ENVIRONMENTAL ANALOGS IN THE SEARCH FOR STRESS-TOLERANT LANDSCAPE PLANTS

by Mark P. Widrlechner

Abstract. This paper reviews briefly the climatic and edaphic factors related to tree adaptation. Photoperiod regimens, the timing and severity of low temperatures, and high temperature-moisture interactions all are important climatic determinants of adaptation for which adequate data have been widely recorded. Edaphic factors that injure trees in managed environments are more difficult to extrapolate to natural systems, but natural soils that are poorly drained, calcareous, alkaline, or saline may be initial foci for seeking tough trees. A project to identify promising new landscape plants for the north-central United States, by examining climatic, edaphic, and floristic factors in Eastern Europe, is presented as a case study.

Index Words. climate, soil, plant introduction, evaluation, Eastern Europe, north-central United States

In the search for tough trees that thrive in stressful environments, much of our attention should be directed toward tree populations in nature. By analyzing the selective pressures under which natural tree populations have evolved, potentially valuable germplasm can be identified for horticultural evaluation. Evaluation data may lead to superior germplasm that can be directly introduced into the trade, or, more likely, can help identify populations valuable for selection and breeding programs.

Many stresses faced by trees are complex functions of the local growing conditions and, accordingly, serve as selective pressures driving local adaptation, for populations unadapted to such stresses will be injured directly (e.g., extreme low temperature or drought injury) or indirectly by their predisposition to infestation by pathogens and other pests (17,38,39). Our goal should be to minimize injuries and mortality in nurseries and managed landscapes, thereby reducing production, maintenance, and replacement costs. As tree maintenance budgets tighten, interest in such low-input landscapes continues to grow (47).

How can we simplify and quantify the complex environmental relationships leading to adaptation or to injury, and thereby focus our search for tough trees? Ideally, such quantification would emphasize environmental factors that are predictable by existing records and are correlated with stresses analogous to those faced by trees under managed conditions.

Environmental factors with the broadest application to tree adaptation are functions of local climates and soils. The quantity, quality, and timing of light, moisture, and heat potentially available to trees are climatic functions, whereas the availability of moisture and nutrients is greatly influenced by soil characteristics. Of course, edaphic and climatic effects are not clearly separable, because climate and vegetation continually interact with the parent material to produce soil (5).

Climatic factors

We can begin simplifying complex environmental relationships by examining various climatic and edaphic features in light of previous research on woody plant adaptation. Since trees have extended juvenile periods, the evolution of climatic adaptation of tree populations in nature is affected both by long-term, seasonal climatic cycles that are, to varying degrees, predictable and by the frequency and severity of relatively infrequent, extreme conditions, which may be impossible to predict without extensive data.

The annual photoperiod regimen, a direct function of latitude, is one of the most predictable climatic features. The photoperiod regimen may serve as a phenological signal to trees and shrubs for the induction of vegetative growth and flowering (22) and subsequent cessation of growth leading to autumnal cold hardening (16). [These phenomena are reviewed in detail by Salisbury (36).] Cultivation of natural populations for evaluation or direct use in latitudes significantly removed from their provenance often interferes with evolved phenological patterns, resulting in poor growth

and winter injury (25,30). Attempts to cultivate natural tree populations that overlook a provenance's latitude risk failure.

Low winter temperatures predicted from medium to long-term (20-100 year) records are widely used to relate tree adaptation to low-temperature injury (14). The most common measure, mean annual minimum temperature, serves as the basis of important hardiness zone maps for North America (6, 34) and for Europe (14). Other studies have evaluated January mean temperatures in comparison with mean annual minimum temperature to predict the survival of selected woody plants in the north-central United States (50) or incorporated the monthly mean of daily minimum temperatures of the coldest month (MMDM) into multiple regression equations and maps for general woody plant adaptation in Canada (28, 29). The MMDM also was the climatic statistic that was most congruent with boundaries of forest plant communities in Florida (13).

Extreme low temperatures may be at least as important as mean low temperatures in causing injury. Temperatures below -40°C disrupt a common physiological adaptation, winter survival through freezing avoidance produced by free water supercooling in xylem tissue (33) and overwintering buds (35). In plant tissues, supercooling fails at or slightly above -40°C, the spontaneous nucleation point of supercooled water. The frequency of such extreme events has been correlated with the northern limits of the natural ranges of many trees in North America (12,35). Some genera, such as *Prunus* (33), include both species that rely on supercooling and others with poorly understood mechanisms that allow survival below -40°C.

Photoperiod reduction, decreasing autumn temperatures, and the physiological status of the plant can interact to acclimate woody plants to winter conditions (11). Record low temperatures during the normal acclimation period producing massive tree mortality have been well documented in trade literature (2,43). Such losses can be characterized by monitoring changes in low-temperature tolerance during the autumn and early winter in relation to on-site temperature data (26).

Whereas the timing and severity of low temperatures are limiting factors in the northern distribution of woody plants in North America, the limiting role of insufficient warmth during the growing season in Scandinavia has been well documented (40). The effects of insufficient warmth on plant distribution can be observed both on vegetative growth and development, and on sexual reproduction [see especially the works of Pigott and Huntley (31,32) on *Tilia cordata*]. These effects are not limited to Scandinavia, but also occur at other northern or montane sites. Ouellet and Sherk (28) reported that the mean frost-free period and the mean daily maximum temperature of the warmest month were statistically significant factors in multiple regression analyses of the relationship between climatic factors and woody plant adaptation across Canada. In contrast, my colleagues and I (50) found no significant effects of July mean temperatures on the survival of woody plants from Yugoslavia in the north-central United States.

Extremely high summer temperatures also induce stress, either directly to species that have evolved in alpine or otherwise cool conditions (9) or, indirectly, in concert with low relative humidities (23) or inadequate soil moisture, producing drought injury. A broad range of mathematical formulas has been proposed (7) for estimating the potential of temperature, moisture, and other factors, such as wind and insolation, to effect transpiration and thus to induce possible stress. These measures are generally known as potential evapotranspiration (PE).

Long-term moisture deficits and surpluses can be analyzed by comparing PE with mean annual precipitation. One method of expressing the balance between PE and precipitation, Mather and Yoshioka's (24) moisture index, has helped predict the distribution of plant communities (24) and is a statistically significant variable, along with January mean temperatures, in predicting the survival of woody plants from Yugoslavia at test sites in the north-central United States (50).

Mean monthly or seasonal precipitation records have also been analyzed in conjunction with temperature data to predict woody plant survival in Canada (28) and the distribution of natural plant communities in North America (21,41). The rela-

tionship of woody plant adaptation to precipitation extremes producing serious droughts or floods has not been studied systematically, except for specific phenomena, such as relationships between leaf abscission and drought (1). Drought severity can be quantified with the Palmer Drought Severity Index or with Palmer's Z-Index (18), but no reports where these indices are compared with plant distribution have been found. However, Borchert's (4) classic study of climatic factors corresponding to the distribution of grassland vegetation in the Great Plains and Midwest described interesting relationships between plant communities and patterns of July precipitation and temperature in drought years. His findings suggest that variability in the balance between PE and precipitation may be as important as is the overall balance. The effects of abnormally high precipitation are problematic, depending on the physiological status of the plant (winter floods vs. summer floods), and on drainage and other soil conditions that can influence root distribution (20).

Clearly, the photoperiod regimen, low temperatures, and interaction of high temperatures and moisture are all important determinants of woody plant adaptation. As we consider these factors in our search for tough trees, we would be wise to base our search on actual conditions faced by plants in our target environments (pre-identified managed landscapes), which may differ widely from conditions recorded at nearby weather stations (46), and on plant performance data previously collected under these or similar environments.

Edaphic Factors

Soils of managed landscapes, especially those in urban areas, have been greatly modified by human activity and often bear little resemblance to nearby undisturbed soils (8,47). Human disturbance creates soils that may be saline from deicing salts, alkaline from irrigation, calcareous from discarded construction materials, or compacted by construction machinery or other traffic. Finally, natural soil profiles are often disrupted when topsoil is removed before new construction. These disturbances produce soils with low oxygen-holding capacities and chemical compositions unlike those commonly found in natural forest soils (3,8,42,45).

Although direct analogs to human-disturbed soils may be rare in nature, the processes of alkalization, calcification, salinization, and hardening all can occur during soil genesis (5) and are associated with particular soil types. When appropriate soil types are identified and detailed maps are available, it may be possible to employ this information to focus the search for tough trees, as has been proposed by Ware (45).

In the absence of detailed soil maps, knowledge of topographic and general landscape features [such as karsts (dissected limestone near the surface), extensive flood plains, or salt flats] can help focus the search. Certain plant groups are also indicators of soil drainage or chemistry: willows (*Salix* spp.) prefer poorly drained, seasonally flooded soils and deciduous azaleas (*Rhododendron* spp.) prefer nutrient-poor, acidic soils. Detailed distribution information for such indicator species may partly substitute for direct soil mapping data.

Case Study

With this very long "preface" complete, I will now describe an ongoing effort to locate and acquire potentially useful trees and shrubs native to Eastern Europe, for testing in the north-central United States. This project began in a rather unsystematic fashion in the mid-1970s, with the introduction to the United States of a diverse set of woody plant populations from the former nation of Yugoslavia (50). Many of these populations were evaluated at sites throughout the north-central United States as part of the NC-7 Regional Ornamental Trials, a long-term project to evaluate new landscape plants and to increase the future diversity of well-adapted plants found in commerce (48).

The 10-year evaluation results of Yugoslavian landscape plants indicated that only about a third of the populations survived and generally performed well throughout the north-central United States, another third failed at the colder or drier sites, and the remaining third failed at all sites (50). Statistically significant multiple-regression models, based on low winter temperatures and

Table 1. Criteria for future exploration for woody landscape plants in Eastern Europe [from (50)].

1. January mean temperatures ≤ -5°C
2. Moderate, annual moisture deficits
3. July mean temperatures ≥ 18°C
4. Elevations ≤ 1000 meters

moisture conditions at test sites, explained 84% of variation for first-year survival and 56% of variation for overall survival across all sites (50). From these results and an analysis of climatic conditions in the former nation of Yugoslavia, my colleagues and I (50) developed a set of four criteria (Table 1) for locating Eastern European sites with environments more closely analogous to those found in the north-central United States.

These criteria are now being employed to focus future plant acquisition in Eastern Europe. First, it was necessary to analyze climatic and topographic data to determine which sites, if any, met the four criteria. I found that much of central and northern Ukraine, and adjacent portions of Belarus, the Russian Federation, and Moldova, along with two small areas in the foothills of the southern Carpathian Mountains in central Romania met all criteria (49). A literature review of natural plant communities was then performed to ensure that the criteria did not identify grassland sites lacking useful woody plants. Patterns of plant communities in these regions of Eastern Europe include mixed and deciduous woodlands, grasslands, and transitional communities similar to those found in Minnesota and Wisconsin (49).

It has not yet been possible to find soil maps for the Eastern European regions, and fine-scale vegetation maps are only now being prepared for publication (27). Thus, current efforts are focusing on developing contacts with botanical gardens in these regions known to collect and share seeds from natural populations (15) and identifying promising species. Nineteen botanical gradens have been identified for contact in the near future. And relevant floras (10,19,37,44) have been consulted to develop a comprehensive list of woody plants native to the region. This comprehensive list, along with habitat descriptions, aids our effort to identify promising species in three ways.

Table 2. Selected trees and shrubs from Eastern Europe

Commonly cultivated species for which superior ecotypes are desired:
Acer campestre and *platanoides*
Carpinus betulus
Cornus mas
Euonymus europaeus
Fraxinus excelsior
Ligustrum vulgare
Tilia cordata
Indicator species for calcareous soils (C) and poor drainage (D):
Acer pseudoplatanus (C)
Alnus glutinosa and *incana* (D)
Corylus avellana (C)
Cotinus coggygria (C)
Cytisus podolicus (C)
Euonymus verrucosus (D)
Fraxinus excelsior (D)
Genista tinctoria (C)
Juniperus communis (C)
Populus alba and *nigra* (D)
Quercus pubescens (C)
Salix (many species) (D)
Ulmus laevis (D)
Taxonomically diverse plant groups:
Crataegus
Cytisus and related genera
Rosa
Salix
Thymus

First, the list is being checked for those European landscape plants that are commonly cultivated in our region, with an emphasis on those that are poorly adapted to colder and drier areas, such as the northern Great Plains. Collections from Ukraine and surrounding areas, which meet the climatic criteria, should be better adapted to the harsher climates of the north-central United States than are those from sites farther south or west in Europe. Second, habitat information is being checked for species that are potential indicators for calcareous, alkaline, saline, and poorly drained soils. Finally, the list gives some indication of patterns of genetic diversity as reflected in species diversity within genera. Genetically diverse genera, although perhaps unsuitable for direct introduction, may be particularly interesting sub-

jects for future breeding and selection. A few examples identified by these analytical methods are listed in Table 2.

The true test of this program remains to be conducted. How will plants identified in this fashion perform at diverse sites in the north-central United States? Perhaps we will discover important limiting factors overlooked initially. Alternatively, we might be too successful. Our network of trial site cooperators will be warned that these introductions could be so well adapted that they might invade natural plant communities; they should manage these plants accordingly. We hope to begin acquiring and evaluating these plants during the next few years and ultimately find a broad array of tough new trees and shrubs.

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Résumé. Cet article résume de façon brève les facteurs climatiques et édaphiques reliés à l'adaptabilité des arbres. Les régimes de photopériode, la période et la sévérité des températures basses, et les interactions entre les hautes températures et l'humidité représentent tous des facteurs climatiques importants qui sont déterminant pour l'adaptabilité et pour lesquels des données adéquates ont été largement consignées. Les facteurs édaphiques qui affaiblissent les arbres en milieu aménagé sont plus difficiles à extrapoler des systèmes naturels, mais les sols naturels qui sont mals drainés, calcaires, alcalins ou salins peuvent être initialement visés pour rechercher les arbres plus résistants. Un projet pour identifier de nouveaux végétaux prometteurs dans le domaine de l'aménagement paysager pour le Centre-Nord des États-Unis au moyen d'un examen des facteurs floristiques, climatiques et édaphiques propres à l'Est de l'Europe est présenté comme cas d'étude.

Zusammenfassung. Diese studie gibt einen kurzen Überblick über die klimatischen und bodenbedingten Faktoren bezüglich der Baumadaption. Die Photoperiode, die Dauer und Strenge von tiefen Temperaturen und die Interaktionen zwischen hoher Temperatur und Feuchtigkeit sind alle wichtige klimatische Determinanten der Anpassung, für die entsprechende Daten weitläufig erhoben wurden. Bodenbedingte Faktoren, die in einem bewirtschafteten Umfeld Bäume verletzen, sind schwieriger zu mutmaßen als in einem natürlichen System, aber natürliche, gewachsene Böden die eine geringe Durchlässigkeit haben, kalkreich, basisch oder salzig sind, möglicherweise erste Anhaltpunkte bei der Suche nach widerstandsfählgen Bäumen sein. In einer Fallstudie ist ein Projekt dargestellt, welches vielversprechende neue Pflanzen für Landschaften im Norden und Zentrum der Vereinigsten Staaten anhand der Untersuchungen von klimatischen, edaphischen und floristischen Faktoren in Osteuropa, identifizieren soll.