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Evaluation of Asian, European, and North American Elm (*Ulmus* spp.) Biotypes To Feeding by Spring and Fall Cankerworms[1]

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Abstract

Nearly 40 different Asian elm *(Ulmus* spp.) biotypes, growing at The Morton Arboretum, Lisle, IL, were evaluated in laboratory bioassays and in the field for suitability and feeding preference of the spring cankerworm *Paleacrita vernata* (Peck) and the fall cankerworm, *Alsophila pometaria* (Harris). No-choice and multiple-choice laboratory feeding studies, and field defoliation surveys revealed that *U. castaneifolia*, *U. changii*, *U. chenmoui*, *U. davidiana*, *U. elongata*, *U. gaussenii*, *U. glaucescens* var. *lasiophylla*, *U. japonica*, *U. lamellosa*, *U. lanceaefolia*, *U. macrocarpa*, *U. parvifolia*, *U. propinqua*, *U. propinqua* var. *suberosa*, *U. prunifolia*, *U. pseudopropinqua*, *U. taihangshanensis*, *U. wallichiana*, *U. wilsoniana*, *U. wilsoniana*-98, and the simple and complex hybrids *U. davidiana* x *U. japonica*, *U. davidiana* x *U. propinqua*, *U. japonica* x *U.* 'Morton'-Accolade™, *U.* 'Morton'-Accolade™ x *U. japonica-pumila*, *U.* 'Morton Glossy'-Triumph™, and *U.* 'Morton Plainsman'-Vanguard™ x *U. davidiana*, were less suitable for larval development and pupation and less preferred by spring and fall cankerworm larvae. *Ulmus americana*, *U. glaucescens*, *U. szechuanica*, and the simple and complex hybrids *U. davidiana* x *U.* 'Morton'-Accolade™, *U. szechuanica* x *U. japonica*, *U.* 'Morton'-Accolade™, *U.* 'Morton Red Tip'-Danada Charm™ and *U.* 'Morton Plainsman'-Vanguard™ were more suitable for and more preferred by spring and fall cankerworm larvae. Rankings for larval development time were highly correlated with larval longevity, but the proportion of larvae pupating was correlated neither with larval longevity nor with larval development time. Pupal fresh weights also were correlated neither with larval longevity nor with larval development time. Mean fecal pellet weights were correlated with the proportion of larvae pupating, but were not correlated with pupal fresh weights. *Ulmus chenmoui*, *U. glaucescens* var. *lasiophylla*, *U. lamellosa*, *U. macrocarpa*, *U. propinqua*, *U. prunifolia*, and *U. pseudopropinqua* all showed medium to heavy leaf pubescence and were less suitable and less preferred by spring and fall cankerworms. Asian elms were least preferred by cankerworm larvae, followed in order of increasing preference by European and North American elms.

Index words: spring cankerworm, fall cankerworm, suitability, preference, *Ulmus*, *Alsophila pometaria*, *Paleacrita vernata*.

Significance to the Nursery Industry

The research project reported here evaluated the suitability and preference of nearly 40 different elm biotypes for spring cankerworm *Paleacrita vernata* (Peck) and fall cankerworm, *Alsophila pometaria* (Harris) larval development. Spring and fall cankerworms have the potential to be serious leaf-feeding insect pests of nursery, forest, and landscape trees. Heavy populations of cankerworms can result in total defoliation of trees early in the growing season. Twenty Asian elm species and six simple and complex Asian elm hybrids were identified as being less suitable and less preferred by spring and fall cankerworm larvae. In addition, Asian elms, as a group, appear to be resistant to Dutch elm disease (DED). Many of the same species also are less suitable for the elm leaf beetle (*Xanthogaleruca luteola*), Japanese beetle (*Popilliae japonica*), and elm leafminer (*Fenusa ulmi*) all potentially damaging pests of nursery and landscape elms. Identification of elm biotypes resistant to DED and the above leaf-feeding insect pests will be a critical component of plant health care (PHC) strategies for elms. This wealth of Asian elm biotypes provides a rich source of genetic material for future elm breeding programs, reducing the need for insecticidal and fungicidal treatments.

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Introduction

Larvae of spring cankerworm, *Paleacrita vernata* (Peck), and fall cankerworm, *Alsophila pometaria* (Harris), are important pests primarily of elm (*Ulmus* spp.), apple (*Malus* spp.), oak (*Quercus* spp.), linden (*Tilia* spp.) and beech (*Fagus* spp.). Larvae are present in early spring and feed until mid June in a given year. When populations are heavy, feeding damage can be severe with entire trees being completely defoliated by early summer (1, 5). Repeated heavy defoliation by spring and fall cankerworms, during the critical photosynthetic period for the tree, can promote plant stress and require the tree to use valuable food reserves to refoliate. It is widely recognized and understood that stressed plants are more susceptible to invading secondary insect pests and plant pathogens. In some cases, these secondary invaders may be lethal to the tree. In addition, the presence of silk produced by the larvae and loss of the tree's aesthetic qualities due to severe defoliation can be very alarming and disconcerting to homeowners. Insecticidal sprays can be effective in preventing feeding damage, but they are not always practical or feasible for large trees in city and suburban landscape, park, and parkway plantings.

With the renewed interest and success in development of new elm cultivars for Dutch elm disease resistance (2, 14) and reduced feeding preference by the elm leaf beetle *Pyrrhalta luteola* Müller (6, 7, 8, 9, 11, 12) and Japanese beetle, *Popillia japonica* Newman (6, 10, 13), elms have the

potential once again to be a major focus in landscape and shade-tree plantings. In addition, the recent accessibility and procurement of Asian elm seed sources has added greatly to the number of potential elm (*Ulmus* spp.) biotypes available for breeding and hybridization (15, 16). Overall, Asian elms (*Ulmus* spp.) have proven to be resistant to Dutch elm disease and show varied resistance to the elm leaf beetle, Japanese beetle, and elm leafminer, *Fenusa ulmi* Sundevall (6, 7, 8, 9, 10, 11, 12, 13). The Asian hybrids *U.* 'Morton'-Accolade™, *U.* 'Morton'-Glossy-Triumph™, *U.* 'Morton Red Tip'-Danada Charm™, and *U.* 'Morton Plainsman'-Vanguard™ recently have been introduced into the nursery trade with more candidate elms to follow in the next several years.

Ulmus is considered a preferred host of spring and fall cankerworms. However, to the best of our knowledge, no study has examined the relative resistance of *Ulmus* species to feeding by spring and fall cankerworms, with the exception of the study by Dix et al. (3) on the feeding preference of spring cankerworm for Siberian elm, *U. pumila* L., clones. Therefore, we conducted a study with the following objectives: to conduct an initial screening of Asian, European, and North American elm (*Ulmus*) biotypes for relative resistance to feeding damage by spring and fall cankerworms; to determine if any Asian, European, and North American elm biotypes share comparable levels of resistance to spring and fall cankerworms as well as to elm leaf beetle, Japanese beetle, and elm leafminer; and to determine if Asian elm biotypes as a group are less preferred by spring and fall cankerworms relative to European, and North American elms.

Results from this study will give clearer direction and support to development of elm biotypes as part of a comprehensive breeding program for resistance to Dutch elm disease and to the elm leaf beetle, Japanese beetle, and elm leafminer.

Materials and Methods

No-choice laboratory larval feeding trials. No-choice larval feeding trials were conducted during the 1999 growing season, using first and early second instar larvae. Thirty-eight different elm biotypes were evaluated for relative resistance to larval feeding (refer to Table 1 for a listing of elms tested). Candidate elm biotypes were 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) 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 4 cardinal directions. The leaf samples included the terminal 15 cm (5.9 in) of elm 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 5C (41F) for a maximum of 2 days. Leaves collected from each test tree were combined for the laboratory bioassays. Three individual trees (replicates) of each elm progeny group were evaluated. *Ulmus americana* L., a preferred host of spring and fall cankerworms, served as the standard species.

First and early second instar larvae were used in the no-choice and multiple-choice feeding trials. The larvae were collected from infested *U. americana* trees at Hinsdale, IL, and at the elm collection at The Morton Arboretum, Lisle, IL, placed in plastic bags and transported to the laboratory. No attempt was made to separate fall and spring cankerworm larvae. A random sample of larval field populations revealed a 2:1 ratio of fall cankerworm to spring cankerworm larvae, respectively. Upon arrival at the laboratory, one larva was placed in each of 10 petri dishes (0.6 × 10.0 cm) with foliage from the test elm biotype. The petri dishes were examined daily for larval mortality, evidence of feeding, and pupation. Foliage was replaced every 2 days. Petri dishes were placed in clear plastic ziplock bags to prevent drying of the foliage and were held in an incubator under a photoperiod of 16:8 (L:D) at approximately 25C (77F). Each of the three trees (replicates) of each elm biotype was assayed with 10 individual larvae. The bioassay for a given larva was terminated at pupation. Larval longevity was the difference in days from the date the larvae were introduced to the foliage until death. Larval development time was the difference in days from introduction to the foliage until prepupation. At the time of pupation (within 12 hr), individual pupae were weighed (nearest 0.1 mg) 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 biotype for all three single tree replicates. At the termination of the no-choice larval feeding bioassay trial, the remaining leaf tissue in each petri dish was removed leaving only the fecal pellets. Fecal pellets were dried in an oven at 50C (122F) and then weighed (nearest 0.1 mg).

Multiple-choice laboratory larval feeding trial. About 10 first and early second instar spring and fall cankerworms were placed into each of 10 plastic petri dishes (0.6 × 15.0 cm). Each petri dish served as a replicate. A total of 7 studies were carried out. Depending on the study, four to seven leaf discs 2.54 cm (1 in) in diameter, with each disc representing one each of the different elm biotype choices, were placed into each dish and randomly arranged around the perimeter. Within each dish, the larvae had 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 ~25C (77F). Condensation of water on the lid of the petri dish indicated a high relative humidity. The dishes were examined daily for 5 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. For the fourth study, leaf trichomes were physically removed from the leaf of each elm biotype choice by using a glass slide and gently scraping the upper and lower leaf surfaces along the long axis of the leaf and then perpendicular to the long axis. Each leaf was examined under a microscope to ensure that the trichomes had been removed. A leaf disc 2.54 cm (1 in) in diameter was cut from the leaf as described previously.

1998–2000 field defoliation survey. In late June and early July of 1998, 1999, and 2000, a visual field defoliation survey was conducted on 43 different Asian, European, and North American elm biotypes growing in the elm collection and elm breeding nursery at The Morton Arboretum, Lisle, IL. Depending on availability, three to five trees were evaluated for each elm biotype.

Measures of suitability and preference. The measure of suitability of each elm biotype for spring and fall canker-

Table 1. Mean ± SEM of larval longevity, larval development time, percent pupation, pupal fresh weights, and dried fecal pellet weights for spring and fall cankerworms feeding on Asian elm (*Ulmus* spp.) biotypes, 1999.

Biotype[z]	Larval longevity days[y]	Larval development time, days[x]	Percent pupation	Pupal fresh weight (mg)	Fecal pellet weight (mg)
U. americana (standard)	6 ± 0.5ab	11 ± 0.6ab	43 ± 4.2b	28.6 ± 1.7b	22.9 ± 3.1b
U. bergmanniana	6 ± 0.5ab	7 ± 1.4a	0 ± 0.0a	—	9.3 ± 2.3ab
U. bergmanniana var. *lasiophylla*	5 ± 0.4a	7 ± 0.5a	7 ± 0.6a	32.0 ± 4.2b	10.7 ± 3.6ab
U. castaneifolia	7 ± 1.2b	—[w]	0 ± 0.0a	—	0.0 ± 0.0a
U. changii	6 ± 0.5ab	—	0 ± 0.0a	—	0.1 ± 0.1a
U. chenmoui	8 ± 0.8b	—	0 ± 0.0a	—	0.1 ± 0.1a
U. davidiana	7 ± 0.9b	—	0 ± 0.0a	—	0.7 ± 0.4a
U. davidiana x *U. japonica*	7 ± 1.1b	—	0 ± 0.0a	—	0.4 ± 0.3a
U. davidiana x *U. propinqua*	6 ± 0.6ab	—	0 ± 0.0a	—	0.0 ± 0.0a
U. davidiana x *U.* 'Morton'-Accolade™	15 ± 1.0c	21 ± 1.5c	27 ± 2.2b	27.9 ± 4.0b	34.1 ± 7.6b
U. elongata	6 ± 0.4ab	—	0 ± 0.0a	—	0.0 ± 0.0a
U. gaussenii	8 ± 0.6b	—	0 ± 0.0a	—	0.6 ± 0.4a
U. glaucescens	9 ± 0.6b	13 ± 0.7b	40 ± 3.5b	30.1 ± 1.8b	26.3 ± 4.0b
U. glaucescens var. *lasiophylla*	2 ± 0.0a	11 ± 0.0ab	0 ± 0.0a	5.6 ± 0.5a	5.6 ± 2.2a
U. japonica	7 ± 0.5b	—	0 ± 0.0a	—	0.0 ± 0.0a
U. japonica x *U.* 'Morton'-Accolade™	2 ± 0.0a	—	0 ± 0.0a	—	3.9 ± 1.8a
U. lamellosa	7 ± 0.6b	11 ± 2.1ab	7 ± 0.8a	41.6 ± 15.6b	15.6 ± 2.5ab
U. lanceaefolia	4 ± 0.2a	—	0 ± 0.0a	—	0.0 ± 0.0a
U. macrocarpa	6 ± 0.3ab	—	0 ± 0.0a	—	0.0 ± 0.0a
U. parvifolia	14 ± 0.8c	16 ± 1.0bc	10 ± 1.0ab	30.1 ± 13.2b	23.8 ± 5.5b
U. propinqua	10 ± 0.5b	14 ± 1.0b	0 ± 0.0a	—	0.9 ± 0.4a
U. propinqua var. *suberosa*	3 ± 0.1a	7 ± 1.7a	7 ± 0.9a	41.7 ± 31.4c	5.0 ± 2.3a
U. prunifolia	4 ± 0.2a	—	—	—	0.0 ± 0.0a
U. pseudopropinqua	1 ± 0.0a	—	0 ± 0.0a	—	0.0 ± 0.0a
U. pumila	1 ± 0.0a	16 ± 2.5bc	10 ± 1.0ab	17.8 ± 2.6a	13.5 ± 3.7ab
U. szechuanica	7 ± 0.4b	14 ± 0.5b	37 ± 2.9b	36.5 ± 3.0b	30.1 ± 4.5b
U. szechuanica x *U. japonica*	6 ± 0.3ab	16 ± 0.6bc	40 ± 3.7b	28.4 ± 2.8b	36.1 ± 4.5b
U. taihangshanensis	9 ± 0.7b	—	0 ± 0.0a	—	0.0 ± 0.0a
U. wallichiana	2 ± 0.0a	—	0 ± 0.0a	—	0.3 ± 0.1a
U. wilsoniana	9 ± 0.7b	—	0 ± 0.0a	—	1.4 ± 1.0a
U. wilsoniana-98	6 ± 0.2ab	—	0 ± 0.0a	—	1.4 ± 0.0a
U. 'Morton'-Accolade™	10± 0.9b	15 ± 0.7b	47 ± 4.2b	29.2 ± 2.4b	37.0 ± 4.7b
U. 'Morton'-Accolade™ x *japonica-pumila*	1 ± 0.0a	—	0 ± 0.0a	—	0.0 ± 0.0a
U. 'Morton Glossy'-Triumph™	7 ± 1.0b	—	0 ± 0.0a	—	0.0 ± 0.0a
U. 'Morton Red Tip'-Danada Charm™	7 ± 1.2b	16 ± 1.1c	47 ± 3.6b	28.3 ± 2.6b	28.8 ± 3.6b
U. 'Morton Plainsman'-Vanguard™	7 ± 1.1b	18 ± 1.5bc	43 ± 3.2b	19.6 ± 1.6a	37.0 ± 4.4b
U. 'Morton Plainsman'-Vanguard™ x *U. davidiana*	11± 0.6b	—	0 ± 0.0a	—	5.8 ± 2.4b
U. 'Morton Plainsman'-Vanguard™ x *U. japonica-wilsoniana-pumila*	11± 0.8b	20 ± 1.7bc	10 ± 0.0ab	51.8 ± 8.0 d	30.6 ± 3.8b
Significance	0.001	0.001	0.001	0.001	0.001

[z]Values within columns followed by the same letter are not significantly different (P < 0.05; Student-Neuman-Keuls (SNK) multiple comparison test).

[y]Larval longevity is the difference in days from the date the larvae were introduced to the foliage until death.

[x]Larval development time is the difference in days from introduction to the foliage until prepupation.

[w]None of the larvae reached the prepupal stage.

worm larvae was defined by mean larval longevity, mean larval development time, mean proportion of larvae pupating, mean pupal fresh weight, and mean dried fecal pellet weight in the no-choice larval feeding trials, and preference was measured using the mean proportion of leaf tissue removed in the multiple-choice larval feeding trials, and the percent field defoliation survey rating (PFDSR).

Statistical analysis. Measures of suitability and preference were subjected to analysis of variance (ANOVA) by using biotype as the main effect. Proportion of larvae pupating on each tree were arcsin transformed before analysis to correct for non-normality. Means of significant effect (5%) were compared with a Student–Newman–Keuls (SNK) multiple comparison test. A coefficient of correlation was calculated for the rankings for mean larval development time with mean larval longevity, mean proportion of larvae pupating, mean pupal fresh weights, and mean fecal pellet weights. All data are presented as original means ± SEM. Data were analyzed using SigmaStat for Windows (4).

Results and Discussion

No-choice laboratory larval feeding trial. Of the 38 Asian elm biotypes tested, spring and fall cankerworm larvae had the shortest longevity (<6 d, mean = 2 d) when feeding on the 11 biotypes of *U. bergmanniana* var. *lasiophylla* Schneider, *U. glaucescens* var. *lasiophylla*, *U. japonica* x *U.* 'Morton'-Accolade™, *U. lanceaefolia* Roxburgh, *U. propinqua* var. *suberosa* Koidzumi, *U. prunifolia* Cheng, *U. pseudopropinqua* Wang et Li, *U. pumila* L., *U. wallichiana* Planchon, and the complex hybrid *U.* 'Morton'-Accolade™ x *U. japonica-pumila*. Larvae lived the longest on *U. parvifolia* and the complex hybrid *U. davidiana* x *U.* 'Morton'-Accolade™ (>13 day, mean = 15 day) (Table 1).

Table 2. Mean percentage ± SEM of leaf tissue consumed by spring and fall cankerworm larvae in multiple-choice studies on Asian elm (*Ulmus* spp.) biotypes.

Biotype[z]	Mean percentage of leaf tissue consumed
Study 1	
U. japonica	64 ± 8.5b
U. pumila	88 ± 6.5b
U. davidiana	84 ± 6.7b
U. propinqua	67 ± 8.8b
U. davidiana x *U. japonica*	42 ± 9.7a
U. davidiana x *U. propinqua*	51 ± 9.6b
U. szechuanica	58 ± 10.0b
U. americana (standard)	76 ± 8.2b
Significance	< 0.003
Study 2	
U. glaucescens	75 ± 7.8ab
U. glaucescens var. *lasiophylla*	82 ± 6.6b
U. lamellosa	63 ± 8.1ab
U. macrocarpa	60 ± 8.4ab
U. propinqua	39 ± 9.0a
U. americana (standard)	93 ± 4.3b
Significance	< 0.0001
Study 3 (trichomes present)	
U. glaucescens var. *lasiophylla*	78 ± 9.9a
U. lamellosa	83 ± 8.7b
U. macrocarpa	71 ± 8.2a
U. americana (standard)	83± 11.6b
Significance	= 0.03
Study 4 (trichomes removed)	
U. glaucescens var. *lasiophylla*	91 ± 8.5b
U. lamellosa	83 ± 11.9b
U. macrocarpa	46 ± 12.2a
U. americana	49 ± 12.8a
Significance	= 0.02
Study 5	
U. japonica	72 ± 7.5c
U. pumila	60 ± 9.3c
U. wilsoniana	35 ± 7.7b
U. 'Morton'-Accolade™	25 ± 6.9a
U. 'Morton Glossy'-Triumph™	24 ± 8.3a
U. 'Morton Plainsman'-Vanguard™	58 ± 10.2c
U. americana (standard)	71 ± 8.6c
Significance	<0.0001
Study 6	
U. davidiana	89 ± 6.1b
U. davidiana x *U. japonica-wilsoniana-pumila*	62 ± 8.6ab
U. davidiana x *U.* 'Morton'-Accolade™	45 ± 8.1a
U. 'Morton'-Accolade™	61 ± 8.3ab
U. 'Morton Plainsman'-Vanguard™	73 ± 9.1a
U. 'Morton Plainsman'-Vanguard™ x *U. davidiana*	46 ± 8.0a
U. 'Morton Plainsman'-Vanguard™ x *U. japonica-wilsoniana-pumila*	64 ± 8.3ab
U. americana (standard)	96 ± 2.9b
Significance	< 0.0001

Table 2. Mean percentage ± SEM of leaf tissue consumed by spring and fall cankerworm larvae in multiple-choice studies on Asian elm (*Ulmus* spp.) biotypes (continued).

Biotype[z]	Mean percentage of leaf tissue consumed
Study 7	
U. changii	18 ± 7.5b
U. lanceaefolia	0 ± 0.0a
U. prunifolia	2 ± 0.2a
U. pseudopropinqua	1 ± 0.0a
U. taihangshanensis	1 ± 0.0a
U. americana (standard)	7 ± 1.8b
Significance	< 0.0005

[z]Values within a column followed by the same letter within a given study are not significantly different (P < 0.05; Student-Neuman-Keuls (SNK) multiple comparison test).

Larvae had the shortest development time when feeding on *U. bergmanniana* Schneider, *U. bergmanniana* var. *lasiophylla*, and *U. propinqua* var. *suberosa* (<8 days, mean = 7 days) compared to larvae feeding on *U. davidiana* x *U.* 'Morton'-Accolade™, *U. glaucescens*, *U. parvifolia*, *U. propinqua*, *U. pumila*, *U. szechuanica*, *U. szechuanica* x *U. japonica*, *U.* 'Morton'-Accolade™, *U.* 'Morton Red Tip'-Danada Charm™, *U.* 'Morton Plainsman'-Vanguard™, and *U.* 'Morton Plainsman'-Vanguard™ x *U. japonica-wilsoniana-pumila* (>12 d; mean = 16 d) (Table 1). Larval development time was significantly correlated with larval longevity ($R^2 = 0.33$; P = 0.02).

Larvae feeding on 23 of the 38 (61%) elm biotypes failed to pupate (Table 1). A significantly greater proportion of larvae pupated when feeding on *U. americana* (standard), *U. davidiana* x *U.* 'Morton'-Accolade™, *U. glaucescens*, *szechuanica* x *U. japonica*, *U.* 'Morton'-Accolade™, *U.* 'Morton Red Tip'-Danada Charm™, and *U.* 'Morton Plainsman'-Vanguard™ (>26%, mean = 36%) as compared to 3 biotypes with < 8% (mean = 7%) reaching the pupal stage (Table 1). The proportion of larvae pupating was not correlated with larval longevity ($R^2 = 0.07$; P = 0.12) nor with larval development time ($R^2 = 0.18$; P = 0.09) nor with pupal fresh weight ($R^2 = 0.12$; P = 0.67).

Larvae feeding on *U. americana*, *U. bergmanniana* var. *lasiophylla*, *U. davidiana* x *U.* 'Morton'-Accolade™, *U. glaucescens*, *U. lamellosa*, *U. parvifolia*, *U. propinqua* var. *suberosa*, *U. szechuanica*, *U. szechuanica* x *U. japonica*, *U.* 'Morton'-Accolade™, *U.* 'Morton Red Tip'-Danada Charm™, and *U.* 'Morton Plainsman'-Vanguard™ x *U. japonica-wilsoniana-pumila* had significantly greater pupal fresh weights (>27.0 mg, mean = 33.9 mg) compared to larvae feeding on *U. glaucescens* var. *lasiophylla*, *U. pumila*, and *U.* 'Morton Plainsman'-Vanguard™ with fresh pupal weights <20 mg (mean = 11.7 mg) (Table 1). Pupal fresh weights were correlated neither with larval longevity ($R^2 = 0.13$; P = 0.19) nor with larval development time ($R^2 = 0.00$; P = 0.95).

Fecal pellet weights for larvae feeding on the more suitable elm biotypes were significantly greater (>22.0 mg, mean = 30.7 mg) compared to larvae feeding on less suitable elms (<16.0 mg, mean = 1.2 mg) (Table 1). Fecal pellet weights were highly correlated with the proportion of larvae pupating ($R^2 = 0.82$; P < 0.0001), but fecal pellet weights were not correlated with pupal fresh weights ($R^2 = 0.02$; P = 0.64).

Table 3. Field defoliation survey ratings (FDSR's) for Asian, European, and North American elm (*Ulmus* spp.) biotypes for spring and fall canker-worm feeding damage.

Biotype[z]	Percent field defoliation survey rating[y]		
	1998	1999	2000
Asian Elms			
U. bergmanniana	—[x]	1.0 ± 0.1ab	0.8 ± 0.0a
U. bergmanniana var. *lasiophylla*	—	1.0 ± 0.0a	0.5 ± 0.1a
U. castaneifolia	0.0 ± 0.0a	0.0 ± 0.0a	0.6 ± 0.1a
U. chenmoui	1.0 ± 0.0ab	1.0 ± 0.1ab	0.8 ± 0.1a
U. davidiana	1.0 ± 0.0ab	1.0 ± 0.2ab	0.5 ± 0.0a
U. davidiana x *U. japonica*	1.0 ± 0.2ab	1.0 ± 0.0ab	0.5 ± 0.0a
U. davidiana x *U. propinqua*	0.9 ± 0.1ab	0.9 ± 0.0ab	0.3 ± 0.0a
U. davidiana x *U.* 'Morton'-Accolade™	0.0 ± 0.0a	0.0 ± 0.0a	0.5 ± 0.0a
U. gaussenii	0.8 ± 0.0ab	1.1 ± 0.2ab	0.4 ± 0.1a
U. glaucescens	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a
U. glaucescens var. *lasiophylla*	0.0 ± 0.0a	0.0 ± 0.0a	0.5 ± 0.1a
U. japonica	1.4 ± 0.4b	1.4 ± 0.4ab	0.8 ± 0.2a
U. lamellosa	0.3 ± 0.3ab	0.1 ± 0.0a	0.0 ± 0.0a
U. macrocarpa	0.0 ± 0.0a	0.0 ± 0.0a	0.5 ± 0.0a
U. parvifolia	0.3 ± 0.0a	0.2 ± 0.0a	0.2 ± 0.0a
U. propinqua	1.2 ± 0.0ab	1.1 ± 0.1ab	0.5 ± 0.0a
U. pumila	1.0 ± 0.0a	1.2 ± 0.1a	1.0 ± 0.3ab
U. szechuanica	1.0 + 0.0ab	0.9 ± 0.0ab	0.6 ± 0.1a
U. szechuanica x *U. japonica*	1.0 ± 0.0ab	1.1 ± 0.1ab	0.0 ± 0.0a
U. wilsoniana	1.4 ± 0.4ab	1.3 ± 0.2ab	1.7 ± 0.5b
U. 'Morton'-Accolade™	1.0 ± 0.0ab	1.2 ± 0.1ab	1.0 ± 0.2ab
U. 'Morton Glossy'-Triumph™	1.0 ± 0.0ab	1.1 ± 0.2ab	0.5 ± 0.1a
U. 'Morton Red Tip'-Danada Charm™	1.2 ± 0.2ab	1.0 ± 0.0ab	0.5 ± 0.1a
U. 'Morton Plainsman'-Vanguard™	1.0 ± 0.0ab	0.9 ± 0.1ab	0.5 ± 0.0a
U. 'Morton Plainsman'-Vanguard™ x *U. davidiana*	1.1 ± 0.0ab	0.9 ± 0.0ab	0.3 ± 0.0a
Mean	0.8	0.7	0.5
European Elms			
U. carpinifolia	2.6 ± 0.2b	2.5 ± 0.4b	1.5 ± 0.2ab
U. elliptica	0.2 ± 0.2ab	0.1 ± 0.0a	0.5 ± 0.0a
U. foliaceae	2.3 ± 0.3b	2.1 ± 0.2b	1.0 ± 0.0a
U. glabra	1.6 ± 0.6ab	1.3 ± 0.1ab	0.5 ± 0.0a
U. glabra-wallichiana x *U.* x *hollandica* 'Lobel'	2.0 ± 0.0ab	2.1 ± 0.2ab	2.0 ± 0.3b
U. glabra-wallichiana x open pollinated 'Dodoens'	1.0 ± 0.0ab	1.2 ± 0.1ab	1.0 ± 0.1a
U. laevis	1.8 ± 0.2ab	2.0 ± 0.2b	1.8 ± 0.2ab
U. procera	1.2 ± 0.4ab	1.3 ± 0.1ab	1.0 ± 0.1a
U. sukaczevii	1.0 ± 0.0ab	1.1 ± 0.1ab	2.3 ± 0.4b
U. x *hollandica*	2.4 ± 0.2b	2.2 ± 0.4ab	1.7 ± 0.2ab
Mean	1.6	1.6	1.3
North American Elms			
U. alata	1.2 ± 0.1a	1.0 ± 0.1a	0.0 ± 0.0a
U. americana	2.6 ± 0.2b	3.0 ± 0.3b	2.6 ± 0.4b
U. crassifolia	1.2 ± 0.1a	1.0 ± 0.1a	1.0 ± 0.1a
U. pumila x *U. rubra*	2.0 ± 0.0b	2.1 ± 0.2ab	1.5 ± 0.2a
U. rubra	2.0 ± 0.2ab	2.1 ± 0.2ab	2.0 ± 0.3ab
U. serotina	1.0 ± 0.0ab	1.3 ± 0.0ab	0.0 ± 0.0a
U. thomasii	2.7 ± 0.3b	2.5 ± 0.2b	0.5 ± 0.0a
Mean	1.8	1.9	1.1

[z]Values within columns followed by the same letter are not significantly different ($P < 0.05$; Student-Neuman-Keuls (SNK) multiple comparison test).
[y]PFDSR: 1 = very light (1–10% defoliation); 2 = light def. (11–20%); 3 = moderate def. (21–30%); 4 = heavy (31–50%); 5 = very heavy (>50% def.)
[x]Not surveyed due to a lack of available trees (replicates) in the field.

Multiple-choice laboratory larval feeding trial. In Study 1, *U. davidiana* x *U. japonica* was least preferred (42% of leaf tissue consumed) as compared to *U. japonica*, *U. pumila*, *U. davidiana*, *U. propinqua*, *U. davidiana* x *U. propinqua*, *U. szechuanica*, and *U. americana* (standard) where 51–88% of the leaf tissue was removed (Table 2).

In the second study, *U. propinqua* was least preferred (39% leaf tissue consumed) compared to *U. glaucescens* var. *lasiophylla* and *U. americana* (standard) with 82% and 93% leaf tissue consumed, respectively. *Ulmus glaucescens*, *U. lamellosa*, and *U. macrocarpa* were intermediate in preference with 60–75% leaf tissue consumed (Table 2).

Multiple-choice studies three and four evaluated the effect of trichomes and the removal of trichomes on larval feeding preference. In Study 3, larvae fed the least on *U. glaucescens* var. *lasiophylla* and *U. macrocarpa* compared to *U. lamellosa* and *U. americana* (standard) (Table 2). However, when trichomes were physically removed (Study 4), larval feeding preference shifted to *U. glaucescens* var. *lasiophylla* (91% of leaf tissue consumed) compared to *U. americana* (standard) and *U. macrocarpa*. Mean proportion of leaf tissue consumed was constant in both studies for *U. lamellosa* at 83% (Table 2). Overall, there was no significant difference in leaf tissue consumed for larvae feeding on leaf discs of *U. glaucescens* var. *lasiophylla*, *U. lamellosa*, and *U. macrocarpa* with trichomes present versus leaf discs with trichomes removed, for these same species.

Study 5 evaluated larval feeding preference for simple and complex hybrids with *U. japonica*, *U. wilsoniana*, and *U. pumila* parentage. Larvae fed the least on the complex hybrids of *U.* 'Morton'-Accolade™ (25% of leaf tissue consumed), and *U.* 'Morton Glossy'-Triumph™ (24% leaf tissue consumed) compared to *U. japonica*, *U. pumila*, *U. wilsoniana*, *U.* 'Morton Plainsman'-Vanguard™ and *U. americana* (standard) (Table 2).

Study 6 compared larval feeding preference of simple and complex hybrids with *U. davidiana*, *U. japonica*, *U. wilsoniana*, and *U. pumila* parentage. *Ulmus davidiana* x *U.* 'Morton'-Accolade™ and *U.* 'Morton Plainsman'-Vanguard™ x *U. davidiana* were least preferred (<47% leaf tissue consumed) as compared to *U. davidiana* and *U. americana* (standard) with 89% and 96% of leaf tissue consumed, respectively. The complex hybrids of *U. davidiana* x *U. japonica-wilsoniana-pumila*, *U.* 'Morton'-Accolade™, *U.* 'Morton Plainsman'-Vanguard™ x *U. japonica-wilsoniana-pumila*, and *U.* 'Morton Plainsman'-Vanguard™ were intermediate in preference (61–73% leaf tissue consumed) (Table 2). In Study 7, we evaluated the feeding preference of cankerworm larvae on newly acquired elms from temperate regions of China. *Ulmus changii* and *U. americana* (standard) were more preferred than *U. lanceaefolia Roxburgh*, *U. prunifolia* Cheng et L.K. Fu, *U. pseudopropinqua* Wang et Li, and *U. taihangshanensis* S.Y. Wang (<3% leaf tissue consumed) (Table 2).

1998, 1999, and 2000 field defoliation surveys. Overall, Asian elms were the least preferred (mean FDSR = 0.7, very light feeding damage). European elms had a mean FDSR = 1.5 (light feeding damage), and North American elms had a mean FDSR = 1.6 (light feeding damage) (Table 3). Within the European elms, *U. carpinifolia* Gled, *U. laevis*, and the hybrids *U. glabra-wallichiana* x *U.* x *hollandica* 'Lobel', and *U.* x *hollandica* showed (mean PFDR = 2.6) the highest PFDR's (1.5–2.0). Preferred North American elms included *U. americana*, and *U. thomasii* Sargent (mean PFDR = 1.9) (Table 3). Field defoliation survey ratings were not consistent with the no-choice larval feeding trials for the more highly preferred biotypes. (Tables 1 and 3). The least suitable species in the no-choice laboratory larval feeding trials (ie. *U. lamellosa*, *U. macrocarpa*) were more consistent with mean FDSRs of <1.1 (Tables 1 and 3). Rankings for the field defoliation survey were consistent over the three study year but slightly lower in 2000 (Table 3).

Leaf pubescence may play a role in feeding preference and suitability. Dix et al. (3) suggests that trichome density may influence the amount of leaf area consumed by spring cankerworm, *P. vernata* on certain *U. pumila* clones. In our study, *Ulmus chenmoui*, *U. glaucescens* var. *lasiophylla*, *U. lamellosa*, *U. macrocarpa*, *U. propinqua*, *U. propinqua* var. *suberosa*, *U. prunifolia*, and *U. pseudopropinqua* all have medium to heavy leaf pubescence and were least preferred by spring and fall cankerworms. These same three biotypes also are least preferred by the Japanese beetle and the gypsy moth (10).

As a group, Asian elm biotypes appear to be less preferred by the spring and fall cankerworm. Many of these same biotypes also show resistance to feeding by the elm leaf beetle, elm leafminer, and Japanese beetle (6, 7, 8, 9, 10, 11, 12, 13). Field defoliation studies indicate the European elm biotypes of *U. elliptica* and *U. glabra* are least preferred. Among North American elm biotypes, *U. serotina* and *U. thomasii* are least preferred as examined in this study. Further studies are needed to examine potential resistance of simple and complex hybrids including the above species.

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