Palatability and Suitability of the Ulmaceae for Spongy Moth Larval Development (Lepidoptera: Lymantriidae)[1]

Fredric Miller[2]* and **George Ware**[3]

Abstract

Fifty-nine *Ulmus* taxa, varieties, and cultivars and six *Zelkova* taxa and cultivars were evaluated in no-choice (NC) and multiple-choice (MC) laboratory feeding bioassays for suitability and preference for spongy moth larvae (*Lymantria dispar* L.). *Ulmus* 'Morton Stalwart'-Commendation™, *U.* 'Morton Red Tip'-Danada Charm™, 'Frontier', 'Homestead', 'Regal', and *U. elliptica* were found to be the most suitable (suitability ratios of > 0.90). *Ulmus gausennii*, and *U. carpinifolia* were the least suitable (suitability ratio < 0.5). The remaining *Ulmus* and *Zelkova* taxa were either unsuitable (i.e. larvae failed to pupate) or were moderately suitable (suitability ratios 0.54 to 0.86). Dry frass weight was a moderate predictor of larval longevity. Feeding preference was moderately correlated with larval longevity and percent larval survival. Leaf thickness and toughness does not appear to affect larval survival, pupal fresh weight, or frass production. Asian elm leaves possess both glandular and straight trichomes but they did not affect larval suitability. Hybridization significantly affected host susceptibility and appears to contribute to an "*U. pumila* and *U. carpinifolia* factor" for host preference, susceptibility, and suitability. There appears to be a rich pool of *Ulmus* and *Zelkova* taxa for potential use in future tree breeding programs.

Species used in this study: *Lymantria dispar* L; *Malus sylvestris* Mill.; *Quercus palustris* Munchh.; *Ulmus alata* Michx.; *U. americana* L.; *U. bergmaniana* C.K.Schneid.; *U. carpinifolia* Gled;, *U. castaneifolia* Hemsl.; *U. chenmoui* Cheng; *U. crassifolia* Nutt.; *U. davidiana* Planch.; *U. elliptica* K.Koch.; *U. foliaceae* Gilbert; *U. gaussenii* Cheng; *U. glabra* Hudson; *U. glaucescens* Franch.; *U–. glaucescens* Franch. var. *lasiocarpa* Rehd.; *U. japonica* Sarg.; *U. laevis* Pall.; *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.; Henry; *U. prunifolia* Cheng et L.K. Fu; *U. pseudopropinqua* Wang et Li; *U. pumila* L.; *U. serotina* Sarg.; *U. sukaczevii* Andr.; *U. szechuanica* Fang; *U. taihangshanensis,* S.Y. Wang; *U. thomasii* Sarg.; *U. wilsoniana* Schneid.; *Zelkova serrata* (Thunb.) Mak.; *Z. carpinifolia* (Pall.) K. Koch.; *Z. schneideriana* Hand.-Mazz,; *Z. sinica* C.K. Schneid.

Index words: Host plant resistance, *Lymantria dispar*, preference, suitability, *Ulmus*, *Zelkova*.

Significance to the Horticulture Industry

Fifty-nine *Ulmus* and six *Zelkova* taxa, varieties, and cultivars were evaluated for suitability and preference for spongy moth (*Lymantria dispar*) larvae. *Ulmus* 'Morton Stalwart'-Commendation™ and *U.* 'Morton Red Tip'-Danada Charm™, 'Frontier', 'Homestead', 'Regal', and *U. elliptica* were the most suitable for spongy moth larval development and pupation. *Ulmus gausennii*, and European elm *U. carpinifolia* were the least suitable. The remaining *Ulmus* and *Zelkova* taxa were either unsuitable (i.e. larvae failed to pupate) or were intermediate in suitability for larval development. Physical leaf characteristics (i.e. leaf thickness and toughness) differed by geographic origin with Asian and European elm leaves thicker than North American elms, and Asian elm leaves tougher than European and North American elm leaves. Overall, leaf thickness and toughness were related, but did not appear to affect larval survival, pupal fresh weight, or dry frass production. Additionally, Asian elm leaves appear to possess both glandular and straight trichomes, but their presence did not affect larval suitability. Hybridization appears to contribute to an '*U. pumila* and *U. carpinifolia* factor' which significantly affected host suitability and preference. Results reported here, suggest there is a rich pool of *Ulmus* and *Zelkova* taxa for use in tree breeding programs in order to develop resistant trees to invasive lethal insect pests such as Asian long-horned beetle (ALB) [*Anoplophora glabripennis* (Motschulsky, 1853)], emerald ash borer (EAB) (*Agrilus lanipennis* Fairmaire, 1888), and diseases including Dutch elm disease (DED) (*Ophiostoma* spp.), and elm yellows (*Candidatus Phytoplasma ulmi*) for use in landscapes and urban reforestation efforts, 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 in the mid-19th century, the spongy moth (*Lymantria dispar,* L.) (Lepidoptera: Lymantriidae) is still considered one of the most destructive and persistent pest of nursery crops, landscape plants, and rural and urban forest trees. Spongy moth larvae feed on over 500 woody plant species (Forbush and Fernald 1896, Liebhold et al. 1995), preferring oaks (*Quercus* spp.) (Barbosa and Krischik 1987), and certain other hardwood species (Elkinton and Liebhold 1990, Shields, et al. 2003).

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[2] Senior Scientist, Entomology, The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL 60532.

[3] Research Associate (Deceased), Dendrology, The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL 60532.

*Corresponding author email: fmento84@gmail.com.

Chronic defoliation can lead to trees that may be predisposed to abiotic factors such as drought, and biotic factors including lethal secondary wood-boring insects and pathogens, for example, the two-lined chestnut borer (*Agrilus bilineatus*) Weber) and pathogens such as *Armillaria* root rot [*Armillaria mellea,* (Vahl) P. Kumm]. Common to most woody landscape and forest trees, host plant resistance for *L. dispar* has historically been compiled from anecdotal field studies and observations (Forbush and Fernald 1896, Mosher 1915) and while helpful, these studies require some level of interpretation as for host susceptibility, preference, and suitability. More recently, Liebhold et al. (1995) ranked over 600 North American angiosperm and gymnosperm tree species as to their susceptibility to the spongy moth based on previous field and laboratory tests. These susceptibility and suitability rankings were based on spongy moth defoliation, larval abundance, growth and survival, larval foliage preference, pupal weights, and ratio of pupal weight on the host to the pupal weight on white oak (*Q. alba* L.) (standard host) (Liebhold et al. 1995). Concurrently, extensive studies have focused on the relative susceptibility and suitability of oaks (*Quercus* spp.) because of the importance of the genus in the ecology and sustainability of eastern and mid-western North American and European forests (Barbosa and Capinera 1977, Barbosa and Greenblatt 1979, Barbosa et al. 1983, Lechowicz and Jobin 1983, Lechowicz and Mauffette 1986, Mauffette et al. 1983, Miller and Hanson 1989a,b, Montgomery 1991, Miller et al. 1991, Davidson et al. 1999, Foss and Rieske 2003, Rieske et al. 2003, Shields et al. 2003, Miller 2008, Milanovic et al. 2014). However, of the over 600 tree species listed in Liebhold et al. (1995), only *U. americana* and *U. parvifolia* are listed with suitability rankings of 2 and 1, respectively, and no rankings are provided for *Zelkova* taxa.

In recent years, a wide variety of Asiatic woody plant species, including *Ulmus* and *Zelkova* taxa, has been discovered and developed for possible use in tree breeding programs and for increasing plant diversity in urban forests and landscapes (Ware 1992, 1995). With the recent loss of millions of North American ash (*Fraxinus* spp.) trees to the emerald ash borer (EAB) (*Agrilus planipennis,* Fairmaire), and maples (*Acer* spp.) and other hardwoods to the Asian long-horned beetle (ALB) [*Anoplophora glabripennis* (Motschulsky, 1853)], there is an important and critical need for the development, and availability of new urban tree species for replanting in EAB and/or ALB affected areas, and to minimize the economic impact on communities and municipalities for the need for chemical protection from spongy moth defoliation (Poland and McCullough 2006, Raupp et al. 2006, Sydnor et al. 2007, Kovacs et al. 2010, Sadof et al. 2011, Vannatta et al. 2012, Hauer and Peterson 2017, Herms et al. 2019). With the exception of the aforementioned North American species of *U. americana* and the Asian species of *U. parvifolia* (Liebhold et al. 1995), to the best of our knowledge, no comprehensive studies have been conducted on the relative suitability and preference of recently acquired and developed *Ulmus* and *Zelkova* taxa of North American, Eurasian, and Asian parentage for spongy moth development and reproduction. Here, we report the results of a series of no-choice (NC) and multiple-choice (MC) laboratory feeding bioassays to determine the relative feeding suitability and preference of *Ulmus* and *Zelkova* taxa for spongy moth larval development and reproduction. Results from this study will contribute to the use of existing and additional *Ulmus* and *Zelkova* taxa in landscape and urban forest plantings, which will minimize the need for application of chemical insecticides, and contribute to more diverse landscapes and urban forest settings.

Materials and Methods

No-Choice (NC) laboratory larval feeding trials (Suitability). No-choice (NC) larval laboratory feeding trials were conducted using newly hatched first instar larvae as previously described by Miller and Wiegrefe (2021). Fifty-nine different elm taxa were evaluated for relative resistance to larval feeding (refer to Table 1 for a listing of *Ulmus* and *Zelkova* taxa, hybrids, varieties, and cultivars tested). Candidate elms are growing at The Morton Arboretum, Lisle, IL, and ranged from a height of 3 to 10 m (9.8 – 32.8 ft) with a diameter at breast height (dbh) (1.37 m) of 5 to 20 cm (1.9 – 7.9 in).

Leaves for the laboratory bioassays were randomly collected from ground level from the canopy of the tree at all four cardinal directions. The leaf samples included the terminal 15 cm (5.9 in) of branches. Samples consisted of an equal portion of actively growing and senescent foliage for each tree. Only fully expanded leaves were used. Leaf samples were taken in this way to compensate for leaf quality within trees. Leaf samples were held in cold storage in plastic bags at 5 C (41 F) for a maximum of 2 days. Leaves collected from each test tree were combined for the laboratory bioassays. Three individual trees (replicates) of each taxon were evaluated. *Malus sylvestris* and *Quercus palustris*, both highly preferred hosts of the spongy moth (*L. dispar*), served as reference species.

Newly emerged first and second instar spongy moth larvae were used in the no-choice (NC) and multiple-choice (MC) feeding trials, and were reared from overwintering egg masses collected from infested trees on the grounds of The Morton Arboretum, Lisle, IL. Upon collection, the eggs masses were placed in brown kraft paper bags, and held in a refrigerator at approximately 40 F until needed. In early May, the egg masses were placed in an incubator under a photoperiod of 16:8 (L:D) hour at approximately 25 C (77 F). Upon hatching, each larva was randomly selected and one larva each was placed in each of 10 snap-cap plastic vials (2.5 cm × 7.5 cm) (1 in × 3 in) with foliage from the test taxon. The vials were examined daily for larval mortality, evidence of feeding, and pupation. Foliage was replaced every 2 days. Vials were placed in plastic trays, and were held in an incubator under a photoperiod of 16:8 (L:D) hour at approximately 25 C (77 F). Each of the three trees (replicates) of each taxon was assayed with 10 individual larvae for a total of 30 spongy moth larvae per taxon. The bioassay for a given larva was terminated at adult emergence. Larval longevity was defined as the difference in days from the date the larva was introduced to the foliage until death or pre-pupation. At the time of pupation (within 12 hr), each individual

Table 1. Ulmaceae evaluated in no-choice (NC) and multiple-choice (MC) feeding trials for suitability for spongy moth larval development and fecundity, and feeding preference.

Taxa, Hybrid, Variety or Cultivar Asian taxa, hybrids, cultivars, and varieties	Parentage
U. bergmaniana	
U. bergmaniana var. *lasiophylla*	
U. chenmoui	
U. davidiana	
U. davidiana × 'Accolade'	
U. davidiana × *U. japonica-wilsoniana-pumila* ('Leatherleaf')	
U. gaussenii	
U. elongate	
U. glaucescens	
U. glaucescens var. *lasiophylla*	
U. japonica	
'New Horizon'	*U. japonica* × *U. pumila*
U. laciniata	
U. laciniata var.nikoense	
U. lamellosa	
U. macrocarpa	
U. multinervis (syn. *U. castaneifolia*)	
U. parvifolia	
U. propinqua	
U. propinqua var. suberosa	
U. prunifolia	
U. pseudopropinqua	
U. pumila	
'Sapporo Autumn Gold'	*U. pumila* × *U. japonica*
U. szechuanica	*U. pumila* × *U. japonica*
U. szechuanica × *U. japonica*	
U. taihangshensis	
U. wilsoniana	
Simple and complex Eurasian elm hybrids	
'Frontier'	*U. carpinifolia* × *U. parvifolia*
'Homestead'	*U. pumila* × (*U* × *hollandica* 'Vegeta' × *U. carpinifolia*) × *U. pumila-pinnato-ramosa* × *U. carpinifolia* 'Hoersholmiensis'
'Pioneer'	*U. glabra* × *U. carpinifolia*
'Regal'	(*U.* × *hollandica* 'Vegeta' × *U. carpinifolia*) × (*U. pumila* × *U. carpinifolia* 'Hoersholmiensis')
'Patriot'	
'Urban Elm' × *U. wilsoniana* 'Prospector'	
'Prospector'	*U. wilsoniana*
'Urban Elm'	N-148 *U.* × *hollandica* 'Vegeta' × *U. carpinifolia* × *U. pumila*
'Morton'Accolade	*U. japonica* × *U. wilsoniana*
'Morton Stalwart' Commendation	*U. carpinifolia* × *U. pumila* × *U. wilsoniana*
'Morton Red Tip' Danada Charm	*U. japonica* × *U. wilsoniana*
'Morton Glossy' Triumph	*U. pumila* × *U. japonica* × *U. wilsoniana*
'Morton Plainsman' Vanguard	*U. pumila* × *U. japonica*
'Accolade' × *U. japonica*	(*U. japonica* × *U. wilsoniana*) × *U. japonica*
'Accolade' × *U. pumila*	(*U. japonica* × *U. wilsoniana*) × *U. pumila*
'Vanguard' × *U. davidiana*	(*U. pumila* × *U. japonica*) × *U. davidiana*
'Vanguard' × *U. japonica-wilsoniana-pumila*	(*U. pumila* × *U. japonica*) × *U. japonica* × *U. wilsoniana* × *U. pumila*
North American elm taxa and cultivars	
U. alata	
U. crassifolia	
U. serotina	
U. thomasii	
'Jefferson'	*U. americana*
'Liberty'	*U. americana*
European elm taxa	
U. carpinifolia	
U. elliptica	
U. foliaceae	
U. glabra	
U. microcarpa	
U. procera	
U. sukaczevii	
***Zelkova* taxa and cultivars**	
Zelkova carpinifolia	
Z. schneideriana	
Z. serrata	
Z. serrata 'Green Vase'	
Z. serrata 'Village Green'	
Z. sinica	
Reference Taxa	
Malus sp.	
Quercus palustris	

pupa was weighed (nearest 0.01 g) to obtain the pupal fresh weight. The proportion of larvae reaching pupation was calculated by recording each larva that pupated in each petri dish within a given taxon for all three single tree replicates. At the termination of the no-choice (NC) larval feeding trial, the remaining leaf tissue in each petri dish was removed leaving only the fecal pellets. Fecal pellets were dried in an oven at 50 C (122F) and then weighed (nearest 0.1 mg).

Multiple-Choice (MC) (Preference) laboratory larval feeding trials. As previously described by Miller and Wiegrefe (2021), ten first instar spongy moth larvae were placed into each of 10 plastic petri dishes (0.6 cm × 15.0 cm) (0.24 in by 6.0 in). Each petri dish served as a replicate. A total of nine studies were conducted. Depending on the study, two to four leaf discs (2.54 cm diameter), with each disc representing one each of the different elm taxon choices, were placed into each dish and randomly arranged around the perimeter. Within each dish, the larvae had equal access to all foliage discs. The petri dishes were placed in clear plastic bags to prevent drying of the leaf discs and were held in an incubator under a photoperiod of 16:8 (L:D) hour ∼25 C (77 F). Condensation of water on the lid of the petri dish indicated a high relative humidity. The dishes were examined daily for 3 days. Each day, the foliage discs were removed from the dishes, replaced, and visually evaluated using a defoliation template for the proportion of leaf tissue removed by larval feeding. New foliage discs were arranged randomly around the perimeter of each dish to eliminate possible bias.

Measuring elm leaf thickness and toughness (Suitability). As previously described by Miller and Ware (2022), prior to using the leaves for the NC laboratory feeding trials, 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^{TM} 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 suitability and preference. Suitability of each taxon for spongy moth larvae was defined by larval longevity, percent larval survival, percent of larvae pupating, pupal fresh weight, percent adult emergence, and dried fecal pellet weight in the no-choice (NC) larval feeding trials. Preference was measured using the percent of leaf tissue removed in the multiple-choice (MC) larval feeding trials. The male and female suitability ratio was calculated as the quotient of the MPW and FPW for each respective *Ulmus* taxon over the MPW and FPW of the reference taxon, *Q. palustris,* respectively. Male and female suitability rankings were defined using the following scale: suitability ranking 1 > 0.9; 2 > 0.5 to 0.9; 3 < 0.5 (Liebhold, et al. 1995, Miller and Hanson 1989a,b).

Statistical analysis. Measures of suitability and preference were subjected to analysis of variance (ANOVA) by using taxon as the main effect. The percent of larvae pupating was arcsin transformed before analysis to correct for non-normality. Means of significant effect (5%) were compared with Dunn's test. A coefficient of correlation was calculated for the rankings for larval development time with larval longevity, proportion of larvae pupating, pupal fresh weights, percent adult emergence, and fecal pellet weights. All data are presented as original means ± SEM. Data were analyzed using Jandel Scientific (1992).

Results and Discussion

No-Choice (NC) laboratory larval feeding trials (Suitability). A summary of the suitability of *Ulmus* and *Zelkova* taxa for spongy moth larval longevity and dry frass weight is presented in Table 2 for larvae that did not reach pupation, and in Table 3 for larval longevity (days), percent male and female larval survival to pupation, percent pupation and adult male and female emergence, pupal fresh weights, and dry frass weight.

Spongy moth larvae not pupating. Averaged across all 59 *Ulmus* species tested in this study, *s*pongy moth larvae lived a mean of six days (range=3-12 days), and no larvae pupated when feeding on 66% of *Ulmus* taxa (Table 2); two exceptions being larvae feeding on 'Accolade' (3% larval survival), and the European species, *U. microcarpa* (5% of larval survival), but none of the larvae pupated (data not shown). Additionally, averaged across all six *Zelkova* taxa tested, spongy moth larvae feeding on these taxa lived a mean of four days (range=3-4 days), and none reach pupation (Table 2). Our results are consistent with a study by Miller and Hanson (1989a,b) who found that 1st instar spongy moth larvae feeding on *Z. serrata* died, and 2nd instars developed into pre-pupae, but then died.

Dry frass weights. Consistent with other suitability measures, larvae that lived the longest on highly suitable hosts (i.e. 'Commendation', 'Danada Charm') produced significantly greater dry frass weights (F=86.7, P<0.001) compared with all of the remaining *Ulmus* taxa. The reverse was also true. Dry frass weights for the highly preferred standards of *M. sylvestris* and *Q. palustris* were 2,188 g and 1,498 g, respectively. Dry frass weight was a moderate predictor of larval longevity (R=0.53, P<0.001) (Tables 2 and 3).

Spongy moth larval longevity and percent larval survival to pupation. Larvae lived significantly longer (F=8.6; P<0.001) (mean=28 days; range=20-35 days) when feeding on the simple and complex hybrids of 'Frontier', 'Pioneer', 'Regal', 'Urban' elm; the North American cultivar, *U. americana* 'Liberty'; and European taxa of *U. elliptica, U. foliaceae*, and *U. sukaczevii* compared with larvae feeding on the remaining *Ulmus* taxa and living less than 11 days. Larvae feeding on *U. gausennii*, 'Homestead', 'Vanguard', *U. carpinifolia*, and *U. procera* lived an intermediate number of days (mean= 16 days; range=14-18 days) (Table 3). Significantly more male and female larvae survived to pupation when feeding on *U. gaussennii*, 'Triumph', *U. carpinifolia*, *U. procera*, and *U. sukaczevii* compared with the

Table 2. Suitability (±SE) of Ulmaceae for spongy moth larvae that failed to complete development and did not pupate^{z}.

Taxa	Larval longevity (±SE) (days)^{y}	Dry frass weight (±SE) (mg)
Asian Elm Taxa, Varieties, and Hybrids		
U. bergmanniana	5±1.05a	1.0±0.0a
U. bergmanniana var. *lasiophylla*	8±1.59a	34.8±0.02ab
U. castaneifolia	6±0.92a	7.0±0.08a
U. chenmoui	4±0.47a	0.0a
U. davidiana	5±1.38a	0.0a
U. davidiana × 'Accolade'	10±2.13a	69.1±0.11b
U. davidiana × *U. japonica*	9±1.80a	7.0±0.05a
U. davidiana × *U. propinqua*	5±0.47a	0.0a
U. davidiana × *U. japonica-wilsoniana-pumila* ('Leatherleaf')	3±0.16a	0.0a
U. elongata	4±1.55a	0.0a
U. glaucescens	4±0.30a	0.0a
U. glaucescens var. *lasiophylla*	2±0.00a	0.0a
U. japonica	4±2.22a	0.0a
U. japonica × *U. pumila* 'New Horizon'	4±0.50a	0.0a
U. laciniata var. *nikkoense*	8±1.65a	2.5±0.02a
U. macrocarpa	4±0.44a	0.0a
U. multinervis (syn. *U. castanefiolia*)	3±0.15a	0.0a
U. parvifolia	5±0.32a	0.0a
U. propinqua	6±0.47a	12.0±0.1a
U. propinqua var. *suberosa*	10±2.02a	4.2±0.04a
U. prunifolia	2±0.08a	0.0a
U. pseudopropinqua	5±0.74a	0.6±0.00a
U. pumila	5±1.47a	23.5±0.24a
'Sapporo Autumn Gold' (*U. pumila* × *U. japonica*)	1±0.00a	0.0a
U. szechuanica × *U. japonica*	10±0.38a	0.0a
U. taihangshanensis	4±0.37a	0.0a
U. wilsoniana	5±1.3a	21.0±0.25a
Simple and Complex Eurasian Elm Hybrids		
'Accolade'	6±1.8a	0.0a
'Accolade' × *U. japonica*	4±0.22a	0.0a
'Accolade' × *U. pumila*	5±1.1a	0.9±1.7a
'Patriot' ('Urban elm' × *U. wilsoniana* 'Prospector')	4±0.3a	0.0a
'Vanguard' × *U. davidiana*	3±0.3a	0.0a
'Vanguard' × *U. japanese-wilsoniana-pumila* ('Leatherleaf')	11 ± 2.1a	65.2 ± 0.06b
North American Elm Taxa and Cultivars		
U. alata	5±0.6a	0.0a
U. crassifolia	7±0.8a	0.0a
U. serotina	4±0.5a	0.0a
U. thomasii	2±0.1a	0.0a
European Elm Taxa		
U. glabra	3±0.3a	0.0a
U. microcarpa	5±0.7a	0.7±0.8a
***Zelkova* Taxa and Cultivars**		
Zelkova carpinifolia	3±0.3a	0.0a
Z. schneideriana	3±0.3a	0.0a
Z. serrata	3±0.3a	0.0a
Z. serrata 'Green Vase'	4±0.2a	0.0a
Z. serrata 'Village Green	4±0.2a	0.0a
Z. sinica	3±0.3a	0.0a
Malus sylvestris (reference)	16±1.1b	2,188.0±2.2c
Quercus palustris (reference)	10±1.2b	1,498.0±1.6c
Significance:	**NS**	**F=30.2** **P<0.001**

^{z}Values within columns followed by the same letter are not significantly different. (Dunn' Test; P<0.05).

^{y}Means represent 10 larvae for each of three single tree replicates per taxon.

remaining *Ulmus* taxa (male larvae, F=5.7, P<0.001, female larvae, F=14.2, P<0.001). Larvae feeding on the highly preferred standards of *M. sylvestris* and *Q. palustris* lived a mean of 16 and 10 days respectively with greater than 30% to 60% of male and female larvae pupating (Table 3). Collectively, for all *Ulmus* taxa evaluated, percent larval longevity was moderately correlated with larval survival (R=0.69, P<0.001), but was a weak predictor of percent pupation (R=0.30, P=0.02). Percent larval survival was highly related to the percentage of larvae pupating (R=0.81, P<0.001).

Table 3. Suitability (±SE) of Ulmaceae for male (M) and female (F) spongy moth larval development, pupation, adult emergence, and dry frass weight[z].

		% Larval survival		% Pupation		% Adult emergence		Pupal fresh wt. (PFW)		Dry frass wt.
Taxa	**Larval longevity,[y] (days)**	**M**	**F**	**M**	**F**	**M**	**F**	**M (g)**	**F (g)**	**(mg)**
Asian Elm Taxa, Varieties, and Hybrids										
U. gaussennii	14±0.52ab	47±7.4b	63±6.2b	17±2.0ab	0a	17±2.0b	0a	0.255±0.04a		243.0±0.21c
U. laciniata	12±2.33ab	7±0.6a	0a	10±0.9a	0	0a	0a	0.302±0.04a		127.0±0.19b
U. lamellosa	4±0.32a	37±3.3ab	0a	3±0.3a	0a	0a	0a	0.289±0.04a		14.0±0.09a
U. szechuanica	6±0.55a	3±0.3a	7±0.6a	3±0.3a	0a	0a	0a	0.460±0.07b		64.0±0.09b
Simple and Complex Eurasian Elm Hybrids										
'Commendation'	8±0.58a	39±3.9ab	47±5.2b	37±3.8b	23±2.8b	37±3.8c	23±2.8b	0.486±0.08b	0.912±0.23ab	1299.0±0.32e
'Danada Charm'	10±1.19a	40±3.9ab	47±5.4b	40±3.9b	13±1.8ab	40±3.9c	13±1.8b	0.441±0.06b	0.935±0.11b	1235.0±0.33e
'Frontier' (*U. carpinifolia* × *U. parvifolia*)	26±2.8b	47±5.1ab	47±4.8b	23±2.4b	23±1.6b	0a	0a	0.564±0.06b	0.934±0.22ab	618.0±0.12c
'Homestead' (*U. pumila* × European hybrid)	17±3.0ab	33±3.4ab	47±4.8b	10±1.3a	13±0.9ab	0a	0a	0.480±0.04b	0.684±0.07a	307.0±0.12c
'Pioneer' (*U. glabra* × *U. carpinifolia*)	21±2.9b	20±0.5ab	0a	3±0.30a	0a	0a	0a	0.438±0.03b		304.0±0.06c
'Regal' (*U. pumila* × European hybrid)	30±4.2b	37±4.2ab	4±0.4b	13±1.1ab	3±0.3a	0a	0a	0.426±0.03b		568.0±0.16c
'Triumph'	7±1.6a	47±5.1b	0a	3±0.3a	0a	0a	0a	0.350±0.04a		63.0±0.06b
'Urban elm'	20±0.05b	20±5.0a	0a	20±0.05a	0a	0a	0a	0.426±0.03b		312.0±0.04c
(N-148 *U.* × *hollandica* 'Vegeta' × *U. carpinifolia* × *U. pumila*)										
'Vanguard'	16±3.8ab	37±4.2ab	40±3.9ab	37±0.8a	10±1.2a	0a	0a	0.388±0.05ab	0.610±0.08a	201.0±0.13c
North American Elm Taxa and Cultivars										
U. americana 'Jefferson'	8±1.5a	10±1.2ab	7±0.6a	0a	0a	0a	0a	0.374±0.04a		171.0±0.12c
U. americana 'Liberty elm'	30±3.0b	40±3.9ab	0a	27±0.4b	0a	0a	0a	0.372±0.04a		889.0±0.11d
European Elm Taxa (N=5)										
U. carpinifolia	18±1.1ab	47±5.1b	7±0.6a	7±0.6a	0a	0a	0a	0.262±0.05a		197.0±0.08c
U. elliptica	27±3.4b	37±4.2ab	47±5.1b	13±1.9ab	17±1.9ab	0a	0a	0.488±0.08b	0.740±0.09a)	523.0±0.11cd
U. foliacea	35±2.9b	40±3.9ab	47±5.1b	33±3.6b	17±1.8ab	0a	0a	0.450±0.03b	0.670±0.07a	856.0±0.12d
U. procera	15±0.4ab	47±5.0b	57±6.3b	13±1.2a	0a	0a	0.409±0.03ab		227.0±0.08c	
U. sukaczevii	32±0.34b	53±6.1b	53±6.1b	23±1.9bc	3±0.3a	0a	0a	0.363±0.04a	**0.618±0.7a**	522.0±0.11cd
Malus spp. (reference)	16 + 1.1ab	60±4.6c	30±2.8ab	60±4.6c	30±3.2c	60±4.6d	30±2.8b	0.527±0.06b	0.857±0.09ab	2188.0±2.2e
Quercus palustris (reference)	10±1.2a	37±4.2ab	40±3.7b	37±4.2b	33±3.3c	37±4.2c	33±3.3b	0.536b±0.05b	1.097±1.12b	1498.0±1.6e
Significance:	**F=8.6**	**F=5.7**	**F=14.2**	**F=6.1**	**F=4.1**	**F=13.8**	**F=6.8**	**F=4.3**	**F=4.5**	**F=86.7**
	P<0.001	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**

[z] Values within columns followed by the same letter are not significantly different. (Dunn's Test; $P<0.05$). M=male and F=female larvae.

[y] Means represent 10 larvae for each of three single tree replicates per taxon.

Table 4. Suitability (±SE) of *Ulmus* for adult female spongy moth fecundity^{z}.

Taxa	Mean # of eggs laid per ovipositing female (±SE)	Percent females ovipositing (±SE)
'Commendation'	255+39.2a	90+0.10a
'Danada Charm'	323+9.5ab	50+0.29a
Malus sylvestris (reference)	227+41.8a	90+0.10a
Q. palustris	516+7.0b	100+0.00a
Significance:	**F=20.9** **P<0.001**	***NS***

^{z}Values within columns followed by the same letter are not significantly different. (Dunn' Test; P<0.05).

Table 5. Mean (±SE) percent spongy moth larval survival by geographic origin of *Ulmus*.

Geographic Origin	N	Mean % larval survival^{z} (±SE)
Asian taxa, hybrids, cultivars, varieties	31	2±1.2a
European taxa	6	31±10.3b
Simple and Complex Eurasian Hybrids	15	31±6.7b
North American taxa	6	14±11.9ab
Significance:		**F=8.6** **P<0.001**

^{z}Values within columns followed by the same letter are not significantly different. (Dunn' Test; P<0.05).

Spongy moth pupation, pupal fresh weights, adult emergence, and fecundity. A mean of 10% (range=3%-17%) of male larvae, and no female larvae pupated when feeding on Asian taxa of *U. gausennii, U. laciniata, U. lamellosa* and *U. szechuanica*. A mean of 20% (range=3-40%) of male larvae and a mean of 14% (range=3%-23%) of female larvae pupated when feeding on the complex Eurasian hybrids of 'Commendation' 'Danada Charm', 'Frontier', 'Homestead', 'Regal', 'Triumph', and 'Vanguard' (Table 3). Thirty-seven percent of the remaining male pupae and 23% of female pupae; and 40% of male pupae and 13% of female pupae emerged as adults having developed on the complex Eurasian hybrids 'Commendation' and 'Danada Charm', respectively. A mean of 24% of male and 10% of female larvae pupated when feeding on the European taxa of *U. elliptica, U. foliaceae, U. procera*, and *U. sukeczvii*. Twenty-seven percent (27%) of male larvae feeding on the North American cultivar U. *americana* 'Liberty' pupated, but no female larvae pupated. For the highly preferred standards of *M. sylvestris* and *Q. palustris*, 60% and 37% of male larvae and 30% and 33% of female larvae pupated, respectively, and a like percentage of adult male and female moths emerged. The percentage of larvae pupating was highly correlated with percent adult emergence (R=0.94, P<0.001).

Overall, female spongy moth pupae were significantly heavier (mean=0.816g; range=0.610-1.290g) by 2.5 times compared with male spongy moth pupae (mean=0.323g; range=0.255-0.564g) (t = 22287.000, P = <0.001) (Table 3). Male pupae developing on *U. szechuanica*, 'Commendation', 'Danada Charm', 'Frontier', 'Homestead', 'Pioneer', 'Regal', *U. elliptica*, and *U. foliaceae* were significantly heavier compared with male pupae developing on *U. gausennii*, *U. laciniata*, *U. lamellosa*, 'Triumph', *U. americana* cultivars 'Jefferson' and 'Liberty', *U. carpinifolia*, and *U. sukaczevii*. Male pupae developing on 'Vangard', and *U. procera* had intermediate pupal fresh weights (PFW) (F=4.3; P<0.001). Female pupae developing on 'Danada Charm' and 'Frontier' and the highly preferred standard of *Q. palustris* were significantly heavier compared with pupae developing on 'Homestead', 'Vanguard', *U. elliptica*, and *U. foliaceae*, Female pupae developing on 'Commendation' and the highly preferred standard, *M. sylvestris* had intermediate PFWs (F=4.5; P<0.001). Male and female PFWs for the highly preferred species of *M. sylvestris* and *Q. palustris* were 0.527g and 0.536g, and 0.865g and 1.097g, respectively and were comparable with other studies (Miller and Hanson 1987, Miller and Wiegrefe 2021) (Table 3). PFWs were moderately correlated with larval longevity (R=0.53, P<0.001) and percent adult emergence (R=0.64, P<0.001).

Significantly more male and female moths emerged when completing development on 'Commendation' and 'Danada Charm (13% to 40%) compared with all of the remaining *Ulmus* taxa (male moths, F=13.8, P<0.001, female moths, F=6.8, P<0.001) (Table 3). Additionally, compared with all of the remaining *Ulmus* taxa, a significantly greater number of male moths completed development on *U. gaussennii*, but no female moths emerged when developing on this taxon. Percent adult emergence for both male and female moths for the reference species of *M. sylvestris* and *Q. palustris* was slightly higher (30% to 60%), respectively. Adult female spongy moths laid significantly more eggs per ovipositing female when developing on the highly preferred standard of *Q. palustris* (516 eggs) compared with 'Commendation' (255 eggs) and the highly preferred standard of *Malus* spp. (227 eggs). Ovipositing females laid an intermediate number of eggs when developing on 'Danada Charm' (323 eggs) (F=20.9; P<0.001) (Table 4). Ninety percent to 100% of emerging females laid eggs on 'Commendation', 'Danada Charm', and *Q. palustris* (standard) compared with only 50% of emerging adult females laying eggs on *M. sylvestris* (standard), but there was no significant difference in the percent females ovipositing (F=1.0; P=0.15) (Table 4). The number of eggs laid per ovipositing female was highly correlated with the percentage of females ovipositing (R=0.96, P=0.04).

Larval survival by geographic origin. Overall, female larvae had a significantly higher (t=2.9; P=0.008) survival rate (47%) compared with male larvae (41%), and the mean percent larval survival (i.e. larvae living to pupation) differed significantly (F=8.6; P<0.001) by geographic origin (Table 5). Spongy moth larvae feeding on simple and complex Eurasian hybrids and European taxa both had a mean survival rate of 31% (Eurasian range=0%-48%; European range=0%-56%) compared with larvae feeding on Asian taxa with <2% of larvae surviving to pupation (range=0%-64%). ***Note*** that spongy moth larvae survived to pupation on only four out of 26 Asian taxa tested, namely *U. gausennii* (male=47%; female=63%), *U. laciniata* (male=7%; female=10%), *U. lamellosa* (male=37%; female=0%), and *U. szechuanica* (male=3%; female=7%) (Tables 3 and 5). Larvae feeding on North American taxa had an intermediate mean percent

Table 6. Suitability ratios and suitability rankings for spongy moth pupae developing on *Ulmus* taxa.

Taxa	Male suitability ratio[z]	Female suitability ratio	Male suitability ranking[y]	Female suitability ranking
U. gausennii	0.48	—[x]	3	—
U. lamellosa	0.54	—	2	—
U. laciniata	0.56	—	2	—
U. szechuanica	0.86	—	2	—
'Commendation'	0.91	0.83	1	2
'Danada Charm'	0.82	0.85	2	2
'Frontier'	1.05	0.85	1	2
'Homestead'	0.90	0.62	1	2
'Pioneer'	0.76	—	2	—
'Regal'	0.79	1.18	2	1
'Triumph'	0.65	—	2	—
'Urban elm'	0.81	—	2	—
'Vanguard'	0.72	0.56	2	2
U. carpinifolia	0.49	—	3	—
U. elliptica	0.91	0.67	1	2
U. foliaceae	0.84	0.61	2	2
U. procera	0.76	—	2	—
U. sukaczevii	0.68	0.56	2	2
U. americana 'Liberty'	0.69	—	2	—
Means	0.75	0.75	1.9	1.9

[z] Male and female suitability ratio equals the quotient of the MPW and FPW for each respective *Ulmus* taxon over the MPW and FPW of the reference taxon, *Q. palustris,* respectively.

[y] Male and female suitability ranking is defined using the following scale: Suitability ranking 1 > 0.9; 2 > 0.5 to 0.9; 3 < 0.5 (Taken from Liebhold, et al., 1995).

[x] No larvae pupated.

survival rate of 14% (range=0%-39%), but like the Asian taxa, the only larvae that survived to pupation were those feeding on the *U. americana* cultivar 'Liberty' (Tables 3 and 5).

Suitability ratios and rankings. Suitability ratios (SRs), for male and female spongy moth larvae that pupated, when feeding on *Ulmus* taxa, are summarized in Table 6. The overall mean male pupal SR was 0.77 (moderate) and 0.75 (moderate) for female pupae. The mean male SR for Asian taxa was 0.61 (moderate) (range=0.48 to 0.86). No female larvae pupated when feeding on Asian taxa. The mean male pupal SR was 0.84 (range=0.71-1.05) (moderate), and 0.81 (range=0.75-0.84 (moderate) for female larvae developing on simple and complex Eurasian hybrids. Male larvae feeding on the European taxa of *U. elliptica, U. foliaceae*, and *U. sukaczevii* had a mean male pupal SR of 0.84 (range=0.68-0.91) (moderate), and a mean female pupal SR of 0.67 (range=0.59-0.78) (moderate) (Table 6). These results suggest that the majority of the *Ulmus* taxa tested in this study have low (SR< 0.5) to moderate (SR=0.5 to 0.9) host suitability for male and female spongy moth larvae feeding, development, and pupation. Host suitability significantly affected male and female pupal weights. (t = 22287.000, P = <0.001) with female pupae being 2.5 times heavier than male pupae (male = 0.323 g versus female = 0.816 g). Overall, male pupae had a low suitability ranking (value=3, pupa < 700 mg) and female pupae had a moderate suitability ranking (value=2, 700 mg < pupa < 1,000 mg) (Miller and Hanson 1989a, b). Suitability rankings for male pupae for both of the standards of *Malus sylvestris* and *Q. palustris* were 3 (0.527g and 0.536g), and 2 (0.857g) and 1 (1.097g) for female pupae, respectively. Male and female pupal weights in our study were comparable with other studies for another highly preferred host, *Q. macrocarpa* (male=0.339g, female=0.886g) (Miller and Hanson, 1989a,b, Miller and Wiegrefe 2021b). Percent male and female larval development survival was not correlated with male and female suitability ratings (SRs) (male, R=0.21, P=0.45; female, R=0.55, P=0.20). However, both male and female pupal fresh weights (PFW) were very strong predictors of suitability (male: R=0.85, P<0.001, female: R=0.99, P<0.001). Liebhold et al. (1995) does not provide any SR values for *Ulmus* taxa, therefore prohibiting any direct comparisons among *Ulmus* taxa evaluated in this study, but Liebhold et al. (1995) does indicate that 11 *Ulmus* taxa have moderate suitability rankings (value=2), with the exception of *U. parvifolia* which is rated low (value=1).

Multiple-Choice (MC) laboratory feeding trials (Preference). A summary of the nine MC studies is presented in Table 7. In MC study #1, spongy moth larvae preferred 'Commendation' over 'Danada Charm' (t=8.2; P<0.001). When larvae were given a choice in MC study #2 between 'Commendation' and 'Accolade', significantly more 'Commendation' and *U. pumila* leaf tissue was consumed compared to larvae feeding on 'Accolade' (F=19.9, P<0.001). In MC study #3, when larvae were presented a choice between 'Accolade' and 'Danada Charm', neither were preferred with <10% of leaf tissue consumed. In MC study #4, spongy moth larvae were allowed to choose between 'Vanguard' and its *U. japonica* and *U. pumila* parentage. Significantly more leaf tissue was consumed by larvae feeding on *U. pumila* as compared to larvae feeding on 'Vanguard' and *U. japonica* (F=18.4, P<0.001). Spongy larvae preferred *U. davidiana* foliage over the other Davidiana complex species of *U. japonica* and *U. wilsoniana* in MC study #5 (F=17.5, P<0.001). When examining elm taxa of Eurasian parentage, 'Frontier' was more highly preferred over 'Pioneer' and *U. carpinifolia* in MC study #6 (F=4.4, P=0.04). In MC study #7, the complex hybrid 'Homestead' was highly preferred followed by *U. pumila.* The complex hybrid, 'Regal', was least preferred and 'Urban' elm was moderately preferred (F=7.8, P=0.002). In MC study #8, there was no significant difference in preference when larvae fed on 'Patriot', *U. wilsoniana*, and 'Urban' elm. In the final MC study, #9, as before, 'Frontier' was highly preferred as compared to *U. carpinifolia*, which was moderately preferred and *U. parvifolia* which was least preferred (F=8.9, P=0.004). For the *Ulmus* taxa evaluated in the multiple-choice (MC) preference studies, larval longevity was highly correlated with percent larval survival (R=0.83, P<0.001) for the same taxa evaluated in the NC feeding studies.

Elm leaf thickness and inner and outer leaf toughness. A summary of elm leaf thickness and inner and outer leaf toughness by geographic origin and taxon is presented in Tables 8 and 9, respectively. Asian and European elms had significantly thicker leaves (1.5X) compared with North American elms (F=70.0, P<0.001), and Asian elm leaves

Table 7. Mean (±SE) percent leaf tissue removed for spongy moth larvae feeding on Asian elm taxa and hybrids, and simple and complex Eurasian taxa in multiple choice (MC) feeding preference studies.

Taxa	% Leaf tissue consumed[z,y,x] (±SE)
Study #1	
U. 'Morton Stalwart-Commendation™ (*U.* 'Morton'-Accolade™ × *U. pumila-carpinifolia*)	18±1.9b
U. 'Morton Red Tip'-Danada Charm™ (*U.* 'Morton'-Accolade™ × *U. pumila*)	4±1.8a
Significance	**t=8.2 P<0.001**
Study #2	
U. 'Morton Stalwart-Commendation™ (*U.* 'Morton'-Accolade™ × *U. pumila-carpinifolia*)	17±2.8b
U. 'Morton'-Accolade™ (*U. japonica* × *U. wilsoniana*)	1±0.5a
U. pumila	12±2.0b
Significance	**F=19.9 P<0.001**
Study #3	
U. 'Morton Red Tip'-Danada Charm™ (*U.* 'Morton'-Accolade™ × *U. pumila*)	6±2.1a
U. 'Morton'-Accolade™ (*U. japonica* × *U. wilsoniana*)	9±2.2a
Significance	**NS**
Study #4	
U. 'Morton Plainsman'-Vanguard™ (*U. japonica* × *U. pumila*)	12±1.9a
U. japonica	0±0.0a
U. pumila	24±6.3b
Significance	**F=18.4 P<0.001**
Study #5	
U. davidiana	12±2.4b
U. japonica	1±0.5a
U. wilsoniana	3±1.5a
Significance	**F=17.5 P<0.001**
Study #6	
'Frontier' (*U. carpinifolia* × *U. parvifolia*)	66±15.5b
'Pioneer' (*U. glabra* × *U. carpinifolia*)	31±7.9a
U. carpinifolia	32±5.8a
Significance	**F=4.4 P=0.04**
Study #7	
'Homestead' (*U. pumila* × complex European hybrids)	62±13.8c
'Regal' (*U. hollandica* × *U. carpinifolia* × *U. pumila* × *U. carpinifolia*)	2±1.2a
'Urban' elm (*U. hollandica* x *U. carpinifolia*) × *U. pumila*	21±8.3ab
U. pumila	49±10.6b
Significance	**F=7.8 P=0.002**
Study #8	
'Patriot' ('Urban' elm × *U. wilsoniana* 'Prospector')	3±1.2a
U. wilsoniana	1±1.0a
'Urban' elm	0±0.0a
Significance	**NS**
Study #9	
'Frontier' (*U. carpinifolia* × *U. parvifolia*)	71±8.7b
U. carpinifolia	33±18.3ab
U. parvifolia	1±1.0a
Significance	**F=8.9 P=0.004**

[z] Values within columns, within a study, followed by the same letter are not significantly different (Dunn's test, P<0.05).

[y] Means represent approximately ten larvae in each of five to ten single replicate petri dishes per study.

[x] Mean percent leaf tissue consumed was visually estimated at 36-72 hours after larvae were introduced into the petri dishes.

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). There was no significant difference between inner and outer leaf toughness for all elms tested (Table 8). Leaf thickness was moderately correlated with inner and outer leaf toughness (inner R=0.36; P=0.02; outer R=0.42, P<0.006), and inner leaf toughness was strongly correlated with outer leaf toughness (R=0.94, P<0.001). Of the 21 Asian elm taxa evaluated, *U. castaneifolia* had significantly thicker leaves and *U. gausenni*, *U. glaucescens*, *U. japonica*, *U. pumila*, and *U. szechuanica*; and the complex hybrids of 'Accolade', 'Commendation', and 'Vanguard' had the thinnest leaves. Leaves of all of the remaining 12 Asian elm taxa were intermediate in thickness (F=353.3, P<0.001). Leaves of *U. bergmaniana*, *U. gausenni*, *U. japonica*, and *U. pumila* were the most tender (least tough) compared with the toughest leaves of *U. glaucescens* var. *lasiophylla*, *U. macrocarpa*, and 'Triumph'. Leaves of all 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) (Table 9).

For the simple and complex Eurasian hybrids, Frontier, Homestead and Regal had significantly thinner and more tender leaves than Patriot, Pioneer, and Prospector (thickness, F = 47.4, P<0.001; inner toughness, F=17.2, P<0.001; outer toughness, F=17.8, P =<0.001). Among European elms, *U. foliaceae* had the thinnest leaves and *U. procera* and *U. sukaczevii* had significantly thicker leaves (F=44.2, P<0.001). *Ulmus elliptica* and *U. procera* had significantly tougher leaves compared with *U. sukaczevii* (inner toughness, F=30.6, P<0.001; outer toughness, F=4.9, P<0.001).The North American elm *U. thomasii* had significantly thinner leaves compared with *U. alata* and *U. crassifolia* (F=40.4, P<0.001). There was no significant difference in 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=4.4, P<0.005).

Elm leaf thickness, inner and outer leaf toughness, and suitability. For all of the elm taxa tested, larval longevity was not correlated with leaf thickness (R=0.16, P=0.32), inner leaf toughness (R=0.30, P=0.06), or outer leaf toughness (R=0.29, P=0.07). Likewise, percent larval survival was not correlated with leaf thickness (R=0.14, P=0.40) or inner (R=0.17, P=0.30) and outer leaf toughness (R=0.22, P=0.17). Additionally, leaf thickness and leaf toughness were not good predictors of the amount of dry frass weight produced (thickness: R=0.14, P=0.0.41; inner toughness: R=0.01, P=0.97, outer toughness: R=0.01, P=0.87) or pupal fresh weight (thickness R=0.15, P=0.37; inner toughness: R=0.11, P=0.51, outer toughness: R=0.10, P=0.47).

In summary, of the 59 *Ulmus* and six *Zelkova* taxa, hybrids, varieties, and cultivars tested in this study, the vast majority of *Ulmus* and all of the *Zelkova* taxa were found not to be suitable for spongy larval development, pupation, and adult reproduction. Results from this study, provides new insight into the potential of *Ulmaceae* for use in future tree breeding programs.

Leaf tissue chemical analysis, and its influence on host suitability and preference was beyond the scope of this study and was not examined. However, we will discuss the effect of physical plant traits (i.e. leaf thickness, toughness, and pubescence), the relationship between elm host plant phenology and larval feeding, and possible effects of hybridization on host suitability and preference of *Ulmus* taxa.

Leaf thickness, and inner and outer leaf toughness, host suitability and preference. Physical plant traits, such as leaf toughness and thickness, can greatly influence invertebrate

Table 8. Leaf thickness and leaf toughness (±SE) for *Ulmus* taxa, hybrids, and cultivars by geographic origin.

Taxa	Thickness[y] (±SE) (mm)	Inner	Toughness (g/cm) (±SE) Outer
Asian[z]	0.282±0.02b	30.71±0.03a	29.71±0.28b
European[z]	0.325±0.04b	24.90±0.03a	23.32±0.26a
North American	0.198±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**

[z] Includes simple and complex Eurasian hybrids.

[y] Values within columns, within a study, followed by the same letter are not significantly different (Dunn’s test, P<0.05).

Table 9. Leaf thickness and leaf toughness (±SE) for Asian, Eurasian, European, and North American *Ulmus* taxa, hybrids, and cultivars[z].

Taxa	Thickness (±SE) (microns)	Inner	Toughness (g) (±SE) Outer
Asian Taxa			
U. bergmaniana	328±9.83bc	11.61±0.46a	11.61±0.46a
U. castaneifolia.	411±12.3c	30.98±1.24c	28.85±1.15d
U. chenmoui	373±11.2bc	28.17±1.13c	24.04±0.96c
U. davidiana	274±8.23b	31.66±1.27d	28.12±1.12d
U. gausennii	173±5.18a	12.79±0.51a	12.61±0.50a
U. glaucescens	213±6.40a	22.59±0.90b	19.19±0.77b
U. japonica.	178±5.33a	12.93±0.52a	10.57±0.42a
U. lamellosa	378±11.4bc	58.97±2.36g	59.88±2.40h
U. macrocarpa	368±11.0bc	37.83±1.51e	44.72±1.79g
U. parvifolia	269±8.08b	38.65±1.55e	30.35±1.21e
U. propinqua	305±9.14b	29.08±1.16c	22.23±0.89b
U. prunifolia	318±9.53b	30.89±1.24c	28.99±1.16d
U. pseudopropinqua	371±11.1b	25.31±1.01c	24.72±0.99c
U. pumila	203±6.10a	14.92±0.60a	14.42±0.58a
U. taihangshanensis	257±7.70b	38.15±1.53e	35.06±1.40f
U. wilsoniana	302±9.07b	33.43±1.34d	29.98±1.20e
Complex Eurasian Hybrids			
‘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** **P=<0.001**	**F=254.4** **P=<0.001**	**F=303.0** **P=<0.001**
New Complex 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** **P=<0.001**	**F=17.2** **P<0.001**	**F=17.8** **P<0.001**
European Taxa			
U. carpinifolia	254±7.62b	18.05±0.72c	17.60±0.83b
U. elliptica	335±10.1c	20.87±0.83d	20.68±0.66b
U. foliaceae	221±6.63a	17.96±0.72d	16.51±0.54ab
U. glabra	277±8.31c	14.52±0.58b	13.52±0.70ab
U. procera	345±10.4d	21.23±0.85d	17.42±0.47b
U. sukczevii	338±10.1d	12.34±0.49a	11.70±0.95ab
Significance:	**F= 44.24** **P=<0.001**	**F=30.6** **P<0.001**	**F=4.9** **P<0.001**
North American Taxa			
U. alata	218±6.55c	26.44±1.06a	23.63±0.88b
U. crassifolia	241±7.24c	25.31±1.01a	21.95±0.83ab
U. serotina	193±5.79b	23.32±0.93a	20.87±0.69ab
U. thomasii	1.57±4.72a	25.17±1.01a	17.15±0.74ab
U. americana	1.78±5.33b	24.40±0.98a	18.55±0.74ab
Significance:	**F=40.4** **P=<0.001**	**NS**	**F=4.84** **P=0.005**

[z] Values within columns, within a study, followed by the same letter are not significantly different (Dunn’s test, P<0.05).

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.). 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 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* Aiton) leaves were more important than leaf margin spines in deterring edge feeding caterpillars. In a previous study by Miller and Ware (2022), they determined that Asian and European elm leaves were significantly thicker than North American elm leaves, and Asian elm leaves were tougher than European and North American elm leaves. Additionally, elm leaf thickness was weakly correlated with inner and outer leaf toughness, but inner and outer leaf toughness was strongly related. Recently, Miller and Wiegrefe (2021) found that spongy moth development was not correlated with the thickness of *Carpinus* leaves but was related to inner and outer leaf toughness. Additionally, 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 the present study, elm leaf thickness and inner and outer leaf toughness were not good predictors of larval longevity, pupation, pupal fresh weights, or frass production. Schneider (1980) reported that it takes approximately three days for newly hatched fall cankerworm (*Alsophila pometaria* Harris) larvae to starve to death which is consistent with our results, in this study, where spongy moth larvae lived an average of only 3-5 days when feeding on a majority of *Ulmus* and *Zelkova* taxa.

Our results are similar to larval feeding studies by Miller (2000) and Miller et al. (2001) where they found that the majority of these same Asian elm taxa were unsuitable for spring cankerworm [*Paleacrita vernata* (Peck, 1795)] and fall cankerworm [*Alsophila pometaria* (Harris, 1841)] larval development and pupation. Similarly, less than 30% of spongy moth larvae feeding on thin, thick, tough or tender leaves of 'Regal', 'Frontier', *U. foliaceae*, and *U. sukaczevii* survived, and none pupated or emerged as adult moths. In contrast, spongy moth larvae feeding on either the thin, thick, or tougher leaves of 'Commendation' and 'Danada Charm' had over 50% larval survival, and an equal proportion of larvae developing into adults. Studies by Cunningham and Dix (1983) and Dix et al. (1996) found that Siberian elm (*U. pumila*) clones with thicker leaves had significantly higher rates of percent defoliation and thinner Siberian elm leaves experienced less feeding by the spring cankerworm (*Paleacrita vernata*) (Peck). They suggest that spongy moth larvae may prefer to feed on trees with thicker leaves because of the increased feeding efficiency that would be offered by leaves with a greater weight per unit area. Their findings are consistent with our study where *U. pumila* leaves were significantly thinner and less tough compared with other *Ulmus* taxa, and spongy moth larvae only lived a mean of five days, and none reached pupation. Spongy moth larvae tend to feed inward from the leaf margins, toward the mid-vein, eventually consuming the entire leaf. It would seem reasonable that more tender elm leaves would be more palatable for younger larvae to feed on, but that does not appear to be the case in this study. It is possible that older larvae are able to feed on tougher and thicker leaves, but again, that was not consistently observed in this study. Thinner leaves on trees may also mature more rapidly, thus accumulating tannins and cellulose faster than trees with smaller and thicker leaves (Feeny 1970). Feeny (1970) also documented the deterioration in quality of oak leaves as food for Lepidoptera larvae during leaf maturation. The development of Lepidoptera larvae on oaks was adversely affected by tannin and cellulose accumulation in the leaf tissues and cell walls, respectively.

The amount of leaf tissue removed in the multiple-choice (MC) studies by larvae feeding on Asian taxa was consistent with larval longevity and percent larval survival in the no-choice (NC) feeding trials, suggesting that other factors (i.e. leaf chemistry, pubescence) besides leaf thickness and toughness may be responsible for host preference and may play a more important role in the suitability and preference of elms for spongy moth larval development. Paluch et al. (2009) found significant differences in the total phenolic content of 13 of some of the same Asian elm taxa and cultivars evaluated here, but no significant differences were identified between spongy moth larval longevity, pupal fresh weight, or percent adult emergence with regard to total leaf phenolic content. In another study, Paluch et al. (2008) found that Asian elms belonging to the David complex (i.e. *U. propinqua, U. japonica, U. wilsoniana*) possessed a much larger diversity of leaf terpenes, phenolics, alkaloids, and lipids. More specifically, the diversity of lipids showed a significant effect relating to David complex parentage suggesting that elms belonging to this complex are better suited for spongy moth larval development than other elms. However, in this study, none of the larvae feeding on members of the David complex survived to pupation. It appears that host suitability relies on a complexity of leaf chemical composition, and that generalist herbivorous insects, such as the spongy moth, might selectively use host plants containing a larger diversity of compounds (Schultz 1988, Paluch et al. 2008).

Host plant phenology and susceptibility, and spongy moth larval suitability and preference. Spongy moth, and spring and fall cankerworm egg hatch occurs between 100 and 200 DD_{50} and which corresponds closely with adult elm leafminer emergence (Miller and Ware 2014, Orton, 2007). In an elm leafminer study by Miller and Ware (2014), they observed considerable variability in spring elm leafing out phenology for many of the same less suitable Asian elm taxa evaluated in this study. For example, less suitable elms, such as *U. davidiana*, *U. japonica*, *U. lamellosa*, *U. pumila*, and others tend to begin leafing out at approximately the same time as initial spring (*P. vernata*) (Peck) and fall cankerworm (*Alsophila pometaria* Harris) egg hatch, and adult leafminer emergence, but suffer no or negligible feeding damage from either insect (Miller and Ware 2014, Miller et al. 2001a). Other less preferred Asian, European, and North American elms, such as

U. parvifolia, U. wilsoniana, *U. carpinifolia*, and *U. thomasii*, are typically breaking bud or just flowering, and generally do not leaf out until after cankerworm and spongy moth larval feeding is well underway, and peak adult elm leafminer emergence has passed. This phenological pattern suggests that these taxa possibly avoid feeding damage, and appear less susceptible (Miller and Ware 2014, Miller et al. 2001). Conversely, field observations have revealed that European species such as *U. elliptica*, *U. glabra*, *U. laciniata*, and *U. sukaczevii*, consistently leaf out at approximately the same time of initial cankerworm, spongy moth, and elm leafminer insect feeding and oviposition, respectively, and these same species were found to be suitable for spongy moth larval development, and moderately to highly susceptible to elm leafminer feeding damage. Witter and Waisamer (1978) also observed that population levels of tortricid caterpillars on early flushing aspen clones were higher than those on late flushing aspen clones. Because the emerging 2nd-stage tortricid larvae were synchronized with their food source, they had higher survival and less dispersal than larvae on unsynchronized leaves. The strong correlation between leafing out phenology of the aforementioned *Ulmus* taxa and their relative susceptibility, suitability, and preference suggests a spectrum of apparent resistance for spongy moth larval feeding and development. Many of these same Asian taxa evaluated in this study have also been shown to be less suitable for other leaf-feeding insects such as the elm leaf beetle (*Pyrrhalta luteola* Muller), and Japanese beetle (*Popillia japonica* Newman, 1841) (Miller and Ware 1997, 1999, 2014; Miller et al. 1999, 2001a,b, Bosu et al. 2007, Bosu and Wagner 2007, Condra et al. 2010, Griffin et al. 2017). These phenological traits should be more fully explored in future elm tree breeding programs.

Hybridization, suitability, and preference of Ulmus taxa for spongy moth larvae. Hybridization may have both a positive and/or negative influence on host suitability and preference for spongy moth larvae (Paige and Capman 1993, Orians 2000, Cheng et al. 2010, Lopez-Caamal 2014). In this study, *U. carpinifolia*, *U. pumila*, and members of the David complex (i.e. *U. japonica, U. wilsonsiana, U. propinqua*) appear to affect feeding preference by spongy moth larvae compared with other *Ulmus* taxa. For example, in the multiple-choice (MC) laboratory feeding bioassays, when a much less suitable or preferred taxon such as *U. parvifolia*, is crossed with a preferred taxon, such as *U. carpinifolia*, to form 'Frontier' suitability and preference increases significantly. Conversely, when the more suitable and preferred *U. carpinifolia* is hybridized with the much less suitable *U. glabra* to form 'Pioneer', there is no appreciable change in suitability or preference. Further, when the preferred *U. pumila* is included in complex hybrids, such as 'Homestead', 'Regal', 'Commendation', 'Urban elm', and 'Vanguard', larval suitability and preference also increases, but the opposite is also true for the *U. pumila* × *U. japonica* hybrids of 'Cathedral' and 'New Horizon' where preference decreased. When the very unsuitable and much less preferred *U. wilsoniana* or *U. japonica* are both included in the complex hybrids of 'Patriot', 'Accolade', and 'Danada Charm', suitability and preference is significantly reduced. Results reported here suggest that *U. carpinifolia* and *U. pumila* tend to increase preference in simple and complex hybrids, but members of the David elm complex such as *U. wilsoniana* and *U. japonica* tend to decrease suitability and preference. Hybrids containing *U. glabra* and *U. parvifolia* parentage do not appear to have a significant effect on the suitability or preference for spongy moth larval feeding and development. The reason for this hybrid effect is not clear. A similar phenomenon, the "*U. pumila* and *U. carpinifolia* factors" has been observed in other studies with elms (*Ulmus* spp.). For example, when Siberian elm (*U. pumila*) is incorporated into hybrids with other taxa it appears to affect the susceptibility, suitability, and preference of elms to an extensive herbivorous insect guild including Japanese beetle, elm leaf beetle spring and fall cankerworm, elm leafminer (Miller and Ware 1997, 1999, 2014, Miller et al. 1999 2001a,b, Bosu and Wagner, 2007, Bosu et al. 2007, Condra et al. 2010; Griffin et al. 2017). In all likelihood, elm leaf chemistry may play a role in host preference and suitability (Paluch et al., 2008, 2009).

Elm leaf trichomes and host suitability. 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, Pillemer and Tingey 1976, Roberts et al. 1979, Southwood 1986, Peter et al. 1995, Dix et al. 1996, Werker 2000, Dalin and Bjorkman 2003, Bosu and Wagner 2007, Dalin et al. 2008, Kariyat, et al. 2018). Conversely, trichomes may also play a role in attracting herbivores to the host plant (Southwood 1986) and 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, 2006, Potter et al. 1998, Miller and Ware 1999, Miller 2000, Miller et al. 2001a,b, Dalin et al. 2008).

In a previous study, Miller and Ware (2022), found some interesting contrasts in elm leaf trichome density and morphology on the abaxial (lower) and adaxial (upper) leaf surfaces of the pubescent elm taxa of *U. chenmoui*, *U. glauscens, U. lamellosa, U. macrocarpa,* and *U. propinqua* (Fig. 1 and 2 a,b,c,d). Namely, 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* (Fig. 1d, 2d) and upper leaf surface of *U. propinqua* (Fig. 1c) are very dense and thick, fine, straight, and of even length, with some curvature on the upper leaf surface. In contrast, the leaf trichomes on the lower and upper surfaces (Fig. 2 a,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. 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) (Fig. 1a, 2b). However, in this study, leaf trichome density (i.e. pubescence) does not appear to be a good indicator of

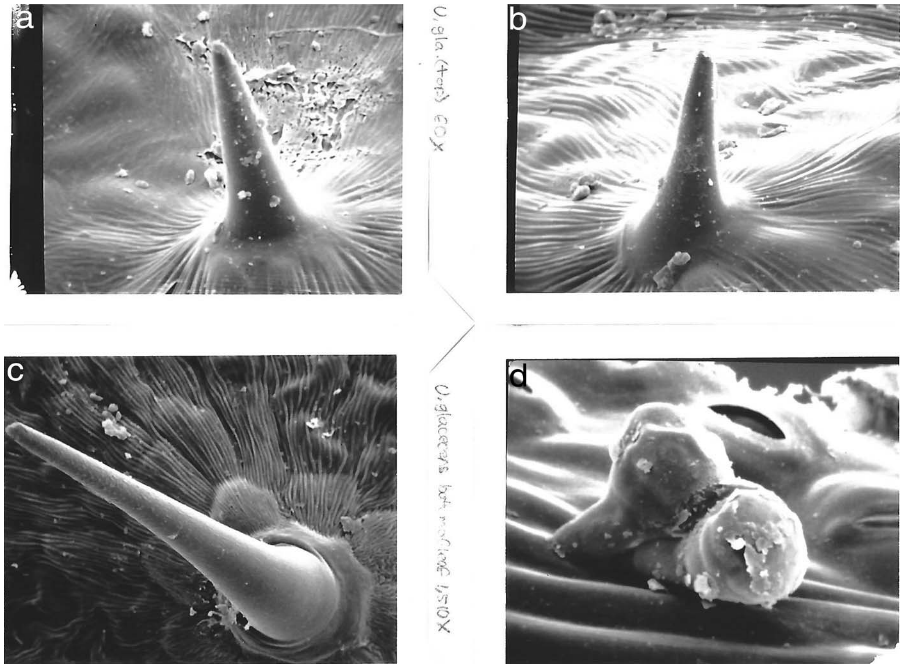

Fig. 1. **a, b, c, d. Elm leaf trichomes. a. (upper left) *U. lamellosa*, upper surface (840X), b. (upper right) *U. glaucescens*, upper surface (60X), c. (lower left) *U. propinqua*, upper suface (620X), d. (lower right) *U. glaucescens*, lower surface (1,510X).**

suitability for spongy moth larvae. With the exception of *U. gausenii*, and *U. lamellosa*, neither pubescent, or non-pubescent Asian elm taxa were suitable for spongy moth larval development and pupation. Our results are consistent with studies by Miller (2000) and Miller et al. (2001) where they found that these same Asian elm taxa were not suitable for spring and fall cankerworm development. They also found, in multiple choice studies, that there was no significant difference in leaf tissue consumed for spring and fall cankerworm larvae feeding on leaf discs of *U. glaucescens* var. *lasiophylla*, *U. lamellosa*, and *U. macrocarpa* with trichomes present versus leaf discs with trichomes removed. Conversely, Miller and Wiegrefe (2021) found that pubescent leaves of certain *Carpinus* taxa were less

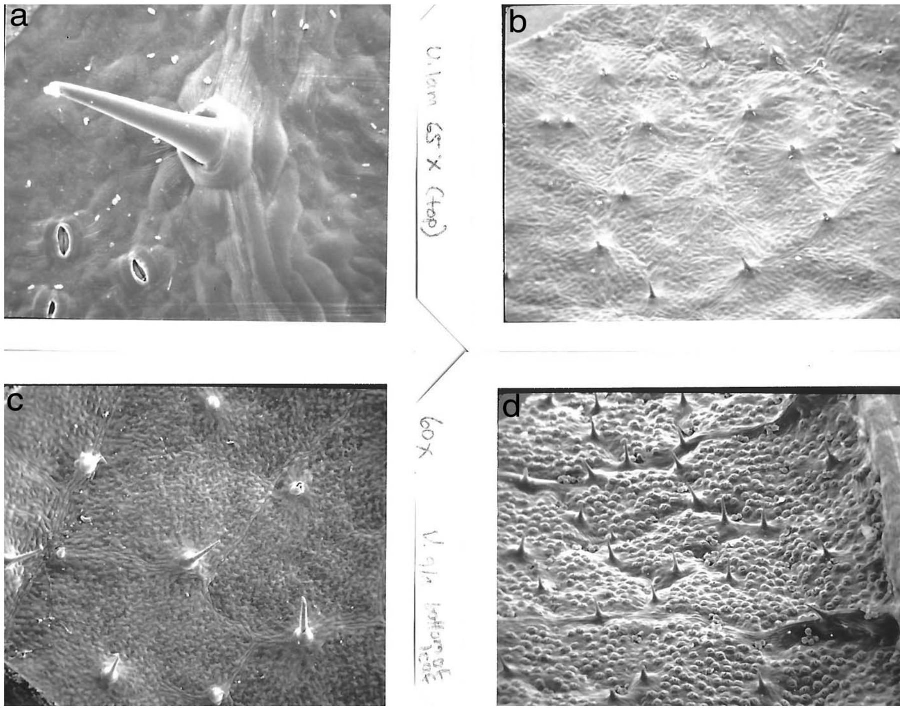

Fig. 2. **a,b,c,d. Elm leaf trichomes. a. (upper left) *U. macrocarpa*, lower surface (430X), b. (upper right) *U. lamellosa*, upper surface (65X), c. (lower left) *U. macrocarpa*, upper surface (63X), d. (lower right) *U. glaucescens*, lower surface (60X).**

suitable and less preferred by spongy moth larvae, but there was no relationship between the amount of leaf tissue removed and trichome density.

Host suitability and suitability rankings (SRs). Liebhold et al. (1995) does not provide any specific SR values for *Ulmus* taxa, therefore prohibiting any direct comparisons for specific *Ulmus* taxa evaluated in this study. However, using SR's from this study, as previously described by Montgomery (1991) and Liebhold et al. (1995), we found a strong correlation between both male and female pupal weights and host suitability. Suitability appears to have a significant effect on both male and female pupal weights with females weighing nearly 2.5 times more than males. Of all of the elm taxa tested in this study, the complex Eurasian hybrids of 'Commendation', 'Danada Charm', 'Frontier', and 'Vanguard' appear to be moderately suitable (value=2 or $0.5 < \text{ratio} < 0.9$) (Montgomery, 1991) for larval development, and of these same taxa, only 'Commendation' and 'Danada Charm' appear to be suitable for spongy moth reproduction. With the above exceptions, all of the remaining *Ulmus* and *Zelkova* tested here do not appear to be suitable for spongy larval development and reproduction.

In conclusion, many of the aforementioned taxa are presently in the horticulture trade and are performing well as parkway and landscape trees due to their resistance to Dutch elm disease (DED), and elm yellows, and most sap-feeding and leaf-feeding insect pests (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 or high spongy moth, Japanese beetle, elm leaf beetle, elm leafminer, and elm flea weevil [*Orchestes ulmi* (Linnaeus, 1758)] populations (Miller 2000, Miller et al. 2001a,b, Condra et al. 2010, Potter and Redmond 2013, Griffins et al. 2017). Elm and *Zelkova* spp. selections should be based on hardiness zones and growth characteristics when planning for future urban tree and landscape plantings, and overall performance should be tempered with tolerance and/or resistance to local insect and disease pressure.

Some of the Asian elms species evaluated in this study including *U. szechuanica,* and *U. parvifolia* and cultivars, members of the David elm complex (i.e. *U. davidiana*, *U. japonica, U. propinqua*, and *U. wilsoniana*), North American taxa of *U. alata, U. crassifolia, U. serotina, U. thomasii*; European taxa of *U. glabra*, *U. microcarpa*, *U. rubra U. sukaczevii;* and *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 and their resistance to DED and herbivorous insect pests particularly where spongy moth populations are sporadic or absent (Ware 1992, 1995, Miller et al. 1999, 2001, Miller 2000, Warren 2000, Hartman, et al. 2007, Brady et al. 2008, McPherson et al. 2008, Dirr 2009, Condra et al. 2010, Potter and Redmond 2013, Griffin et al. 2017, Giblin and Gilman 2021). It is apparent that physical leaf factors do not play a major role in the susceptibility, suitability, and preference of Ulmaceae for spongy moth larval development and reproduction; therefore, more research is needed to better identify possible 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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