the 11 pubescent elm taxa evaluated in paired single taxon NC feeding studies, adult Japanese beetles removed significantly less leaf tissue on five taxa including *U. chenmoui*, *U. gausenii*, *U. glaucescens* var. *lasiophylla*, *U. lamellosa*, and *U. macrocarpa* where trichomes were present, but trichome densities ranged from 184 to 512 per mm² on *U. gausenii* and *U. lamellosa* leaves, respectively. Conversely, adult Japanese beetles feeding on *U. glaucescens* leaves removed significantly more leaf tissue on leaves with trichomes present compared with leaves where the trichomes had been removed ($t=4.2$, $P<0.0002$). Why this occurred is not clear. *Ulmus glaucescens* leaves have the highest density of trichomes (581 per mm²) compared with the other pubescent elm taxa, but adult Japanese beetles

removed significantly more leaf tissue from *U. glaucescens* leaves with trichomes present compared with leaves where the trichomes had been removed ($t=4.2$, $P<0.0002$). The leaves of *U. glaucescens* are significantly thinner and much less tough than the other pubescent elm taxa studied here which may allow for greater adult beetle feeding. Additionally, *U. glaucescens* leaves contain a combination of non-glandular and glandular trichomes, and it is possible that the glandular trichomes may act as a feeding attractant (Dalín and Bjorkman, 2003, Valkama et al. 2003, Ventrella and Marinho 2008) and/or the non-glandular trichomes found on *U. glaucescens* leaves do not serve as a significant feeding deterrent. Dalín et al. (2008) found that the leaf beetle (*Phratora vulgatissima*) was capable of removing non-glandular trichomes when feeding on willow (*Salix viminalis*) leaves. However, our findings here contradict a study by Miller et al. (1999), where they found *U. glaucescens* to have low susceptibility in NC laboratory feeding studies, and a low field defoliation rating. However, for the remaining six pubescent elm taxa, there was no significant difference in leaf tissue removed with respect to trichome density.

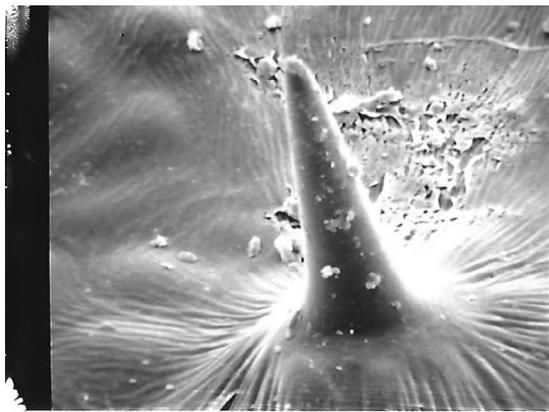
In a recent study, Miller and Wiegrefe (2021) found that the pubescent leaves of *Carpinus japonica* and *C. tschonoskii* differed in their suitability for adult Japanese beetles. Pubescent *C. tschonoskii* leaves, with trichomes present, were less susceptible, preferred, and suitable for feeding by adult Japanese beetles, pubescent *C. japonica* leaves were found to be highly susceptible and preferred for feeding but were less suitable for Japanese beetle reproduction. Additionally, 'Patriot' elm has pubescence on the underside of the leaf, and in NC feeding studies had significantly less leaf tissue removed by elm leaf beetles compared to 'Homestead' and 'American Liberty' (Townsend et al. 1995). However, in our study, feeding by adult Japanese beetles on 'Patriot', which has similar adult feeding habits to elm leaf beetle, was significantly higher in our NC studies. This suggests that leaf pubescence is not universal in preventing feeding by herbivorous insects. Our findings are consistent with a field study conducted by Condra et al. (2010), where they found that there was no overall relationship between Japanese beetle injury and elm leaf pubescence ratings, and their mean pubescence rating did not differ between their six most and least resistant elm taxa. Further study is required to determine these inconsistencies in feeding susceptibility preference, and suitability, and the role of leaf trichomes in host plant resistance.

Leaf trichome morphology and susceptibility. Plants have the ability to produce glandular (chemical-producing) and non-glandular trichomes. These trichomes may vary in the morphology and diversity among plant species, and even genetically within individual plant species (Southwood 1986, Agarwal 1999, 2000, Werker 2000, Dalín and Bjorkman 2003, Valkama et al. 2003, Ventrella and Marinho 2008). Non-glandular trichomes function in structural defense and have low nutritional value compared with glandular trichomes which may provide both structural and chemical defense and may contain terpenes and alkaloids that act as feeding deterrents or toxins (Levin 1973, Shade et al. 1979, Robinson et al. 1980, Rautio et al.

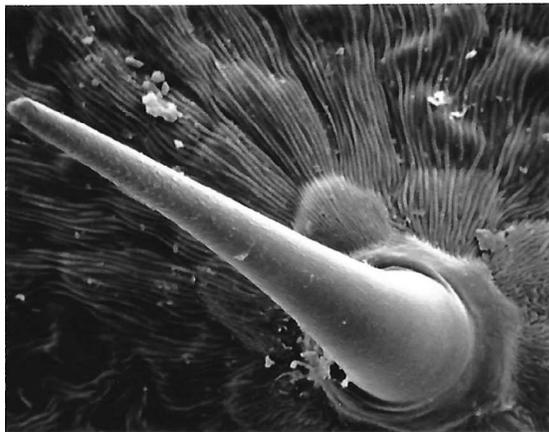
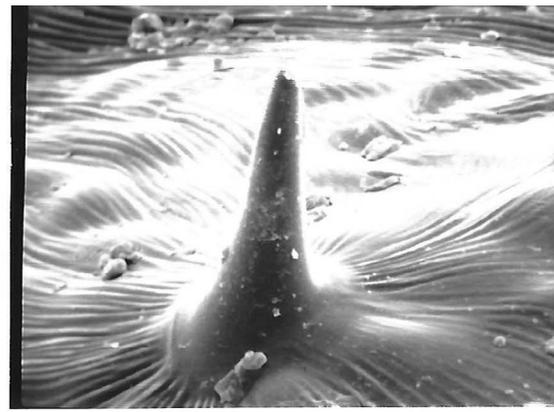
2002, Valkama et al. 2003, Ventrella and Rarinho 2008, War et al. 2012). Many studies have demonstrated that the presence of simple and glandular trichomes may deter or impede feeding susceptibility, preference, and/or oviposition by leaf-feeding beetles such as the alfalfa weevil (Danielson 1987), alfalfa blotch leafminer (MacLean and Byers 1983), blackvine weevil (Doss et al. 1987), Colorado potato beetle (Casagrande 1982), cereal leaf beetle (Hoxie et al. 1975) and Japanese beetle (Potter et al. 1998, Miller and Ware 1999a, Miller 2000 Miller et al. 2001b, Held 2004, Condra et al. 2010, Miller and Wiegrefe 2021). In the aforementioned Japanese beetle studies, leaves of *Tilia*, *Ulmus*, and *Carpinus* taxa with thick trichome mats, long upright hairs, and moderate to dense leaf pubescence had less leaf area consumed compared to more glabrous leaves or leaves with very sparse trichome density.

While not thoroughly examined in this study, trichome morphological traits (i.e. simple or glandular, and length) may also be a factor in attracting the herbivore to the host plant and for oviposition (Lill et al. 2006). For example, certain wheat varieties with long, erect trichomes deter leaf-beetle oviposition much more than varieties with a sparse growth of short trichomes (Hoxie et al. 1975, Roberts et al. 1979). Some glandular trichomes emit adhesives, resins, and/or mixtures of aldehydes, alkanes, and esters entrapping and/or killing the herbivorous insect (Webb et al. 1971, Schalk and Stoner 1976, Kennedy and Yamamoto 1979, Johnson et al. 1980a,b, Ryan et al. 1982, Tingey and Laubengayer 1986, Yencho and Tingey 1994). Simple trichome morphology may demonstrate antibiotic effects contributing to host plant resistance. Hooked trichomes can impale young leafhopper nymphs, puncture eggs of leaf feeding beetles, and impair movement of young leaf feeding caterpillars (Pillemer and Tingey 1976, Wellso, 1979, Ramalho et al. 1984). Conversely, trichomes may also play a role in attracting herbivores to the host plant (Southwood 1986).

Electron microscopy and observations by the authors of leaf trichomes on the abaxial (lower) and adaxial (upper) leaf surfaces of the elm taxa of *U. chenmoui*, *U. glaucescens*, *U. lamellosa*, *U. macrocarpa*, and *U. propinqua* revealed some interesting contrasts (Figures 1a,b,c,d and 2 a,b,c,d). For example, adult Japanese beetles removed the greatest amount of leaf tissue from *U. chenmoui* leaves when trichomes were present. In a study by Miller et al. (1999), *U. chenmoui* was found to be highly susceptible and preferred by Japanese beetles. Trichomes on the lower leaf surface of *U. chenmoui* are of medium density, uneven length, and not all are upright. On the upper leaf surface, trichomes are scattered with bulbous bases, some curving and of uneven lengths. Trichomes on the lower leaf surface of *U. glaucescens* (Figures 1d, 2d) and upper leaf surface of *U. propinqua* (Figure 1c) are very dense and thick, fine, straight, and of even length, with some curvature on the upper leaf surface. In this study, *U. glaucescens* and *U. propinqua* had moderate amounts of leaf tissue removed which is consistent with a study by Miller et al. (1999) where both taxa were moderately susceptible and more preferred. In contrast, the leaf trichomes on the lower and upper surfaces (Figures 2 a,



U. glaucescens 60X



U. glaucescens both surfaces 1,510X

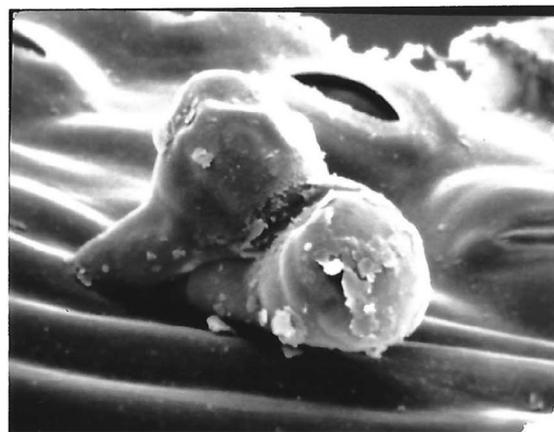


Fig. 1a, b, c, d. Elm leaf trichomes. a. (upper left) *U. lamellosa*, upper surface (840X), b. (upper right) *U. glaucescens*, upper surface (60X), c. (lower left) *U. propinqua*, upper surface (620X), d. (lower right) *U. glaucescens*, lower surface (1,510X).

c) of *U. macrocarpa* are of medium density, but have a bulbous base which may suggest they are glandular, and possess feeding deterrent chemicals making the leaf less palatable. This is evidenced in our study by minimal leaf feeding by adult Japanese beetles on *U. macrocarpa* leaves when trichomes are present, and is consistent with a study by Miller et al. (1999) where they found *U. macrocarpa* was not susceptible to feeding or preferred by Japanese beetles. The trichomes on *U. lamellosa* leaves are scattered and many tend to be broken off during the growing season, giving the leaves a very rough or sandpapery feel (author's personal observations) (Figures 1a, 2b). This sandpapery feel may account for the lower level of feeding in this study, and in a study by Miller et al. (1999), for adult feeding susceptibility and preference. Additionally, Miller and McMahan (in press) found that the "sandpapery" upper leaf surface of *Fraxinus chinensis* was less susceptible to feeding the adult emerald ash borer (*Agilus planipennis*).

Leaf trichome morphology and suitability. The relationship between trichome density and morphology, and host suitability is unclear. Collectively, of the 11 pubescent Asian elms evaluated in this study, there was no significant difference in total eggs laid, eggs produced per female, or eggs produced per ovipositing female (Data not shown). However, a significantly higher percentage of females oviposited when feeding on leaves with the trichomes

removed compared with leaves with trichomes present (Data not shown). It is possible that trichome morphology (simple vs. glandular) may be a factor in host suitability (Peter et al. 1995). Adult female Japanese beetles feeding on the long, thin, and fine trichomes of *U. chinmoui*, laid a similar number of eggs compared with leaves where the trichomes had been removed. Further, adult females laid significantly more eggs when feeding on *U. glaucescens* and *U. propinqua* leaves, both with similar trichome structure and lacking glandular trichomes, than on leaves where the trichomes had been removed. Conversely, trichome morphology differed considerably between *U. lamellosa* and *U. macrocarpa* leaves, but adult female beetles laid significantly more eggs when feeding on *U. macrocarpa* leaves with bulbous (i.e. glandular) trichomes present, and on *U. lamellosa* with short, but simple trichomes. While glandular trichomes are generally considered to possess feeding deterrent chemicals, it possible that they may exude chemicals that enhance their suitability for certain herbivorous insects such as the Japanese beetle (Southwood 1986). Further studies are needed to better understand the relationship between trichome morphology, and chemistry, and their role(s) in host susceptibility, preference, and suitability for the Japanese beetle, and other herbivorous insect pests.

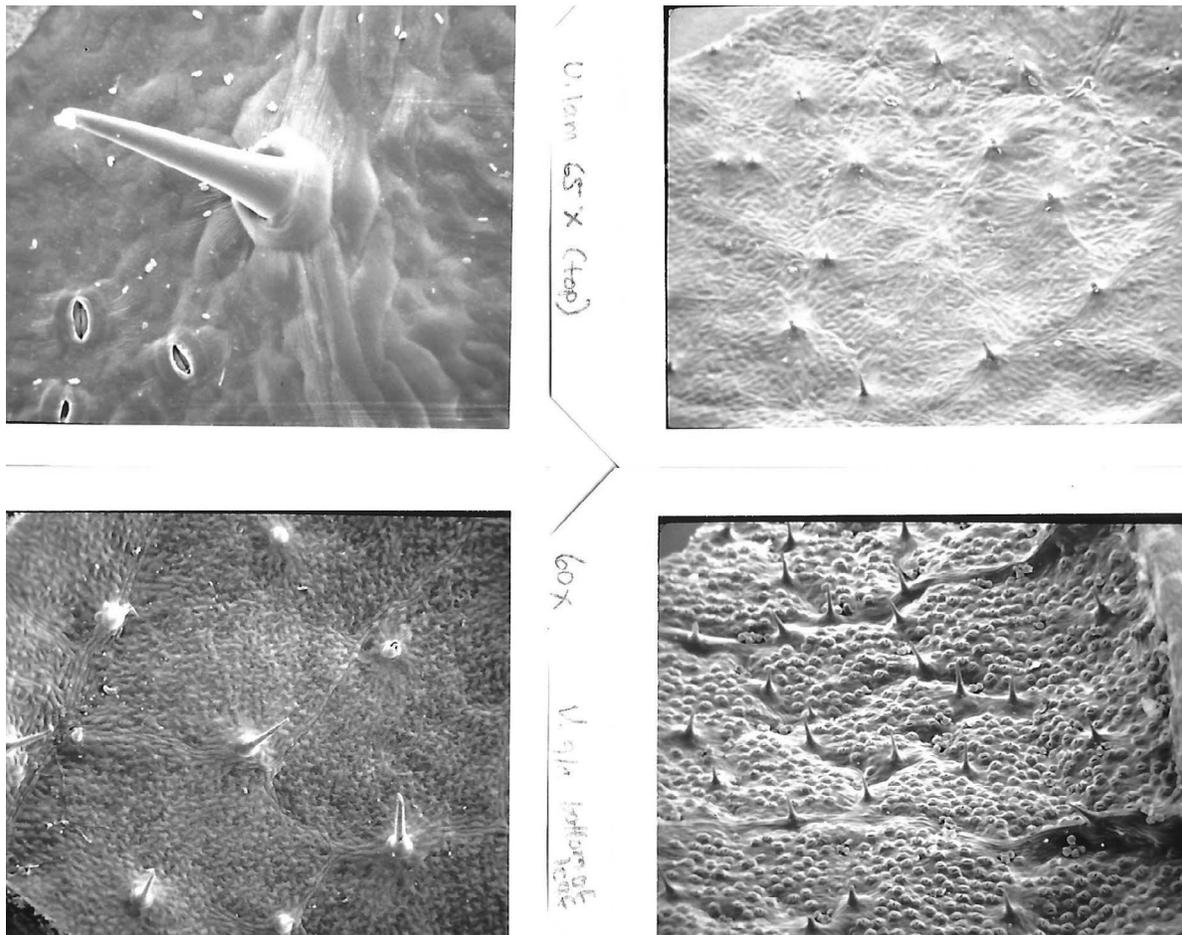


Fig. 2a,b,c,d. Elm leaf trichomes. a. (upper left) *U. macrocarpa*, lower surface (430X), b. (upper right) *U. lamellosa*, upper surface (65X), c. (lower left) *U. macrocarpa*, upper surface (63X), d. (lower right) *U. glaucescens*, lower surface (60X).

In conclusion, the complex Asian hybrids of ‘Accolade’, ‘Commendation’, ‘Danada Charm’, ‘Triumph’, ‘Vanguard’, the simple and complex Eurasian hybrids of ‘Homestead’, ‘Prospector’, and ‘Cathedral’, and recently developed American elm cultivars (i.e. ‘Valley Forge’, ‘Jefferson’, ‘New Harmony’) are already in the trade, and are performing well as parkway and landscape trees due to their resistance to DED, and/or elm yellows, and most sap-feeding and leaf-feeding insect pests (Santamour and Bentz 1985, Smalley and Guries 1993, Sinclair et al. 2000, Jacobs et al. 2003, Costello et al. 2004, Bosu et al. 2007, Herath et al. 2010, Griffin et al. 2017). However, there may be some use limitations for some of the above taxa in settings with chronic and/or heavy elm leaf beetle, elm leafminer, and elm flea weevil (*Orchestes ulmi*) populations (Guries and Smalley, 1994, Miller, 2000, Miller and Ware 2001a,b,c,d 2014, Miller et al. 2003, Condra et al. 2010, Potter and Redmond 2013, Griffins et al. 2017). Elm selection should be based on hardiness zones, growth characteristics, and tempered with regard to resistance and/or tolerance to local insect and disease pressure when planning for future urban tree plantings

Ulmaceae taxa evaluated in this study, including *U. parvifolia* and cultivars, members of the David elm complex (i.e. *U. japonica*, *U. wilsoniana*, *U. propinqua*), North American taxa of *U. rubra* and *U. serotina*,

European taxa including *U. suberosa* and *U. sukaczewii*, and certain *Zelkova* taxa and cultivars, should be considered in future tree breeding efforts because of their desirable horticultural attributes, their ability to tolerate harsh urban growing conditions, their resistance to DED, and feeding damage by herbivorous insect pests, particularly where chronic Japanese beetle populations are sporadic or absent (Ware 1992, 1995, Miller et al. 1999, 2001, Warren 2000, Hartman et al. 2007, Brady et al. 2008, McPherson et al. 2008, Dirr 2009, Condra et al. 2010, Giblin and Gilman 2010, Potter and Redmond 2013, Griffin et al. 2017). More research is needed to better identify the physical and chemical factors involved with Ulmaceae host plant resistance, and how these factors might be incorporated into a more comprehensive tree breeding program.

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