Relative Susceptibility, Preference, and Suitability of *Carpinus* Taxa for the Japanese Beetle (Coleoptera: Scarabaeidae) [1]

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Abstract

Nineteen *Carpinus* taxa were evaluated in no-choice and multiple-choice laboratory feeding bioassays for susceptibility, preference, and suitability for the adult Japanese beetle (*Popillae japonica* Newman). No-choice laboratory feeding bioassays revealed that only three *Carpinus* taxa, *Carpinus caucasica* Grossh., *Carpinus tschonoskii* Maxim., and the hybrid *Carpinus caroliniana* x C. *coreana*, were significantly less susceptible and less suitable to feeding and for reproduction by Japanese beetles. Leaf tissue removed was related to the amount of frass produced, but was not related to leaf thickness, inner or outer leaf toughness, or fecundity. Frass production did not reflect fecundity. Hybridization may have either a positive or negative effect on host susceptibility, preference, and suitability. When a moderately preferred species such as *C. caroliniana* Walter or *C. betulus* L. is crossed with a species of equal or higher susceptibility, (i.e. *C. coreana* Nakai, Blume, or *C. laxiflora* (Sieb. and Zucc.) Blume) feeding preference increases. A "*C. tschonskii* factor" (Maxim.) appears to affect susceptibility and preference. There does not appear to be a large pool of *Carpinus* taxa suitable for future tree breeding programs in areas where Japanese beetle outbreaks are common. Potential use of *Carpinus* taxa in urban landscapes and forests is discussed.

Index words: Susceptibility, preference, suitability, Japanese beetle, *Popillia japonica*, *Carpinus*.

Species used in this study: *Carpinus betulus* L., *C. caroliniana* Walter, *C. caucasica* Grossh, *C. cordata* Blume, *C. coreana* Nakai, *C. fargesii* Franch, *C. japonica* Blume, *C. laxiflora*, (Sieb. and Zucc.) Blume, *C. orientalis* Mill, *C. tschonoskii* Maxim, *C. turczaninowii* Hance, *C. betulus* x *tschonoskii*, *C. caroliniana* x *betulus*, *C. caroliniana* x (*C. betulus* x *tschonoskii*), *C. caroliniana x cordata*, *C. caroliniana x coreana*, *C. caroliniana* x *orientalis*, *C. caroliniana* x *tschonoskii*, *C. caroliniana* x *coreana*, *C. cordata* x *C. japonica*, and, *Sassafras albidum* (Nutt.) Nees.

Significance to the Horticulture Industry

Nineteen *Carpinus* taxa were evaluated in a series of no-choice and multiple-choice laboratory feeding bioassays for susceptibility, preference, and suitability for the adult Japanese beetle (*Popillae japonica*). In this study, only *C. causica, C. tschonoskii,* and the hybrid *C. caroliniana* x *C. coreana*, were significantly less susceptible to feeding by adult Japanese beetles, the remaining *Carpinus* taxa being moderately to highly suitable for adult Japanese beetles. Feeding susceptibility does not appear to reflect feeding preference or reproductive suitability. Physical leaf traits such as leaf thickness and toughness do not present a clear picture of host suitability (i.e. fecundity). Additionally, hybridization may have both a positive and/or negative influence on host susceptibility, preference, and suitability. There appears to be a "*C. tschonskii* factor" affecting susceptibility and preference with the hybrids of *C. betulus* x *tschonoskii* and *C. caroliniana* x *tschonoskii* being less susceptible and less preferred. Based on the findings in this study, there does not appear to be a large pool of *Carpinus* taxa suitable for future tree breeding programs in areas where chronic Japanese beetle outbreaks are common. However, *C. betulus*, *C. caroliniana*, *C. cordata, C. japonica,* and *C. tschonoskii*, and their related hybrids, may have future breeding potential for use in areas where chronic Japanese beetle populations are low or rare due to their broad hardiness range, ability to tolerate varied soil conditions, minimal maintenance, and their use in landscape and urban forest replanting efforts.

Introduction

Since its introduction into the United States in the early 20th century, the Japanese beetle, *Popillia japonica* Newman, is still one of the most destructive and difficult nursery crop, landscape plant, and urban forest pests to control. Adult Japanese beetles feed on over 300 species of wild and cultivated plants including, but not limited to, members of the Rosaceae, Malvaceae, Vitaceae, Polygonoceae, Aceraceae, Ulmaceae, and Salicaceae (Fleming 1972, Held 2004, Ladd 1986, 1987, 1989, Potter and Held 2002). Highly preferred hosts include linden (*Tilia* spp.), sassafras (*S. albidum* (Nutt.) Nees) and purple plum (*Prunus cerostifera* Ehrh.*)*, all of which may be completely defoliated. Common to most woody landscape plants, host plant resistance for *P. japonica* is poorly documented (Raupp et al. 1992), with susceptible or resistant plant lists being compiled from anecdotal descriptions and field observations (Fleming 1972, Hawley and Metzger 1940). In addition, no-choice laboratory bioassays conducted by Ladd (1987, 1989) have revealed considerable variations in

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feeding preference by *P. japonica* among plant species listed by Fleming (1972) as being either favored hosts, minor hosts, or non-host species.

While there have been a number of studies evaluating the relative susceptibility and feeding preference of species, cultivars, and/or varieties of common Japanese beetle hosts, most of these have focused on ornamental landscape plants and shade trees. Held (2004), Miller and Ware (1999a), Miller et al. (1999), Miller et al. (2001b), and Rowe and Potter (1996) evaluated the susceptibility, preference, and suitability of species and cultivars of elm (*Ulmus* spp.), linden (*Tilia* spp.) crape myrtle (*Lagerstroemia* spp.), and crabapple (*Malus* spp.), for feeding by adult beetles. Further, feeding damage ratings for *P. japonica* were conducted by Ranney and Walgenbach (1992) on a wide selection of cultivars and varieties of birch (*Betula* spp.), cherry (*Prunus* spp.), and crabapple (*Malus* spp.) during one growing season. Spicer et al. (1995) found consistent differences in defoliation to 42 different cultivars of flowering crabapples and Potter et al. (1998), and Condra et al. (2010) observed significant relative differences in susceptibility for a variety of flowering crabapples, lindens, roses (*Rosa* spp.) and elms to defoliation by Japanese beetles.

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 hardwood species to the Asian long-horned beetle (ALB) (*Anoplophora glabripennis* Motschulsky), there is a critical need for the development and availability of new urban tree species for replanting in EAB- and ALB-affected areas, and to minimize the need for chemical protection from Japanese beetle feeding. To the best of our knowledge, no studies have been conducted on the susceptibility, preference, and suitability of recently acquired and developed *Carpinus* taxa of North American, European, and Asian parentage for feeding by adult Japanese beetles.

Therefore, the objectives of this study were to determine the relative susceptibility, feeding preference, and suitability of *Carpinus* taxa of North American, European, and Asian parentage for the adult Japanese beetle by conducting a series of no-choice and multiple-choice laboratory feeding bioassays, and to determine what role, if any, physical plant factors (i.e. trichomes, leaf thickness, and leaf toughness) may play in the relative susceptibility, preference, and suitability of *Carpinus* taxa for adult Japanese beetle defoliation. Results from this study will hopefully contribute to future tree breeding programs and the eventual use of *Carpinus* taxa in urban landscapes and forests, minimizing the need for application of chemical insecticides, and providing for a more diverse urban forest landscape.

Materials and Methods

Japanese beetle no-choice (NOC) laboratory feeding bioassays. A series of laboratory no-choice bioassay feeding studies were conducted on 19 different *Carpinus* taxa to determine their relative susceptibility to feeding by adult Japanese beetles as previously described by Miller and Ware (1999) and Miller et al., (1999, 2001b). Refer to Table 1 for a complete listing of *Carpinus* taxa evaluated. Sassafrass (*S. albidum*), a preferred Japanese beetle host, served as the standard reference (Fleming 1972). Candidate *Carpinus* taxa used in the study were growing in The Morton Arboretum (TMA) tree breeding nursery production area in Lisle, Illinois, and ranged in height from 2 to 4 m (6.6 to 13.1 ft), with diameters at breast height of 5.1-10 cm (2.0-3.9 in).

For the laboratory NOC and multiple choice (MC) bioassay feeding tests, approximately 40 fully developed *Carpinus* leaves, for each *Carpinus* taxon to be tested, were randomly selected from the terminal 15 cm (6 in) of each of four mid-canopy branches, from all four cardinal directions for each tree. The leaves were brought back to the TMA entomology lab and held in cold storage in plastic zip-lock bags at 5 C (41 F) for a maximum of 2 d. The leaves for each *Carpinus* taxon tested, from each single tree replicate, were combined for the NOC laboratory bioassays. Depending on availability, one to three single tree replicates of each *Carpinus* taxa were evaluated. Adult male and female Japanese beetles used in the NOC and MC feeding bioassays were field-collected from host plants growing on the grounds of TMA. Upon collection, the adult Japanese beetles were held in clear, 30 $\times$ 30 $\times$ 30 cm (12 $\times$ 12 x12 in), plexiglass cages under a photoperiod of 16:8 (L:D) at 25 C (7 F). While being held in the cages (no longer than 12 hours), the Japanese beetles were allowed to feed on fresh crabapple foliage to insure predisposition to feeding. Prior to the beginning of the feeding trials, the Japanese beetles were sexed and one adult male/female beetle pair was placed into each of 10 clear plastic petri dishes (10.0 by 0.6 cm) (4 by 0.23 in) along with foliage of the specific *Carpinus* taxon to be tested. Each Japanese beetle pair was used only once. Petri dishes were placed in clear plastic zip-lock bags to prevent drying of the foliage, and were held in an incubator-growth chamber under a 16:8 (L:D) photoperiod at $\sim$ 25 C. Condensation of water on the inner lid of the petri dish indicated a high relative humidity. There were 10 dishes (sub-replicates) for each of one to three single tree replicates per taxa for a total of 10 to 30 beetle pairs per taxa. Petri dishes were examined daily for beetle mortality and evidence of feeding. Foliage was replaced every 2 d. Old foliage was removed from the petri dish, and independently visually rated by two different individuals using a defoliation template to determine the percent leaf tissue (nearest 5%) removed. At the end of seven days, both the remaining foliage and fecal pellets were removed from each petri dish and the fecal pellets were oven dried and weighed (nearest mg). The measure of susceptibility for each *Carpinus* taxon was defined by the mean percentage of leaf tissue removed, and the mean dried fecal pellet weights. The bioassays were terminated after 7 days.

Japanese beetle multiple-choice (MC) laboratory feeding bioassays. As described previously by Miller and Ware (1999) and Miller et al. (1999, 2001b), one adult male/female beetle pair was placed into each of 10 plastic petri dishes (replicates) (15.0 by 0.6 cm). Three to five circular leaf disks 2.54 cm (1 in) in diameter were placed into and

Table 1. **Summary of mean percent leaf tissue removed, dry fecal weight, total eggs, and male and female longevity for adult Japanese beetles feeding on *Carpinus* taxa**

Taxa[z]	Mean % Leaf Tissue Removed	Mean Dry Fecal Weight (mg)	Total Eggs	Male Longevity	Female Longevity
Carpinus betulus	41±3.8b	13.5±2.9ab	20±0.9a	14±0.4a	14±0.6a
Carpinus betulus x *C. tschonoskii*	38±3.5b	14.0±4.5ab	95±1.8b	14±0.4a	14±0.6a
Carpinus caroliniana	52±3.6b	20.6±2.8bc	118±2.1b	13±0.6a	14±0.4a
Carpinus caroliniana x *C. betulus*	57±3.1c	20.9±2.5bc	108±2.1b	14±0.0a	14±0.4a
Carpinus caroliniana x (*C. betulus* x *tschonoskii*)	46±4.3b	26.9±2.4c	2±0.07a	14±0.3a	14±0.3a
Carpinus caroliniana x *C. cordata*	42±4.5b	28.9±4.1c	28±1.3b	21±0.0b	21±0.8b
Carpinus caroliniana x *C. coreana*	33±7.2a	13.8±2.0ab	6±0.1a	14±0.5a	13±0.7a
Carpinus caroliniana x *C. laxiflora*	50b±2.7	25.0±3.1c	1±0.2a	13±0.3a	14±0.7a
Carpinus caroliniana x *C. orientalis*	65±4.1c	23.3±4.2bc	6±0.15a	14±0.3a	14±0.4a
Carpinus carolinana x *C. tschonoskii*	50±2.8b	16.6±4.7ab	30±0.7b	14±0.2a	13±0.6a
Carpinus caucasica	25±3.9a	1.01±1.2a	10±0.2a	14±0.2a	14±0.1a
Carpinus cordata	47±5.1b	28.7±4.1c	3±0.2a	14±0.0a	14±0.4a
Carpinus cordata x *C. japonica*	64±4.1c	20.1±2.6ab	0±0.0a	21±0.0b	21±0.7b
Carpinus coreana	90±4.2d	34.7±3.0d	2±0.1a	7±0.1a	7±0.1a
Carpinus fargesii	77±6.1c	25.9±2.2c	0±0.0a	18±0.2b	19±0.2b
Carpinus japonica	90±4.6d	51.5±6.3e	21±1.1a	14±0.0a	15±0.7a
Carpinus laxiflora	45±3.6b	30.3±2.9d	87±1.6b	10±0.2a	10±0.2a
Carpinus tschonoskii	15±3.3a	7.0±2.2a	29±1.5b	7±0.3a	7±0.3a
Carpinus turczaninowii	74±3.3c	21.3±2.4ab	12±0.6a	17±0.2b	17±0.2b
Sassafrass albidum (preferred species)	90±3.5d	60.1±4.1e	200±3.9c	21±0.0b	21±0.0b
Blank			0±0.0a		
Significance	**F=10.1 P<0.001**	**F=43.6 P<0.001**	**F=23.8 P=0.002**	**F=101.9 P<0.001**	**F=104.8 P<0.001**

[z]Mean within columns followed by the same letter are not significantly different (Dunn's test; P<0.05)

randomly arranged around the perimeter of each dish, depending on the number of taxa to be evaluated for a given MC bioassay. The leaf tissue disks were cut from fresh fully mature leaves using a #10 cork-borer. Beetles had access to all foliage sections. The petri dishes were examined daily for 7 days. Each day, the foliage discs were removed from the dishes, replaced, and independently visually rated by two individuals for the amount of leaf tissue removed (nearest 5%) using a defoliation template. New foliage discs were arranged randomly in the dish each day to eliminate possible bias. The measure of preference for each *Carpinus* taxon tested was defined by the mean percentage of leaf tissue removed.

Leaf trichome multiple-choice (MC) laboratory feeding bioassay. In order to determine the effect of trichome density, on feeding preference, a MC study was conducted as described previously except that only *C. tschonskii* was tested in paired choices. *Carpinus tschonskii* was selected because it was the least preferred of all 19 *Carpinus* taxa tested, and was the only taxon that had pubescent leaves. Leaf trichomes were removed from the leaves using a glass microscope slide by gently scraping the upper and lower leaf surfaces exerting enough pressure to remove the trichomes but not enough to tear or rupture the leaf epidermis. Feeding preference was evaluated as described above.

No-choice NOC laboratory adult female fecundity bioassay. In order to assess the suitability of *Carpinus* taxa for Japanese beetle reproduction, a NOC laboratory fecundity bioassay was conducted. As previously described by Rowe and Potter (2000) and Ranney and Walgenberg (1992), one adult male/female pair of field-collected adult Japanese beetles was placed into a 5.7 L (6 qt) capacity ClearView™ plastic container (Sterilite®, Townend, MA) with a corresponding plastic lid with drilled holes to provide for air circulation and to minimize mold. Ten single plastic container replicates were used for each of one to three trees of each taxon tested, depending on availability, for a total of 10 to 30 Japanese beetle pairs. Prior to introducing the male/female Japanese beetle pair, approximately 5 cm (2 in) of finely sifted moist silt loam soil and foliage of the candidate *Carpinus* taxon were added to each plastic container. Foliage was kept turgid and fresh using a floral water pik and the soil was misted, as needed, to maintain moisture. The boxes containing the beetles and foliage were kept at room temperature (approximately 21 C or 70 F) in the laboratory under natural day length. The boxes were examined every third day for beetle mortality, and the foliage was replaced as needed. At 7, 14, and 21 days from the initiation of the experiment, the soil in each box was examined for eggs. The total number of eggs and Japanese beetle mortality for each plastic container was recorded. The fecundity study was terminated after 21 days.

Measuring Carpinus leaf toughness and thickness. Prior to using the leaves for the NOC laboratory feeding trials, each leaf was measured for leaf thickness, and inner and outer leaf toughness. Leaves were collected in the field as previously described. In the lab, 10 leaves of each taxon tested were used to determine leaf thickness and inner and outer leaf toughness. Leaf thickness was determined by measuring the thickness of each leaf (nearest micron) approximately one-half the distance from the leaf margin to the mid-rib using a Vernier caliper. Inner and outer leaf toughness was determined to the nearest gram using a Chatillon™ digital force meter (pentrometer) (Greensboro, N.C.) applied to within 0.5 cm (0.2 in) from the edge of the leaf for measuring outer toughness, and in the center of the leaf adjoining the mid-rib for inner toughness, respectively.

Measures of susceptibility, preference, and suitability. Measures of susceptibility for adult Japanese beetles feeding on *Carpinus* taxa was defined as the percent leaf tissue removed and dry fecal pellet weight in the NOC feeding bioassays. Preference was determined by the amount of leaf tissue removed in the MC feeding bioassays. Host suitability was determined by counting the total number of eggs laid per female (i.e. fecundity) and male and female longevity.

Statistical Analysis. Measures of susceptibility, preference, and suitability were subjected to analysis of variance (ANOVA) using taxon as the main effect. Means of significant effect (5%) were compared with the Dunn's test. Coefficients of correlation were calculated by regression analysis for the rankings for the mean percent leaf tissue removed with mean dry fecal pellet weight, leaf thickness, inner and outer leaf toughness, and fecundity; and fecal weight with fecundity. Percent leaf tissue removed for each taxon was arcsine transformed before analysis to correct for non-normality. All data are presented as original means $\pm$ standard error of the mean (SEM). Data were analyzed using the SigmaStat for Windows (Jandel Scientific 1992).

Results and Discussion

No-choice (NOC) feeding bioassays (Susceptibility). A summary of mean percent leaf tissue removed, mean dry frass weights, total eggs laid per female, and male and female longevity, for the 19 *Carpinus* taxa evaluated, is presented in Table 1. Two taxa, *Carpinus coreana,* and *C. japonica* were highly susceptible to feeding with 90% of the leaf tissue removed (F=10.1; $P<0.0001$). *Carpinus betulus*, *C. caroliniana*, *C. cordata*, *C. fargesii*, *C. laxiflora*, and *C. turczaninowii* and the hybrids of *C. betulus* x *tschonoskii, C. caroliniana* x *betulus*, *C. caroliniana* x (*C. betulus* x *tschonoskii*), *C. caroliniana x cordata, C. caroliniana x coreana, C. caroliniana* x *orientalis, C. caroliniana* x *tschonoskii,* and *C. cordata* x *C. japonica*, were moderately susceptible to feeding by adult beetles with a range of 38-77% (mean=58%) of leaf tissue removed. *Carpinus caucasica*, *C. tschonoskii* and the hybrid of *C. caroliniana* x *coreana* were the least susceptible to adult feeding with 15-33% (mean=24%) of leaf tissue removed (Table 1). The standard (highly preferred host) of *S. albidum* had 90% of the leaf tissue removed.

Dried fecal pellet weights (Susceptibility). There were also significant differences between *Carpinus* taxa for mean dry fecal pellet weights (F=43.6; P<0.0001) (Table 1). Adult Japanese beetles feeding on *C. caucasica* (1.0 mg) and *C. tschonoskii* (7.0 mg) produced significantly less frass compared to the highly susceptible taxa of *C. coreana* (34.7 mg), *C. japonica* (51.5 mg), and the highly preferred standard *S. albidum* (60.1 mg). Adult beetles feeding on the remaining *Carpinus* taxa produced intermediate fecal pellet weights ranging from approximately 13.5 to 30.3 mg (mean=21.9 mg) (Table 1). Mean percent leaf tissue removed was correlated with mean dry fecal pellet weight (R = 0.65; P=0.001).

Adult female fecundity (Suitability). Adult female beetles laid significantly fewer eggs (less than 22 eggs; mean=7 eggs) when feeding on *C. betulus, C. cordata, C. coreana, C. fargesii, C. japonica*, and *C. turczaninowii;* and the hybrids of *C. caroliniana* x (*C. betulus* x *tschonoskii*), *C. caroliniana* x *coreana*, , *C. caroliniana* x *laxiflora*, *C. caroliniana* x *orientalis*, and *C. cordata* x *japonica* compared to the highly preferred (standard) of *S. albidum* with a total of 200 eggs (F=23.8; P=0.002) (Table 1). The remaining *Carpinus* taxa were moderately suitable for egg production with a total of 28 to 118 eggs (mean=73 eggs) (Table 1). Adult female survival was 88% after seven days for beetles laying a total of at least 20 eggs or more and virtually all adult female oviposition occurred between seven and fourteen days of starting the study (data not shown). Adult female beetle survival on the remaining taxa was 30% and 23% after 14 and 21 days, respectively (data not shown). Male and female adult Japanese beetle longevity in the fecundity study was consistent with Japanese beetle longevity in the NOC feeding bioassays. Additionally, female fecundity was not related to the percentage of leaf tissue removed (R = 0.19; P=0.48) or the amount of frass produced (R = 0.11, P=0.69).

Adult male and female longevity (Suitability). In the NOC feeding bioassays, adult male and female Japanese beetles lived significantly longer (18 to 21 days) on the hybrids of *C. caroliniana* x *cordata* and *C. cordata* x *japonica*, *C. fargesii*, and the preferred host, *S. albidum* compared to Japanese beetles feeding on the remaining *Carpinus* taxa, which lived 7-14 days (male = F=101.9; P<0.001; female = F=104.8; P<0.001) (Table 1). Females feeding on the highly susceptible *C. coreana* (90% leaf tissue removed) and the least susceptible *C. tschonoskii* (15% leaf tissue removed) lived only one week, the same amount of time as the blank (starvation control). The reason for the shorter adult Japanese beetle longevity on the highly susceptible *C. coreana,* is not clear. In this study, the amount of *Carpinus* leaf tissue removed by adult Japanese beetles was correlated with frass production, but the amount of leaf tissue removed was not correlated with *Carpinus* leaf thickness or toughness. These findings are supported by the fact that *C. coreana* has much thicker leaves than *C. tschonoskii*, but both taxa have comparable leaf toughness. This suggests that adult longevity and subsequent Japanese beetle fecundity was more likely a function of leaf chemistry and the provision of adequate nutrition from the leaves than the physical leaf characteristics. However, leaf chemistry was not explored in this study.

Multiple-choice(MC) feeding bioassays (Preference). A summary of the 11 MC feeding studies is presented in Table 2. In MC-1, adult Japanese beetles removed significantly less leaf tissue when feeding on the *C. caroliniana* x *C. cordata* hydrid (32%) compared to the parents, *C. caroliniana* and *C. cordata,* with 53% and 70%,

Table 2. Multiple-choice (MC) feeding studies for adult female Japanese beetles feeding on *Carpinus* taxa

Taxa [z,y]	Mean % Leaf Tissue Removed
Study 1	
Carpinus caroliniana	53±7.5b
Carpinus caroliniana x *C. cordata*	32±5.6a
Carpinus cordata	70±6.7b
Significance	**P < 0.001 (F = 8.2)**
Study 2	
Carpinus caroliniana	24±6.9ab
Carpinus caroliniana x *C. coreana*	57±9.0b
Carpinus coreana	20±7.3a
Significance	**P = 0.002 (F = 12.9)**
Study 3	
Carpinus caroliniana	25±6.5a
Carpinus caroliniana x *C. laxiflora*	85±7.2b
Carpinus laxiflora	17±6.8a
Significance	**P < 0.001 (F = 24.0)**
Study 4	
Carpinus cordata	24±8.6a
Carpinus cordata x *C. japonica*	76±8.0b
Carpinus japonica	92±5.0b
Significance	**P < 0.001 (F = 19.9)**
Study 5	
C. betulus	41±7.9a
C. fargesii	27±7.6a
C. turczaninowii	86±6.7b
Significance	**P <0.001 (F = 22.8)**
Study 6	
C. caroliniana x *U. cordata*	8±4.9a
C. cordata	14±6.3a
C. coreana	36±8.5b
C. fargesii	17±6.7a
C. laxiflora	8±4.3a
Significance	**P <0.02 (F = 11.9)**
Study 7	
Carpinus betulus	22±6.9b
Carpinus betulus x *tschonoskii*	4±4.2a
Carpinus tschonoskii	4±4.1a
Significance	**P = 0.01 (F = 10.7)**
Study 8	
Carpinus caroliniana	65±4.9b
Carpinus caroliniana x *tschonoskii*	8±4.4a
Carpinus tschonoskii	6±4.3a
Significance	**P<0.0001 (F = 32.5)**
Study 9	
Carpinus betulus	23±7.5b
Carpinus betulus x tschonoskii	5±3.9a
Carpinus caroliniana	56±8.8c
Carpinus caroliniana x (*C. betulus* x *tschonoskii*)	5±3.5a
Carpinus tschonoskii	3±3.7a
Significance	**P<0.0001 (F = 41.5)**
Study 10	
Carpinus betulus	19±5.1a
Carpinus betulus x *caroliniana*	15±4.7a
Carpinus caroliniana	71±7.9b
Significance	**P<0.0001 (F = 41.5)**
Study 11	
Carpinus tschonoskii (with trichomes)	14±4.3a
Carpinus tschonoskii (with trichomes removed)	24±6.9a
Significance	**P = 0.06 (t = 787.5)**

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

[y]Means represent 10 petri dishes (replicates) containing one adult male-female beetle pair, and allowed to feed for 72 hours

respectively (F=8.2; P<0.001). These results are consistent with the no-choice feeding study results for these same taxa where beetles fed more on *C. caroliniana* and *C. cordata* compared to the hybrid (Tables 1 and 2). When given a choice in MC-2**,** adult beetles fed significantly less on *C. coreana* compared to the *C. caroliniana* x *C. coreana* hybrid, and *C. caroliniana* was intermediate in preference (F=12.9; P=0.002). The MC-2 results were the reverse of the NOC studies for these same taxa where the parent species, *C. caroliniana* and *C. coreana*, had 52% and 90% of leaf tissue removed, respectively. However, the *C. caroliniana* x *C. coreana* hybrid had the second lowest amount of leaf tissue removed after *C. tschonoskii* (Tables 1 and 2). Results from MC-3 revealed the hybrid *C. caroliniana* x *C. laxiflora* was highly preferred (85% leaf tissue removed) compared to the parent species of *C. caroliniana* and *C. laxiflora* (F=24.0; P<0.001) (Table 2) and were consistent with the NOC studies for the parent species. MC-4 revealed that both *C. japonica* and the hybrid *C. cordata* x *C. japonica* were highly preferred (76%-92% leaf tissue removed) compared to *C. cordata* alone (24% leaf tissue removed) (F=19.9; P<0.001). Consistent with the NOC feeding studies, *Carpinus cordata* experienced moderate feeding damage while *C. cordata* x *C. japonica* and *C. japonica* were heavily fed upon (64% to 90% leaf tissue removed) (Tables 1 and 2). The MC-5 study revealed *C. turczaninovii* is highly preferred compared to *C. betulus* and *C. fargesii* (F=22.8; P<0.001). All three of these *Carpinus* species were moderately to highly susceptible to feeding in the NOC studies (41% to 77% leaf tissue removed) (Tables 1 and 2). MC-6 examined preference between five moderate to highly susceptible *Carpinus* taxa. *Carpinus coreana* was the most preferred (36%) with significantly more leaf tissue removed compared to *C. caroliniana* x *C. cordata*, *C. cordata*, *C. fargesii,* and *C. laxiflora* (F=11.9; P<0.02). Results from MC-6 are consistent with the NOC feeding studies for these same taxa where *C. coreana* had the highest amount (90%) of leaf tissue removed (Tables 1 and 2). In MC-7, *Carpinus betulus* and the hybrid *C. betulus* x (*C. betulus* x *tschonoskii*) had significantly more leaf tissue removed compared to the hybrid *C. betulus* x *tschonoskii* and *C. tschonoskii* (F=10.7; P=0.01); the leaf tissue removed is consistent with the NOC feeding studies (Tables 1 and 2). In MC-8, *C. caroliniana* was clearly preferred over *C. tschonoskii* and the *C. caroliniana* x *C. tschonoskii* hybrid (F=32.5; P<0.0001). *Carpinus caroliniana* and the *C. caroliniana* x *C. tschonoskii* hybrid were both moderately preferred (50-52% leaf tissue removed) in the NOC study compared to *C. tschonoskii* alone (15% leaf tissue removed (Tables 1 and 2). Significantly more leaf tissue was removed by beetles in MC-9 when feeding on *C. betulus* and *C. caroliniana* compared to *C. tschonoskii* and their respective hybrids (F=41.5; P<0.0001). These same hybrids had less leaf tissue removed in the NC feeding trial (Tables 1 and 2). In MC-10, *C. caroliniana* was highly preferred over *C. betulus* and the hybrid *C. betulus* x *caroliniana* (F=41.5; P<0.0001). All three of these taxa were moderately preferred in NC feeding studies (Tables 1 and 2). Study MC-11 examined the presence or absence of

Table 3. **Summary of leaf thickness, and inner and outer leaf toughness of *Carpinus* taxa.**

		Toughness (gm)	
TAXA[z]	**Thickness (microns)**	**INNER**	**OUTER**
Carpinus betulus	250.00±25.0d	17.8286±5.9b	19.5657±1.0b
Carpinus betulus x (C. betulus x tschonoskii)	145.00±13.0ab	16.3657±4.8ab	14.4457±2.1ab
Carpinus betulus x C. tschonoskii	180.00±18.0b	19.5657±5.7bc	17.0057±2.5ab
Carpinus caroliniana	202.50±14.0c	17.3714±4.9b	15.0857±3.2ab
Carpinus caroliniana x (C. betulus x tschonoskii)	175.00±17.5b	15.2686±6.1a	13.8057±1.4ab
Carpinus caroliniana x C. cordata	202.50±40.2c	16.2743±5.2ab	16.9143±1.5ab
Carpinus caroliniana x C. coreana	222.50±44.1c	21.5771±5.6bc	23.3143±2.1c
Carpinus caroliniana x *C. laxiflora*	162.50±10.7b	16.6857±1.2ab	15.0400±1.2ab
Carpinus caroliniana x C. orientalis	212.50±11.0c	48.8343±14.6**c**	45.0743±5.4d
Carpinus carolinana x C. tschonoskii	190.00±9.5b	16.4571±4.2ab	14.7200±1.6ab
Carpinus cordata	145.00±11.6ab	21.0286±8.6bc	15.8171±2.1ab
Carpinus cordata x C. japonica	170.00±13.6b	16.0914±4.1ab	14.7200±2.0ab
Carpinus coreana	207.50±22.1c	19.4743±5.2bc	19.2000±1.8b
Carpinus fargesii	180.00±10.8b	19.8400±5.3ab	18.5600±1.6ab
Carpinus japonica	117.50±8.9a	9.9657±2.1a	8.9600±1.0a
Carpinus laxiflora	125.00±6.2ab	16.0000±4.0ab	14.9943±1.3ab
Carpinus orientalis	207.50±21.6c	27.8857±8.7bc	29.9886±3.2bc
Carpinus tschonoskii	157.50±10.9ab	16.9143±4.8ab	17.0057±1.6ab
Carpinus turczaninowii	207.50±21.1c	17.0057±4.2ab	15.3600±1.6ab
Significance:	**F=116.6 P<0.001**	**F=62.2 P<0.001**	**F=68.1 P<0.001**

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

trichomes on adult Japanese beetle feeding preference. Adult beetles fed less (14% of leaf tissue removed) on *C. tschonoskii* leaves with trichomes present compared to leaves where the trichomes had been mechanically removed (24% leaf tissue removed). The amount of leaf tissue removed in MC-11 (14%), with trichomes present, is consistent with the percent leaf tissue removed in the NOC (15%) and related MC (4%-6%) feeding studies (Tables 1, 2). Overall, feeding preference and host susceptibility were not related. However, (MC 6) was the only study in which the amount of leaf tissue removed by the hybrid *C. carolinana* x *C. cordata, C. cordata, C. coreana, C. fargesii*, and *C. laxiflora* strongly reflects the NC feeding bioassays for these same taxa (R = 0.90, P = 0.037).

Carpinus leaf thickness and toughness. A summary of leaf thickness and inner and outer leaf toughness of *Carpinus* taxa is presented in Table 3. *Carpinus betulus, C. caroliniana, C. orientalis* Mill., *C. turczaninowii*, and the hybrids of *C. caroliniana* x *C. cordata*, *C. caroliniana* x *C. coreana*, *C. caroliniana* x *C. orientalis, C. cordata* x *C. japonica* had significantly thicker leaves while *C. japonica* and *C. tschonoskii* had the thinnest leaves (F=116.6; P<0.001). Leaves of the hybrid *C. caroliniana* x *laxiflora*, and the species, *C. cordata*, and *C. laxiflora* were intermediate in thickness. Inner leaf portions of the hybrids *C. betulus* x *tschonoskii*, *C. caroliniana* x *coreana*, *C. caroliniana* x *orientalis,* and species, *C. betulus* and *C. cordata*, were significantly tougher than the inner leaf portions of *C. japonica* leaves. Inner leaf toughness for the remaining taxa was intermediate (F=62.2, P<0.001). Outer leaf toughness was less variable with only the leaves of *C. caroliniana* x *cordata* and *C. caroliniana* x *orientalis* being significantly tougher than *C. japonica* (F=68.1, P<0.001). Outer leaf toughness for the remaining *Carpinus* taxa was intermediate (Table 3). Leaf thickness was correlated with outer leaf toughness (R = 0.50, P=0.03), but was not related to inner leaf toughness (R = 0.40, P=0.09).

Effect of leaf thickness and toughness on feeding susceptibility, preference, and host suitability of Carpinus taxa. Percent leaf tissue removed was not related to leaf thickness (R = 0.08, P=0.77), inner leaf toughness, (R=0.01, P=0.97) or outer leaf toughness (R = 0.33, P=0.90). Additionally, leaf thickness (R = 0.09; P=0.79), inner leaf toughness (R = 0.08; P=0.74) and outer leaf toughness (R = 0.20, P=0.41) were not good predictors of fecundity.

Results from this study provide new insight into the relative susceptibility, preference, and suitability of *Carpinus* taxa for feeding and reproduction by adult Japanese beetles, and for the potential use of these taxa in an overall tree breeding program. The invasive, exotic Japanese beetle feeds on a wide variety of woody plant hosts, and variation in host susceptibility, preference, and suitability can be quite strong even within genera (Held 2004, Miller and Ware 1999a, Miller et al. 1999, 2001b, Potter and Held 2002, Potter et al. 1998, Ranney and Walgenbach 1992, Rowe and Potter 2000, Spicer, et al. 1995). Plants protect themselves from herbivores by using either physical plant traits, chemical defenses, or a combination of both, and that is likely the case with *Carpinus* taxa (Dalin and Bjorkman 2003, Doss et al. 1987, Fulcher et al. 1998, Hoxie et al. 1975, Johnson et al. 1980a,b, Matsuda and Senbo 1986, Meredith and Schuster 1979, Patton et al. 1997, Potter and Kimmerer 1988, Ranney and Walgenbach 1992, Rowe and Potter 2000, Ryan et al., 1982, Southwood, 1986, Tingey and Laubengayer 1986, War et al. 2012**).** Chemical analysis of the leaf tissue to investigate the influence on host susceptibility, preference, and suitability was beyond the scope of this study and was not examined; however, we did attempt to examine and will discuss possible physical plant traits (i.e. leaf thickness, toughness, and pubescence) of *Carpinus* leaves and their possible role in host susceptibility, preference, and suitability for adult Japanese beetles.

Susceptibility, preference and suitability of Carpinus taxa. In this study, only three *Carpinus* taxa, *C. caucasica, C. tschonoskii,* and the hybrid *C. caroliniana* x *C. coreana*, were significantly less susceptible to feeding by adult Japanese beetles, with the remaining *Carpinus* taxa moderately to highly susceptible for feeding by adult Japanese beetles. Further, feeding susceptibility and frass production do not appear to necessarily reflect feeding preference or reproductive suitability for the *Carpinus* taxa as evaluated in this study. For example, taxa evaluated in the MC studies were not necessarily the most preferred or more suitable for Japanese beetle reproduction. The reason(s) for the lack of correlation between host susceptibility, feeding preference, and reproductive suitability is/are not clear. Physical plant traits, such as leaf toughness and thickness, can be main factors affecting invertebrate feeding, and usually correlate with leaf fiber and lignin content (Graca and Zimmer 2005). Agrawal and Fishbein (2006) found leaf toughness could be used to predict herbivory of many plants including milkweeds (*Asclepias* spp.), and Raupp (1985) found that the toughness of willow (*Salix* spp.) leaves reduced leaf beetle feeding due to mandibular wear. Condra et al. (2010) and Miller et al. (1999) found that the thicker and tougher leaves of certain Asian elm species were much less susceptible to feeding by Japanese beetles both in the field and in no-choice laboratory bioassay feeding studies. Potter and Kimmerer (1988) found that the thick glabrous cuticle and tough leaf margins of American holly (*Ilex opaca* Aiton) leaves were more important than leaf margin spines in deterring edge-feeding caterpillars. In this study, leaf thickness and outer leaf toughness were weakly related ($R=0.50$, $P=0.03$), but leaf thickness and toughness were not reflective of host susceptibility or preference. For example, *C. betulus* and *C. caroliniana* leaves are similar, but *C. betulus* leaves are thicker in texture (Dirr 2009). Adult beetles feeding on the thicker *C. betulus* leaves, in both the NOC and MC feeding studies, removed a similar amount of leaf tissue as beetles feeding on *C. caroliniana* leaves. Conversely, Japanese beetles feeding on the thicker leaves of *C. coreana* and *C. turczaninowiii*, in the NOC feeding studies, removed 90% and 74% of leaf tissue, respectively, but when given a choice in MC-2 and MC-5, Japanese beetles removed only 20% of the leaf tissue when feeding on *C. coreana* compared with 86% for *C. turczaninowii*. Additionally, the thicker leaves of the hybrids of *C. betulus* x *C. tschonoskii, C. caroliniana* x *C. cordata, C. caroliniana* x *C. coreana, C. caroliniana* x *C. orientalis,* and *C. caroliniana* x *C. tschonoskii* were found to be moderately to highly susceptible to feeding by Japanese beetles. The thin and more-tender leaves of *C. laxiflora and C. japonica* ranged from moderate to high susceptibility for adult beetle feeding in the NOC, but when given a choice, preference was low for *C. laxiflora*, and high for *C. japonica*. Conversely, Rowe and Potter (2000) found that Japanese beetles fed the same on sun and shade rose leaves (*Rosa variety floribunda* 'Class Act') of equal toughness and on the thicker sun and thinner shade rose leaves. Similar conflicting results were reported by Keathley and Potter (2008) for both preferred and non-preferred hosts of Japanese beetle. It appears that leaf thickness and toughness are not good predictors of host feeding susceptibility or preference for *Carpinus* taxa.

Additionally, leaf thickness and toughness do not present a clear picture of host suitability (i.e. fecundity) and may or may not affect Japanese beetle reproduction. For example, adult beetles feeding on the thicker and tougher leaves of *C. coreana*, *C. fargesii*, *C. turczaninowii,* and the hybrids of *C. caroliniana* x *C. cordata,* and *C. caroliniana* x *C. coreana, C. caroliniana* x *C. orientalis* laid significantly fewer eggs (less than 30 eggs) compared to 40 to 60 eggs per adult female when feeding on a suitable host (Fleming, 1972). Japanese beetles feeding on the thinner and more-tender leaves of *C. japonica* and *C. cordata* also laid fewer eggs (less than 22 eggs). Conversely, adult beetles feeding on the thicker leaves of *C. caroliniana*, and the hybrids of *C. betulus* x C. *tschonoskii* and *C. caroliniana* x *C. betulus* laid three to four times as many eggs (118, 95, 108 eggs, respectively), and these taxa appear to be highly suitable for Japanese beetle reproduction. Keathley and Potter (2008) found that the fecundity of Japanese beetles feeding on the tougher leaves of susceptible Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch) was comparable to *S. albidum*, a highly preferred host, but they also reported that Japanese beetles feeding on the resistant and thin leaves of *Cornus florida* L. laid less than 15 eggs per cohort. In our study, fecundity for beetles feeding on *S. albidum* was comparable to egg production in the study by Keathley and Potter (2008). In contrast to Keathley and Potter (2008), in our study, beetles feeding on thinner and more-tender *C. laxiflora* leaves were significantly more fecund (87 eggs). It appears that physical leaf qualities other than thickness and toughness are more important for determining suitability for adult Japanese beetles.

Leaf trichomes may also help protect plants from insect herbivores, specifically as it relates to feeding, growth, survival, and oviposition. Feeding may be negatively correlated with trichome density, which is generally considered a "soft weapon" in plant defense compared to other plant traits (Dalin et al 2008, Levin 1973, 2006, Miller 2000, Miller and Ware 1999a, b, Miller et al. 2001a,b,c, Potter et al. 1998). Plants have the ability to produce glandular (chemical-producing) and non-glandular trichomes. They may vary in morphology and genetics, and even within individual plant species (Agrawal 1999, 2000, Dalin and Bjorkman 2003, Southwood 1986, Werker 2000). Non-glandular trichomes function in structural defense and have low nutritional value while glandular trichomes provide both structural and chemical defense and may contain terpenes and alkaloids that act as feeding deterrents or toxins (Levin 1973, Rautio et al. 2002, War et al. 2012). In this study, the low feeding susceptibility of the two pubescent taxa, *C. japonica* and *C. tschonoskii*, is consistent with other feeding studies which have demonstrated that the presence of simple and glandular leaf trichomes may act as a feeding deterrent and/or contribute to non-preference feeding and oviposition for adult Japanese beetles (Condra et al. 2010, Held 2004, Miller 2000, Miller and Ware 1999a,b, Miller et al. 2001b, Potter et al. 1998). In the aforementioned studies, leaves of *Tilia* and *Ulmus* taxa with thick trichome mats, long upright hairs, and moderate to dense leaf pubescence had less leaf area consumed compared to more glabrous leaves or leaves with very sparse trichome density. While feeding susceptibility and preference were not correlated in this study, several of the MC studies did reveal preference patterns that may be related to leaf pubescence and may be partially responsible for differences in susceptibility and preference. *Carpinus tschonoskii* possess pubescent (villous) leaves corrugated with silky hairs along the veins (Krussman 1976) while *C. japonica* leaves possess soft pubescent hairs on the upper and lower leaf surfaces only (Krussman 1976). In MC studies 7, 8, and 9, when given a choice, adult Japanese beetles removed significantly less leaf tissue when feeding on *C. tschonoskii* alone, or on the hybrids of *C. betulus* x *C. tschonoskii* and *C. caroliniana* x *C. tschonoskii*. In contrast, the soft pubescent hairs found on *C. japonica* leaves apparently do not provide enough of a feeding deterrent as this host was highly preferred in the no-choice and multiple-choice feeding studies.

Removal of leaf trichomes is known to increase feeding damage (Bauer et al. 1991, Fordyce and Agrawal 2001, Loe, et al. 2007). In MC study 11, adult Japanese beetles removed more leaf tissue (24%) when feeding on *C. tschonoskii* leaves where the trichomes had been physically removed, compared to leaves with trichomes present (14% leaf tissue removed). Our results are consistent with Miller and Ware (1999) and Miller et al. (2001b), who found that in single, paired multiple choice feeding studies, adult female Japanese beetles removed significantly more leaf tissue (21% to 33%) when trichomes were removed from pubescent Asian elm (*Ulmus* spp.) leaves. Since adult Japanese beetles skeletonize the leaves, leaving the main veins intact, the presence of leaf surface trichomes may have more of an effect on feeding susceptibility and preference compared to trichomes on the leaf veins and midrib.

The role of leaf pubescence in host suitability is not clearly understood. In this study, leaf and leaf vein pubescence appears to affect host suitability (i.e. fecundity) for adult female Japanese beetles when skeletonizing the pubescent leaves of *C. tschonoskii* and *C. japonica*. Further, the pubescent leaf veins of *C. cordata* also appeared to reduce host suitability but not feeding preference, suggesting that pubescent leaf veins and midribs may provide some level of protection. However, female fecundity on non-pubescent taxa of *C. betula, C. cordata, C. fargesii, C. japonica*, and *C. turczaninovii* was equally low. Miller, F. (unpublished data) found that adult female Japanese beetles feeding on pubescent *Tilia tomentosa* Moench., and *T. tomentosa* 'Erecta' leaves laid significantly fewer eggs compared to other less pubescent *Tilia* taxa. In another related study, they found that female beetles feeding on highly pubescent elms were more fecund compared to beetles feeding on less pubescent *Ulmus* taxa.

Male and female adult longevity was apparently not affected by host susceptibility or suitability. Fleming (1972), states that captive male and female beetles lived 9 to 74 days and 17 to 105 days, respectively. When the beetles were not fed or refrained from feeding, male beetles may live an average of seven days and females nine days (Fleming, 1972). In this study, with the exception of male and female Japanese beetles that lived seven days, feeding on the pubescent leaves of *C. tschonokii* and non-pubescent leaves of *C. coreana*, male and female adult longevity was very consistent (13 to 14 days) across all *Carpinus* taxa; some beetles lived up to 19 to 21 days on *C. fargesii,* the hybrid *C. cordata* x *C. japonica,* and the highly preferred *S. albidum*. Adult longevity in this study is similar to other studies for Japanese beetles feeding on susceptible *Rosa, Sassafras, Prunus*, *Tilia* and *Ulmus* taxa (Keathley and Potter 2008, Miller, F. (unpublished data), Miller 2000, Miller and Ware 1999a,b, Miller et al., 2001b, Rowe and Potter 2000). The reason for the shorter adult Japanese beetle longevity on the highly susceptible *C. coreana* is not clear. In this study, the amount of *Carpinus* leaf tissue removed by adult Japanese beetles was correlated with frass production, but the amount of leaf tissue removed was not correlated with *Carpinus* leaf thickness and toughness. *Caprinus coreana* has much thicker leaves than *C. tschonoskii*, but both taxa have comparable leaf toughness. This suggests that physical leaf characteristics may not be a factor in adult Japanese beetle longevity and subsequent fecundity. Results from this study suggest that the more susceptible and preferred *Carpinus* taxa are not necessarily the most suitable hosts for Japanese beetles. While these taxa may lack effective chemical leaf feeding deterrents, they may possess other chemicals that affect overall fecundity of adult female beetles and/or may not provide adequate nutrition for adult longevity even with moderate or extensive adult Japanese beetle feeding.

Hybridization, susceptibility, preference, and suitability of Carpinus taxa for adult Japanese beetles. Hybridization may have both a positive or negative influence on susceptibility, preference, and suitability for adult Japanese beetles, and may be polygenic, and not the result of single gene expression (Cheng et al., 2011, Fritz, et al., 1999, Paige and Capman, 1993). It is well known that secondary metabolites are a common chemical defense employed by plants against herbivorous insects and hybridization may increase the variation of secondary metabolites affecting herbivore resistance (Cheng et al. 2011, Fulcher et al. 1998, Orians 2000, Patton et al. 1997, Rieseberg and Ellstrand 1993). Most secondary metabolites (SMs) in hybrids may also be present in the parents, but hybrids may miss some parental secondary metabolites or have novel ones (Cheng et al. 2011, Lopez-Caamal and Tovar-Sanchez 2014, Paige and Capman 1993). For example, in the MC-2 and MC-3 feeding studies, the hybrids of *C. caroliniana* x *C. coreana* and *C. caroliniana x C. laxiflora* were moderately to highly preferred by adult Japanese beetles, respectively, while their respective parent species were much less preferred. In contrast, the parent species were observed to be moderately to highly susceptible in the NOC feeding study. While not examined in this study, it is possible that in the hybrids tested in MC-2 and MC-3, some secondary metabolites (SMs) that did act as feeding deterrents in the parents did not act as feeding deterrents in the hybrids. Another hypothesis is that novel SMs were formed in the hybrids that acted as less of a deterrent, resulting in higher feeding preference for the hybrids.

Additionally, there appears to be a "*C. tschonskii* factor" affecting susceptibility and preference. In the no-choice and multiple-choice feeding studies, *C. tschonskii* was one of the least susceptible species tested, and susceptibility and feeding preference decreased for the hybrids of *C. betulus* x *tschonoskii* and *C. caroliniana* x *tschonoskii*. The reason for this is not clear, but is probably related to the potential effects of hybridization outlined above, leaf chemistry, and to a lesser extent, leaf pubescence. A similar phenomenon, the "*U. pumila* factor" has been observed in elms (*Ulmus* spp.): when Siberian elm (*U. pumila* L.) is incorporated into hybrids with other taxa, it appears to affect the susceptibility, preference, and suitability of elms to extensive defoliating insect guilds including Japanese beetle, elm leaf beetle (*Pyrrhalta luteola* Muller), spring cankerworm (*Paleacrita vernata* Peck, fall cankerworm (*Alsophila pometaria* Harris), and elm leafminer (*Fenusa ulmi* Sundevall) (Condra et al. 2010, Miller and Ware 1994, 1997, 1999a, Miller et al. 1999, 2001a,b,c, 2014).

The results presented here and from others, focusing on physical leaf traits, strongly suggest there are other factors, such as leaf chemistry (Fulcher et al. 1998, Held 2004, Keathley and Potter 2008, Ladd, 1986, 1987, 1989, Paluch et al. 2008, Patton et al.,1997, Potter and Held, 2002, Potter et al. 1998, Ranney and Walgenbach 1992, Rowe and Potter 2000, Spicer et al. 1995), and hybridization (Cheng et al. 2011, Orians 2000, Patton et al. 1997, Rieseberg and Ellstrand 1993), that may be affecting the host susceptibility, preference, and suitability of *Carpinus* taxa for Japanese beetle feeding, longevity, and reproduction. Based on the findings in this study, there does not appear to be a large pool of *Carpinus* taxa suitable for future tree breeding programs in areas where Japanese beetle outbreaks are common. However, a few *Carpinus* taxa may have potential in areas where chronic Japanese beetle feeding level is absent or rare. With the exception of *C. caroliniana*, and the hybrids of *C. betulus* x *C. tschonoskii* and *C. caroliniana* x *C. betulus*, the vast majority of the *Carpinus* taxa tested here were susceptible to adult beetle feeding but not very suitable for Japanese beetle reproduction. In an ornamental or urban forestry landscape, moderate to heavy adult feeding would be a liability and unacceptable, but at the same time, a reduction in female reproductive capacity might offset the aesthetics of leaf-feeding damage and reduce the need for intensive and regular chemical host plant protection.

The *Carpinus* genera consist of a number of small to medium-sized deciduous trees which are distributed across the temperate regions of the northern hemisphere. Known for their hard wood, the majority of the species are common to Asia with several species native to Europe, and only two to eastern North America. Most are slow growing and can tolerate a wide hardiness range and a variety of soil conditions (i.e. moisture, pH, and texture) (Krussman 1976, Dirr 2009). *Carpinus coreana* (Korean hornbeam) is native to Korea and is a medium sized tree, hardy to Zone 5. *Carpinus fargesii* is a hardy fast-growing tree native to China, and like *C. laxiflora,* can thrive in a variety of soils, including heavy clays which are common in many urban soils. The Oriental hornbeam (*C. orientalis*) does quite well on calcareous and disturbed soils and is drought tolerant (Krussman 1976, Dirr 2009). Species such as *C. betulus, C. cordata*, and *C. tschonoskii* still may have utility in future plant breeding programs because of minimal maintenance (i.e. pruning) and their use as screens, hedges, and group plantings. Recently, Sjoman et al. (2019) determined that *C. betulus* and *C. orientalis* genotypes growing in the warmer and drier ecosystems of the Republic of Georgia may have a better use capacity than as an urban street tree in central and northern European cities. In order to make better use of the genotypic and phenotypic attributes of *Carpinus* taxa for use in urban and forest landscapes where chronic defoliation is common, further studies are needed to determine the factor(s) responsible for Japanese beetle feeding susceptibility and preference, and host suitability.

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