Insights Into Woody Plant Adaptation and Practical Applications

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Introduction

Since its inception in 1954, the NC7 Regional Ornamental Plant Trials have evaluated 623 different accessions of woody landscape plants under a wide range of environments across the North Central U.S. and at other locations with similar climatic conditions. The evaluation of replicated field plantings at multiple locations has a long tradition in forestry (Langlet, 1971; Wright, 1976) beginning with common-garden trials of tree populations in the 1700s and leading to the development of modern, replicated designs in Europe in the early 1900s. By evaluating many provenances of the same species at numerous sites, considerable knowledge has been accumulated about tree adaptation in relation to geographic origin and to climatic and edaphic conditions at the evaluation sites. This knowledge has been valuable in matching forest trees to appropriate production sites and has facilitated the breeding and selection of superior tree populations for timber and Christmas trees (Wright, 1976).

Although based on a similar model of long-term, multi-site evaluation, the design and goals of the NC7 Trials are subtly different than those of classical provenance testing in forestry (Widrlechner, 1990). The NC7 Trials have distributed a different set of species for testing in nearly every year of its 50-year existence. The goal of the NC7 Trials has been to diversify the range of well-adapted landscape plants cultivated in the North Central U.S. by searching for new and promising landscape plants not commonly found in the nursery trade. Trial-site cooperators at more than 30 sites (Table 1) evaluate those plants under a wide range of environmental conditions for a ten-year test. Data are collected on plant survival, growth, injury, and phonological and aesthetic characteristics. For plants distributed since 1984, these data are compiled in a master database accessible on the Internet (North Central Regional Plant Introduction Station, 2004). Occasionally, new cultivars have emerged from the NC7 Trials and introduced into commerce through the cooperating institutions (Becker, 2000).

From the late 1950s until the early 1980s, the performance of NC7 trial plants was summarized in the form of individual five- and ten-year reports published internally. These rather obscure reports are now being prepared for posting on the Internet. After the discontinuation of these publications, reports on the best performing plants at individual trial sites were prepared for trade journals (e.g., Iles and Widrlechner, 1992; Schutzki and Widrlechner, 1996). While these publications were notable in describing valuable characteristics (and the range of adaptation) for individual accessions, until the 1990s little research resulted from the NC7 Trials to compare multiple populations of the same species or otherwise generate data that could be generalized to understand woody-plant adaptation throughout the region. One notable exception was an evaluation of Ligustrum populations that resulted in the selection and release of 'Cheyenne' privet (Dodge et al., 1965).

Geographic and Climatic Analyses

The first opportunity to generate a data set that could easily be analyzed to gain insight into some of the key

factors that affect regional, woody landscape-plant adaptation presented itself in the 1980s. At that time, ten years of evaluation data had been collected on the performance of a diverse assemblage of trees and shrubs resulting from a project conducted in the 1970s with scientists in the former nation of Yugoslavia. Multiple-regression analyses were performed to test the effects of climatic variables on plant survival of 27 accessions collected as part of that project, representing 16 different species of trees and shrubs native to Slovenia, Croatia, and Bosnia & Herzegovina, at 14 NC7 Trial sites (Widrlechner et al., 1992).

During the 1990s, another opportunity arose to analyze the role climatic variables play in plant adaptation. A plant exploration to northern Japan in 1982 resulted in the distribution of numerous woody plants in the NC7 Trials in 1984 and 1985. Widrlechner et al. (1998) reported the results of multiple-regression analyses testing climatic effects on plant survival of 17 accessions from that exploration, representing 11 species tested at 12 NC7 Trial sites.

Taken together, the results of these two studies demonstrated the importance of both low winter temperatures and annual moisture balance in determining woody-plant adaptation in the North Central U.S. In general, woody plants from Yugoslavia were better adapted to cultivation in the North Central U.S. than were those from northern Japan. There was significant overlap between average annual moisture balance at Yugoslav collection sites and at some of the wetter NC7 Trial sites. Low winter temperatures differed significantly between collection sites and trial sites, but generally low-temperature injury or loss was problematic only at the colder trial sites (Widrlechner et al., 1992). In contrast, none of the NC7 trial sites participating in the study of Japanese plants had an average annual moisture surplus as high as that of even the driest of the Japanese collection sites. This mismatch was manifest in considerable loss of Japanese plants during the droughts of the late 1980s. Of the Japanese collections, only Rosa rugosa PI 479562, collected from a drought-prone beach in Hokkaido, performed well across sites (Widrlechner et al., 1998).

Another notable feature of the Yugoslav study was a test conducted on three different measures of low-winter temperature in the multiple-regression analyses. A comparison of January mean temperature, mean annual minimum temperature (the statistic used to define USDA hardiness zones), and the proportion of years with minimum temperatures below -32°C across the 14 trial sites for a 15-year period indicated that all three measures were highly correlated and that each of them contributed to very similar multiple-regression models for the prediction of plant survival (Widrlechner et al., 1992). Although it is likely that extreme low-temperature events and monthly mean winter temperatures are not highly correlated when comparing highly variable, continental sites to highly moderate, maritime sites, such comparisons can reasonably be made within the typical range of sites in the North Central U.S. This is helpful because data on January mean temperatures are more readily accessible than those for extreme low-temperature events.

An opportunity for an independent validation of a plant-survival model based on evaluations of plants from the former nation of Yugoslavia arose when Leege and Murphy (2000) analyzed plant survival and growth of Austrian pines (Pinus nigra Arnold) planted at Saugatuck Dunes State Park in southwestern Michigan. They noted that survival was higher than mean values reported at NC7 Trial sites in Widrlechner et al. (1992) and attributed the difference to this species' high tolerance of sand-dune conditions. Had they entered moisture balance and low temperature data from southwestern Michigan into the overall plant-survival model presented by Widrlechner et al. (1992), they would have discovered that the model provided a reasonable estimate of Austrian pine survival at their location. Climatic data from Allegan County, Michigan, near the pine plantings, resulted in a predicted survival rate of 71% (Widrlechner, 2001), while their study reported a 16-32 year survival rate of ca. 80% (Leege and Murphy, 2000).

One other notable example of climatic comparison to gain insight into woody plant adaptation remains unpublished. In 1984, an exploration to collect native trees and shrubs from Colorado and eastern Utah resulted in the distribution of 12 accessions in the NC7 Trials between 1986 and 1992. In general, plant performance and long-term survival was poor, with many losses likely attributable to foliar and vascular disease. Climatic analysis would suggest that introducing woody plants from significantly drier regions into the North Central U.S. may be problematic. Of these 1984 collections, only Forestiera neomexicana PI 495889, collected near a stream bed in Montrose County, Colorado, performed well (North Central Regional Plant Introduction Station, 2004).

Practical Applications
I see three broad areas for the practical application of these insights into the importance of low winter temperatures and annual moisture balance in limiting regional woody-plant adaptation:
1. targeted germplasm exploration,
2. risk-assessment modeling, and
3. matching species with appropriate sites for cultivation.

However, being able to apply this information on a practical basis requires access to certain types of information. First, one must locate reliable data on low winter temperatures and moisture balance. Winter hardiness-zone maps are quite helpful in visualizing geographic variation in low winter temperatures and have been produced for North America (Cathey, 1990), Europe (Heinze and Schreiber, 1984), Ukraine (Widrlechner et al., 2001), China (Widrlechner, 1997a), Japan (Hayashi, 1990), and Australia (Dawson, 1991). Moisture balance maps are more difficult to locate. Carter and Mather (1966) puyblished a comprehensive set of moisture-balance maps for the world; however, the coarse scaling and zonation used in these maps limit their utility. The Atlas of the Climatic Resources of China (China Meteorological Administration, 1994) and the Oxford Regional Economic Atlas for Western Europe (Cartographic Department of Clarendon Press, 1971) also include useful moisture-balance maps, but neither is quite as detailed as the moisture-balance map created by Widrlechner (1999) for the North Central U.S.

Another useful way to visualize relationships between the range of woody-plant adaptation and climatic variables, including winter temperatures and moisture balance, was presented in graphical form for more than 400 species of woody plants in North America by Thompson et al. (2000). Their atlas includes native range maps and displays plots of January and July mean temperatures and moisture balance for the range of values represented across each species' native range.

Second, for the best results, practical applications should incorporate other important factors, beyond low winter temperatures and moisture balance, that influence woody-plant adaptation. For example, in planning plant explorations, floristics and plant ecology cannot be ignored. A target region that meets climatic criteria, but where local conditions have favored grasslands over woody vegetation may be a very poor source of new trees or shrubs.

Important environmental factors worthy of our attention include photoperiod regimens at the sites of collection and cultivation and local soil composition and hydrology. These factors have been reviewed by Widrlechner (1994a) and Ware (1994). In particular, many of the soils of the North Central U.S. formed under grasslands and/or over glacial till or other calcium-rich parent material, often producing calcareous or alkaline, poorly-drained soils that limit tree growth (Ware, 1990). These soils resemble the human-modified substrates found in urban areas, which typically include calcareous construction debris and/or high concentrations of dissolved salts (Ware 1984, 1994). Ware (1983, 1994) pointed out the parallels between flood plains and calcareous savannas

as natural habitats and urban planting sites as cultivated "habitats," suggesting that these natural habitats would be valuable locations for plant exploration.

1. Targeted Germplasm Exploration

The history of plant exploration for woody-landscape plants includes many examples of travel to distant, rugged lands with high biological diversity and pristine plant communities. These areas are exciting sources of new species and often capture the imagination of adventurous explorers (Spongberg, 1990). In contrast, targeted plant explorations specifically for locating new sources of genes for pest and/or stress tolerance, while common in agronomic and vegetable crops, are relatively rare for ornamental horticulture.

Ware (1983) proposed using climatic analogs to target plant explorations for stress-tolerant landscape plants adapted to the North Central U.S. However, there are many climatic variables that can be used to compare climates from different regions, and it is not always clear which variables are most highly correlated to woody-plant adaptation. For example, Kawase's (1979) failure to consider moisture balance as a criterion for a collection trip to northern Japan in 1982 resulted in collections that were poorly suited for the intended target environment (Widrlechner et al., 1998).

Climatic insights gained from the NC7 Trials could be used to create criteria for the geographic targeting of sources of tolerance to drought, high humidity and rainfall, and extreme temperature conditions for future cultivar improvement through breeding. Similar criteria can be developed to create appropriate matches between typical climates in the North Central U.S. and those of other parts of the world for explorations that are more focused on landscape-plant evaluation and commercial introduction.

Based on the results of the evaluations of plants from the former nation of Yugoslavia (Widrlechner et al., 1992), I began evaluating climatic conditions at sites in central and eastern Europe that potentially would be better sources of European trees and shrubs adapted to the North Central U.S. The results of these studies were published in two reports (Widrlechner 1994a, 1994b) that identified large parts of the forest-steppe transition zone in Ukraine as having good climatic matches to sites in the North Central U.S. In addition to comparisons of low winter temperatures and moisture balance, these studies included latitude, elevation, soil type, and floristics as criteria to identify appropriate collection sites. In 1997 and 1998, I collaborated with Dr. Robert Schutzki at Michigan State University and Drs. Vasily Yukhnovsky and Victor Sviatetsky at the National Agricultural University of Ukraine to develop and submit an exploration proposal to the U.S. National Plant Germplasm System with the endorsement of the Woody Landscape Plant Crop Germplasm Committee.

In September 1999, our team spent about three weeks exploring the forest-steppe transition zone in Ukraine and collected 89 accessions, including many of our targeted species of trees and shrubs. The results of this exploration, including a combined hardiness-zone and trip-route map, are summarized in a report by Widrlechner et al. (2001). Between 2001 and 2004, 19 accessions collected in Ukraine were distributed for evaluation in the NC7 Trials. Various aspects of this trip will be discussed by Dr. Schutzki in the next presentation.

The use of key climatic factors, in concert with analyses of soils, floristics, and additional environmental variables, also has been investigated for China (Widrlechner, 1997b) and for the South Central U.S. (Widrlechner, 2003). The Midwest Plant Collecting Collaborative has been using the analysis for the South Central U.S. to help plan an exploration in the Ozark and Ouachita Mountains in October, 2004.

2. Risk-assessment Modeling and Invasive-species Research

Explorations based on climatic matching, with goals of locating new plants that are well adapted to local

environmental conditions, may run the risk of introducing populations that have problematic combinations of climatic adaptation and reproductive or other biological characteristics that make them likely candidates for escape from cultivation. As we gain a better understanding of the damage that can be caused by invasive, non-native plants (Pimentel et al., 2000), there is increasing urgency for practical tools to predict whether new introductions are potentially invasive. As researchers work to develop such tools, an obvious question is whether we can use the insights gained from our experiences about woody-plant adaptation in the North Central U.S. to help predict the likelihood that non-native woody plants may escape from cultivation and potentially become pests.

Since 1999, when I was asked to contribute to a workshop on invasive species in Iowa, I've been conducting research to help answer that question. If climatic analogs are correlated with woody-plant adaptation, then a good first step would be to examine the native ranges of species that have already naturalized. I began by creating a composite native-range map for 28 non-native woody plants that were known to naturalize in Iowa. The two parts of the world that had the highest concentration of naturalizing species, in central Europe and northeastern Asia, also exhibited January mean temperatures and moisture balance indices resembling Iowa conditions (Widrlechner, 2001). This an interesting correspondence raised the question as to whether most non-native woody plants (not just naturalizing ones) that are cultivated in Iowa came from regions of similar climate. I then collaborated with Dr. Jeffery Iles to compile and analyze the native ranges of 72 non-native woody plants commonly cultivated in Iowa that were not known to naturalize (Widrlechner and Iles, 2002). The native ranges of those species were more diffusely distributed around the temperate world than were the naturalizing species and did not correspond closely to climatic analogs. We mapped the proportions of naturalizing species among the entire set of 100 species evaluated (Widrlechner and Iles, 2002) and learned that more than half the regions with the most naturalizing species also had significantly higher proportions of naturalizing species, generally confirming the findings of the first study (Widrlechner, 2001).

Dr. Iles and I expanded our team to include Dr. Janette Thompson, an urban forester, and Dr. Philip Dixon, a statistician. We developed a new geographic statistic, called the range-wide geographic-risk value, or G, to quantify a species' native range in terms of its relative risk of naturalization in Iowa (Widrlechner et al., 2004). We calculated values for G for each of the 100 species in the earlier studies. We were then able to incorporate G into three risk-assessment models that combined a species' geography with its biological and life-history traits to assign it to one of three categories: accept for introduction (not likely to naturalize), reject (likely to naturalize), and further analysis needed (Widrlechner et al., 2004). We tested our three models against an existing risk-assessment model developed for North America by Reichard and Hamilton (1997). Each of the three models was at least as powerful and accurate in its assignment of the set of 100 species for Iowa as was Reichard and Hamilton's (1997) model. We now plan to validate our models on independent data sets collected in other parts of the North Central U.S. with a goal of developing powerful and accurate regional risk-assessment models. It will be interesting to see how factors that influence woody-plant naturalization vary throughout the region and to determine whether such variation is correlated to geographic differences in woody-plant adaptation.

3. Matching species/populations with appropriate sites for cultivation

The sites where landscape trees and shrubs are planted today often resemble minefields. One can search out the best plants to face typical hazards or one can modify sites to make them more amenable to woody-plant growth (Ware, 1983, 1984). But the commonly used construction and site-preparation practices that lead to inhospitable growing conditions are difficult to change, and complete rehabilitation of damaged sites can be costly and time consuming. Until the conservation of native soils and the retention of more natural hydrological systems are widely integrated into construction plans, finding the right plants to meet challenging conditions will be

increasingly important.

Since the inception of the NC7 Trials, the project has collected, summarized and shared evaluation data to help horticulturists and nursery professionals define geographic limits for woody-plant adaptation within the North Central U.S. This has generally been accomplished on a species-by-species basis, first through the in-house publication of five and ten-year reports and later through the summarization of results on the Internet (North Central Regional Plant Introduction Station, 2004).

Although these reports are useful in describing plant growth and overall performance under a range of climatic conditions typically found in the North Central U.S., I suspect the actual use of these reports by horticultural professionals will be quite limited. This could be rectified two ways. First, we should consider packaging existing data into a more accessible format for landscape professionals, perhaps resembling "The Right Tree Handbook" (Pellett et al., 1991). Second, we may want to reconsider the existing evaluation format to build in notes beyond damage due to cold, drought, flooding, animal predation, etc., taking advantage of specific, limiting conditions noted (or managed) by cooperators, that might be valuable in matching plants to challenging urban sites and in reducing the risk of future invasive pests. The content of plant-performance summaries posted on the Internet (North Central Regional Plant Introduction Station, 2004) could be expanded with the intent of sharing information useful in matching plants to appropriate sites for a broader audience.

Future Directions
As the NC7 Trials begin their second half century, I'd like to share just a few thoughts on future directions in relation to data analysis and building upon the insights gained from past work, realizing that Dr. Jason Griffin and our panel will be examining future directions for the NC7 Trials in greater depth.

First, as we continue to accumulate evaluation data from new plant populations from more parts of the world, the value of these data should increase commensurately. The extended duration of the Trials with many dedicated cooperators located at a relatively constant set of sites retaining their trial plants well past the 10-year evaluation period, may also allow us to examine the effects of longer-term, regional climatic change on woody-plant adaptation.

Second, the recent distributions of Ukrainian plants in the NC7 Trials give us an excellent opportunity to validate the concept of targeted explorations as a way to increase the likelihood of introducing well-adapted plant populations. In the unlikely event that our climatic-matching hypothesis is not as robust as expected, I would hope that we would gain insight into the importance of some unexpected climatic or environmental variable(s) in determining plant adaptation. I also hope that the approach used to plan and conduct the Ukrainian trip can be repeated for other parts of the world with climates and soils analogous to those in the North Central U.S. The increasing sophistication of Geographic Information Systems (GIS) in applying climatic and other geographic criteria to plans for plant exploration should make this process more efficient and effective (Greene and Guarino, 1999; Williams, in press).

Third, just as GIS is transforming our ability to manipulate georeferenced data, the development of expert systems has the potential for synthesizing insights we have gained through years of plant observation, formal evaluation, and statistical analysis and taking them to a new level of refinement. Two areas that can benefit greatly from expert systems are the development of reliable, easy-to-use, protocols to assess risks of plant invasiveness and to match woody landscape plants with appropriate growing conditions.

In this age of technological developments, the combination of appropriate technical tools and insights gained by

our network of dedicated cooperators, through keen observation and a willingness to collect and share such information, is a very powerful one. I am most grateful to have such fine and experienced cooperators and can only encourage those that follow us to build upon these relationships and insights.

Table 1. NC7 Regional Ornamental Plant Trial Sites

State	Site and location
Alaska	Alaska Plant Materials Center, Palmer
Colorado	Colorado State Univ., Ft. Collins
Connecticut	Univ. of Connecticut, Storrs
Illinois	Chicago Botanic Garden, Glencoe
	Southern Illinois Univ., Carbondale
	The Morton Arboretum, Lisle
	Univ. of Illinois, Urbana
Iowa	Bickelhaupt Arboretum, Clinton
	Iowa State Univ., Ames
Kansas	City of Dodge City
	Kansas State Univ. John C. Pair Horticultural Center, Haysville
	Kansas State Univ., Olathe
	USDA/NRCS Plant Materials Center, Manhattan
Maine	Univ. of Maine, Orono
Michigan	Michigan State Univ., East Lansing
	USDA/NRCS Plant Materials Center, East Lansing
Minnesota	Univ. of Minnesota Landscape Arboretum, Chanhassen
	Univ. of Minnesota North Central Res. Center, Grand Rapids
	Univ. of Minnesota Southern Res. Center, Waseca
	Univ. of Minnesota West Central Res. Center, Morris
Missouri	Univ. of Missouri, New Franklin
	USDA/NRCS Plant Materials Center, Elsberry
Nebraska	Nebraska Statewide Arboretum, Lincoln
	Univ. of Nebraska West Central Res. Center, North Platte
New Hampshire	Univ. of New Hampshire, Durham
North Dakota	North Dakota State Univ., Absaraka
	North Dakota State Univ., Carrington
	North Dakota State Univ., Dickinson
	USDA/NRCS Plant Materials Center, Bismarck
Ohio	Mt. Airy Forest Arboretum, Cincinnati
	The Dawes Arboretum, Newark
	The Holden Arboretum, Kirtland
Rhode Island	Univ. of Rhode Island, Kingston
South Dakota	South Dakota State Univ., Brookings
Vermont	Univ. of Vermont, Burlington
Wisconsin	Univ. of Wisconsin, Madison

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