Suitability and Feeding Preference of Selected North American, European, and Asian Elm (*Ulmus* spp.) Biotypes to Elm Leaf Beetle (Coleoptera: Chrysomelidae)[1]

Fredric Miller[2] and George Ware[3]
The Morton Arboretum
4100 Illinois Route 53, Lisle, IL 60532

Abstract

Recently introduced North American elm cultivars, simple and complex elm hybrids of European and Asian parentage, and simple Asian hybrids of *U. pumila* and *U. japonica* parentage growing at The Morton Arboretum, Lisle, IL, were evaluated in laboratory bioassays for ovipositional response, and feeding preference and suitability for larvae and adults of the elm leaf beetle, *Xanthogaleruca luteola* (Müller). Larval and adult no-choice and adult multiple-choice feeding studies revealed that the North American cultivars of *U. americana* 'Jefferson' and *U. americana* 'Valley Forge', *U. americana* (diploid form), and *U. americana* were the least preferred for feeding and reproduction by the elm leaf beetle. Among simple and complex European hybrids, 'Homestead', 'Patriot', and 'Prospector' were least preferred and least suitable for larval development, feeding, and reproduction by adult elm leaf beetles. Hybrids of 'Frontier', 'Pioneer', and 'Regal'; the simple Asian hybrids of 'Cathedral' and 'New Horizon'; and *U. pumila* were more highly preferred for feeding and suitable for reproduction. The least preferred and least suitable North American biotypes of *U.* x *americana* 'Jefferson', *U. americana* 'Valley Forge', and *U. americana* (diploid form), simple and complex European hybrids of 'Homestead', 'Patriot', and 'Prospector', show promise for use in areas where the elm leaf beetle is persistent and for future elm breeding programs.

Index words: *Xanthogaleruca luteola*, elm leaf beetle.

Species used in this study: American elm (*U. americana* Linn.); smooth-leaved elm (*U. carpinifolia* Gleditsch); Scots elm (*U. glabra* Hudson); Siberian elm (*U. pumila* Linn.); 'Jefferson' elm (*U.* x *americana)*;'Valley Forge' elm (*U. americana)*; 'Frontier' elm (*U. carpinifolia* x *U. parvifolia)*; 'Homestead' elm (*U. pumila* x [(*U.* x *hollandica* 'Vegeta' x *U. carpinifolia*) x (*U. pumila-pinnato-ramosa* x *U. carpinfolia* 'Hoersholmiensis')]; 'Pioneer' elm (*U. glabra* x *U. carpinifolia*); 'Regal' elm (*U.* x *hollandica* 'Vegeta' x *U. carpinifolia*) x (*U. pumila* x *U. carpinifolia* 'Hoersholmiensis'); 'Patriot' elm ('Urban' elm x *U. wilsoniana* 'Prospector'); 'Prospector' elm (*U. wilsoniana)*; 'Urban' elm (N-148 (*U.* x *hollandica* 'Vegeta' x *U. carpinifolia*) x *U. pumila*); *U. glabra* 'Camperdownii'; 'Sapporo Autumn Gold' elm (*U. pumila* x *U. japonica*); 'Cathedral' elm (*U. pumila* x *U. japonica)*; 'New Horizon' elm (*U. japonica* x *U. pumila).*

Significance to the Nursery Industry

With the recent development and acquisition of North American, European, and Asian elm biotypes, elms once again have the opportunity to grace our urban landscapes and forests. However, limited studies have been conducted on the insect resistance of North American and European elm cultivars, and certain simple and complex Asian hybrids. More specifically, very little is known about the susceptibility of these elm biotypes for the elm leaf beetle, Japanese beetle, *Popillae japonica* Newman, elm leafminer, *Fenusa ulmi* Sundevall, spring cankerworm, *Paleacrita vernata* (Peck), and fall cankerworm, *Alsophila pometaria* (Harris). Development and identification of North American, European, and Asian elm biotypes, resistant to Dutch elm disease (DED) and the aforementioned leaf-feeding insect pests will greatly add to our pool of elm genetic material for future elm breeding programs.

In this study, we report on the preference and suitability of 18 elm biotypes for elm leaf beetle larval development, and adult preference and suitability. The results presented here provide a more comprehensive data base of preference and suitability of North American, European, and Asian elm biotypes for the elm leaf beetle, and provide further direction for future elm breeding programs for resistance to elm leaf beetles and other leaf-feeding insect pests, eventually resulting in a reduction in the need for chemical pesticides.

[1]Received for publication February 5, 2002; in revised form March 21, 2002. The authors gratefully acknowledge **The Horticulture Research Institute, 1000 Vermont Avenue, NW, Suite 300, Washington, DC 20005**, for their support in partial funding of this project.

[2]Professor of Horticulture, Joliet Junior College, Agriculture & Horticulture Sciences Department, 1215 Houbolt Road, Joliet, IL 60431.

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

Introduction

Extensive breeding and selection programs have focused on insect-resistant trees for forest and landscape uses (1, 2, 3, 4, 9, 11, 23, 24, 25, 26, 32). United States Department of Agriculture genetic improvement programs are currently being carried out on elms with efforts concentrated on Dutch elm disease (DED) resistance (24, 27, 28, 29, 30, 31) but, more recently include resistance to the elm leaf beetle, *Xanthogaleruca luteola* (Müller).

The elm leaf beetle (*X. luteola* Müller) is a common defoliator of elms (*Ulmus* spp.) and is a significant pest affecting urban elm trees in most parts of the United States (33). It is originally from Europe and was imported into the United States in the 1830s.

Previous efforts have focused on the preference for and suitability of various elm species and their hybrids for feeding by elm leaf beetle (5, 6, 7, 8, 12, 13, 14, 15, 16, 18, 19, 20, 21, 34). In all of these studies, suitability was defined as the mean number of eggs laid per adult female beetle and mean percent of females ovipositing in no-choice feeding studies. Preference was defined as the mean percent of leaf tissue removed in multiple-choice feeding studies. Siberian elm, *Ulmus pumila* L. was highly preferred while Chinese elm, *U. parvifolia* Jacq. was least preferred. Miller and Ware (14, 15) and Hall (5) demonstrated that *U. japonica* Sarg. and *U. wilsoniana* Schneid. were somewhat intermediate in suitability.

To the best of the author's knowledge, only two previous studies have been conducted that include the insect resistance of North American and European elm biotypes (7, 12). In these studies, certain European species were found to be more suitable than North American or Asian species. In addition, very little is known about the susceptibility of the more recently developed and acquired North American cultivars, particularly for the elm leaf beetle, Japanese beetle, *Popillae japonica* Newman, (17) elm leafminer, *Fenusa ulmi* Sundevall, spring cankerworm, *Paleacrita vernata* (Peck), and fall cankerworm, *Alsophila pometaria* (Harris) (2, 22). Within the simple and complex North American, European, and Asian elm hybrids, Santamour and Bentz (24) state that *U. wilsoniana* 'Prospector' and 'Patriot' elm are resistant to elm leaf beetle and 'Frontier' has moderate resistance to the beetle. Townsend et al. (30) found 'Homestead' elm to be highly suitable for and preferred by the elm leaf beetle. In contrast, no mention is made of the relative susceptibility of 'Cathedral', 'New Horizon', 'Pioneer', 'Regal', and 'Sapporo Autumn Gold' (24). 'Urban' elm is reported to be somewhat susceptible to the elm leaf beetle (24, 30).

The experiment summarized here first examined the suitability of 18 elm biotypes for larval development of the elm leaf beetle. Second, adults reared from the larval suitability study were utilized in a no-choice study of these same elm biotypes. The results provide a more comprehensive picture of the suitability and preference of North American, European, and Asian elm biotypes for the elm leaf beetle and provide further direction for future elm breeding programs for resistance to elm leaf beetles and other leaf feeding insects such as the Japanese beetles, elm leafminer, and spring and fall cankerworms.

Materials and Methods

No-Choice larval suitability laboratory bioassay. Biotypes used in all studies are listed in Table 1. We used newly emerged and unfed elm leaf beetle (*X. luteola*) larvae hatching from eggs laid on the foliage of *U. pumila* seedlings. These seedlings were growing in 7.6-liter pots and covered with light screen mesh to prevent beetles from escaping. Seedlings were held in the laboratory at 25C (77F) and under 16:8 hr (L:D) photoperiod. Adult beetles were reared from late instar larvae and pupae collected from *U. pumila* trees at North Platte, NE, and shipped overnight to The Morton Arboretum, Lisle, IL. On arrival, these larvae and pupae were held in clear Plexiglas cages in an incubator at 25C (77F) and 16:8 (L:D) hr photoperiod. As adults emerged, they were released onto *U. pumila* seedlings and allowed to feed, mate, and oviposit.

For the host suitability test, we used 24-hr-old *X. luteola* larvae. Neonates of *X. luteola* initially cluster at or near the egg mass before initiation of feeding. These were randomly selected from an egg mass and transferred to a single leaf of the test elm that was placed in a plastic petri dish (0.6 × 10.0 mm). Ten such petri dishes were used for each single tree replicate and there were three trees per elm biotype. Petri dishes were placed into a clear plastic bag to retain moisture. The petri dishes were checked daily for larval mortality, evidence of feeding, prepupation, pupation, and adult emergence.

Candidate elm biotypes growing at The Morton Arboretum were approximately 2 m (6.6 ft) high and growing in 8 liter (2.1 gal) pots. Leaves for the bioassays were randomly collected from the trees from all four cardinal directions. The leaf samples included the terminal 15 cm (5.9 in) of elm branches. Only fully expanded leaves were used. Leaf samples were taken in this way to compensate for variation in leaf quality within trees. Leaf samples were held in cold-storage in plastic bags at 5C (41F) for a maximum of 2 days. Leaves collected from each test tree for each biotype were combined for the bioassays. Larval bioassays ceased when larvae died or when adults emerged.

Proportion of larvae pupating was calculated by totaling pupae on each tree of a given elm biotype. Larval suitability for each biotype was defined as the mean development time from larva to adult, mean proportion of larvae pupating, mean percent adult emergence, and mean pupal weight.

Table 1. North American elm cultivars, species and simple and complex elm cultivars of European and Asian parentage, and simple hybrids of *U. pumila* and *U. japonica* parentage evaluated in elm leaf beetle studies.

Biotype	Parentage
Study 1 — North American elm biotypes	
'Jefferson'	*U.* x *americana*
'Valley Forge'	*U. americana*
U. americana (diploid form)	
U. americana	
Study 2 — European elm species and simple and complex biotypes of European and Asian parentage	
'Frontier'	*U. carpinifolia* x *U. parvifolia*
'Homestead'	*U. pumila* x [(*U.* x *hollandica* 'Vegeta' x *U. carpinifolia*) x (*U. pumila-pinnato-ramosa* x *U. carpinfolia* 'Hoersholmiensis')]
'Pioneer'	*U. glabra* x *U. carpinifolia*
'Regal'	(*U.* x *hollandica* 'Vegeta' x *U. carpinifolia*) x (*U. pumila* x *U. carpinifolia* 'Hoersholmiensis')
'Patriot'	'Urban' Elm x *U. wilsoniana* 'Prospector'
'Prospector'	*U. wilsoniana*
'Urban' elm	N-148 (*U.* x *hollandica* 'Vegeta' x *U. carpinifolia*) x *U. pumila*
U. carpinifolia	
U. glabra	
U.glabra 'Camperdownii'	
U. pumila (reference species)	
Study 3 — Simple hybrids of *U. pumila* and *U. japonica* parentage	
'Sapporo Autumn Gold'	*U. pumila* x *U. japonica*
'Cathedral'	*U. pumila* x *U. japonica*
'New Horizon'	*U. japonica* x *U. pumila*

Adults emerging from the larval suitability experiment were placed in standard plastic petri dishes on leaves of the same test elms. Methods for this bioassay were conducted as previously described by Miller and Ware (19). Suitability for a biotype was defined as the mean number of eggs laid per female and the mean percentage of ovipositing females. Mean preovipositional period (POP), male longevity, and female longevity also were determined as previously described by Miller and Ware (14, 15, 16, 18, 19, 20, 21).

No-Choice adult suitability laboratory bioassays. No-choice laboratory feeding assays (14, 15, 17, 18, 19, 20, 21) were conducted on 2000 second generation (early-mid August) adult elm leaf beetles. Four North American elm biotypes, 10 species, simple and complex hybrids of European and Asian elm parentage, and three simple hybrids of *U. pumila* and *U. japonica* parentage were evaluated. *Ulmus pumila* is a highly preferred host of the elm leaf beetle, and served as the reference in all of the studies. Candidate elm biotypes and leaf sampling were identical to the study above, except that leaf samples were held in cold storage for a maximum of 2 days. Three individual trees of each elm biotype were evaluated.

Adult beetles emerged from field-collected third instars and pupae shipped overnight from sites in and around North Platte, NE. Upon arrival, the pupae were sexed and held under a photoperiod of 16:8 (L:D) hr at ca. 25C (77F).

One newly emerged, unfed male and one female were placed together in each of 10 plastic petri dishes (10.0 × 0.6 cm) with foliage from the test elms. Petri dishes were examined daily and the foliage inspected for evidence of feeding and oviposition. Fecundity and beetle mortality were recorded. Foliage was replaced every 2 days. Beetles that died within the first 3 days were replaced with newly emerged, unfed adults, to ensure that healthy beetles had an opportunity to feed on test elms. Petri dishes were placed in clear plastic bags to prevent drying of the foliage and were held under a photoperiod of 16:8 (L:D) hr at ca. 25C (77F). Condensation of water on the lid of the petri dish indicated a high relative humidity. Each of the 3 trees for every biotype was assayed with 10 pairs of beetles. Bioassays were terminated after 21 days.

Mean number of eggs laid per female was calculated by totaling all of the eggs laid by each adult female in each individual petri dish within a given biotype during the 21-day study. We also determined the overall percentage of females that oviposited on each biotype, and the mean preovipositional period. Male and female longevity from the date that the beetles were introduced to the foliage was also determined. Adult beetles that were still alive at the end of 21 days were assigned longevities of 21 days. The measure of suitability for each biotype was defined by the mean number of eggs laid per female and the mean percent of females ovipositing in the no-choice feeding study (14, 15, 16, 18, 19, 20, 21).

Multiple-Choice laboratory bioassay adult feeding study. A male/female pair of newly emerged, unfed, adult beetles was placed in each of 10 plastic petri dishes (15.0 × 0.6 cm). Each adult pair served as a replicate. Into each dish was placed four to five circular foliage discs (1 cm in diameter), 1 each of each biotype to be evaluated, evenly spaced and touching the outside perimeter of the dish. Beetles had access to all foliage sections. The petri dishes were examined daily for 7 days. Each day, the leaf discs were removed, replaced, and evaluated for percent leaf tissue removed by adult feeding. New foliage sections were arranged randomly each day. Percent leaf area removed was estimated visually (nearest 5%) using a defoliation template and recorded. Preference was defined using the results from the mean percent of leaf tissue removed in the multiple-choice feeding study (16, 18).

Statistical analysis. Proportional data were arcsin square root transformed to correct for non-normality. Measures of suitability and preference including mean eggs laid/female, percent females ovipositing, preovipositional period, male longevity, female longevity and percent leaf tissue removed were subjected to Analysis of Variance (ANOVA) using biotype as the main effect, followed by the Student-Newman-Keuls (SNK) multiple comparison test using SigmaStat for Windows (10). All data are presented as original means ± SEM.

Results and Discussion

No-Choice larval suitability laboratory bioassay for North American elm biotypes. The length of larval survival on North American biotypes was not significant with a range of 3 to 7 days (mean = 6 days) (Table 2). Larvae fed *U. americana* had a significantly longer larval to adult development time (46 days) compared to larvae fed *U.* x *americana* 'Jefferson' (26 days) and the reference species of *U. pumila* (31 days). A significantly greater proportion of larvae pupated when fed leaves of *U.* x *americana* 'Jefferson', and *U. pumila* (reference) compared with *U. americana* of seedling origin. Larvae fed *U. americana* 'Valley Forge' and the diploid form of *U. americana* failed to reach pupation. Significantly more adults emerged when fed *U.* x *americana* 'Jefferson' and *U. pumila* (reference) as compared to *U. americana*. There was no significant difference in pupal weights for larvae fed *U.* x *americana* 'Jefferson', *U. americana*, and *U. pumila* (Table 2).

All adults that emerged from larvae reared on *U.* x *americana* 'Jefferson' and *U. americana*, in study #1, were male beetles and thus no male/female pairings were possible resulting in no eggs being laid. Adult beetles reared from larvae fed *U. pumila* (reference) laid a mean of 75 eggs per female with 100% of females ovipositing (Table 3). Adult female beetles fed the reference species, *U. pumila*, had a mean preovipositional period of 7 days, and male and female beetles each lived 21 days. This is consistent with previous studies (14, 15, 16, 18, 19, 20, 21) (Table 3).

No-Choice larval suitability for European elm species and simple and complex biotypes of European and Asian elm parentage. Elm leaf beetle larvae lived significantly longer when fed 'Pioneer' than on the remaining ten elm biotypes; and lived the shortest time on 'Prospector' (2 days). Among European and Asian biotypes in study #2, development from larva to adult was significantly longer (30 days) on 'Patriot' elm compared to the other 10 biotypes (22–24 days; mean = 23 days) (Table 2). A significantly smaller proportion of larvae reached pupation when fed 'Patriot' and *U. carpinifolia* compared to 'Pioneer', 'Frontier', and 'Regal', and all larvae fed on 'Homestead' and 'Prospector' failed to pupate. Percent adult emergence was significantly higher on 'Frontier' and 'Pioneer', and intermediate on 'Regal', *U. glabra*, *U. glabra* 'Camperdownii', and *U. pumila*. The proportion of adults emerging was significantly lower on 'Patriot' and *U. carpinifolia*, and no adults emerged from larvae fed 'Home-

Table 2. Development of elm leaf beetle larvae feeding on North American elm biotypes, species and simple and complex biotypes of European and Asian elm parentage, and simple hybrids of *U. pumila* and *U. japonica* parentage.

Biotype[z]	Larval survival (days)	Development time (Larval to adult) (days)	Pupation (%)	Adult emergence (%)	Pupal weight (mg)
Study 1 — North American elm biotypes					
U. x *americana* 'Jefferson'	7 ± 1.5a	26 ± 2.3a	10 ± 0.2b	10 ± 0.2b	11.3 ± 1.0a
U. americana 'Valley Forge'	3 ± 0.0a	—[y]	—[x]	—[x]	—[x]
U. americana-diploid form	7 ± 0.9a	—[y]	—[x]	—[x]	—[x]
U. americana	5 ± 0.9a	46 ± 3.2b	3 ± 0.1a	3 ± 0.1a	11.0 ± 0.9a
U. pumila (reference)	7 ± 1.3a	31 ± 2.9a	17 ± 0.3b	17 ± 0.3b	11.6 ± 0.9a
Significance		<0.001	<0.001	<0.001	
Study 2 — European elm species and simple and complex biotypes of European and Asian elm parentage					
'Frontier'	6 ± 1.6ab	24 ± 0.8a	30 ± 1.0b	30 ± 1.0b	13.2 ± 0.9b
'Homestead'	3 ± 0.2ab	—[y]	—[x]	—[x]	—[x]
'Pioneer'	11 ± 2.0c	23 ± 0.4a	27 ± 0.9b	27 ± 0.9b	14.3 ± 0.6b
'Regal'	5 ± 1.0ab	24 ± 0.4a	23 ± 0.8b	20 ± 0.8ab	13.8 ± 0.5b
'Patriot'	4 ± 1.0ab	30 ± 1.2b	3 ± 0.0a	3 ± 0.0a	7.9 ± 0.5a
'Prospector'	2 ± 0.1a	—[y]	—[x]	—[x]	—[x]
U. glabra	5 ± 1.2ab	23 ± 1.0a	17 ± 0.7ab	13 ± 0.6ab	10.0 ± 0.5b
U. glabra 'Camperdownii'	8 ± 2.8bc	22 ± 0.9a	20 ± 0.7ab	20 ± 0.9ab	13.6 ± 1.1b
U. carpinifolia	5 ± 1.0ab	22 ± 0.9a	3 ± 0.0a	3 ± 0.0a	13.0 ± 1.1b
'Urban' elm	7 ± 2.4ab	—[y]	20 ± 0.7ab	0 ± 0.0a	16.5 ± 0.7b
U. pumila (reference)	8 ± 1.6bc	22 ± 0.6a	10 ± 0.9ab	10 ± 0.8ab	17.6 ± 0.3b
Significance	<0.001	<0.001	<0.001	<0.001	<0.001
Study 3 — Simple hybrids of *U. pumila* and *U. japonica* parentage					
'Sapporo Autumn Gold'	6 ± 2.7a	—	—	—	—
'Cathedral'	6 ± 1.2a	25 ± 2.1a	30 ± 0.8b	25 ± 0.9b	12.8 ± 1.1a
'New Horizon'	6 ± 0.9a	23 ± 1.6a	30 ± 0.8b	30 ± 0.8b	12.4 ± 1.2a
U. pumila (reference)	7 ± 1.4a	22 ± 1.7a	7 ± 0.6a	7 ± 0.6a	8.3 ± 0.4a
Significance	<0.001	<0.001	<0.001	<0.001	<0.001

[z]For each study, values ± SEM within columns within a study followed by the same letter are not significantly different (P = 0.05; Student-Newman-Keuls multiple comparison test).

[y]No larvae completed development.

[x]No larvae pupated.

stead', 'Prospector', and 'Urban' elm. Larvae fed 'Patriot' elm had a significantly lower pupal weight compared to the remaining eight European and Asian elm biotypes (Table 2).

Adult female beetles reared from larvae fed on 'Regal' laid significantly more eggs per female (mean = 155 eggs/female) compared to 'Frontier' (mean = 30 eggs/female) (Table 3). 'Pioneer' was intermediate in suitability with 99 eggs laid/female and no eggs were laid by females fed *U. carpinifolia*. All females laid eggs when fed 'Frontier' and 'Regal' but only 60% of females laid eggs on 'Pioneer' (Table 3). No adults emerged from larvae fed 'Homestead' and 'Prospector', and all beetles emerging from larvae reared on 'Patriot', *U. glabra*, *U. glabra* 'Camperdownii', and 'Urban' elm were males and thus no male/female pairings were possible (Table 3).

There was no significant difference in the preovipositional period (POP) for adult female beetles laying eggs on European and Asian elms and there was no significant difference in male and female longevity in this study (Table 3).

No-Choice larval suitability laboratory bioassay for simple hybrids of U. pumila *and* U. japonica *parentage*. In study #3, there was no significant difference in length of larval survival and larvae fed 'Cathedral' and 'New Horizon' had a similar larva to adult development time as those consuming the highly preferred species, *U. pumila*. Larvae fed 'Sapporo Autumn Gold' failed to pupate (Table 2). A significantly greater proportion of larvae pupated and emerged as adults when fed 'Cathedral' (> 25%) and 'New Horizon' (30%) compared to the reference species of *U. pumila* (7%). No adults emerged from larvae fed 'Sapporo Autumn Gold'. There was no significant difference in pupal weights for larvae fed 'Cathedral', 'New Horizon', and the reference species, *U. pumila* (Table 2.) Larval to adult development time and pupal weights for larvae fed *U. pumila* are consistent with previous studies (12,19).

There was no significant difference in the number of eggs laid per female for beetles fed 'Cathedral' (mean = 23 eggs/female) and 'New Horizon' (mean = 45 eggs/female). The rankings for percent female ovipositing were similar (Table 3).

There was no significant difference in the preovipositional period for adult female beetles fed 'New Horizon' and 'Cathedral'. Male beetles lived a significantly longer time when fed 'New Horizon' (mean = 21 days) compared to beetles fed 'Cathedral' (mean = 11 days). There was no significant difference in female longevity for female beetles fed either 'New Horizon' or 'Cathedral' (Table 3).

No-Choice laboratory adult feeding study for North American elm biotypes. Adult female beetles laid significantly more eggs per female on *U. americana* and the highly preferred host, *U. pumila,* as compared to < 6 eggs/female on 'Jefferson', 'Valley Forge', and the diploid form of *U. americana*. The ranking for percent of females ovipositing was similar to the ranking for the number of eggs laid/female (Table 4).

Table 3. Mean ± SEM number of eggs laid per female, percent females ovipositing, preovipositional period, male longevity, and female longevity for adult *X. luteola* reared in the larval suitability experiment.

Biotype[z]	N[y]	Eggs laid per female	Females ovipositing (%)	Preovipositional period (d)	Male longevity (d)	Female longevity (d)
Study 1 — Simple and complex biotypes of European and Asian parentage						
'Frontier'	2	30 ± 11.8a	100 ± 0.0b	13 ± 3.8a	21 ± 0.0a	21 ± 0.0a
'Pioneer'	2	99 ± 54.2ab	60 ± 0.2a	10 ± 0.3a	21 ± 0.0a	21 ± 0.4a
'Regal'	3	155 ± 69.6b	100 ± 0.0b	6 ± 0.7a	17 ± 3.7a	20 ± 1.3a
Study 2 — Simple hybrids of *U. pumila* and *U. japoncia* parentage						
'Cathedral'	1	23 ± 12.8a	75 ± 0.1a	12 ± 0.9a	11 ± 2.1a	17 ± 2.6a
'New Horizon'	2	45 ± 15.8a	100 ± 0.0a	9 ± 3.2a	21 ± 0.5b	20 ± 0.6a
U. pumila (reference)	3	75 ± 55.1	100 ± 0.0	7 ± 0.5	21 ± 0.0b	21 ± 0.1a

[z]For each study, values within columns within a study followed by the same letter are not significantly different (P = 0.05; Student-Newman-Keuls (SNK) multiple comparison test).

[y]Number of adult male/female *X. luteola* pairs reared from the larval suitability experiment.

There were no significant differences in the preovipositional period (POP) for beetles fed foliage from North American biotypes. Male and female beetles lived significantly longer when fed the reference species, *U. pumila* (14–16 days) compared with the four remaining *U. americana* cultivars (< 8 days). Within a given biotype, male and female beetles lived the same amount of time (± 2 days) (Table 4).

No-Choice laboratory adult feeding study for simple and complex biotypes of European and Asian elm parentage. In study #2, adult females beetles fed 'Frontier', 'Pioneer', and 'Regal' laid significantly more eggs (> 56 eggs/female) compared to beetles fed 'Homestead', 'Patriot', and 'Prospector' (< 10 eggs/female). The percentage of females ovipositing followed the same ranking for these same biotypes (Table 4).

There was no significant difference in the preovipositional period (POP) for adult females fed European and Asian biotypes. Within a given biotype, male and female beetles lived approximately the same number of days (mean = 7–8 days ± 1 day). Male and female beetles fed 'Regal' lived a significantly longer time (10–12 days, mean =11 days) compared with the remaining five cultivars, on which adult beetles lived 4–9 days (mean = 6 days) (Table 4).

Significantly more eggs were laid per female on the highly preferred host, *U. pumila* (102 eggs/female) compared to 'Sapporo Autumn Gold' (63 eggs/female), 'Cathedral' (21

Table 4. Mean ± SEM number of eggs laid per adult female, mean percent females ovipositing, preovipositional period, male longevity, and female longevity of *X. luteola* adults on North American elm biotypes, simple and complex elm biotypes of European and Asian elm parentage, and simple hybrids of *U. pumila* and *U. japonica* parentage.

Biotypes[z]	Mean eggs laid per female[y]	Female ovipositing (%)[y]	Preovipositional period (d)[y]	Male longevity (d)[y]	Female longevity (d)[y]
Study 1 — North American elm biotypes					
U. x *americana* 'Jefferson'	0 ± 0.0a	0 ± 0.0a	—	5 ± 0.5a	6 ± 0.6a
U. americana 'Valley Forge'	0 ± 0.0a	0 ± 0.0a	—	4 ± 0.4a	5 ± 0.3a
U. americana-diploid	5 ± 2.6a	10 ± 0.0a	8 ± 1.0a	5 ± 0.9a	7 ± 1.1a
U. americana	32 ± 13.1b	40 ± 0.0b	6 ± 0.8a	7 ± 0.7a	7 ± 0.6a
U. pumila (reference)	68 ± 14.3b	60 ± 0.0b	6 ± 0.9a	14 ± 1.8b	16 ± 2.6b
Significance	<0.0001	<0.0003		<0.001	<0.001
Study 2 — Simple and complex biotypes of European and Asian elm parentage					
'Frontier'	57 ± 17.8b	40 ± 1.0b	6 ± 0.8a	7 ± 0.7a	8 ± 0.7a
'Homestead'	9 ± 3.5a	30 ± 0.2ab	7 ± 0.7a	5 ± 0.5a	6 ± 0.6a
'Patriot'	1 ± 0.3a	20 ± 0.2ab	4 ± 0.3a	6 ± 0.6a	5 ± 0.5a
'Pioneer'	82 ± 21.2b	60 ± 1.1b	6 ± 0.8a	9 ± 0.8a	9 ± 0.8a
'Prospector'	0 ± 0.0a	0 ± 0.0a	—	5 ± 0.4a	4 ± 0.3a
'Regal'	75 ± 14.4b	63 ± 1.6b	6 ± 0.8a	10 ± 1.0b	12 ± 1.1b
Significance	<0.0001	<0.0001		<0.0001	<0.0001
Study 3 — Simple hybrids of *U. pumila* and *U. japonica* parentage					
'Sapporo Autumn Gold'	63 ± 24.3a	50 ± 1.1b	3 ± 0.3a	9 ± 0.8a	12 ± 1.0a
'Cathedral'	21 ± 9.0a	35 ± 0.4a	3 ± 0.3a	9 ± 0.8a	9 ± 0.9a
'New Horizon'	30 ± 10.0a	35 ± 0.4a	3 ± 0.3a	8 ± 0.7a	12 ± 1.2a
U. pumila (reference)	102 ± 20.1b	50 ± 0.6b	6 ± 0.7a	21 ± 2.0b	21 ± 2.0b
Significance	<0.0001	<0.0001		<0.0001	<0.0001

[z]For each study, values within columns within a study followed by the same letter are not significantly different (P = 0.05; Student-Newman-Keuls multiple comparison test).

[y]Mean eggs laid per female, percent females ovipositing, preovipositional period, male longevity, and female longevity are based on 10 male/female pairs of adult beetles for each of three individual trees per biotype.

eggs/female), and 'New Horizon' (30 eggs/female). The rankings for percent females ovipositing were similar to the rankings for the number of eggs laid/female (Table 4). There were no significant differences in the preovipositional period (POP) for beetles fed 'Sapporo Autumn Gold', 'Cathedral', 'New Horizon' or the reference species, *U. pumila*. Within a given biotype, male and female beetles lived the same length of time (± 3–4 days). Male and female beetles lived significantly longer (21 days) on the highly preferred *U. pumila* as compared to the other hybrids (Table 4).

Multiple-Choice laboratory adult feeding study. In study #1, the highly preferred *U. pumila* had significantly more leaf tissue removed (22%) compared to the other North American elm cultivars which had < 4% of leaf tissue removed. These results are consistent with the no-choice feeding studies where 'Jefferson', 'Valley Forge', and *U. americana* (diploid form) demonstrated low suitability (< 6 eggs laid/female) (Tables 3 and 4).

When the highly preferred host, *U. pumila*, was removed, in study #2, beetles consumed signficantly more leaf tissue from 'Valley Forge', the diploid form of *U. americana*, and *U. americana* compared to 'Jefferson'. Feeding preference was somewhat consistent with the no-choice feeding studies for these same species (Tables 3 and 4).

No significant difference in leaf tissue removed, was observed in study #3, when beetles were given a choice between 'Frontier', 'Pioneer', *U. glabra*, *U. glabra* 'Camperdownii', and *U. carpinifolia*. In the no-choice study, 'Frontier' and 'Pioneer' were more suitable (Tables 3 and 4).

In study #4, when adult beetles were given a choice between 'Homestead', 'Regal', 'Urban' elm, *U.* x *hollandica* 'Vegeta', and *U. carpinifolia*, beetles removed significantly more leaf tissue from 'Urban' elm and *U.* x *hollandica* 'Vegeta'. 'Homestead' was less suitable (mean = 9 eggs/female) in no-choice studies, but adult females laid significantly more eggs on 'Regal' (mean = 75 eggs/female) (Tables 3 and 4). Hall (5) and Hall and Townsend (6) found 'Urban' elm to have moderate to high suitability (31–151 eggs/female) and to be moderately preferred when presented with a choice between the highly preferred *U. pumila* and the less preferred *U. wilsoniania* and *U. parvifolia*. When beetles were offered a choice, 'Urban' elm was moderately preferred along with the highly preferred *U. pumila* and the less preferred *U. wilsoniana* and *U. parvifolia*.

When given a choice, in study #5, adult beetles removed a significantly greater amount of foliage from 'Urban' elm leaves as compared to 'Patriot' and 'Prospector' leaves. In the no-choice studies, 'Patriot' and 'Prospector' demonstrated very low suitability (< 2 eggs laid per female). 'Urban' elm has been shown to have high suitability and moderate preference for adult elm leaf beetles (5, 6).

In study #6, adult beetles feeding on 'Cathedral' and 'Sapporo Autumn Gold', removed significantly more leaf tissue than beetles fed 'New Horizon'. These results are not consistent with the no-choice studies where adult females fed 'Cathedral', 'New Horizon', and 'Sapporo Autumn Gold' laid means of 63 eggs/female, 30 eggs/female, and 21 eggs/female, respectively (Tables 3 and 4).

In the final study (#7), no significant difference in feeding preference was observed for beetles fed 'Frontier', 'Homestead', 'Pioneer', and 'Regal' and mean percent leaf tissue removed was < 6%. In no-choice studies, 'Frontier', 'Pioneer', and 'Regal' were found to be more suitable for egg laying (> 56 eggs laid per female) while 'Homestead' was found to be less suitable (< 10 eggs laid per female) (Tables 3 and 4).

Overall, results from the no-choice larval suitability; no-choice adult suitability, and multiple-choice adult feeding pref-

Table 5. Mean ± SEM percent leaf tissue removed in multiple choice bioassays by *X. luteola* on North American elm biotypes, European elm species and simple and complex biotypes of European and Asian elm parentage, and simple hybrids of *U. pumila* and *U. japonica* parentage.

Biotype[z]	Leaf tissue removed (%)
Study 1	
U. x *americana* 'Jefferson	0 ± 0.0a
U. americana 'Valley Forge'	0 ± 0.0a
U. americana-diploid form	3 ± 0.3a
U. americana	0 ± 0.0a
U. pumila (reference)	22 ± 0.4b
Significance	<0.001
Study 2	
U. americana 'Jefferson'	1 ± 0.0a
U. americana 'Valley Forge'	10 ± 0.5c
U. americana-diploid form	5 ± 0.3b
U. americana	4 ± 0.2b
Significance	<0.001
Study 3	
'Frontier'	1 ± 0.0a
'Pioneer'	7 ± 0.0a
U. glabra	5 ± 0.0a
U. glabra 'Camperdownii'	4 ± 0.0a
U. carpinifolia	3 ± 0.0a
Significance	<0.001
Study 4	
'Homestead'	2 ± 0.0ab
'Regal'	0 ± 0.0a
'Urban' elm	4 ± 0.0b
U. x *hollandica* 'Vegeta'	9 ± 0.0b
U. carpinifolia	0 ± 0.0a
Significance	<0.0001
Study 5	
'Prospector'	2 ± 1.1a
'Patriot'	1 ± 0.0a
'Urban'	21 ± 2.5b
Significance	<0.0001
Study 6	
'Cathedral'	21 ± 3.1b
'New Horizon'	12 ± 2.3a
'Sapporo Autumn Gold'	21 ± 2.5b
Significance	<0.0001
Study 7	
'Frontier'	2 ± 0.8a
'Homestead'	2 ± 0.8a
'Pioneer'	5 ± 1.3a
'Regal'	3 ± 1.1a

[z]For each study, values within a column within a study followed by the same letter are not significantly different (P = 0.05; Student-Newman-Keuls (SNK) multiple comparison test).

erence studies are consistent. Elm biotypes that had low suitability for larvae and adults were also less preferred. The one exception occurred with the elm biotypes of European and Asian elm parentage, for example, 'Frontier', 'Pioneer', and 'Regal' were more suitable in the adult no-choice suitability studies, but were less preferred in the adult multiple-choice feeding preference studies. Santamour and Bentz (24) report that 'Frontier' has moderate resistance to elm leaf beetle.

The strong influence of *U. pumila* parentage on suitability in simple and complex hybrids is demonstrated in this study particularly with 'Sapporo Autumn Gold', 'Cathedral', 'New Horizon', and 'Regal' and is consistent with previous studies (14, 15, 19, 21).

'Prospector' and 'Patriot' both consistently demonstrated low suitability and preference in all of the studies conducted here and is consistent with a study by Townsend et al. (30) where female beetles feeding on 'Patriot' laid a mean of 53 eggs/female. In this study, female beetles laid a mean of one egg/female. The influence of *U. wilsoniana* in 'Prospector', a *U. wilsonsiana* cultivar, and 'Patriot', a complex hybrid containing *U. wilsonsiana*, is consistent with previous studies involving suitability and preference of *U. wilsoniana* for elm leaf beetles and larvae (6, 14, 15, 16, 19, 21, 30, 31).

Female and male longevity were very similar suggesting that host suitability had no effect in this study and is consistent with studies involving other Asian elm biotypes (14, 15, 16, 18, 19, 20, 21).

The lack of oviposition and failure of larvae to complete development on the North American elm biotypes of 'Jefferson' and 'Valley Forge', and the simple and complex biotypes of European and Asian elm parentage, namely 'Homestead', 'Patriot', and 'Prospector', suggest that all of these biotypes look promising for use in areas where there are chronic elm leaf beetle defoliation events. Long term studies are needed on their horticultural attributes and their use in landscapes and urban forest settings.

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