

PROGRESS IN THE DEVELOPMENT OF BORER-RESISTANT WHITE-BARKED BIRCHES

by Frank S. Santamour, Jr.

Abstract. This paper presents a thorough and comprehensive review of the current state of knowledge regarding the hosts of the bronze birch borer (*Agrilus anxius*) and biochemical and genetics studies designed to identify and develop borer-resistant white-barked birches. Both older and heretofore unpublished observations and experiments are evaluated to provide a framework for future research. Based on the hypothesis that the presence of the chemical rhododendrin in the inner bark of birches is the key to their susceptibility to the borer, the finding that *Betula nigra* and *B. maximowicziana* do not contain this compound, and that *B. davurica*, *B. occidentalis*, and *B. papyrifera* have low levels, increased experimentation with these species is encouraged. Some low-rhododendrin, and potentially borer-resistant, hybrids have also been discovered and are awaiting large-scale propagation for long-term trials.

Key Words. Birch; bronze birch borer; resistance; hybridization; selection.

The bronze birch borer, *Agrilus anxius* Gory, is the major lethal pest of white-barked birches in landscapes throughout most of the United States and Canada. The larvae of this native buprestid beetle form extensive mines in the cambial-phloem region beneath the bark, leading to the death of large branches and entire trees. The selection and development of superior white-barked and borer-resistant trees is a monumental challenge to geneticists and horticulturists. The published literature dealing with this broad area of research is widely scattered and often not fully documented. This paper is an attempt to bring together all of the information necessary to understand and appreciate both the current state of the science and the future directions of research necessary to achieve this goal.

TAXONOMIC CLASSIFICATION OF *BETULA*

As with most genera of plants, the taxonomic history of *Betula* is long and involved, and this is not the place for a full discussion of that topic. Suffice it to

say that most of the modern "standard" references by Rehder (1949, 1958) and Krüssmann (1960) recognized 4 infrageneric series within the genus. More recently, Vassiljev (1969) proposed the division of the genus into 5 subgenera, and Jong (1993) and Natho (1976) have agreed with this proposal. The major change in Vassiljev's classification is the creation of 2 subgenera to include the species formerly classified in series *Costatae*. A further refinement by Jong (1993) was the removal of *B. davurica* from affiliation with the major white-barked species (e.g., *B. papyrifera*) to the group of "costate" birches included in subg. *Neurobetula*.

Taxonomic classification can frequently be used as a guide to interspecific crossabilities, with hybridization between species in the same category being more likely than crosses between species in different categories. In the hierarchy of infrageneric classes (series, section, subgenus) the rank of "subgenus" implies nearly generic differences and, in many genera, crosses between species belonging to different subgenera are very rare or impossible. Therefore, in view of the known crossabilities between species categorized in Vassiljev's various subgenera, I do not fully agree with that ranking. On the other hand, there are valid reasons for the recognition of 5 classes, at whatever rank. Thus, in the following list, I have used Vassiljev's subgeneric scheme (with appropriate synonymy) to classify all of the species mentioned in this paper.

Subgenus *Betulenta* V. Vassil. (Series *Costatae* Regel; Section *Eubetula* Regel, Series *Costatae* Regel; in part)
B. alleghaniensis Britt., *B. grossa* Sieb. & Zucc., *B. lenta* L., *B. uber* (Ashe) Fern.

Subgenus *Betulaster* (Spach) V. Vassil. (Series *Acuminatae* Regel; Section *Betulaster* (Spach) Regel, Series *Acuminatae* Regel)

B. alnoides Buch.-Ham., *B. luminifera* Winkl., *B. maximowicziana* Reg.

Subgenus *Neurobetula* V. Vassil. (Series *Costatae* Regel; Section *Eubetula* Regel, Series *Costatae* Regel; in part)

B. albosinensis Burk., *B. costata* Trautv., *B. davurica* Pall., *B. ermanii* Cham., *B. nigra* L., *B. raddeana* Trautv., *B. utilis* D. Don, including var. *jacquemontii* Henry (*B. jacquemontii* Spach) and var. *occidentalis* (Kitam.) Ashburner & Schilling

Subgenus *Betula* (Series *Albae* Regel; Section *Eubetula* Regel, Series *Excelsae* Koch; Series *Excelsae* Koch)

B. cordifolia Reg., *B. occidentalis* Hook. (*B. fontinalis* Sarg.), *B. papyrifera* Marsh., *B. pendula* Roth, *B. platyphylla* Suk., *B. populifolia* Marsh., *B. pubescens* Ehrh., *B. resinifera* Britt.

Subgenus *Chamaebetula* (Opiz) V. Vassil. (Series *Humiles* Koch; Section *Eubetula* Regel, Series *Humiles* Koch)

B. fruticosa Pall., *B. glandulifera* (Reg.) Butler, *B. glandulosa* Michx., *B. humilis* Schrank., *B. nana* L., *B. pumila* L.

CHEMICAL CRITERIA FOR SPECIES AND HYBRID IDENTIFICATION

Although it would seem reasonable to assume that the identification of birch taxa using traditional morphological criteria would be a simple matter, the statement by Jong (1993) that "most arboreta and botanic gardens have less than 50% of their birches correctly labeled" is a cause for concern. The fact that birches may hybridize rather freely in the wild and in cultivation is an added impediment to proper identification.

Recently, Santamour and Lundgren (1996) utilized the production and inheritance of a chemical called platyphylloside in the inner bark of birch twigs to question or verify the identity of many species and hybrids in some of the world's major arboreta. In their survey of more than 70 taxa, they found platyphylloside in relatively few species. However, the presence of this compound in *B. papyrifera*, *B. platyphylla* var. *japonica*, and *B. pubescens* and its absence from *B. populifolia* allowed them to conclude that the cultivar widely grown as *B. platyphylla* var. *japonica* 'Whitespire' was really *B. populifolia*. The identification of some trees labeled as *B. maximowicziana* and *B. jacquemontii* (*B. utilis* var. *jacquemontii*) in several arboreta were shown to be incorrect, but it was impossible to discern their true identity. The absence of platy-

phylloside from *B. occidentalis* showed that this taxon definitely should not be classified as a variety of *B. papyrifera*. Hybrids derived from controlled pollination between platyphylloside-positive and platyphylloside-negative species always contained platyphylloside. The platyphylloside test is simple enough to be performed in any laboratory, and it will be useful in the future as an aid in clarifying the identities and relationships of the confusing assemblage of European white-barked birches. This test could also be very useful in verifying certain interspecific hybrids developed in any birch breeding program. In this connection, and especially in regard to later sections of this paper, it should be noted here that *B. davurica*, *B. nigra* (river birch), *B. occidentalis*, *B. maximowicziana*, and *B. utilis* var. *jacquemontii* do not contain platyphylloside.

BIRCH TAXA RESISTANT AND SUSCEPTIBLE TO THE BRONZE BIRCH BORER

Unfortunately, our current knowledge of the relative susceptibilities of various birches to the bronze birch borer is largely based on anecdotal and observational evidence rather than on long-term experimentation. Fisher (1928) listed *B. papyrifera*, *B. alba* L. (which includes both *B. pendula* and *B. pubescens*), *B. populifolia*, *B. lenta*, and *B. lutea* (= *B. alleghaniensis*) as hosts. Barter and Brown (1949) added *B. fontinalis* to this list and, although various authors have considered this taxon as *B. papyrifera* var. *occidentalis*, it is now believed to be *B. occidentalis*, a species distinct from *B. papyrifera*. Weaver (1978) based his observations on trees growing at the Arnold Arboretum in Massachusetts and rated *B. pendula*, *B. populifolia*, and *B. albosinensis* as susceptible, with *B. papyrifera* being slightly less susceptible. Weaver listed *B. davurica*, *B. ermanii*, and *B. maximowicziana* (monarch birch) as probably resistant species.

I give a great deal of credibility to the report by Ronald (1980), which examined various birches for borer damage following 3 drought years in Manitoba. A susceptible rating was given to *B. ermanii*, *B. glandulifera*, *B. papyrifera*, *B. pendula*, *B. platyphylla*, and *B. populifolia*, but Ronald noted no borer damage on *B. albosinensis* var. *septentrionalis*, *B. alleghaniensis* (as *B. lutea*), *B. davurica*, *B. lenta*, and *B. occidentalis*. The replicated trials of Santamour (1982), based on an evaluation after 10 years in the field, indicated that the most susceptible species was *B. platyphylla*

var. *japonica*. Both *B. pendula* and *B. pubescens* were also highly susceptible, but the survival of *B. papyrifera* was higher than that of the other species. (As of 1997, only 3 of 32 trees of *B. papyrifera* and none of the other species had survived). Johnson and Lyon (1991) also listed *B. papyrifera*, *B. pendula*, and *B. pubescens* as susceptible but rated *B. platyphylla* var. *japonica*, *B. maximowicziana*, and *B. nigra* as resistant or more tolerant. David G. Nielsen, (OARDC, personal communication) has confirmed the borer-resistance of *B. nigra* and the susceptibility of *B. platyphylla* var. *japonica* and *B. populifolia* in his studies. It would appear that the widespread planting and observation of *B. nigra* 'Heritage' since its introduction in 1979 (Santamour and McArdle 1989) has confirmed its resistance over a wide geographical area. Nielsen considered *B. maximowicziana* to be susceptible but noted few emergence holes in this species. My own experience with monarch birch is similar to that of Nielsen, but I would rate it as very much less susceptible than the common run of white-barked species. Where *B. papyrifera* is climatically adapted, as it was in Nielsen's test in Ohio, it may also be less susceptible than the European or Japanese white birches.

It is axiomatic that when any "new" tree is introduced to the American nursery trade, our lack of long-term experience might suggest that it is "resistant" to all of the ills that befall its relatives. This is especially true of *B. utilis* var. *jacquemontii* (*B. jacquemontii*). Although no truly scientific studies have been reported, I conclude, on the basis of discussions with experienced nurserymen and horticulturists, that this taxon is quite susceptible to the bronze birch borer.

In summary, the following taxa possess a degree of borer resistance that could be utilized in breeding and selection programs: *B. davurica*, *B. maximowicziana*, *B. nigra*, *B. occidentalis*, and *B. papyrifera*.

THE BIOCHEMISTRY OF BORER RESISTANCE

Santamour (1990a) provided evidence that the chemical rhododendrol could act as a stimulant to oviposition by mated female borers. Rhododendrol was not found in the inner bark of healthy birch branches, and it was hypothesized that rhododendrol was formed by natural hydrolysis of rhododendrin during senescence of cambial and phloem tissue. This

senescence could be caused by drought stress, and it is well known that stressed trees are more commonly attacked than healthy trees (Barter and Brown 1949; Santamour 1990b).

Some early work (Santamour and Vettel 1978) suggested that there was no relationship between rhododendrin content and borer resistance, but this research was based on the (then) inadequate knowledge of the host range of the borer as well as some incorrect tree identities. However, aided by their work on platyphylloside for species identification, Santamour and Lundgren (1997) recently re-studied the rhododendrin situation in more than 50 birch taxa. The natural hydrolysis of rhododendrin to rhododendrol in drought-stressed birch branches was definitely proved, and the levels of rhododendrin were quantified in many taxa. The absence of rhododendrin in *B. nigra* determined earlier (Santamour and Vettel 1978; Santamour 1990) was confirmed, and *B. maximowicziana* was also found to contain no rhododendrin. Two other species, *B. davurica* and *B. occidentalis*, were found to contain exceedingly low levels of rhododendrin, as did some trees of *B. papyrifera*. Thus, this list of no- or low-rhododendrin taxa corresponds quite well with the list of species with potential borer resistance presented earlier in this paper.

As examples, the contents of rhododendrin (dry weight basis) in the inner bark of taxa susceptible to the bronze birch borer were *B. platyphylla* var. *japonica* (2.0%), *B. pendula* (0.6%), *B. populifolia* (2.2%), *B. pubescens* (3.3%), and *B. utilis* var. *jacquemontii* (1.2%). The bark of several trees of both *B. davurica* and *B. occidentalis* contained between 0.02% and 0.06% rhododendrin. Some individuals of *B. papyrifera* had up to 0.4% rhododendrin, but others had levels as low as 0.05%.

As good as the correlation between resistance and rhododendrin levels may appear, even with the prospect of a cause-and-effect relationship, we still do not have all of the answers. To quote from Santamour and Lundgren (1997), "Unfortunately, we do not presently know what levels of rhododendrin or what degree and extent of 'stress' are necessary to make a tree 'susceptible' to borer." However, the rhododendrin-resistance relationship appears to be real, and the selection or development of low-rhododendrin trees may be a major path to resistance.

PLANTING OF POTENTIALLY RESISTANT TAXA IN THE LANDSCAPE

Can we take advantage of what we know or suspect about borer resistance to plant resistant selections in the landscape? The answer is that we already have. The widespread planting of *B. nigra* 'Heritage' since its introduction in 1979 (Santamour and McArdle 1989) has provided an opportunity to evaluate this cultivar under a broad range of climatic conditions—and it and the species can be considered highly resistant to attack by *A. anxius*.

In recent years, however, several (unpublished) reports of possible bronze birch borer infestations of *B. nigra* have been circulated. Indeed, there may be another beetle of the genus *Agrilus* that attacks *B. nigra*. Both Fisher (1928) and Knull (1930) reported rearing populations of the alder-birch borer, *A. pensus* Horn (as *A. betulae* Fisher), from dead trees of river birch. It is, perhaps, unlikely that this borer is a major pest of birches, but some caution should be exercised by those reporting *A. anxius* on *B. nigra*.

The published literature on the performance of *B. maximowicziana* in various localities indicates that this species is not widely adaptable as a landscape tree. Santamour and Clausen (1979) reported a total lack of survival after 2 years in the field in Lake Tomahawk, Wisconsin. Survival on an adverse site in Beltsville, Maryland, was only 28% after 7 years (Santamour 1983), and no trees survived more than 12 years. A more recent study (Widrlechner et al. 1998) reported poor survival (0% to 23%) of 3 seedlots tested at various locations in the north central United States. In addition, D.G. Nielson (personal communication) reported poor adaptability of this species in his test plots in Wooster, Ohio.

On the other hand, the cultivation of monarch birch at the Morris Arboretum of the University of Pennsylvania in Philadelphia has been quite successful. Following my 1976 determination that trees growing in Philadelphia's Fairmount Park as *B. maximowicziana* were not properly identified, the Morris Arboretum made a concerted effort to introduce this species from various wild and cultivated sources. Of 24 trees planted from accessions prior to 1980, 15 had survived (as of 1994) and were strong, upright trees with reasonably white bark. These trees were definitely true to species on morphological and biochemical grounds (Santamour and Lundgren

1996). No borers have been noted in these trees. I did see a single borer emergence hole in a tree (1078-76-C) at the Arnold Arboretum in Jamaica Plain, Massachusetts, and the bark of this tree was even whiter than that of the Morris trees.

The accumulated experiences of horticulturists who have experimented with the planting of *B. papyrifera* would indicate that this species is not well-adapted very far south of its native range, but there are exceptions. Japanese white birch (*B. platyphylla* var. *japonica* [Miq.] Hara) may be more adaptable to warmer climates, but, despite the single listing of this taxon as "more tolerant or resistant" (Johnson and Lyon 1991), both the species and the recently introduced cultivar 'Fargo' (Cheng et al. 1997) will probably be highly susceptible to the borer.

The bark of the true *B. occidentalis* specimens I have seen in arboreta is definitely not white. Neither can I say that I have been very impressed with the bark "whiteness" of similar specimens of *B. davurica*. Still, both taxa have the potential to cross with white-barked species. This situation will be discussed later.

WHITE BARK—HOW WHITE AND HOW SOON?

The widespread acceptance of *B. nigra* 'Heritage' by the nursery trade and the American public is proof that the bark of a birch need not be as white as the paper in this journal to have a significant impact on urban and suburban landscapes. One major reason for this popularity is that the whitish bark develops at an early age, and both the nurseryman and the landscaper are assured that this trait will persist for many years. Early bark whitening is certainly not characteristic of *B. papyrifera*, and after the 5 to 7 years necessary to develop attractive white bark, the bronze birch borer will have detected any stressed trees. Similarly, the development of whitish bark in *B. maximowicziana* requires an extended period of time.

On the other hand, early bark whitening is normal in some of the taxa that are definitely or possibly susceptible to the bronze birch borer: *B. pendula*, *B. platyphylla* var. *japonica*, *B. populifolia*, *B. pubescens*, *B. utilis* var. *jacquemontii*, and *B. ermanii*. Thus, for a new selection or cultivar to be widely accepted, it should not only be borer resistant but also have white bark at an early age. The creation of such trees will probably require hybridization.

HYBRIDIZATION INVOLVING *BETULA NIGRA* AND *B. MAXIMOWICZIANA*

Because *B. nigra* and *B. maximowicziana* are the 2 major whitish-barked species that totally lacked rhododendrin, it would be of interest to know the potential of these species for interspecific hybridization. Therefore, in the following sections, I have attempted to develop a chronological examination of published works, with some personal observations added, on this subject.

Betula nigra

The published information available concerning interspecific hybridization involving *B. nigra* is not especially convincing with regard to the actual crossabilities of this species or the verification of control-pollinated or garden-origin hybrids. Woodworth (1931) reported that his cross of *B. pumila* with *B. nigra* had "proved successful to the extent that embryos were formed." The seeds had not yet germinated at the time of publication of his report.

Johnson and Heimburger (1946) germinated 48 seedlings from their cross of *B. papyrifera* with *B. nigra*, which gave a "fair" seed set and "low" germination. Their study involved numerous crosses in many genera, but they provided no criteria to verify any particular interspecific hybrid. They stated, "For the most part, the hybridity of the seedlings has been proved, or strongly indicated by various criteria. In some crosses, however, hybridity is assumed on the basis of seedling production under conditions that largely precluded the possibility of self- or chance-pollination."

Delevoy (1948) described the leaves and twigs and illustrated the leaves of suspected garden-origin hybrids derived from open-pollination of *B. nigra* in 1936 in Belgium. These hybrids were considered to be *B. nigra* × *B. ermanii* and *B. nigra* × *B. maximowicziana*. Apparently, these trees had not yet reached sexual maturity in 1948, since there was no mention of male or female catkins.

Clausen (1966) reported the results of 3 years of controlled pollination studies with many birch species. These crosses had been attempted on bottle-grafted branches of the female parents in a greenhouse and in no interspecific combination were more than 9 female catkins pollinated. He stated that "interspecific crosses with *B. nigra* as either female or male parent have been difficult to make, and only a

few seedlings have resulted from the successful crosses." As a female parent, *B. nigra* failed to set viable seed in crosses to *B. lenta*, *B. papyrifera*, and *B. pubescens*, but some seedlings were produced from crosses to *B. alleghaniensis* and *B. pendula*. No viable seed were set by *B. glandulosa*, *B. lenta*, or *B. pumila* when pollinated with *B. nigra*, but seed from crosses of *B. nigra* on *B. alleghaniensis*, *B. papyrifera*, *B. pendula*, *B. populifolia*, and *B. pubescens* gave 1% or less germination.

A later report from the same project (Clausen 1970) added *B. nigra* × *B. lenta*, *B. nigra* × *B. ermanii* (and reciprocal), *B. nigra* × *B. glandulosa*, *B. nigra* × *B. humilis*, *B. nigra* × *B. nana* (and reciprocal), and *B. nigra* × *B. pumila* to the list of "successful" crosses. No criteria of hybridity beyond that of seedling germination were noted for these hybrids or any other interspecific combination, although Clausen (1973) reported that the cross of *B. nigra* × *B. alleghaniensis* had been "verified." As of 1994, none of the putative hybrids developed in this extensive breeding project were extant in Wisconsin (D. Riemenschneider, personal communication).

In 1973, Dan Milbocker (personal communication), then at the University of Kentucky, crossed a cutleaf weeping birch (probably *B. pendula* 'Laciniata') with *B. nigra*. Milbocker brought 31 seedlings from this cross to Virginia Beach, Virginia, in 1974 when he took a position there with Virginia Polytechnic Institute and State University. Because of poor growth, several trees were removed from his test plots every year until only the 4 best trees were living in 1985. Documented herbarium specimens of these 4 trees, all about 7.6 m (25 ft) tall and 17.7 cm (7 in.) in diameter, were made by F.G. Meyer and P.M. Mazzeo of the U.S. National Arboretum in 1985. In my judgment, based on leaf and catkin morphology, 2 of these specimens appeared to represent true hybrids and the other 2 looked like *B. pendula*. All 4 trees were destroyed between 1985 and 1992 because their bark was not as white as might be desired and there was a need for the nursery space they occupied. This hybrid combination is listed in *A Catalog of Cultivated Woody Plants of the Southeastern United States* (Meyer et al. 1994).

Little (1979) noted that *B. nigra* hybridized with *B. papyrifera*, but he did not provide a literature citation or a Latin binomial for this hybrid. It is possible

that Little drew this information from the work of Johnson and Heimburger (1946) because he also stated that *B. papyrifera* hybridized with *B. lenta*, another cross reported by Johnson and Heimburger (1946). As discussed earlier, none of these hybrids were actually verified.

River birch may be unique among the birches in maturing its seeds approximately 1 month after pollination. Thus, it is possible that the inherent physiological traits of this species might preclude its hybridization, as either a male or female parent, with species that require a longer period of seed maturation. In our limited experience, there may be one other species with characteristics similar to *B. nigra*. In 1975, we received 2 plants, purported to be *B. luminifera* (NA 37061) from Hillier and Sons Nursery in England. This species is classified in subgenus *Betulaster*, along with *B. maximowicziana*. Sprouts arising from below the graft unions indicated that the plants had been propagated on *B. pubescens* rootstocks. In 1977, we used *B. luminifera* as a female parent in crosses with *B. nigra*. To our surprise, not only did the seed mature in 1 month, but the entire catkin was shed at maturity. No viable seed was obtained from this cross or from a 1978 cross that utilized *B. luminifera* as a male parent on *B. nigra*. The grafts failed in 1979, and it is not known if this "abnormal" flowering and fruiting behavior was caused by the incipient graft incompatibility. One other interesting story about *B. luminifera* involves the statement by Krüssmann (1960) that the female catkins were "upright standing, like Christmas candles, hence the name." A similar statement later appeared in Fontaine's (1970) monograph on birch. The female catkins on our plants were definitely not erect, and it can only be assumed that this "candle-like" description resulted from the fact that the herbarium specimen used to illustrate the species in Winkler (1904) was mounted in this way.

In 1985, we crossed *B. populifolia* with *B. nigra* 'Heritage' and obtained a few plants that were different enough to be considered hybrids. My 1990 paper mentioned this hybrid combination and also contained other hybridization data that is repeated (and expanded) here to provide a complete history of our work. To quote, "In 1986, we pollinated 107 female catkins of *B. nigra* 'Heritage' with pollen of 13

different birches representing a wide range of species and hybrids and several levels of ploidy. All of the 279 seedlings raised were apomictic" (apomixis is discussed later in this paper). The trees used as male parents included *B. albosinensis*, *B. grossa*, *B. maximowicziana*, *B. papyrifera*, *B. pendula*, *B. platyphylla* var. *japonica*, *B. pubescens*, true hybrids of *B. platyphylla* var. *japonica* × *B. papyrifera*, *B. pendula* × *B. alleghaniensis*, *B. populifolia* × *B. pendula* and putative hybrids of *B. papyrifera* and *B. pendula* with *B. maximowicziana*. The reference to the seedlings being apomictic means that they resembled the female parent (*B. nigra*) in every way. The putative hybrids of *B. populifolia* × *B. nigra* should not, on the basis of work by Santamour and Lundgren (1996), have contained platyphylloside in the inner bar because both parents lacked this chemical. The presence of platyphylloside showed that these plants were not the expected hybrids.

A further quote from Santamour (1990a): "In 1988, we made 127 crosses of *B. nigra* 'Heritage' on selected plants of *B. populifolia*, *B. populifolia* × *B. pendula*, and true *B. platyphylla* var. *japonica*. Of the 447 seedlings that germinated, only about 50 could be considered as putative hybrids and the rest were apomictic. Hybridity was judged on the basis of leaf isozymes." Later work and observations determined that no true hybrids were obtained.

In 1994, we used 5 isolated trees of *B. nigra* 'Heritage' at the National Arboretum and Longwood Gardens as female parents in crosses with pollen gleaned from several trees of *B. maximowicziana* at the Morris Arboretum. All 87 catkins matured, and the germination from the various seedlots ranged from 2.2% to 41.4%. Unfortunately, all the seedlings resembled *B. nigra*.

Our latest, but perhaps not last, efforts to hybridize *B. nigra* occurred in 1995. Pollen from the trade clone of *B. utilis* var. *jacquemontii* and the cultivar 'Jermyns' were used to pollinate *B. nigra* 'Heritage'. All of seedlings from these crosses were *B. nigra*. On the other hand, *B. nigra* 'Heritage' was used as the male parent to pollinate 37 female catkins of 'Jermyns', and 8 putative hybrids have been outplanted for further observation. Because neither taxa contain platyphylloside, we cannot use this simple test to verify hybridity.

Betula maximowicziana

The monarch birch was first introduced into the United States in 1893 by the Arnold Arboretum of Harvard University. Their specimen No. 1967, documented by herbarium specimens in 1922, was definitely true to species. Woodworth (1931) reported the chromosome number of this plant to be diploid ($2n = 2x = 28$) and used monarch birch as the female parent in crosses to *B. lutea* (= *B. alleghaniensis*) and as the male parent with *B. pumila* and *B. davurica*. As noted in the discussion of *B. nigra* hybrids, Woodworth's crosses were considered successful on the basis of seed production with embryos, but there is no record of seed germination or other data. Smith and Nichols (1941), also at the Arnold Arboretum, reported the successful crossing of *B. mandshurica* (Reg.) Nakai var. *japonica* (Miq.) Sarg. (= *B. platyphylla* Suk. var. *japonica* [Miq.] Hara) with monarch birch, but no living plants or herbarium vouchers that might be used to verify the cross are currently in existence. An open-pollinated seedling (No. 202-50) from No. 1967 was propagated from cuttings as No. 672-54-A, but it was not true *B. maximowicziana*.

A putative natural hybrid between *B. nigra* and *B. maximowicziana* was reported from Belgium. Delevoy (1948) and Klaehn (1952) presumably crossed monarch birch with *B. pubescens* in Germany. Johnsson (1945), in Sweden, verified the diploid chromosome number of monarch birch and reported limited success in crossing *B. maximowicziana* as the male parent with *B. pendula*. In a later paper (1974), he verified this combination as a true hybrid. Kantor (1973) reported that the progeny of a cross of *B. pendula* and *B. maximowicziana* made in 1956 were highly variable and verification required "more detailed study and analysis."

Apparently, the Arnold Arboretum had sent plants of *B. maximowicziana* to the Royal Botanic Gardens (Kew) in England in 1895, and at least 1 tree had flowered by 1909 (W.J. Bean herbarium specimen). Although the tree at Kew died before 1977, it may have been the mother-tree of a putative garden-origin hybrid with *B. utilis* (probably *B. utilis* var. *jacquemontii*). That tree also died before 1977 but is represented in the Kew herbarium and noted as being 50 feet tall and 50 cm in diameter in 1962.

The bark color of the tree was described as "whitish-pink-ochre."

Clausen and Garrett (1969) mentioned the hybrids *B. papyrifera* × *B. maximowicziana* and *B. pubescens* × *B. maximowicziana* that had been made in the early 1950s by Jonathan W. Wright while he was stationed with the U.S. Forest Service at the Morris Arboretum of the University of Pennsylvania in Philadelphia. An herbarium specimen of the Morris tree of monarch birch (No. 75), taken in 1933, is currently in the herbarium of the U.S. National Arboretum. It was true to species, but the hybrids are no longer in existence.

In 1975 and 1976, 2 papers were published on monarch birch. One (Kozel and Smith 1976) mentioned white-barked trees then being sold by Cole Nurseries in Circleville, Ohio; the other (Koller and Blum 1975) discussed and illustrated 2 older, white-barked trees growing at Fairmount Park in Philadelphia. Santamour and Meyer (1977) reported that these trees were not true *B. maximowicziana*. They could verify the existence of only 2 sexually mature trees of this species in the United States, both growing at the Brooklyn Botanic Garden and so spatially separated that they could not interpollinate. In 1976, I determined that the Fairmount Park trees had a tetraploid chromosome number ($2n = 4x = 56$) and concluded that they were probably hybrids between the diploid monarch birch and the hexaploid *B. papyrifera* (Santamour, unpublished data). Open-pollinated progeny of the Fairmount trees were tetraploid or triploid!

In 1977, I attempted to use the verified *B. maximowicziana* trees from the Brooklyn Botanic Garden in our birch hybridization program. With most birches, it was easy to force pollen production from cut branches bearing male catkins in the laboratory or greenhouse. However, the male catkins of monarch birch, although they elongated extensively, never shed pollen. We were able to obtain a minuscule amount of apparently sound pollen by grinding and sieving dried catkins and attempted crosses on *B. papyrifera*, *B. pendula*, *B. populifolia*, and *B. pubescens*. A few seedlings of putative *B. papyrifera* × *B. maximowicziana* and a single plant of *B. pendula* × *B. maximowicziana* were grown for a number of years but were not verified before they succumbed to acci-

dental herbicide damage. I could not, at this time, vouch for the authenticity of these hybrids, although the herbarium specimens are "different." Another 1977 cross was *B. luminifera* × *B. maximowicziana*, between 2 species classified in the same subgenus, but no seedlings were obtained.

After the determination, in 1994, that the inner bark of monarch birch did not contain rhododendrin, work with this species was intensified, using the trees growing at the Morris Arboretum. Once again, the problems of pollen forcing were encountered, and, because monarch birch flowered about 2 weeks later than every other species, it had to be used exclusively as a female parent. The platyphylloside test (Santamour and Lundgren 1996) could be used to verify any true hybrids with species containing this compound, but other combinations would be more difficult to evaluate. From 1994 through 1996, crosses were attempted using a wide range of male parents: *B. nigra* 'Heritage', *B. papyrifera*, *B. platyphylla* var. *japonica*, *B. populifolia*, *B. utilis* var. *jacquemontii*, *B. utilis* var. *jacquemontii* 'Jermyns', and the hybrids *B. populifolia* × *B. pendula* 'Purpurea', *B. populifolia* × *B. platyphylla* var. *japonica*, and *B. platyphylla* var. *japonica* × *B. papyrifera*. Because of the difficulties of time and distance between Washington and Philadelphia, these pollinations were made on receptive female catkins before the trees had shed pollen, but the females were not protected against later intraspecific pollination. Seedlings were grown from all pollinations, but not a single verified hybrid was obtained. Percentage germination of the putative hybrid seed ranged from 0% to 2%, and this low level suggested that the seed were apomictic. Seed germination following open-pollination was not much better, however, and ranged from 1% to 4%.

HYBRIDIZATION INVOLVING *B. DAVURICA*, *B. OCCIDENTALIS*, AND *B. PAPYRIFERA*

Because it was found that the inner bark of trees of *B. davurica*, *B. occidentalis*, and *B. papyrifera* could contain very low levels of rhododendrin (Santamour and Lundgren 1997), it is appropriate to survey the literature on interspecific hybridization involving those taxa.

Betula davurica

There is far less information concerning this species, but Santamour and Lundgren (1977) suggested that its use in future hybridization schemes was warranted because of its low rhododendrin content. There may also be other valid reasons for the further testing and use of this species. Fiori (1984) and Fiori and Dolan (1984) reported that it was the only whitish-barked species of the several that were tested that possessed a high degree of resistance to the birch leafminer (*Fenusa pusilla* Lepeletier). There may also be some problems with the proper identification of the species and questions with regard to its ability to produce reasonably white bark. As of 1998, we were growing specimens of 3 different bona fide accessions from China, and the bark at the bases of 3-year-old trees was already turning white.

Knowledge of the potential crossabilities of *B. davurica* is meager. Zabel (1985) reported on a garden-origin hybrid between *B. davurica* and *B. lenta* growing in a botanic garden in Germany. Woodworth (1931) considered his crosses of *B. davurica* (as female) with *B. japonica* var. *mandshurica* (= *B. platyphylla* var. *japonica*), *B. lutea* (= *B. alleghaniensis*), *B. maximowicziana*, *B. papyrifera*, and *B. pendula* as "successful," as was a cross of *B. maximowicziana* × *B. davurica*. His interpretation of success has been discussed earlier in this paper. Clausen (1973) stated that the cross of *B. davurica* × *B. alleghaniensis* had been verified and cited a personal communication from Albert G. Johnson in January 1962 as proof. An illustration (from Johnson?) provided by Clausen (1973) shows 2 young putative hybrids exhibiting the white bark of *B. davurica* and 2 hybrids resembling *B. alleghaniensis*. One other fact concerning the inheritance patterns that might be expected from using *B. davurica* has recently been provided by McAllister (1993). He found that the trees from Japan and the Kurile Islands were hexaploid with $2n = 4x = 84$ chromosomes, while those from the Asiatic mainland (Korea, China, and what was the Soviet Far East) were octoploid ($2n = 8x = 112$ chromosomes). Thus, McAllister believes that the trees currently being grown as *B. davurica* represent 2 distinct taxa! Obviously, there are some major taxonomic and nomen-

clatural problems that must be resolved before we can truly understand *B. davurica*.

Betula occidentalis

Little (1979) listed 3 hybrid-specific epithets (*B. × andrewsii* A. Nel., *B. × piperi* Britt., and *B. utahensis* Britt.) for natural hybrids between *B. occidentalis* and *B. papyrifera*. Such hybrids, especially advanced generation crosses, could have both white bark and low rhododendrin levels. Campbell G. Davidson at the Morden Research Centre in Manitoba, Canada, is using these hybrids in a breeding and selection program. There are no reports in the literature of other successes or failures of controlled hybridization with this species, although it is likely to cross with any other species in subg. *Betula*.

Betula papyrifera

Paper birch is sexually compatible with other species in subg. *Betula*, and hybridization with key species in other subgenera was reviewed earlier in this paper.

APOMIXIS IN BETULA

A simple definition of apomixis is the development of viable seed in the absence of sexual fertilization. Seedlings that develop from apomictic seed, even though they may vary somewhat in morphology, resemble the species from which they are obtained. Obviously, this characteristic can lead to erroneous conclusions concerning hybridity when species that may possess a low degree of sexual compatibility are hybridized. Pollination, even with pollen from other genera, may stimulate the production of apomictic seed.

The work of Bogdanov and Stukov (1970), although somewhat confusing, demonstrated that normal seedlings of several European birches developed from seed of female catkins that were totally isolated from pollination. Clausen (1966) stated that there was "no evidence of apomixis" in his crosses, but in 1973 he considered apomixis as being responsible for the production of "hybrids" with maternal characteristics. There are many allusions to the possibility or unlikelihood of apomixis in *Betula* scattered throughout the literature, and it would be of little use to discuss these tidbits of information.

My opinion, based on many years of research, is that apomictic seed production is prevalent in *Betula*

and is enhanced by pollination with species that are marginally compatible or totally incompatible with the female parent. The degree of expression of apomixis will probably vary among species and among individuals within species and be influenced by weather conditions, bagging procedures, and other external factors. The possibility of apomixis, therefore, makes it imperative that hybridity be unequivocally verified by morphological cytological, or biochemical analyses, preferably by several techniques.

SOME LOW-RHODODENDRIN HYBRIDS

During the course of our studies on rhododendrin, we analyzed a number of putative natural hybrids that were not reported in that paper (Santamour and Lundgren 1997). Some surprising, interesting, and potentially important results were obtained.

The oldest trees examined were the 2 putative white-barked hybrids of *B. maximowicziana* × *B. papyrifera* that were mentioned earlier as growing in Fairmount Park in Philadelphia. The fact that these trees (planted circa 1932) were still extant and thriving in 1995 might be considered an indication of potential borer resistance, and indeed, both of these trees contained less than 0.1% (approximately 0.04% to 0.06%) rhododendrin. During the late 1970s, several attempts were made to propagate these trees from cuttings but to no avail. Perhaps this failure was providential because the trees, though probably borer resistant, were huge and not well suited for use in landscapes with limited space. At the end of the 1994 growing season, these 2 trees were almost identical: 15.8 m (52 ft) in height, 1.32 m (40 in.) in diameter at 30 cm (12 in.) above ground level, with a crown spread of 22.1 m (73 ft). Furthermore, both trees had huge branches—38 to 61 cm (15 to 24 in.) in diameter—emanating from areas below 1.5 m (4.5 ft) on the trunk. These massive lower branches are somewhat indicative of the involvement of *B. maximowicziana* in their parentage.

The failure to vegetatively propagate these trees prompted personnel at the Morris Arboretum to collect open-pollinated seed from the trees in 1978 and grow their progeny. Some 26 trees of this progeny were outplanted on a variety of sites in 1979 and in November 1994, 18 trees were still alive. Borers may have contributed to the demise of only 1 tree. We

determined the rhododendrin content of 5 of these second-generation hybrids and found that all trees had less than 0.1% rhododendrin. The best of these trees has a rapid growth rate, a delightful landscape form, about 0.04% rhododendrin, and they should be propagated for further testing.

Two putative hybrids between *B. platyphylla* var. *japonica* and *B. papyrifera* at the U.S. National Arboretum also had less than 0.1% rhododendrin. These plants had been grown from seed collected from a tree of *B. platyphylla* var. *japonica* in a Japanese botanic garden in 1960. In 1976, I determined that the chromosome number of these trees was $2n = 4x = 56$, a tetraploid number indicating possible hybridization between the diploid *B. platyphylla* var. *japonica* and the hexaploid *B. papyrifera*. This cytological situation, coupled with morphological traits, indicated possible hybridity. Although neither of these trees, the survivors in a row of 15 trees, has shown any significant borer damage in 25 years, their form is not outstanding. Still, we are beginning to propagate these trees for further testing and are especially interested in seeing whether the early bark-whitening of *B. platyphylla* var. *japonica* is inherited.

Two hybrids of unknown parentage, growing at Longwood Gardens since 1962, contained about 0.1% rhododendrin. Although these trees had been labeled *B. Jacquemontii*, the platyphylloside test indicated that they were not that species. They are large trees with good white bark, and they apparently have not been attacked by the bronze birch borer. We also tested 2 white-barked selections made at the Morden (Manitoba) Research Centre from the second generation of hybrids between *B. occidentalis* and *B. papyrifera*. One tree had 0.08% rhododendrin and the other had 0.16%. Four trees of *B. papyrifera* being evaluated by the Evergreen Nursery Company had rhododendrin levels ranging from 0.12% to 0.18%. The patented cultivar 'Rockimon' (registered as "Rocky Mountain Splendor"), a hybrid of uncertain parentage, had 0.13% rhododendrin. Thus, all of the trees mentioned in this paragraph have low levels of rhododendrin which, if our chemical hypothesis is correct, should be more resistant to the bronze birch borer than the average white-barked birch.

Before we end this discussion, I would like to add a bit of personal experience to indicate that long life and white bark do not necessarily mean that a tree is borer resistant. During the latter phases of our rhododendrin research, I was curious about an isolated, multi-trunked, white-barked birch that had been growing, without competition, in the grassy ellipse area at the U.S. National Arboretum for about 30 years. Although the tree had not been attacked by the bronze birch borer, it defied specific identification and was not used in our breeding program. Analyses in 1996 showed that the tree contained 0.5% rhododendrin and should be classified as potentially borer susceptible. The lack of stress was probably the key to survival for this tree.

THE FUTURE

The development, by selection and breeding, of superior insect-resistant trees is a long-term and high-risk undertaking. Such work is only worth the effort when the product will occupy a unique niche in the landscape. White-barked, borer-resistant birches are such trees. It is hoped that this review of successes and failures, hypotheses and opinions, and suggestions and admonitions will stimulate the next generation of geneticists and horticulturists to continue the quest.

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Résumé. Cet article présente une revue approfondie et détaillée de l'état actuel des connaissances sur les hôtes de l'agrile du bouleau ainsi que sur les études biochimiques et génétiques élaborées pour identifier et développer des bouleaux blancs résistants à ce perceur. À la fois les observations et les expériences plus anciennes et celles non publiées d'avant cette époque sont évaluées afin de bâtir une base pour les recherches futures. En se basant sur l'hypothèse que la présence de la rhododendrine dans l'écorce interne des bouleaux est la clé de leur susceptibilité à l'agrile, la découverte que le *Betula nigra* et le *B. maximowicziana* ne contiennent pas ce composé et que *B. davurica*, *B. occidentalis* et *B. papyrifera* en ont à de faibles concentrations ouvre une porte encourageante sur des recherches accrues sur ces espèces. Certains hybrides à faible rhododendrine, potentiellement résistants à l'agrile,

ont été découverts et sont en attente d'une propagation à grande échelle pour des essais sur de plus longues périodes.

Zusammenfassung. Diese Studie stellt eine gründlichen und umfangreichen Rückblick über den gegenwärtigen Kenntnisstand über die Wirtspflanzen des bronzefarbenen Birkenbohrers (*Agilus anxius*) und über die biochemischen und genetischen Studien, die entwickelt wurden, um käferresistente weiße Birken zu identifizieren und zu züchten. Sowohl die älteren und bisher unveröffentlichten Beobachtungen, als auch die Experimente wurden bewertet, um einen Rahmen für die zukünftige Forschung zu liefern. Basierend auf der Hypothese, daß die Anwesenheit von der Chemikalie Rhododendrin in der inneren Rinde der Birke ein Schlüssel für ihre Anfälligkeit gegenüber diesem Bohrinsekt ist, ermutigten die Ergebnisse, daß *Betula nigra* und *B. maximowicziana* diese Komponente nicht enthalten und *B. davurica*, *B. occidentalis* und *B. papyrifera* nur sehr niedrige Gehalte haben, weitere Experimente mit diesen Arten. Einige, potentiell käferresistente Hybriden mit niedrigem Rhododendringehalt wurden entdeckt und stecken nun in einer großen Vermehrung für Langzeitversuche.

Resumen. Este reporte representa una revisión completa y concienzuda del estado actual del conocimiento sobre los huéspedes del barrenador del abedul (*Agilus anxius*) y estudios bioquímicos y genéticos designados para identificar y desarrollar abedules de corteza blanca resistentes. Observaciones y experimentos, los antiguos y los hasta ahora no publicados, son evaluados para proveer una armazón para futura investigación. Basado en las hipótesis de que la presencia del rododendrin químico en el interior de la corteza de abedules es la llave para su susceptibilidad al barrenador, el hallazgo de que *Betula nigra* y *B. maximowicziana* no contienen este compuesto y que *B. davurica*, *B. occidentalis* y *B. papyrifera* tienen bajos niveles, ha alentado una mayor experimentación con estas especies. Algún rododendrin e híbridos potencialmente resistentes al barrenador han sido descubiertos y están esperando una propagación a larga escala para pruebas a largo plazo.