

DIFFERENTIAL FEEDING BY ADULT JAPANESE BEETLES ON FOLIAGE OF BIRCH (*BETULA*) SPECIES AND HYBRIDS

by Frank S. Santamour, Jr.

It is with great sadness that we mark the passing of Dr. Frank S. Santamour, Jr., Research Geneticist in the Floral and Nursery Plants Research Unit at the United States National Arboretum. Frank was well known to many, and he will be missed as a friend and colleague. Frank served on the editorial board of the Journal in the past, and was currently a member.

In more than 40 years as a professional scientist, Frank authored or co-authored about 275 publications, with more than 200 since he joined the U.S. National Arboretum in 1967. Frank was generally regarded as the world's leading authority on the genetics, breeding, and development of superior landscape trees. Among many other achievements, Frank used biochemical methods to examine graft incompatibility, insect and disease resistance, and to verify interspecific hybrids in several genera. His work on wound compartmentalization and on the correct usage of nomenclature to describe landscape trees was also well known. Frank was a frequent contributor to the Journal of Arboriculture.

Among his many activities and service to professional bodies, Frank was a longtime member of the International Society of Arboriculture (ISA). In addition to service on the Research Committee and the Research Trust of ISA, he was president of ISA's Mid-Atlantic Chapter for 1980–81 and president of ISA itself for 1984–85. He was co-founder of the Metropolitan Tree Improvement Alliance (METRIA) in 1975 and served as assistant director of METRIA for 1976–80, as well as twice acting as program chair.

—Editor

Abstract. Assessment of the relative resistance of various birches to foliar feeding by adult Japanese beetles was complicated by the insects' marked preference for leaves on spur shoots, as opposed to long-shoot leaves, on many trees. Based on the limited numbers of trees tested, the susceptible (most preferred) taxa were *Betula alleghaniensis*, *B. davurica*, *B. nigra*, *B. nigra* 'Heritage', *B. papyrifera*, *B. populifolia*, *B. pubescens*, *B. uber*, and *B. utilis* var. *jacquemontii*, although some resistant individuals of *B. papyrifera* and *B. populifolia* were found. Resistant taxa included *B. lenta*, *B. maximo-wicziana*, *B. pendula*, and *B. platyphylla* var. *japonica*. There was some indication that the factors influencing beetle feeding preferences were inherited.

Key Words. *Betula*; birch; Japanese beetle; *Popillia japonica*; resistance; selection.

Compared to the bronze birch borer (*Agrilus anxius* Gory) and the birch leafminer (*Fenusa pusilla* Lepeletier), the Japanese beetle (*Popillia japonica* Newman) might be considered a minor pest of birches in landscape plantings. Still, when adult Japanese beetle populations are high, the foliar feeding damage inflicted by these insects can be extensive and

unsightly, and can reduce the photosynthetic capacity of the tree. Surprisingly little is known about the relative susceptibilities of the major birch taxa to this polyphagous insect pest.

Most references (Hawley and Metzger 1940; Fleming 1972; Ladd 1987; Johnson and Lyon 1991) listed only the native American gray birch (*Betula populifolia* Marsh.) as being highly susceptible, but two (Fleming 1972; Ladd 1987) noted moderate feeding on the European silver birch (*B. pendula* Roth). More recently, Ranney and Walgenbach (1996) reported observations of beetle feeding on plants, about 1 m (3.3 ft) tall, of nine taxa growing outdoors in containers. Significant feeding occurred only on the American "trade clone" of *B. jacquemontii* Spach (this taxon is more properly classified as *B. utilis* D. Don var. *jacquemontii* Henry (Santamour and Lundgren 1996)). Little or no feeding took place on *B. ermanii* Cham., *B. nigra* L., *B. nigra* 'Heritage', *B. papyrifera* Marsh., *B. pendula*, *B. platyphylla* Suk. var. *japonica* (Miq.) Hara 'Whitespire', *B. platyphylla* var. *szechuanica* (Schneid.) Rehd., or *B. populifolia*.

Santamour and Lundgren (1996) have provided biochemical evidence that 'Whitespire' is really a selection of *B. populifolia*.

The tree genetics project at the U.S. National Arboretum (Washington DC, US) was heavily involved in the genus *Betula*, and thus it seemed reasonable to investigate the susceptibilities to Japanese beetle of some of the parent trees and hybrid progenies that had been used or developed over the years. Furthermore, in 1996, we had developed reasonable protocols (unpublished data) for laboratory assessments of Japanese beetle feeding in *Prunus*. Preliminary replicated studies on *Betula* in 1996 indicated that not only were there highly significant differences in feeding preferences among birch taxa, but similar differences were also exhibited within individual species. Another major finding was that, in some species, there were also significant differences in the amount of beetle feeding between leaves produced on spur shoots and leaves on long shoots on the same tree. It appeared reasonable to quantify and compare differences in beetle damage between species and individuals, the position, and possibly the age of the leaves. Therefore, in 1997, a study was undertaken to more extensively determine the relative susceptibilities of various birches to Japanese beetles.

MATERIALS AND METHODS

Most of the trees used in this study were growing on the grounds of the U.S. National Arboretum in Washington, DC or in test plots at Beltsville, Maryland. The only exceptions were those from the Morris Arboretum of the University of Pennsylvania in Philadelphia (MA-numbers) and from Fairmount Park in Philadelphia (F-numbers).

For all trees, branches were harvested in the field on two different dates, about 2 weeks apart, during the peak season of beetle activity, which occurs from the last week of June through the first week in August. These branches were placed in sealed polyethylene bags, transported to the laboratory in an ice-cooled insulated container, and used for beetle feeding tests on the same day. For each of two replicated trials for each tree, three fully expanded leaves were collected from near the midpoint of the current season's long shoot growth and three leaves were taken from short spur shoots that had developed on the previous year's long shoot. The leaf area that in-

cluded the petiole of each leaf was measured using a LI-COR LI-3100 area meter.

For feeding trials, the petiole of each leaf was immersed in water in a 14 × 45 mm (0.6 × 1.8 in.) shell vial plugged with a sponge to maintain leaf turgidity during the test. The leaf-containing vial was placed on its side on a moistened 9-cm (3.5-in.) diameter filter paper disk in a 150 × 25 mm (5.9 × 1 in.) plastic culture dish. The lid of the dish was kept slightly ajar to allow some air movement in the dish during the 24-hour test. The culture dishes were arranged at random on a laboratory bench, at room temperature (22°C [72°F]), under constant incandescent illumination.

Beetles were collected from traps on the arboretum grounds and separated by sex in the laboratory. Only female beetles were used in the feeding trials. Following sexing, the beetles were maintained without feeding for approximately 24 hours in culture dishes until used. Two female beetles were placed in each leaf-containing dish and were allowed to feed for 24 hours. At the end of this period, the leaves were removed from the dishes, cleaned of all debris, and the leaf area was determined once more. Thus, for each tree, the amount and intensity of feeding was determined on the basis of two replications of three spur leaves and three long-shoot leaves.

It was not deemed appropriate to subject the data from this comparative study to formal statistical analyses, thus precluding the accepted use of the terms "significant" and "nonsignificant." There are, however, biologically and esthetically meaningful differences in feeding preferences that will be presented in the tables and addressed in the following discussion.

RESULTS

Data are presented in Tables 1 through 4 on the amount of foliar tissue eaten and the percentage of leaf area removed by adult female Japanese beetles from the leaves of 33 individual trees during a 24-hour feeding period in the laboratory. The subgeneric classification scheme for birch taxa used here is that proposed by Vassiljev (1969) and outlined in the an earlier paper (Santamour 1999). The organization of the tables is intended to facilitate comparisons both within species and among species in the same breeding pool.

There is a pronounced tendency for beetle preference of spur leaves in several taxa and hybrids and

the variation among individuals of *B. populifolia* (Table 1). Trees of *B. populifolia* from Virginia (NST-6-82 (VA)) and Vermont (NST-7-82 (VT)), the extremes of its natural range, did not differ much in terms of the beetle's preference. It was unfortunate that tree NA 30958 had to be removed some years ago because of ice-storm damage since it was possible that this tree might have possessed some resistance to Japanese beetle. Its selfed progeny and intraspecific hybrids with a highly susceptible tree (NA 32427) showed decreased levels of beetle preference, and the hybrids (BE-27) could be considered resistant. Leaves of *B. pendula* and *B. platyphylla* var. *japonica* were fed on much less than the average tree of *B. populifolia*, and the hybrids between *B. populifolia* and these two taxa were similarly less preferred hosts. It should be noted, however, that the female parent of these interspecific hybrids was NA 30958, a no longer present *B. populifolia* tree that might have shown some resistance. It was informative that the foliage of a red-leaved segregate (Red 46-6) of the cross between *B. populifolia* and *B. pendula* 'Purpurea' was preferred over a green-leaved segregate (Green 45-7) since such a preference had been noted earlier for red-leaved crabapples (Spicer et al. 1995). Although no trees of *B. pubescens* had survived in our provenance tests, the high susceptibility of this species mentioned in earlier papers (Santamour 1979; Santamour and Clausen 1979) seemed to be inherited in hybrids with *B. populifolia*.

Data on beetle feeding on taxa on subg. *Neurobetula* are presented in Table 2. The field susceptibility of the trade clone of *B. utilis* var. *jacquemontii* noted by Ranney and Walgenbach (1992) was confirmed on trees growing in test plots and by our laboratory results. The young trees of *B. davurica* Pall. growing in test plots at the National Arboretum were not heavily attacked by the beetles, but laboratory data indicated that they may be highly susceptible. There was little difference between feeding on short-shoot and long-shoot leaves in the three taxa of this subgenus discussed above, but such a difference occurred in *B. nigra* and *B. nigra* 'Heritage'. Field observations of these two latter taxa on the arboretum grounds confirmed the beetle's preference for short-shoot leaves, but the intensity of feeding was not as high as that determined in the laboratory.

Table 1. Feeding of adult Japanese beetles on spur- and long-shoot leaves of *Betula populifolia*, *B. pendula*, *B. platyphylla* var. *japonica*, and hybrids of *B. populifolia*.

Plant identity	Amount of tissue eaten (cm ²)		% of leaf tissue eaten	
	Spur	Long	Spur	Long
<i>Betula populifolia</i>				
NST-6-82(VA)	6.65	0.13	61.0	0.7
NA 32427	9.86	2.41	57.8	11.8
NST-7-82(VT)	7.71	0.82	50.3	4.2
'Whitespire'(NA 60801)	6.10	1.30	38.6	7.0
NA 30958 × NA 32427 (BE-27-10)	3.33	1.16	23.6	6.7
NA 30958 × SELF (BE-24-4)	3.17	0.06	22.3	0.5
NA 30958 × NA 32427 (BE-27-9)	1.14	1.00	7.6	7.5
<i>Betula pendula</i>				
NST-398(10-3)	1.74	0.11	9.6	0.7
<i>B. platyphylla</i> var. <i>japonica</i>				
NST-397(14-2)	2.82	0.36	12.4	1.6
NST-400(14-3)	2.79	0.14	12.1	0.5
<i>B. populifolia</i> × <i>B. pendula</i>				
NA 30958 × NST-393 (BE-73-2-3)	0.96	0.12	7.2	0.9
NA 30958 × 'Purpurea' (Green 45-7)	1.47	0.08	8.7	0.3
NA 30958 × 'Purpurea' (Red 46-6)	3.04	0.49	24.3	3.2
<i>B. populifolia</i> × <i>B. platyphylla</i> var. <i>japonica</i>				
NA 30958 × NST-396 (BE-77-3-2)	3.28	0.74	14.1	2.8
NA 30958 × NST-396 (BE-77-3-4)	1.52	0.14	8.9	0.6
<i>B. populifolia</i> × <i>B. pubescens</i>				
NA 30958 × NST-405 (BE-80-6-9)	3.61	12.5	24.8	81.2
NA 30958 × NST-405 (BE-80-19-6)	7.34	6.68	50.9	48.2

Beetle feeding preferences on leaves of the three surviving trees (of 32) of *B. papyrifera* from our 1973 provenance test (Santamour and Clausen 1979) are given in Table 3. Two trees of Wisconsin origin (NST-386, 389) were similar in sustaining moderate and roughly equal feeding on both spur leaves and long-shoot leaves. Such equality of feeding was also found on a tree (NST-381) derived from open pollination of an arboretum specimen, but because of the low feeding levels, this tree is rated as resistant. Although the

Table 2. Feeding of adult Japanese beetles on spur- and long-shoot leaves of birch taxa in subg. *Neurobetula*.

Plant identity	Amount of tissue eaten (cm ²)		% of leaf tissue eaten	
	Spur	Long	Spur	Long
<i>B. utilis</i> var. <i>jacquemontii</i> (trade clone)	13.2	12.8	70.6	62.8
<i>B. davurica</i> (BJG-121)	6.19	5.10	62.2	49.8
<i>B. utilis</i> var. <i>jacquemontii</i> 'Jermyns'	10.4	10.2	32.4	35.1
<i>B. nigra</i> 'Heritage'	13.4	2.9	52.2	10.8
<i>B. nigra</i>	0.8	1.1	61.9	4.6

data for beetle feeding on *B. maximowicziana* Reg. foliage would indicate that this tree is also resistant, and it probably is, the appearance of the leaves was somewhat marred because of surface feeding that could not be detected with the LI-COR area meter. Both of the putative F₁ and F₂ hybrids between *B. maximowicziana* and *B. papyrifera* showed higher levels of beetle feeding, perhaps because of the increased genetic involvement of *B. papyrifera*. The putative F₁ hybrid between *B. platyphylla* var. *japonica* and *B. papyrifera* was grown from seed obtained from a Japanese botanic garden, and we had no knowledge of the trees involved in the cross. It is somewhat ironic that these putative hybrids of *B. papyrifera* with *B. maximowicziana* and *B. platyphylla* var. *japonica* had low levels of rhododendrin in their bark and have been selected for further propagation for resistance to the bronze birch borer (Santamour 1999). Apparently, it will be difficult to select trees resistant to both insect pests.

The taxa of subg. *Betulenta* listed in Table 4 were included in the beetle studies primarily because of observations the author had made in 1960–61 while examining and measuring the trees in a 1946 U.S. Forest Service plantation near State College, Pennsylvania. Notes from that study indicated that *B. alleghaniensis* Britt. was heavily attacked by Japanese beetles, while *B. lenta* L. was virtually untouched. Hybrids between these two species were preferred only slightly less than *B. alleghaniensis*. The fact that *B. alleghaniensis* is a hexaploid with 2n = 6x = 84 chromosomes and *B. lenta* is a diploid with 2n = 2x = 28 chromosomes would suggest a dominance of *B. alleghaniensis* traits in the hybrids. Our current labo-

Table 3. Feeding of adult Japanese beetles on spur- and long-shoot leaves of *Betula maximowicziana*, *B. papyrifera*, and hybrids involving these species.

Plant identity	Amount of tissue eaten (cm ²)		% of leaf tissue eaten	
	Spur	Long	Spur	Long
<i>B. maximowicziana</i> (MA 79-081-F)	2.21	0.52	5.3	1.4
<i>B. maximowicziana</i> × <i>B. papyrifera</i> -F ₁ (F-436)	9.31	4.61	23.4	13.4
<i>B. maximowicziana</i> × <i>B. papyrifera</i> -F ₂ (MA 79-080-B)	10.98	8.30	33.9	25.6
<i>B. papyrifera</i> NST-389(25-7)	9.82	10.63	37.8	42.4
NST-386(18-6)	8.46	7.15	34.2	28.6
NST-381(20-4)	0.92	1.00	3.6	3.6
<i>B. platyphylla</i> var. <i>japonica</i> × <i>B. papyrifera</i> NA 16574-1(F ₁)	15.83	16.47	60.0	55.3
BE-12 (F ₂)	11.32	13.26	38.5	48.5

Table 4. Feeding of adult Japanese beetles on spur- and long-shoot leaves of birch taxa in subg. *Betulenta*.

Plant identity	Amount of tissue eaten (cm ²)		% of leaf tissue eaten	
	Spur	Long	Spur	Long
<i>B. alleghaniensis</i> (NA 34710)	14.96	8.92	49.8	29.2
<i>B. uber</i> (NA 37939)	5.97	0.18	49.3	1.9
<i>B. lenta</i> (NA 34709)	5.45	0.06	18.0	0.3

ratory tests tended to confirm the author's earlier field observations on these two species. The rare Virginia round-leaved birch (*B. uber* (Ashe) Fern.) is an endangered species and its genetic relationship to the other taxa is unclear.

DISCUSSION

Most laboratory evaluations of insect preferences are highly artificial and represent worst-case scenarios rather than real-world situations. Such studies are necessary, however, since we seldom have the opportunity to examine "natural" feeding preferences during peak insect infestations in test fields containing a statistically designed mixture of important tree species.

Secondly, there is the matter of which statistic to use as a measure of preference (susceptibility) or non-preference (resistance). In the present study, we have provided data for both the total area of leaf tissue removed by beetles and the percentage of leaf area eaten. Another measure of preference is the weight of fecal pellets produced by the beetles during some standard feeding period (Ladd 1987), but we did not perform such analyses. The most meaningful measure of susceptibility may be the percentage of foliar tissue eaten because, when some critical point is reached, the damaged leaves may fall from the tree and litter the ground beneath it. Also, since we now know that there may be a marked preference for leaves on spur shoots as opposed to those on long shoots, there is the problem concerning the type of leaves to use for comparison. Based on the data in the tables, coupled with limited field observations, it appears reasonable to use some arbitrary measure of "total preference." Perhaps a tree could be considered susceptible if the percentage of leaf tissue consumed on either spur- or long-shoot leaves were over 50% or if the average of both types of leaves were higher than 20%. Using these criteria, 19 of the 33 trees would be classified as susceptible and the remainder as resistant. The to home owner or horticulturist, such subjective ratings of resistance or susceptibility, especially when no trees are actually "immune," might have to be translated into levels of damage, considered acceptable or unacceptable in the landscape.

CONCLUSIONS

Based on this study and on field observations, the following taxa, arranged in descending order of resistance, are less preferred by adult Japanese beetles: *B. maximowicziana*, *B. pendula*, *B. platyphylla* var. *japonica*, and *B. lenta*. The more preferred taxa are *B. papyrifera*, *B. uber*, *B. alleghaniensis*, *B. nigra* 'Heritage', *B. populifolia*, *B. nigra*, and *B. davurica*, with *B. utilis* var. *jacquemontii* the most susceptible. The degree of infraspecific variation that allowed the detection of resistant individuals of *B. papyrifera* and *B. populifolia* might be operative in other species as well, resulting in trees that are more preferred or less preferred than those studied in this test. Although there is a possibility that selective breeding might develop trees that were highly resistant to Japanese beetle feeding, such activity is not as important as

developing trees resistant to the bronze birch borer. Trees determined to be borer resistant should be evaluated for Japanese beetle preference. Studies must, and will, be undertaken to determine the basis, biochemical or otherwise, of the difference in beetle preferences for leaves on spur shoots and on long shoots of the same tree.

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Résumé. L'évaluation de la résistance relative ou de la susceptibilité de divers bouleaux à voir ses feuilles mangées par le scarabée japonais adulte est compliquée par les préférences marquées de l'insecte pour les feuilles sur les pousses latérales de plusieurs arbres par opposition aux feuilles des pousses terminales. En se basant sur la limite des arbres testés, les taxons susceptibles (les plus préférés) sont *Betula alleghaniensis*, *B. davurica*, *B. nigra*, *B. nigra* 'Heritage', *B. papyrifera*, *B. populifolia*, *B. pubescens*, *B. uber* et *B. utilis* var. *jacquemontii*, et ce même si certains individus de *B. papyrifera* et *B. populifolia* se sont montrés résistants. Les taxons résistants (ceux moins préférés) incluent *B. lenta*, *B. maximowicziana*, *B. pendula* et *B. platyphylla* var. *japonica*. Il y a certaines indications que les facteurs qui influencent les préférences d'alimentation du scarabée sont transmis génétiquement.

Zusammenfassung. Die Untersuchung der relativen Widerstandsfähigkeit verschiedener Birken gegenüber dem "Japan"-Käfer wurde durch die deutliche Präferenz des Käfers von Langtrieben gegenüber Kurztrieben verkompliziert. Basierend auf der begrenzten Anzahl getesteter Bäume, erwiesen sich *Betula alleghaniensis*, *B. davurica*, *B. nigra*, *B. nigra* 'Heritage', *B. papyrifera*, *B. populifolia*, *B. pubescens*, *B. uber* und *B. utilis* var. *jacquemontii* als sehr anfällig (höchste Präferenz), obwohl einige resistente Individuen von *B. papyrifera* und *B. populifolia* gefunden wurden. Die resistenten Arten schließen *B. lenta*, *B. maximowicziana*, *B. pendula* und *B. platyphylla* var. *japonica* ein. Es gab Hinweise darauf, daß die Faktoren, die die Präferenz des Käfers beeinflussen, vererbt sein können.

Resumen. Las evaluaciones de la resistencia relativa de ciertos abedules a la alimentación por escarabajos japoneses adultos se complica por la marcada preferencia de los insectos hacia los brotes cortos, en oposición a los largos, en muchos árboles. Con base en un número limitado de árboles probados, los taxa susceptibles (más preferidos) fueron *Betula alleghaniensis*, *B. davurica*, *B. nigra*, *B. nigra* 'Heritage', *B. papyrifera*, *B. populifolia*, *B. pubescens*, *B. uber*, y *B. utilis* var. *jacquemontii*. Sin embargo, se encontraron algunos individuos resistentes de *B. papyrifera* y *B. populifolia*. Los taxa resistentes fueron *B. lenta*, *B. maximowicziana*, *B. pendula*, y *B. platyphylla* var. *japonica*. Hubo alguna evidencia de que los factores que influyen en las preferencias alimenticias de los escarabajos fueron heredados.