

Foliar Traits of Sugar Maples and Black Maples Near 43°N Latitude in the Eastern and Central United States

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ABSTRACT. Selection of sugar maples (*Acer saccharum* Marsh.) and black maples (*Acer saccharum* Marsh. ssp. *nigrum* Desm. or *Acer nigrum* Michx. f.) that will be more resilient than existing cultivars in managed landscapes could be facilitated by defining relationships between geographic origin and foliar traits critical to leaf function. We examined variation in leaf morphology and anatomy of both taxa, known collectively as hard maples, near 43°N latitude and tested for relationships between foliar traits and the longitude of origin from 70° to 94°W longitude. Leaves exposed to direct solar radiation were sampled from up to 20 trees indigenous at each of 42 sites during 1995 and 1996. All leaves from east of 75.84°W and from 92.73°W and further west expressed morphological characters associated with sugar maple and black maple, respectively; leaves with intermediate traits were found between these two longitudes. Leaves from 90° to 94°W had the highest surface area due to increases in the areas of middle and proximal portions of laminae. Up to 1162 trichomes/cm² were present on the abaxial surface of laminae from west of 85°W, while laminae from further east were glabrous or had ≤300 trichomes/cm². Laminae from western habitats also had relatively high stomatal frequency, and stomatal apertures of laminae west of 91°W were particularly narrow. Longitude did not affect specific weight and thickness of laminae, which averaged 5.5 mg·cm⁻² and 90 μm, respectively. Principal component analysis of laminar traits showed existence of two clusters. A large group dominated by data from trees in New England also contained data from trees as far west as ≈93°W longitude; data for trees further west were clustered separately. Although phenotypic continua were defined, laminae west of 93°W were distinct, which suggests trees selected there may function differently in managed landscapes than trees selected from native populations further east.

Sugar maple (*Acer saccharum* Marsh.) is an economically important tree species native to the United States and Canada. Cultivars of sugar maple are among the most highly prized trees for use in managed landscapes because of their uniform crown form and outstanding leaf color during autumn. Many of these taxa are sensitive to the limited space, variable moisture supply, salinity, and compaction common to urban soils. These conditions, combined with extremes in wind, temperature, and irradiance that occur in exposed landscapes, lead to foliar damage and tree decline (Close et al., 1996; Ware, 1983), particularly when cultivars of sugar maple selected in the northeastern United States are used in less mesic or urbanized landscapes (Dirr, 1998). Many commercially important genotypes of sugar maple were selected

for reasons other than their resilience in harsh environments, yet certain cultivars appear less prone than most to stress (Dirr, 1998). Observations of these genotypes suggest foliar traits related to the water economy and physical durability of laminae could be important criteria for selecting additional genotypes. Few data exist on variation in such traits among natural populations of sugar maple and its allied taxa. Defining this variation, and determining whether the range in expression of desirable traits is distributed predictably within a geographic area, would provide a basis on which to rate existing cultivars and to make new selections.

The contiguous distribution of sugar maple extends as far west as central Minnesota and eastern Kansas (Kriebel and Gabriel, 1969; Little, 1971). Between these western extremes, sugar maple is restricted to only eastern portions of Iowa. In contrast, the contiguous range of black maple [*Acer saccharum* Marsh. ssp. *nigrum* Desm. (Desmarais, 1952) or *Acer nigrum* Michx. f. (Rehder, 1940)] extends west to central Iowa but is not more westerly in other states than the distribution of sugar maple (Kriebel and Gabriel, 1969). Thus, central Iowa is the most westerly portion of the contiguous range of black maple where sugar maple does not occur. A region near the 43°N latitude is unique because sugar maple and black maple, both members of the *Saccharina* Pax. section of the *Aceraceae* (hard maples), are geographically separate (allopatric) at different longitudinal extremes that border a region from eastern Iowa to Vermont where both taxa are native (sympatric). Justification for analyzing black maples along with sugar maples includes more than patterns of natural distribution. Black maple has ornamental value (Dirr, 1998) and is the predominant hard maple in portions of the northeastern quadrant of the United States where mean annual precipitation is relatively low (United States Environmental Data Service, 1968) and droughts are relatively common. This precipi-

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Table 1. Latitude, longitude, elevation, and mean annual precipitation and temperature of sites where indigenous black maples and sugar maples were collected in 1995 and 1996. Taxon composition indicates the number of samples judged subjectively to be *Acer nigrum* (first number) out of the total number (second number) of samples.

Site	Year (s) sampled	Longitude (°W)	Latitude (°N)	Elevation (m)	Mean annual		Taxon composition
					Precipitation (cm)	Temp (°C)	
Bradbury Mountain State Park, Maine	1996	70.183	43.905	122	115	7.4	0/10
Harris Farm, Dayton, Maine	1995	71.000	43.500	61	108	6.7	0/10
Kingston State Park, N.H.	1995, 1996	71.059	42.927	40	92	7.3	0/20
Bear Brook State Park, N.H.	1995, 1996	71.353	43.108	198	96	7.7	0/20
Greenfield State Park, N.H.	1995, 1996	71.833	42.958	244	92	7.3	0/20
Fox State Park, N.H.	1995, 1996	71.911	43.142	244	96	7.7	0/20
Hunter Brook Partnership, Brattleboro, Vt.	1996	72.763	42.944	110	112	7.5	0/8
Jamaica State Park, Vt.	1995	72.775	43.107	73	102	6.0	0/10
Green Mountain National Forest, Vt.	1995, 1996	73.118	44.008	488	84	2.0	0/16
Arlington State Park, Vt.	1995	73.204	43.032	701	102	6.0	0/10
Saratoga National Historical Park, N.Y.	1995, 1996	73.625	43.000	61	104	8.3	0/10
Grafton Lakes State Park, N.Y.	1996	73.667	42.750	457	92	8.6	0/10
Pack Forest, Warrensburg, N.Y.	1995, 1996	73.792	43.542	242	89	7.4	0/20
Chenango Valley State Park, N.Y.	1996	75.841	42.213	274	94	7.7	1/9
Fillmore Glen State Park, N.Y.	1996	76.396	42.694	305	97	7.8	0/9
Watkins Glen State Park, N.Y.	1996	76.901	42.369	305	109	7.2	0/10
Allegany State Park, N.Y.	1995, 1996	78.750	42.158	549	119	8.3	0/20
Lakeport State Park, Mich.	1995, 1996	82.496	43.123	183	79	8.6	0/7
Sleepy Hollow State Park, Mich.	1995, 1996	84.413	42.939	244	79	8.6	2/17
Saugatuck Dunes State Park, Mich.	1996	86.208	42.708	202	97	9.9	1/9
Silver Lake State Park, Mich.	1996	86.511	43.679	55	75	4.2	0/10
Kettle Moraine State Forest, Wis.	1995, 1996	88.500	42.867	317	79	3.7	0/18
Village of Maple Bluff, Wis.	1996	89.383	43.075	265	78	4.4	0/10
Abraham Woods, Albany, Wis.	1995, 1996	89.483	42.667	253	102	7.7	0/20
Yellowstone Lake State Park, Wis.	1996	89.987	42.759	279	84	7.2	0/3
Dean Thomas Property, Montfort, Wis.	1995	90.420	42.975	275	79	7.4	1/8
Wildcat Mountain State Park, Wis.	1996	90.561	43.700	305	85	7.8	0/9
Wyalusing State Park, Wis.	1996	91.122	42.992	275	81	7.5	0/10
Yellow River State Forest, Iowa	1995, 1996	91.250	43.167	317	81	7.5	20/20
Wapsipinicon State Park, Iowa	1996	91.283	42.095	293	67	8.8	0/10
Palisades State Park, Iowa	1996	91.506	41.907	244	75	8.9	0/10
Backbone State Park, Iowa	1995	91.559	42.616	342	90	7.6	0/10
Maralie Forest, Frankville, Iowa	1995	91.667	43.208	366	81	8.2	1/4
Volga River Recreation Area, Iowa	1996	91.722	42.865	305	87	7.9	0/10
Echo Valley Recreation Area, Iowa	1996	91.765	42.944	305	87	7.9	0/10
Wentland Woods, Floyd, Iowa	1995, 1996	92.733	43.117	336	84	8.1	10/10
Mather's Woods, Nora Springs, Iowa	1996	92.983	43.150	342	81	8.1	10/10
Pine Lake State Park, Iowa	1995, 1996	93.078	42.371	305	86	8.2	20/20
Claybanks Forest, Nora Springs, Iowa	1996	93.083	43.207	348	88	8.1	10/10
Pammel Woods, Iowa	1995, 1996	93.525	42.500	275	84	7.9	20/20
YMCA Woodland, Iowa	1995, 1996	93.944	42.140	336	84	8.7	20/20
Dolliver Memorial State Park, Iowa	1995, 1996	94.083	42.387	305	86	8.4	20/20

tation pattern was among the reasons Ware (1983) speculated that black maples may be more resistant to drought than sugar maples.

Several of the foliar traits used to distinguish hard maples could also influence their relative resilience in the landscape. Leaves of sugar maple have three to five lobes, are coarsely toothed, and have narrow and deep sinuses (Rehder, 1940). In contrast, leaves of black maple, which often are associated with stipules (Dirr, 1998), have a relatively entire outline because they lack the basal two lobes (Dansereau and Desmarais, 1947). Reduced sinus depth in black maple (Rehder, 1940) might affect convective heat loss (Gottschlich and Smith, 1982) and boundary layer thickness (Baker and Myhre, 1969). Both Desmarais (1952)

and Powers (1967) concluded that leaves of black maple have a greater surface area than those of sugar maple, but relative thickness of laminae is controversial. Powers (1967) stated that laminae of black maple may be thinner than those of sugar maple, yet Preston (1989) listed thicker leaves among the traits that separate black maple from sugar maple. Black maples subjected to drought in a greenhouse had a higher specific leaf weight than did drought-stressed sugar maples (Graves, 1994). Differences in specific weight could be due to leaf thickness or cell size, which both influence leaf water relations (Ashton and Berlyn, 1992; Graves, 1994). Leaves of black maple tend to have more pubescence on abaxial surfaces than leaves of sugar maple (Dansereau

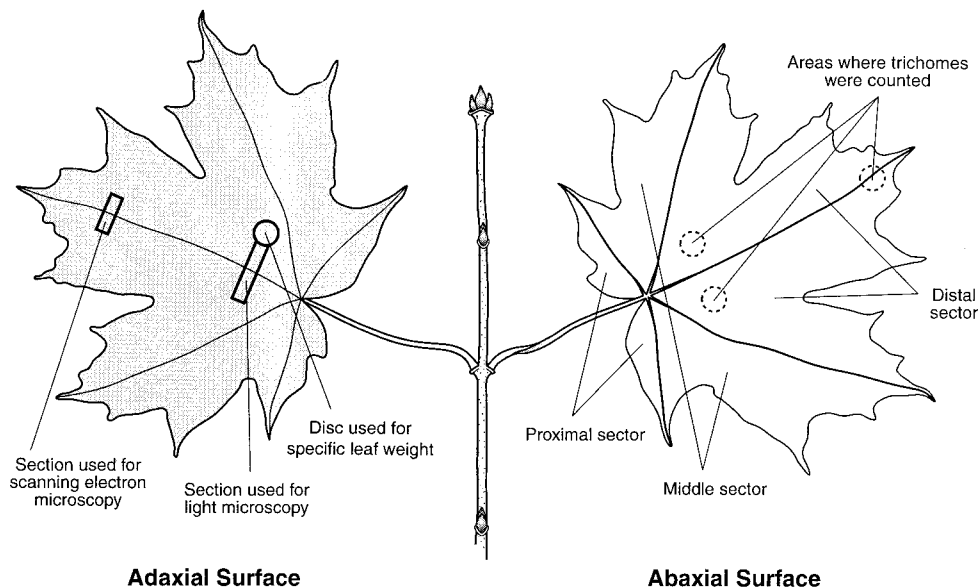


Fig. 1. Schematic representation of the areas on a pair of hard maple leaves from which data were taken. The third oldest pair of leaves from terminal shoots of trees was sampled.

and Desmarais, 1947; Desmarais, 1952; Rehder, 1940). Pubescence could influence leaf water relations by increasing boundary layer resistance (Donselman and Flint, 1982). The extent and patterns of variation in such traits of sugar maples and black maples have not been well defined.

An objective of this research was to test for relationships between longitude of origin and foliar morphological and anatomical traits of sugar maples and black maples along a latitudinal gradient that would include zones of allopatry and sympatry for both taxa. We also sought to define differences between sugar maple and black maple more precisely, and to assess whether foliar characters of the two taxa have remained distinct in their zone of sympatry. Our approach was to measure foliar traits on 537 shoots from trees indigenous near the 43°N latitude and to use regression analyses to test for relationships between those traits and longitude of origin. We also used principal component analysis, a multivariate technique used frequently to reveal relationships among several quantitative variables (Jackson, 1991). The analysis involved development of matrices of variables that were partitioned by an eigenequation. Corresponding eigenvalues, which can solve the eigenequation and render the highest correlation among variables, and eigenvectors, which represent the relative importance of variables, were generated in our analysis. A plot of principal component data was used to test for the existence of populations of hard maples that share traits of potential biological significance to those interested in selecting promising new genotypes.

Materials and Methods

PLANT MATERIAL. A terminal shoot with at least three nodes was collected from each of up to 20 hard maple trees at 24 (1995) and 36 (1996) sites near 43°N latitude from 94°W longitude in Iowa to 71°W longitude in Maine (Table 1). Trees at each site were physiologically mature, had trunk diameters of 5 to 61 cm at ≈1.3 m above ground, and were chosen to represent the foliar diversity of

indigenous hard maples in the area. Samples were collected in July, August, and September. All samples formed the year of collection and had been fully exposed to solar radiation. Shoots were kept between moist paper towels sealed in plastic bags during transport to our laboratory, which was completed within 2 d for all samples. We considered leaves from Dolliver State Park, Pammel Woods, and the YMCA Woodland near 94°W longitude (Table 1) as reference black maples based on their cordate bases, shallow sinuses, pubescence, and texture (Rehder, 1940; Ware, 1983). Subjective comparisons with these references were made to designate each shoot as sugar maple or black maple. The basipetal end of each stem was cut under and held in tap water. The containers of tap water with shoots were then enclosed in plastic bags and kept in a dark cooler at 5 °C for 12 h to rehydrate the leaves.

SURFACE AREA. Laminar surface area of one leaf from the third oldest pair of leaves was determined with a leaf area meter (model 3100, LI-COR, Lincoln, Nebr.). This leaf was then dissected under an Olympus SZ60 microscope (Olympus Optical, Tokyo, Japan) so partitioning of surface area within the lamina could be assessed. While viewing the abaxial surface, a cut was made through the center of the midvein to bisect the leaf. Then a cut was made through each of the two pairs of lateral veins to divide leaves into sectors designated as distal, middle, and proximal (Fig. 1). Surface area of each sector was measured with the leaf area meter. Areas of both halves of the leaf were combined for each sector, expressed as a percentage of the total area for each leaf, and plotted against longitude.

TRICHOME FREQUENCY. Trichomes on the abaxial surface of the leaf used for surface area measurements were counted by viewing three 0.237-cm² areas (Fig. 1) with the Olympus SZ60 microscope. For each leaf, the number of trichomes within 1 cm² was determined as an average of the three areas assessed.

SPECIFIC WEIGHT. A cork borer was used to remove a 0.79-cm² disc from the leaf opposite the one used for surface area and trichome determinations. Discs were taken from the same region of each leaf, 2 to 3 cm above the petiole attachment (Fig. 1). Weight of each leaf disc was determined after it dried at 67 °C for 3 d. Specific leaf weight was calculated by dividing dry weight by disc area.

MICROSCOPY. Two samples were cut transversely perpendicular to the midvein from leaves used to measure specific weight. From each leaf, a sample 10 mm long and 3 mm wide, taken 2 to 3 cm from near the tip of the central lobe (Fig. 1), was preserved in formalin–acetic acid–alcohol (FAA) (Berlyn and Miksche, 1976). These samples were dehydrated in a graded ethanol series and critical-point dried with liquid carbon dioxide. Dried specimens were mounted on brass discs and sputter-coated with gold-palladium. Trichome morphology was examined with a model JSM-5800LV scanning electron microscope (Japan Electron Optic Laboratory, Akishima, Japan). A second sample, 15 mm long and 3 mm wide, was taken from adjacent to the area removed to determine specific leaf weight (Fig. 1) and preserved in FAA.

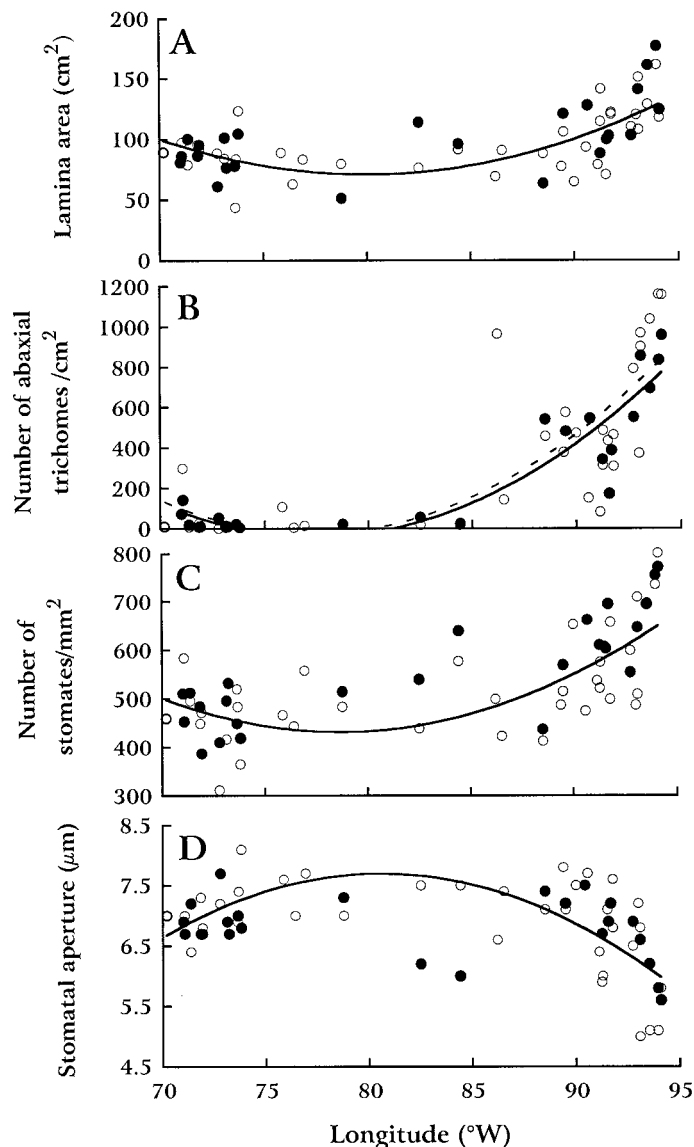


Fig. 2. Foliar traits that varied with longitude for hard maples sampled in 1995 (●) and 1996 (○) from sites near 43°N latitude. Each point is a mean of up to 10 values. (A) Mean lamina area; lamina area = $1820 - 44.2 \text{ longitude} + 0.28 \text{ longitude}^2$; $r^2 = 0.46$, $P = 0.0001$. (B) Trichomes on abaxial leaf surface; for 1995 (solid line), number of trichomes/cm² = $17700 - 458 \text{ longitude} + 2.96 \text{ longitude}^2$; $r^2 = 0.84$, $P = 0.0001$; for 1996 (broken line), number of trichomes/cm² = $18425 - 477 \text{ longitude} + 3.08 \text{ longitude}^2$; $r^2 = 0.64$, $P = 0.0001$. (C) Stomates on abaxial leaf surface; number of stomates/cm² = $5381 - 127 \text{ longitude} + 0.82 \text{ longitude}^2$; $r^2 = 0.52$, $P = 0.0001$. (D) stomatal aperture; stomatal aperture = $-37.5 + 1.12 \text{ longitude} - 0.007 \text{ longitude}^2$; $r^2 = 0.30$, $P = 0.0001$.

A subsection 5 mm long and 3 mm wide removed from the end of each of these samples was rehydrated into water through 50%, 30%, and 10% ethanol and pressed between paper towels at 23 °C. Clear finger nail polish (No. 61, Revlon, New York, N.Y.) was painted on the abaxial surface and allowed to dry for 15 min. Subsections were placed under an Olympus SZ60 zoom stereo microscope with fiber-optic lighting. Forceps were used to lift the dry replica from the sample. Each replica was placed on a glass slide, sealed with a cover slip, and observed with an Olympus BH-2 compound microscope fitted with a micrometer and ocular grid. Stomata within a 0.05-mm² grid were counted. Length and width of three guard cells chosen at random within the same grid, and aperture width between these cells, were measured and averaged.

The remaining subsection was dehydrated in a graded ethanol-tertiary butanol series and embedded in Paraplast-xtra (Oxford Labware, St. Louis, Mo.). Serial transverse sections were cut at 10 µm, stained with safranin-fast green, and observed with the Olympus BH-2 microscope. A randomly selected serial section was used to measure thickness of the entire section, adaxial and abaxial epidermal layers, and mesophyll and palisade parenchyma. Two measurements of total thickness and of each thickness component were taken 5 mm from the midvein and averaged.

DATA ANALYSIS. Analysis of variance (ANOVA) to test the effect of year of collection was performed (Statistical Analysis System [SAS], Cary, N.C.) for each dependent variable. Linear and quadratic relationships between leaf traits and longitude were tested by using regression analyses (SAS). Separate regression models for data from 1995 and 1996 were determined if *F* tests from ANOVA showed a year effect at $P \leq 0.05$. Procedure PrinComp of SAS was used to determine principal component scores based on foliar morphological and anatomical traits that regression analyses showed were related to longitude.

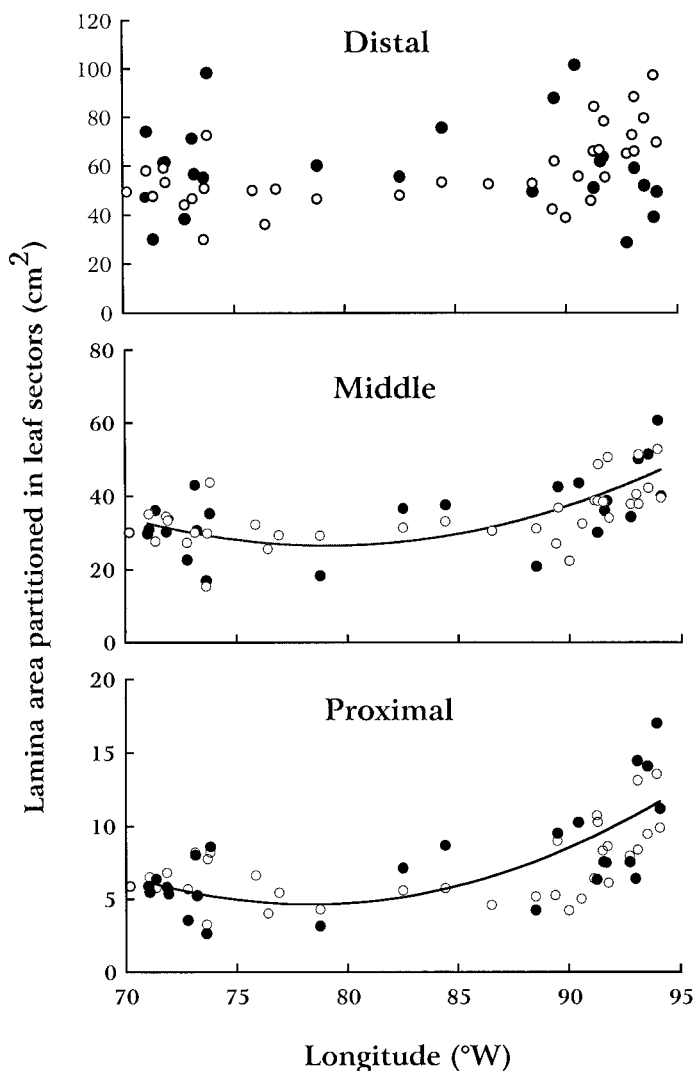


Fig. 3. Relationship between longitude and lamina area partitioned in distal, middle, and proximal sectors of hard maple leaves collected in 1995 (●) and 1996 (○) from sites near 43°N latitude. Each point is a mean of up to 10 values. For the middle sector, area = $546 - 13 \text{ longitude} + 0.083 \text{ longitude}^2$; $r^2 = 0.42$, $P = 0.0001$. For the proximal sector, area = $196 - 4.8 \text{ longitude} + 0.03 \text{ longitude}^2$; $r^2 = 0.45$, $P = 0.0001$. No statistical relationship existed between area partitioned in distal sectors and longitude.

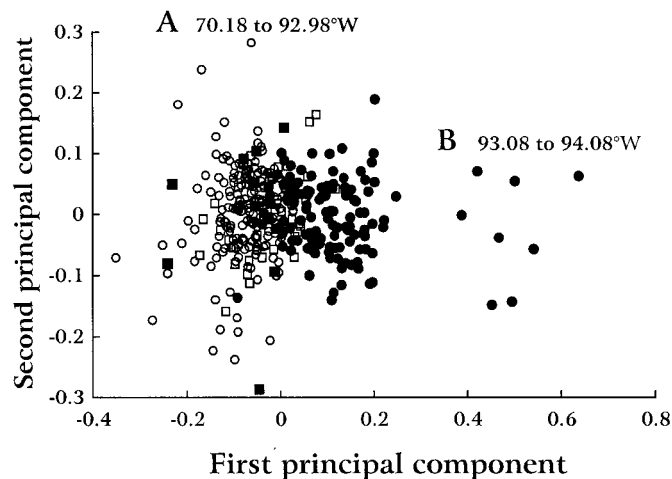


Fig. 4. Plot of the relationship between first and second principal components from the analysis of morphological traits that varied with longitude for hard maple leaves sampled near 43°N latitude. Each point represents the average of samples from each site. Points from four geographical regions have the following symbols: (●) Iowa; (○) New York, New Hampshire, Vermont, and Maine; (■) Michigan; (□) Wisconsin. Note that most plants in group A occur between 70.18° to 92.98°W longitude. Plants in group B were within 93.08° to 94.08°W longitude.

Results

All samples from Pack Forest, N. Y. (73.79°W longitude), and further east were judged subjectively to be sugar maples, while all samples from Wentland Woods, Iowa (92.73°W longitude), and further west were deemed to be black maples (Table 1). Only 26 of the 243 samples from between these two longitudes were considered black maples (Table 1). Mean annual precipitation (Table 1), tended to decrease with increasing longitude (precipitation [mm] = 1567 – 7.87 [longitude]; $r^2 = 0.35$, $P = 0.0001$).

Year of collection did not affect total surface area of laminae nor the area in distal, middle, and proximal sectors. Laminae from westerly sites had the highest surface area, and the relationship of total area and longitude was best fitted by a quadratic regression function (Fig. 2A). Most surface area was partitioned in the distal and middle sectors. Percentages of area in middle and proximal sectors were best represented by quadratic functions (Fig. 3). Specific leaf weight did not vary with longitude and was higher ($P = 0.0043$) in 1996 (5.8 mg·cm⁻²) than in 1995 (5.2 mg·cm⁻²).

Although ANOVA revealed that trichome frequency over all longitudes was higher in 1996 than in 1995, the relationship of trichome frequency and longitude was similar both years (Fig. 2B). Fewer than 200 trichomes/cm² were typical on laminae from east of 87°W. Regression functions predicted trichome frequency increased from ≈0/cm² at 80°W to ≈800/cm² at 94°W (Fig. 2B), and leaves at the most westerly sites had a trichome frequency of nearly 1200/cm². Trichomes were uniseriate and arose from both major and minor veins regardless of the location from which the sample was obtained. Trichome morphology, including surfaces with raised areas ≈2 μm long and ≈4 μm apart, was similar for all samples.

Leaves from the most westerly sites had the highest stomatal frequency on the abaxial surface (Fig. 2C) and smallest stomatal aperture (Fig. 2D). Quadratic regression functions best represented changes in stomate frequency and the width of the stomatal aperture across the region, which did not differ in 1995 and 1996. Guard cell pair length and width, which were not influenced by year or longitude, averaged 17.0 and 17.5 μm, respectively.

Variation in total laminar thickness and its components was not related to year of collection nor longitude. Overall mean thickness of laminae was 90 μm. Mean adaxial and abaxial epidermis thicknesses were 10 and 7.5 μm, respectively. Thickness of the palisade mesophyll averaged 41.5 μm, and mean thickness of spongy mesophyll was 28.5 μm.

Principal component analysis of data from sites sampled in both years showed the first two components accounted for 75% of the variation of traits that related to longitude (Table 2). The first principal component had high positive factor loading of trichome frequency, lamina area, and stomatal density, and high negative factor loading of stomatal aperture. Percentage lamina area in basipetal lobes was the variable that contributed most to the second principal component. The third principal component explained 9.8% of the total variation (Table 2). ANOVA showed that only variation along the axis of the first principal component was significant. The second principal component axis was retained for graphical purposes. A scatter plot depicting the relationship between the first and second principal components based on site averages separated two groups at ≈0.3 of the first principal component (Fig. 4). While group 1 consisted of data from all the states where we sampled, data from Iowa, Wisconsin, and Michigan tended to be clustered away from data from more easterly locations. Group 2 consisted only of plants from four locations in

Table 2. Eigenvalues and eigenvectors of the first three principal components from five foliar traits of hard maples indigenous near the 43°N latitude.

Principal component	Eigenvalue	Percentage variance	Cumulative percentage variance
First	3.12	62.3	62.3
Second	0.64	12.8	75.1
Third	0.49	9.8	84.9
	Eigenvectors		
	First principal component	Second principal component	Third principal component
Variable			
Lamina area	0.462	0.194	0.055
Lamina area in basipetal sectors	0.400	0.816	0.099
Stomatal density	0.462	-0.372	0.272
Trichome frequency	0.467	-0.355	0.408
Stomatal aperture	-0.441	0.179	0.864

central Iowa, Pine Lake State Park, Pammel Woods, YMCA Woodland, and Dolliver Memorial State Park, at 93.08 to 94.08°W longitude. Data on trees in Iowa showed the most heterogeneity along the first principal component.

Discussion

This research broadens the base of knowledge on foliar traits of sugar maples and black maples (Dansereau and Desmarais, 1947; Desmarais, 1952; Kriebel, 1957) by modeling surface area and trichome and stomate frequencies along a geographical gradient. Our data are quantitative evidence that sugar maples in New England and black maples in Iowa represent the ends of a continuum of morphological variation. Whether this continuum represents introgression or simply ecotypic differentiation is not clear; if black maples and sugar maples evolved through allopatric differentiation, the taxa have since coalesced in the current area of sympatry. We also have resolved the conflict in the literature regarding lamina thickness by showing that neither total thickness nor its components varied with longitude. Dimensions of guard cells also were similar across the region. Therefore, more potential exists for selecting genotypes with atypical leaf surface areas and frequencies of trichomes and stomates than exists for selections based on disparate leaf thickness or guard cell dimensions. How surface area of individual leaves and trichome and stomate frequencies should be prioritized as selection criteria still must be resolved by determining the relative impact of these traits on the function of leaves and whole trees.

The positive quadratic relationship of lamina area with longitude (Fig. 2A) is consistent with the results of Desmarais (1952), who showed that black maple had larger leaves than sugar maple, *Acer floridanum* Pax., *Acer leucoderme* Small., and *Acer schneckii* Rehd. Occurrence of large laminae on hard maples at westerly sites contrasts the relationship of leaf size and longitude of another woody plant native to eastern North America. A decrease in area of individual leaves of eastern redbud (*Cercis canadensis* L.) as natural habitats become drier from east to west was considered a drought resistance mechanism by Donselman and Flint (1982). How the large laminae of the hard maples we sampled from westerly sites might relate to differences in water use, heat gain, or susceptibility to physical damage may depend on other traits that could have mitigating effects. For example, the high trichome frequencies of leaves from the most western longitudes (Fig. 2B) may promote relatively large boundary layer resistances to water loss. The large leaves of black maples also have a distinctive, droopy stance (Dirr, 1998; Preston, 1989) that probably buffers abaxial surfaces. Moreover, surface area of individual leaves is not necessarily consistent with total leaf surface area of trees. No measures of entire trees have been made, but total leaf area of seedlings of black maple was less than that of sugar maples of the same age (Graves, 1994). The significance of differences in the partitioning of lamina area among hard maples is unclear. Baker-Brosh and Peet (1997) proposed lobing patterns may represent adaptations for rapid initiation of photosynthesis in newly emerging leaves of temperate woody species. Differences in the degree to which leaf bases of hard maples are cordate or acute (Rehder, 1940) may account for changes in size of middle and proximal sectors of laminae across longitudes (Fig. 3).

The relevance of individual leaf surface area also can be considered in the context of the forest communities in which hard maples occur. Associations of hard maples with other species

lead to distinct vegetation types such as the American linden (*Tilia americana* L.) complex in Iowa (Johnson-Groh, 1985) and the maple–American beech (*Fagus grandifolia* J.F. Ehrh.) forests of eastern North America (Desmarais, 1952). These relationships could create a microclimate that tempers environmental extremes. Plants with large and thin laminae maximize surface area per volume of photosynthetic tissue in forests where radiation is limited (Mooney, 1980). Because we controlled for radiation effects by sampling only sun leaves, we do not know if hard maples vary in how microclimatic factors such as shade affect leaf area and specific weight. The significance of specific leaf weight of hard maples to photosynthetic efficiency, physical durability, and other traits important in managed landscapes merits further attention. Photosynthesis of sugar maples at different altitudes in New Hampshire was correlated negatively to specific leaf weight (Ledig and Korbobo, 1983). No comparative data on the relative plasticity of hard maples from other provenances have been reported, but under comparatively low-radiation conditions in a greenhouse, specific weight of laminae was greater for black maple than for sugar maple (Graves, 1994). Carpenter and Smith (1981) reported that the plasticity index of sugar maples was the third highest among 23 tree species. Plasticity index is the ratio of thickness difference between sun and shade leaves to thickness of sun leaves. Leaves of hard maples from westerly origins might show a comparatively large response to low water supply if they are more phenotypically plastic than other hard maples. Although we found no relationship between longitude and thickness or specific weight of sun leaves, whether the plasticity index of hard maples from disparate provenances varies remains unknown.

Our data on the relationship between trichome frequency and longitude represent the first quantitative comparison of pubescence of black maples and sugar maples occurring in a zone of sympatry and in their allopatric extremes. In contrast to leaves from eastern locations, which lacked or had few trichomes, plants west of 85°W had up to 1200 trichomes/cm² (Fig. 2B). This substantiates previous, unquantified observations of pubescence among hard maples by Dansereau and Desmarais (1947), Desmarais (1952), Dirr (1998), and Graves (1994). The occurrence of trichomes has been associated with xeric environments (Donselman and Flint, 1982; Ehleringer, 1980) and may be a strategy for reducing loss of water vapor from leaf blades (Johnson, 1975; Schuepp, 1993). Varying environmental conditions at a single location can affect trichome development (Johnson, 1975), which may explain the difference between years in the relationship of pubescence with longitude (Fig. 2B).

Stomatal frequency and stomatal aperture displayed positive and negative quadratic relationships with increasing longitude, respectively (Figs. 2C and D). Thus, laminae with the most stomates per unit area and the smallest stomatal apertures tended to be at sites with the least precipitation. These data are consistent with previous observations of other species that occur in a range of environments (Abrams et al., 1992; Carpenter and Smith, 1981; Salisbury, 1927). Stomata provide a major resistance to water loss (Jones, 1983; Ludlow, 1980), and stomatal aperture is related directly to water loss from the plant (Willmer and Fricker, 1996). Under the assumptions that stomatal apertures of all of our samples were affected similarly by our collection and handling procedures, and that regulation of guard cells is similar regardless of provenance, leaves of eastern hard maples may lose more water per unit area than leaves from western regions because of larger stomatal apertures (Salisbury, 1927). Like lamina area and trichome frequency, stomatal frequency and aperture are among the

traits this research indicates could be used as selection criteria for hard maples that might demonstrate improved function in managed landscapes. Plants representing the geographical area we sampled also showed similar patterns of differences in trichome and stomatal frequencies when grown in a common environment (St. Hilaire, 1998). This, and the consistency of data we obtained in 1995 and 1996, indicate that the continua we have defined represent inherent patterns of variation that are stable in different environments.

Results of the principal component analysis could guide attempts to select hard maples with unique traits. The uniformity of absolute eigenvector values among five dependent variables of the first principal component (0.400 to 0.467, Table 2) indicates that each contributed similarly to the variation and merits attention as a potential selection criterion. Hard maples at Pine Lake State Park, Pammel Woods, YMCA Woodland, and Dolliver Memorial State Park (Table 1) were distinct (Fig. 4). Their extreme position and homogeneity on the positive axis of the first principal component imply that hard maples at these locations had high positive scores for lamina area, pubescence, and stomatal frequency, and had high negative scores for stomate aperture. This is consistent with the contention that leaf size and pubescence characterize black maples (Dansereau and Desmarais, 1947; Desmarais, 1952; Powers, 1967; Rehder, 1940), and the results illustrate heterogeneity that could be exploited. All data in group B of Fig. 4 represent trees at 93.08° to 94.08°W longitude. Other trees in (Claybanks Forest) and near (Wentland Woods and Mather's Woods) this longitudinal range (Table 1) were represented in group A (Fig. 4). If lamina area, pubescence, or stomatal traits prove to be important selection criteria, the fact that all trees at and west of 92.73°W longitude were considered black maples (Table 1) shows that selection efforts will require methods to distinguish among phenotypes similar to the naked eye.

Genotypes with aberrant foliar traits may be of interest to those seeking clones of hard maple for planting in managed landscapes within the climatic zones from which we obtained samples. Among the many commonly available cultivars marketed as sugar maple, only two provide an indication of the potential for relatively good stress resistance in germplasm of black maple. 'Greencolumn', a black maple selected in Boone, Co., Iowa, is considered well adapted to landscapes in the Midwest, while 'Green Mountain', which is considered a hybrid of sugar maple and black maple, performs better in dry soils than do many selections of sugar maple (Dirr, 1998). Evaluation of additional genotypes of black maple, particularly those from atypical populations (Fig. 4), is warranted.

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