

FREEMAN MAPLE — ILLUSION AND TRUTH

by Frank S. Santamour, Jr.

Abstract. The application of a scientific name, *Acer x freemanii*, to all hybrids between red maple (*A. rubrum*) and silver maple (*A. saccharinum*) has led to somewhat exaggerated expectations for the performance of Freeman maples in urban landscapes. In this paper, the author draws on 30 years of personal experience with more than 1,000 control-pollinated hybrids to present a more balanced view of the potential of Freeman maples. The difficulties of unequivocal verification of natural hybrids are also discussed.

In recent years, there has arisen a new wave of interest in hybrids between red maple (*Acer rubrum*) and silver maple (*A. saccharinum*) as potential superior trees for urban planting. Such hybrids are known collectively as Freeman maple (*A. x freemanii* E. Murray). Although many new selections and many older ("red maple") cultivars are currently being assigned to this hybrid group (2), none of these trees is the product of controlled hybridization. The identification of these Freeman maples has been based largely on the opinions of trained botanists and horticulturists. Most such diagnoses are probably "right". There is also the possibility that some identifications are "wrong", because of the high degree of morphological variability within both parental species, and the lack of knowledge of the particular parent trees involved in the cross. Whatever the case, and despite the admonitions of many authors that Freeman maples are highly variable, the idea that such hybrids are inherently superior (2 - and personal correspondence) has become prevalent.

Are hybrids between red maple and silver maple inherently superior? Do any hybrids from controlled pollination of known parents exist today? Are some of the parent trees still alive? Have any studies been made on the growth of such hybrids? Are there any non-morphological techniques that will aid in the identification of hybrids? This paper is an attempt to answer these questions.

In March, 1969, Edward Murray chose to distinguish hybrids between red maple and silver maple as *Acer x freemanii* E. Murray, "Hybrida Nova." The name and description, complete with Latin diagnosis, were printed (7) in his self-published, mimeographed "journal," *Kalmia*. The lack of a cited type herbarium specimen to accompany the description was rectified in June, 1969 (8) when he established the holotype (E. Murray #344) in the herbarium of the Morris Arboretum of the University of Pennsylvania in Philadelphia. Isotype specimens were deposited in the herbaria of the Arnold Arboretum of Harvard University in Jamaica Plain, Massachusetts and the U.S. National Arboretum in Washington, DC. The National Arboretum obtained the holotype from the Morris Arboretum in 1985. According to Murray, all of these specimens were collected "from the type tree #404-40 at the Arnold Arboretum sent there by Oliver M. Freeman of the National Arboretum in 1941."

Indeed, it was Freeman, recognized by Murray in *A. x freemanii*, who made the first controlled cross between red and silver maples in 1933 (5). Freeman made the cross in only one direction (red maple as the female parent) and noted a high degree of sexual incompatibility, which he ascribed, in part, to the previously reported (but incorrect) chromosome numbers in the two species. Many of Freeman's hybrids were probably planted on the grounds of the National Arboretum but, at the present time, there is only one tree that we can unequivocally identify as an original Freeman seedling.

The Forest Service Breeding Program

Undoubtedly, Freeman's success in maple hybridization was the basis for the extensive genetics program undertaken by the Northeastern

Forest Experiment Station (USDA-Forest Service) in the late 1930's. Cytological, physiological (rooting), and hybridization studies were carried out under the direction of Dr. Ernst J. Schreiner at the station's laboratory in New Haven, Connecticut. In 1940 and 1941, this work resulted in thousands of seedlings which, because of World War II, were lined out in a Forest Service nursery in Williamstown, Massachusetts. It was not until 1946 that these trees could be outplanted for long-term testing. The three plantations established on Forest Service land at the Beltsville Agricultural Research Center in Beltsville, Maryland in 1946 included 4,269 trees, virtually all of which were red maples or silver maples, including crosses within species and between species as well as clonal propagations of the parent trees. The largest plantation (GP-3-46) contained 2,829 trees planted at a 6-foot by 6-foot spacing in 64 rows ranging from seven to 54 trees in length. Among these trees were 1,304 that could be designated as Freeman maple: 903 trees resulting from crosses between three silver maples as female parents and five red maples as male parents and 401 trees from hybridization between two red maple females and two silver maples as male. In addition, there were 844 intraspecific hybrids involving four red maple females and nine red maple males and 226 intraspecific silver maple hybrids from intercrossing among three trees. Another large block of trees consisted of 241 seedlings from self-pollination of two silver maple parents. The parents used in the crossing program were represented by 18 trees of two (of the three) silver maple clones and 43 trees of eight (of the 13) red maples. Various other red maples in the environs of New Haven had also been utilized in research on vegetative propagation and 84 assorted trees that had been rooted from cuttings were also included. Finally, there were 24 trees from open-pollination of one red maple parent, 32 trees from open-pollination of one silver maple parent, 10 open-pollinated sugar maple seedlings from one parent tree, and three trees of other hybrid combinations that were later determined to be non-hybrids. That's a lot of trees,

and probably because of the large number of progenies and the constraints of time, there was no attempt at statistical replication in this plantation.

The heights of trees in this plantation were measured between 1950 and 1952, but the major (and last) measurement of the tree heights and diameters was done in 1958 (by H.C. Kettlewood, F.S. Santamour, Jr., and E.J. Schreiner) in preparation for the Sixth Northeastern Forest Tree Improvement Conference (NEFTIC) that was held in Beltsville in August, 1958. Without replication, the data could only be analyzed in a straightforward fashion, but it was obvious that the hybrids between red and silver maples were not superior to either parental species. Because of the possibilities of vegetative propagation of the best trees, I assembled a table of heights of the five tallest trees in each of several progenies that were represented by more than 20 trees each. That table was published, anonymously, as a guide to the field sessions of the NEFTIC Conference (1) and is reproduced as Table 1.

Even with the built-in bias of comparing only the tallest trees in each progeny, it can be seen that there were considerable differences between both red and silver maple parents in general and specific combining ability for height growth. Some silver X red progenies were slower-growing than intraspecific red maple crosses and some were faster-growing, although lack of replication precluded attaching any statistical significance to these differences. The best parents appeared to be R61 and S202.

In general, the silver maples (including selfed progenies) grew faster than the red maples or interspecific hybrids during the first four to six years after outplanting but had become decadent by 1958. Data presented in the summary (1) show seemingly significant differences in height (21 ft. vs. 18 ft.) and survival (67% vs. 83%) between progenies from reciprocal crosses in silver maple (S 58 x S 201 and S 201 x S 58). Furthermore, by 1958, less than 5% of the 241 silver maple seedlings derived from selfing had survived.

Table 1. Average height (feet) of the five tallest trees in maple progenies at 17 to 18 years of age (R = red maple; S = silver maple).

Female parent	Male parent			
	R28	R60	R61	R62
R64	16.9	21.4	25.9	20.5
R70	17.5	19.5	25.4	19.9
S58	10.7	14.9	—	24.2
S202	18.1	24.2	29.8	125.6

One further point can be made concerning the presumed superior "adaptability" of silver maple. The other 1,440 trees planted in 1946 were contained in two replicate blocks planted about one mile apart. Each block consisted of 36-tree plots of 12 red maple progenies, 5 silver maple progenies, and three plots of trees derived from vegetative propagation of various trees. Thus, there were 864 red maples and 360 silver maples in these plantings. By 1974, when I began wounding (compartmentalization) studies on these maples, the silver maples had all died out!

Surveys for possible selection of trees for outstanding autumn leaf color were made in 1974 and 1977, but no trees were found that would merit selection. Although it is likely that autumn leaf color was not a major criterion for the choice of trees to be used in the breeding program, a couple of the red maple parent clones showed better leaf color than any of their hybrids with silver maple.

After 1958, the Forest Service lost interest in these plantings and the land, like much of that in the Beltsville area, was parcelled out to other government agencies. However, before the plantings had been abandoned, I had made a study of the cytology (chromosome number and behavior) on many of these trees, and this work will be discussed later. Following my move to the National Arboretum in 1967, these trees were also used in studies of wound compartmentalization (11) and of the cambial enzymes related to graft

incompatibility (13).

Hybrid Identification

Both parent species of Freeman maple, especially red maple, are highly variable in leaf morphology and other easily observed characteristics. Are there any non-morphological criteria that could be used for hybrid identification?

Cytology. Both red maple and silver maple are polyploid species, whereas most other maples are diploid with $2n=26$ chromosomes ($2x13$) in their somatic cells. Before 1965, red maples (at least in the northern part of the species range) had been found to be hexaploid ($2n=6x=78$ chromosomes) or octoploid ($2n=8x=104$ chromosomes) and silver maple was a tetraploid species with $2n=4x=52$ chromosomes. In our study of the chromosomes of the parents and progenies of the Forest Service maples (10), some additional numbers were found. Of the eight red maple parents that were counted, six trees were octoploid, one was hexaploid, and one was septaploid ($2n=7x=91$ chromosomes). The septaploid could easily have arisen from a cross between octoploid and hexaploid individuals. Progeny from the cross between the septaploid and an octoploid tree were 7.5-ploid with 97 or 98 somatic chromosomes.

All of the hybrids between octoploid red maples and tetraploid silver maples were hexaploids ($2n=78$). In view of the 2:1 ratio of red maple chromosomes in these hybrids, and in similar hybrids from natural crossing, red maple characteristics dominate in the progeny. Can we distinguish these hybrids by chromosome behavior at meiosis or pollen abortion? Silver maple goes through meiosis and pollen is produced in the fall preceding flowering but red maple meiosis occurs in the spring (usually late winter) of the flowering season. All of the hybrids I examined produced pollen in the spring, but at early stages of meiosis the silver maple chromosomes could be recognized by their precocious division (a vestige of their inherent capacity for fall pollen production) while the red maple chromosomes were still in a bivalent

condition (10). Such analyses are too time-consuming to be of general utility.

Contrary to popular notions about hybrids, most interspecific hybrids between tree species are fully fertile and produce viable seed. This is especially true at the higher levels of ploidy, when the chromosomes from each parent can pair with other chromosomes from the same species. Thus, with the exception of a few abnormal individuals (10), the male hybrids produced better than 90% good pollen and the female hybrids produced good seed.

Could some of the so-called "red" maples at the hexaploid level actually be hybrids between red and silver maples? Yes, they could, especially if the person performing the identification were not "looking" for hybrids. Are all red maples with hexaploid chromosome numbers hybrids between red and silver maples? No, they are not. In fact, some of the progeny derived from crossing two octoploid red maples turned out to be hexaploid because of abnormal meiosis in the male parent that gave rise to pollen grains with two different chromosome numbers (10). Since the hybrids are fertile, crossing between two known hexaploid hybrids should produce highly variable progenies with individuals varying in morphology from those virtually indistinguishable from either parent to some with almost classic hybrid intermediacy. However, because of the taxonomic dictum that only one hybrid specific epithet can be used to denote plants with a combination of genes from two parental species, even the progeny that strongly resemble either parent would have to be classified as *Acer x freemanii*.

Likewise, the progeny from a hexaploid hybrid backcrossed to a tetraploid silver maple would still have to be called *Acer x freemanii* even though the plants would be pentaploids ($2n=5x=65$). The range of morphological variability within the progeny would be from nearly pure silver maple (with four-fifths of the genes from that species) to intermediate types. Although not especially pertinent to this discussion, the report (4) of a pentaploid chromosome number for *A. drummondii* (*A.*

rubrum var. *drummondii*) is of interest.

Chromosome numbers cannot, then, be used to verify Freeman maples as hybrids. It is highly likely that all octoploids ($2n=104$) would be pure red maples and all tetraploids ($2n=52$) would be pure silver maple. Trees with any euploid or aneuploid numbers between $2n=78$ and $2n=104$ could be red maples but any trees with numbers between $2n=52$ and $2n=104$ could also be the products of interspecific hybridization.

Flowering and sex expression. Although there have been numerous contradictory reports, red maple is generally considered to be functionally dioecious (with male and female flowers on separate trees) and silver maple is monoecious (with male and female flowers on the same tree). The fact is, however, that individual trees of both species may flower entirely male, or female, or produce flowers of both sexes. Also, trees that normally produce flowers of only one sex may occasionally have some flowers of the opposite sex. Jong (6) has provided an excellent summary of the literature up to 1976. More recently, a seven-year study of flowering in 79 red maples found that 55 trees were constant males and 12 were constant females (9). Four basically male trees and 6 basically female trees did produce flowers of the opposite sex during the study period and in only two trees did the flowering fluctuate significantly in different years.

Among the trees used in the Forest Service breeding project, there was a conscious attempt to develop self-pollinated progenies from all parents. Apparently, all 13 red maples (4 females and 9 males) were totally dioecious, at least during the years of controlled pollination. Two of the silver maples were monoecious (and produced selfed progeny) and one tree was used exclusively as a female parent.

In summary, the tendency toward dioeciousness is probably stronger in red maple than in silver maple, and our observations on the interspecific hybrids (Freeman maple) suggest that these progenies resemble red maple in this characteristic. However, a dioecious flowering habit cannot

be used as an indicator of hybridity, and essentially "fruitless" (male) trees may be selected from either of the parent species or their hybrids.

Biochemistry. Delendick (3) found that both red maples and silver maples produced a similar array of flavonoid compounds in their leaves and both species also contained aceritannin, a rather rare substance in the maple family. Oddly, the three putative interspecific hybrids that he examined contained fewer flavonoids than either parent species. Santamour (12) did not find any marked differences between the species in cambial peroxidase enzymes. More recently, Tobolski and Kemery (14) analyzed the variation among seven polymorphic isozymes in vegetative and flower buds of 18 "red maple" cultivars (including 'Armstrong' and four others that have been assigned to *A. x freemanii*) and did not find any isozyme patterns that were unique to the putative hybrids. In fact, 'Armstrong' could not be distinguished from 'Red Sunset' or 'October Glory'. Thus, while there may well be biochemical differences between red and silver maples, our knowledge at this time is not sufficient to distinguish the species or to verify hybridity.

Summary

Individual trees of Freeman maple, whether derived from controlled pollination or natural crossing between red and silver maples, may be better or worse than the "average" tree of either species for urban planting. The performance of such hybrids in any area will be dependent on both the geographic origin (provenance) and the genetic constitution of the individual parent trees. At the present time, there are no foolproof non-morphological criteria that can be used to judge hybridity, and reliance must be placed on the considered opinions of botanists and horticulturists with a broad knowledge of the range of variation within both parent species. When assigning either old or new cultivars to *Acer x freemanii*, horticulturists and nurserymen should bear in mind that the term "hybrid" is not an indication of superiority.

Literature Cited

1. Anonymous (F.S. Santamour, Jr.). 1959. *Field sessions*. Northeastern Forest Tree Improve. Conf. Proc. 6:33-34 (1958).
2. Bachtell, K. R. 1989. *A fortunate blend*. Amer. Nurs. 169 (8):40-43,46,48,50-55.
3. Delendick, T. J. 1990. *A survey of foliar flavonoids in the Aceraceae*. Mem. N.Y. Bot. Gard. 54:1-129.
4. Ellis, W. H. 1963. Revision of Section Rubra of *Acer* in eastern North America excluding *Acer saccharinum* L." Ph. D. Thesis, Univ. Tennessee, 230 p.
5. Freeman, O. M. 1941. *A red maple, silver maple hybrid*. Jour. Hered. 32:11-14.
6. Jong, P. C. De. 1976. *Flowering and sex expression in Acer L. A Biosystematic Study*. Meded. Landbouwhogeschool 76-2, 201 p.
7. Murray, E. 1969. *Acer notes*. Kalmia 1(1):1-4.
8. Murray, E. 1969. *Supplementary notes on Acer*. Kalmia 1(4):18-20.
9. Primack, R. B. and C. McCall. 1986. *Gender variation in a red maple population (Acer rubrum; Aceraceae): A seven-year study of a polygamodioecious Species*. Amer. J. Bot. 73:1239-1248.
10. Santamour, F. S., Jr. 1965. *Cytological studies in red and silver maples and their hybrids*. Bull. Torrey Bot. Club 92:127-134.
11. Santamour, F. S., Jr. 1979. *Inheritance of wound compartmentalization in soft maples*. J. Arboric 5:220-225.
12. Santamour, F. S., Jr. 1982. *Cambial peroxidase isoenzymes in relation to systematics of Acer*. Bull. Torrey Bot. Club 109:152-161.
13. Santamour, F. S., Jr. 1989. *Cambial peroxidase enzymes related to graft compatibility in red maple*. J. Environ. Hort. 7:8-14.
14. Tobolski, J.J., and R.D. Kemery. 1992. *Identification of red maple cultivars by isozyme analysis*. HortScience 27:169-171.

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Résumé. De jeunes sujets, à raison d'une espèce par genre (*Aesculus*, *Ailanthus*, *Celtis*, *Fagus*, *Ginkgo*, *Gleditsia*, *Juglans*, *Koelreutia*, *Liquidambar*, *Maclura*, *Magnolia*, *Pyrus*, *Robinia*, *Sassafras*, *Sophora*, *Ulmus*, *Zelkova*) et de trois espèces pour les genres *Betula* et *Prunus*, étaient inoculés avec quatre nématodes communs de racines (*Meloidogyne* spp.). Des 23 espèces testées, une majorité était susceptible à un ou plusieurs des nématodes en question, mais *Ailanthus altissima*, *Fagus grandifolia*, *Gleditsia triacanthos*, *Juglans nigra*, *Liquidambar styraciflua*, *Maclura pomifera*, *Magnolia grandiflora*, *Prunus avium*, *Pyrus calleryana* et *Sassafras albidum* présentaient une tolérance ou une résistance à tous les nématodes.

Zusammenfassung. Junge Pflanzen einer Art von jeder der 17 Gattungen (*Aesculus*, *Ailanthus*, *Celtis*, *Fagus*, *Ginkgo*, *Gleditsia*, *Juglans*, *Koelreutia*, *Liquidambar*, *Maclura*, *Magnolia*, *Pyrus*, *Robinia*, *Sassafras*, *Sophora*, *Ulmus*, *Zelkova*) und drei Arten jeweils von *Betula* und *Prunus* wurden geimpft mit vier gewöhnlichen Wurzelneematoden (*Meloidogyne* spp.). Von dem 23 getesteten Arten war die Mehrzahl anfällig gegenüber einer oder mehrerer Nematoden, aber *Ailanthus altissima*, *Fagus grandifolia*, *Gleditsia triacanthos*, *Juglans nigra*, *Liquidambar styraciflua*, *Maclura pomifera*, *Magnolia grandifolia*, *Prunus avium*, *Pyrus calleryana* und *Sassafras albidum* reagierten auf alle vier Nematoden tolerant oder resistent.